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Dissociable intrinsic functional networks support noun-object and verb-action processing

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ABSTRACT

The processing mechanism of verbs-actions and nouns-objects is a central topic of language research, with robust evidence for behavioral dissociation. The neural basis for these two major word and/or conceptual classes, however, remains controversial. Two experiments were conducted to study this question from the network perspective. Experiment 1 found that nodes of the same class, obtained through task-evoked brain imaging meta-analyses, were more strongly connected with each other than nodes of different classes during resting-state, forming segregated network modules. Experiment 2 examined the behavioral relevance of these intrinsic networks using data from 88 brain-damaged patients, finding that across patients the relative strength of functional connectivity of the two networks significantly correlated with the noun-object vs. verb-action relative behavioral performances. In summary, we found that verbs-actions and nouns-objects are supported by separable intrinsic functional networks and that the integrity of such networks accounts for the relative noun-object- and verb-action-selective deficits.

1. Introduction

Nouns and verbs, commonly referring to two major types of concepts of the human mind – objects (entities) and actions (events), are the core components that support syntax for all known human languages (Robins, 1952). While grammatical classes (nouns and verbs) and conceptual classes (objects and actions) could be dissociated - there are nouns and verbs referring to concepts that are beyond objects and actions (e.g., abstract words) - object and action naming and comprehension tasks have been the common proxy for studying noun and verb processing in the literature. Classical neuropsychological studies have long established that brain damage can lead to relatively selective impairment to nouns (objects) or verbs (actions), suggesting that they are supported at least partly by segregated brain systems (Breedin, Saffran, & Schwartz, 1998; Caramazza & Hillis, 1991; Damasio & Tranel, 1993; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Goodglass, Klein, Carey, & Jones, 1966; McCarthy & Warrington, 1985; Miceli, Silveri, Villa, & Caramazza, 1984; Zingeser & Berndt, 1988). The brain basis underlying such behavioral dissociation, however, has been elusive.

From the lesion study perspective, there are tendencies that more severe verb-action processing deficit is associated with the left frontal damage, while more severe noun-object processing deficit with damage of the left temporal cortex (Aggujaro, Crepaldi, Pistarini, Taricco, & Luzzatti, 2006; Bates, Chen, Tzeng, Li, & Opie, 1991; Cappa et al., 1998; Damasio & Tranel, 1993; Daniele et al., 1994; Druks, 2002; Glosser & Donofrio, 2001; Lubrano, Filleron, Démonet, & Roux, 2014). Yet there are cases that do not follow this pattern (De Renzi & Di Pellegrino, 1995; Luzzatti, Aggujaro, & Crepaldi, 2006) and that patients with verb-action impairment are rarely caused by a cerebral lesion limited to the frontal or the parietal lobe (Aggujaro et al., 2006). Neuroimaging studies of healthy populations have reported much more distributed regions for the two word/conceptual classes: Preferential activations by verbs-actions were observed in left inferior frontal gyrus, middle and superior temporal gyrus, precentral area, and right cerebellum, while noun-object preferential activations were found in left fusiform gyrus, inferior parietal lobe, inferior frontal gyrus, and right cerebellum (Crepaldi, Berlingeri, Paulesu, & Luzzatti, 2011; Vigliocco, Vinson, Druks, Barber, & Cappa, 2011).

One hypothesis about verb-action and noun-object processing that readily accommodates the neuropsychological and neuroimaging findings is that noun-object or verb-action processing is not attributable to specific circumscribed regions, but rather are supported by networks of many different regions, and it is the integrity of the whole functional

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systems that are predictive of noun-object or verb-action processing skills. Damage to any component of the network, including the connections among the cortical regions, would affect the functional integration of the system and thus compromise the processing of the corresponding word/conceptual class.

We here test this hypothesis explicitly by asking two questions: (1) Are the regions showing preferential activation to a particular word/conceptual class (nouns-objects or verbs-actions) intrinsically more tightly connected, i.e., forming functional networks? (2) Is the integrity of the functional network, i.e., the strength of the functional connectivity, associated with behavioral performances for the corresponding class? In Experiment 1 we employed graph-based brain network analysis methods (Newman, 2006) to examine the intrinsic organization of verb/action- and noun/object-preference brain regions obtained in previous fMRI studies, using resting-state fMRI data in 146 healthy individuals. Experiment 2 tested whether the network functional connectivity strength (FCS) associates with noun-object- or verb-action- behavioral deficits in 88 brain-damaged patients.

Given that object and action naming and comprehension tasks are commonly used in the literature, the conceptual and grammatical origins of the word class distinction in these tasks is difficult to be teased apart (see Vigliocco et al., 2011 for a review). We use nouns-objects and verbs-actions without committing to either dimension, and use noun- and verb-specific networks when referring to relevant brain networks for the sake of simplicity. Also note that noun-object- and verb-action-dissociations similar to studies with Indo-European language have been demonstrated in Chinese using both neuropsychological and neuroimaging approaches (e.g., Bi, Han, Shu, & Caramazza, 2007; Yu, Bi, Han, Zhu, & Law, 2012; Yu, Law, Han, Zhu, & Bi, 2011), we thus considered previous results of both studies using English and those using Chinese in Experiment 1 and tested Chinese speaking patients in Experiment 2.

2. Materials and methods

2.1. Experiment 1: Characterizing the intrinsic functional network organization of verb- and noun-preferential regions in healthy subjects

In this experiment, we examined whether the brain regions previously shown to be preferentially activated by verbs or nouns are intrinsically organized into dissociable functional networks by testing the resting-state functional connectivity (RSFC) pattern using resting-state fMRI data of 146 healthy subjects. First, activation likelihood estimation (ALE) meta-analyses were applied to define verb nodes and noun nodes based on the task-based fMRI activation results. We then examined: (1) Are the within-class (i.e., among the ALE-defined-verb nodes and among the ALE-defined-noun nodes) FCS greater than the between-class (i.e., between ALE-defined-verb nodes and ALE-defined-noun nodes) FCS? (2) Are the nodes, when pulled together, can be partitioned into distinct modules on the basis of the FCS pattern?

2.1.1. Participants

One hundred and forty-six right-handed healthy young participants (76 females; 22.7 ± 2.1 years old; range, 19–30 years old) were recruited from Beijing Normal University for this experiment. Fifty-seven members of this group took part in another scanning session with identical scanning parameters about 6 weeks later, the data of which were used in our validation analyses as the retest dataset. All subjects were from the same cohort reported in our earlier study (Xu, Lin, Han, He, & Bi, 2016). They were native Mandarin speakers with no history of neurological or psychiatric disorders. Each gave written informed consent and the research was approved by the Institutional Review Board of the National Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University.

2.1.2. Image acquisition and preprocessing

Structural and functional imaging data were acquired using a Siemens TrioTim 3-Tesla scanner at the Beijing Normal University Imaging Center for Brain Research. During resting-state fMRI scanning, participants were asked to stay relaxed and to rest with their eyes closed and not fall asleep. T1-weighted three-dimensional magnetization-prepared rapid gradient echo (3D MPRAGE) images were obtained with the following parameters: repetition time (TR) = 2530 ms, echo time (TE) = 3.39 ms, flip angle = 7°, slice thickness = 1.3 mm, slice gap = 0.65 mm, slice in-place resolution = $1.3 \times 1.0\ mm^2$, field of view (FOV) = $256 \times 256\ mm^2$, slice number = 144. Functional images were acquired using an echo planar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, flip angle = 90°, slice thickness = 3.5 mm, slice gap = 0.7 mm, slice in-place resolution = $3.1 \times 3.1\ mm^2$, FOV = $200 \times 200\ mm^2$, slice number = 33, volume number = 200).

Functional imaging data preprocessing was performed using Data Processing Assistant for Resting-State fMRI (DPARSF, available at http://rfmri.org/DPARSF, Chao-Gan & Yu-Feng, 2010). The first 10 volumes of the functional images were discarded before slice timing and head motion correction. In the main dataset, two participants exhibited head motion of > 2 mm maximum translation or 2° rotation and were excluded from the analyses, resulting in 144 remaining subjects (75 females; 22.7 ± 2.3 years old; range, 19–30 years old). Next, each participant's structural images were co-registered to their mean functional images and were subsequently segmented. The functional images were normalized to the Montreal Neurological Institute (MNI) space (resampling voxel size was $3 \times 3 \times 3\ mm^3$) using the parameters obtained during segmentation. Next, linear trend removal, band-pass filtering (0.01–0.1 Hz) and spatial smoothing (6 mm FWHM Gaussian kernel) were applied to the functional images. Finally, some nuisance covariates were regressed out, including rigid-body 6 head motion parameters, white matter signal, and cerebrospinal fluid signal. The residual time series were used in the subsequent network analysis.

2.1.3. Node definition

ALE meta-analyses were used to identify regions showing consistent preferential activation to nouns or verbs across studies as the following procedures.

Literature selection. An influential and comprehensive review written by Vigliocco et al. (2011) summarized the verb- and noun-activation preference results from 26 imaging studies. We selected 20 studies from this summary, with six studies excluded for the following reasons: one reported only the ROI analysis results (Palti, Ben-Shachar, Hendler, & Hadar, 2007); one did not report the number of subjects (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995); two did not find any positive results contrasting verbs and nouns (Fujimaki et al., 1999; Vigliocco et al., 2006); and two did not report the coordinates of the activation differences (Kable, Lease-Spellmeyer, & Chatterjee, 2002; Li, Jin, & Tan, 2004). Two studies that compared noun and verb processing using Chinese language (Yu et al., 2011, 2012) that were published after the review were additionally included for completeness and for having the same language speakers with our current study. As a result, 22 articles (containing 16 fMRI and 6 PET studies) were designated suitable for the meta-analyses. Twenty of them were used for verb-preference ALE meta-analysis, while 11 were involved in a noun-preference ALE meta-analysis (see Table 1). It is important to note that different sets of studies are used in verb > noun and noun > verb activation meta-analysis because many studies do not find both types of activations with many cases finding verb > noun activity with no noun > verb activity. The inconsistency between studies may be related to the complex nature of the noun/verb dissociations (see Section 4).

Types of contrast. We focused on the verbs versus nouns direct comparison in the meta-analyses. Simple effects of verbs or nouns versus baseline were not considered for the following two reasons: (1) The baselines used in each study were quite different, ranging from "resting" to "face picture identification"; (2) The activations observed for the simple effect might be dominated by the cognitive components

Table 1
Overview of the 22 studies included in the ALE meta-analyses.

Paper	Subject number	Mode	Task
Studies used in the verb-preference ALE meta-analysis			
Warburton et al. (1996)	9	PET	Word generation
Tyler, Russell, Fadili, and Moss (2001)	8	PET	Semantic categorization
Tyler et al. (2001)	9	PET	Lexical decision
Tyler et al. (2003)	12	fMRI	Semantic categorization
Tyler, Bright, Fletcher, and Stamatakis (2004)	12	fMRI	Semantic categorization
Bedny and Thompson-Schill (2006)	13	fMRI	Semantic similarity judgment
Davis, Meunier, and Marslen-Wilson (2004)	10	fMRI	One-back synonym-monitoring
Bedny, Caramazza, Grossman, Pascual-Leone, and Saxe (2008)	12	fMRI	Semantic relatedness judgment
Damasio et al. (2001)	20	PET	Picture naming
Tranel, Martin, Damasio, Grabowski, and Hichwa (2005)	10	PET	Picture naming
Saccuman et al. (2006)	13	fMRI	Picture naming
Liljeström et al. (2008)	15	fMRI	Picture naming
Berlingeri et al. (2008)	12	fMRI	Picture naming; Grammatical-class switching
Longe, Randall, Stamatakis, and Tyler (2007)	12	fMRI	Pleasant judgment
Tyler, Randall, and Stamatakis (2008)	15	fMRI	Pleasant judgment
Perani et al. (1999)	14	PET	Lexical decision
Yokoyama et al. (2006)	28	fMRI	Lexical decision
Shapiro et al. (2005)	12	PET	Word inflection
Shapiro, Moo, and Caramazza (2006)	10	fMRI	Word inflection
Yu et al. (2011)	21	fMRI	Semantic relatedness judgment
Yu et al. (2012)	20	fMRI	Semantic associate generation
Studies used in the noun-preference ALE meta-analysis			
Warburton et al. (1996)	9	PET	Word generation
Bedny and Thompson-Schill (2006)	13	fMRI	Semantic similarity judgment
Saccuman et al. (2006)	13	fMRI	Picture naming
Liljeström et al. (2008)	15	fMRI	Picture naming
Siri et al. (2008)	12	fMRI	Picture naming
Berlingeri et al. (2008)	12	fMRI	Grammatical-class switching
Shapiro et al. (2005)	12	PET	Word inflection
Shapiro et al. (2006)	10	fMRI	Word inflection
Burton, Krebs-Noble, Gullapalli, and Berndt (2009)	12	fMRI	Grammaticality judgment
Yu et al. (2011)	21	fMRI	Semantic relatedness judgment
Yu et al. (2012)	20	fMRI	Semantic associate generation

that are shared by nouns and verbs such as visual perception in the case of a visual task, as proposed by Crepaldi et al. (2011). For the verbs-nouns direct contrast, 20 studies reporting 132 verb-activation foci in 287 subjects and 11 studies reporting 59 noun-activation foci in 149 subjects were included (Fig. 1A). A large proportion of these activations were found in the semantic and naming tasks.

Activation likelihood estimation (ALE). All coordinates were transformed onto MNI space (Evans et al., 1993) using the Convert Foci menu in the GingerALE software package (available at http://brainmap.org). These foci were organized into a .txt file according to different subject groups for verbs and nouns, respectively. The ALE analyses were implemented in the GingerALE software package with the settings of the conservative (smaller) mask without excluding foci outside the mask. We chose an ALE algorithm that implements small corrections to minimize within-experiment effects, as described by Turkeltaub et al. (2012). The threshold was set at $P < 0.05$ and was corrected for multiple comparisons using the false discovery rate (FDR) method along with a minimum cluster size of 50 mm^3.

Node extraction. ALE probability maps for verbs and for nouns were constructed from the ALE meta-analyses. All of the peaks extracted from verb- and noun-ALE probability maps were used to form spheres of 4 mm radius within a grey matter mask (N voxels = 67541) that was generated by thresholding (cut off = 0.2) the grey matter probability map in SPM. These spheres were labeled as ALE-defined-verb and noun nodes, respectively.

2.1.4. Edge definition

Edges are represented by the strength of RSFC, measured by the time series correlation coefficients, between the nodes. Specifically, the residual time-series of all voxels within each node were averaged, and then in each subject the Fisher-z transformed average residual time-series correlations across nodes were calculated. The analysis was performed with the Resting State fMRI Data Analysis Toolkit (REST, available at http://www.restfmri.net, Song et al., 2011).

2.1.5. Average FCS comparison on the ALE-defined networks

We first examined whether the nodes showing stronger activation to a particular word class, as obtained from the ALE analyses above, are more strongly intrinsically connected to each other. We compared the mean FCS during the resting-state for within- and between-class nodes across subjects (see similar methods in He et al., 2007; Van Dijk et al., 2010). For each subject, the FCS for each pair of nodes was computed, and then three values were calculated: the average of the FCS within the ALE-defined-noun nodes, that of the FCS within the ALE-defined-verb nodes, and that of the FCS for all the between-class nodes. The paired t-test was conducted to test whether the average FCS for each within-class network was significantly different from that of the between networks.

2.1.6. Network modularity analysis

Another way to elucidate whether the ALE-defined-noun and verb nodes are intrinsically organized as different networks is to explore the modularity structure of these nodes in a data-driven manner. We constructed the network matrix over all the nodes without *a prior* role assignment to perform a modularity analysis (Newman's spectral optimization, Newman, 2006). This approach identifies modules according to the functional connectivity structure of the nodes. We then inspected whether the intrinsic modular structure roughly corresponded to the ALE-defined-verb/noun networks.

Connectivity matrix generation. Averaging strength across subjects for each edge, the group weighted graph matrix was obtained. Given that the negative correlations between two nodes may not be meaningful,

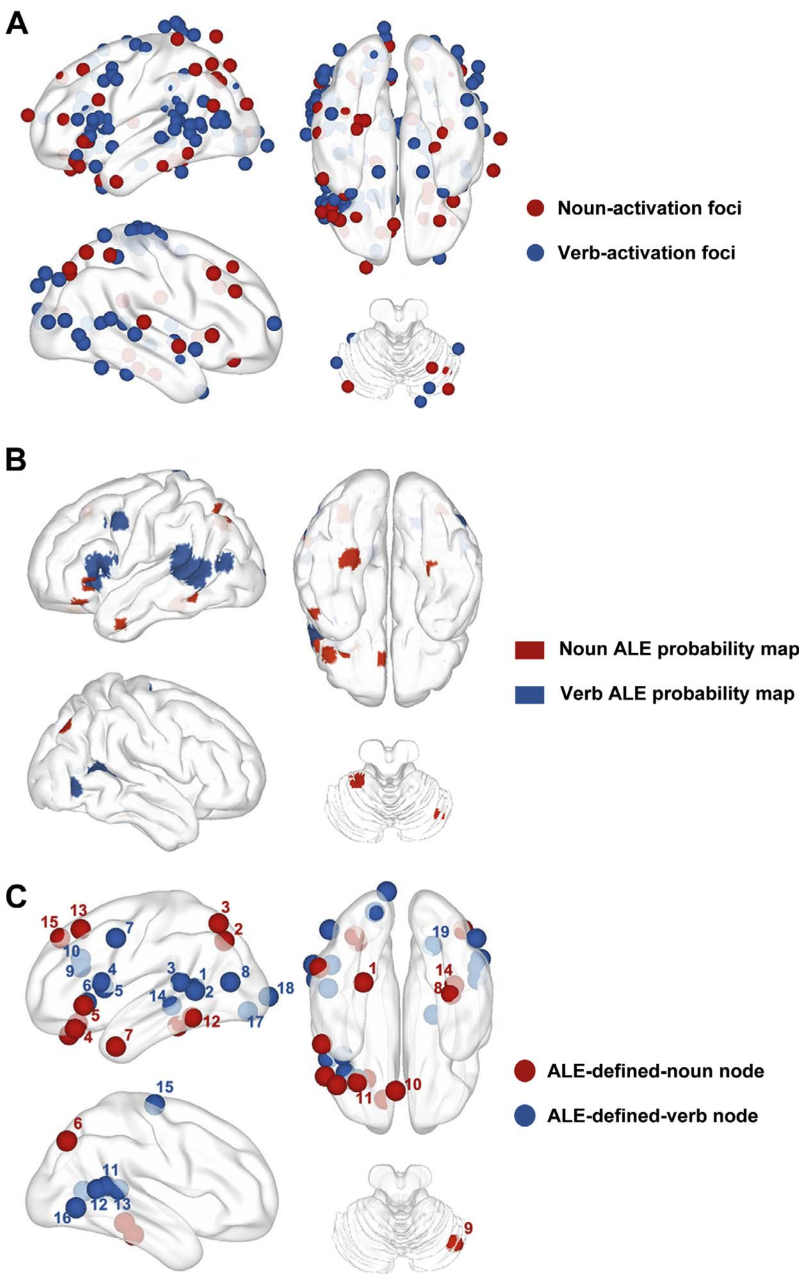

Fig. 1. Node definition. (A) Verb- and noun-activation foci included in the meta-analyses. (B) ALE probability maps of the meta-analyses (threshold: FDR corrected $P < 0.05$, volume $> 50\ \text{mm}^3$). (C) Distribution map of the 19 ALE-defined-verb nodes and the 15 ALE-defined-noun nodes. Arabic numbers for the brain regions correspond to those in Table 2. This and the brain figures below are all visualized with the BrainNet Viewer (Xia, Wang, & He, 2013, http://www.nitrc.org/projects/bnv/).

they were converted to zero and the positive correlations were remained and analyzed in this study. Thus, an n × n RSFC matrix, in which n is the sum number of ALE-defined-verb and noun nodes, was constructed.

Modularity analysis. The n × n weighted graph matrix was input to a Graph-theoretical Network Analysis Toolkit in MATLAB (GRETNA, available at https://github.com/sandywang/GRETNA, Wang et al., 2015) for modularity analysis. The modularity $Q(p)$ for a given partition p of the RSFC network (Newman & Girvan, 2004) is defined as:

$$Q(p) = \sum_{s=1}^{N_m} \left[\frac{l_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right]$$

where N_m is the number of modules, L is the total number of network connections, l_s is the number of connections between nodes in module s, and d_s is the sum of the degrees of the nodes in the modules. The modularity index quantifies the difference between the real number of intra-module connections in the actual network and that of a network in which nodes are connected at random. This module detection process allows us to identify the preference partition p that maximizes $Q(p)$. There are several available optimization algorithms; we partitioned the RSFC network using Newman's spectral optimization algorithm (Newman, 2006). According to Clauset, Newman, and Moore (2004), a Q value above 0.3 is good enough to indicate the significant modules in a network. The difference between Q of the real network and that of random networks was used to generate a Z score, which indicates the significance level. The modularity analyses were conducted for sparsity thresholds ranging from 0.22 to 0.50 in increments of 0.01. The lowest threshold was determined to ensure that the resulting graph was fully connected; the highest threshold was set to remove weak correlations so that only the correlations significantly above zero were included. Note that because almost all of the connections in the matrix were significantly above zero, 80% remained when the significance reached the Bonferroni-corrected level of 0.001. This connection density is deemed too high and we arbitrarily set the highest threshold to 0.50.

2.1.7. Validation analyses

We performed validation analyses using a new test-retest dataset, preprocessing with global signal removal, and additional head motion treatment procedures.

A different (retest) dataset. Fifty-seven (27 females; 23.1 ± 2.3 years old; range, 19–30 years old) of the 146 participants in Experiment 1 took part in another scanning session about 6 weeks (40.94 ± 4.51 days) later (i.e., the second scan session in Lin et al., 2015). We used this later scan to validate our results. This sub-group retest dataset was included in the "Connectivity-based Brian Imaging Research Database (C-BIRD) at BNU" (http://fcon_1000.projects.nitrc.org/indi/CoRR/html/bnu_1.html, BNU 1). Two subjects were excluded due to excessive head motion and 55 participants (26 females; 23.1 ± 2.3 years old; range, 19–30 years old) remained for identical analysis procedures as the main dataset in Experiment 1.

Global signal removal. It remains controversial whether global signal regression should be performed during resting-state fMRI preprocessing (Fox, Zhang, Snyder, & Raichle, 2009; Murphy, Birn, Handwerker, Jones, & Bandettini, 2009). To test the extent to which that our results were reliable across different preprocessing protocols, we performed the same analyses using data with global signal regression for the main dataset.

Head motion. Head motion has been shown to have a confounding effect on RSFC (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012; Power et al., 2014; Van Dijk, Sabuncu, & Buckner, 2012). In order to further exclude the possible effects of head motion, we performed a 'scrubbing' procedure (Power et al., 2012; Yan et al., 2013) during preprocessing of the main dataset. In this scrubbing analysis, functional volumes were deleted based on a framewise displacement >0.5 mm compared with the 1 back and 2 forward neighbors (Power et al., 2012). Different time points remained after scrubbing across subjects. To have a sufficient number of time points for meaningful analyses, two subjects that had too few remaining time points (<150 volumes out of the 190 total time points; i.e., <5 min) were excluded, resulting in 142 healthy subjects for this analysis.

2.2. Experiment 2: Testing the relationship between functional network integrity and behavioral deficits in patients

This experiment further examines the cognitive relevance of the intrinsic noun- and verb-functional networks by testing whether the breakdowns of these functional networks associate with noun or verb deficits. We collected resting-state fMRI data and behavioral data from 88 patients with brain damage, and correlated the relative FCS for the two networks (subtractions of noun network FCS from verb network FCS) with the relative performances on noun and verb processing tasks (subtracting the noun behavioral score from the verb behavioral score) after controlling for potential confounding variables (following similar procedures in Nomura et al., 2010). We also examined whether the potential effect of the FCS is account for by the lesions to the constituent nodes. This correlation approach captures the general relationship between two continuous variables and is possible because of the proper sample size in this Experiment.

2.2.1. Participants

Eighty-eight patients with brain damage (17 females; 45.1 ± 13.4 years old; range, 19–74 years old; 12.9 ± 3.2 years of education; range, 4–19 years of education), all from the China Rehabilitation Research Center, participated in this study voluntarily. Sixty-eight of the patients were from the cohort reported in our earlier study (Han et al., 2013). All were right-handed (Edinburgh Handedness Inventory; Oldfield, 1971). The inclusion criteria were as follows: presenting with brain injury for the first time; at least 1 month elapsed since the onset; no other neurological or psychiatric disease such as schizophrenia or alcohol abuse; and capable of following task instructions. The majority suffered from stroke (n = 71), with remaining suffering from trauma, atrophy, gas poisoning, and electric shock. Thirty-five patients had bilateral lesions, 35 had left hemisphere lesions, 17 had right hemisphere lesions and 1 had brain stem lesion. Detailed information for each patient is shown in the Supplementary Table S1. A lesion distribution map of the 88 patients is presented in Fig. 2A. All subjects were provided written informed consent. This research was approved by the Institutional Review Board of the National Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University.

2.2.2. Behavioral tests design and data preprocessing

To assess the cognitive processing ability of verbs and nouns, four tasks were administered, including an oral picture naming task, a picture associative matching task, a word associative matching task and a word-picture verification task. The four tasks covered pictorial and verbal inputs, oral and nonverbal outputs, reflecting primarily abilities in semantic and oral production, nonverbal comprehension, verbal comprehension, and verbal-nonverbal matching, respectively. All stimuli used in the tasks were words and pictures corresponding to actions (e.g., diving, hugging) and objects (tools, animals, fruits and vegetables, artifacts, and large nonmanipulable objects). Illustrations of picture associative matching are shown in Fig. 2B. The complete stimulus list of all tasks is presented in the Supplementary Table S2. There were no significant differences in term of word frequency across various word categories in any task (see the Supplementary Table S3). For oral picture naming task, there are no significant differences in phonological length across categories (number of syllables, $F = 1.272$, $P = 0.281$). For word-picture verification and word associative matching task, there were no significant differences in word visual complexity across categories (number of strokes, word-picture verification: $F = 0.756$, $P = 0.586$; word associative matching: $F = 1.153$, $P = 0.344$).

In oral picture naming, participants were instructed to name each object or action picture. The word and picture associative matching tasks had an identical structure: in each trial contained three items and the participants need to choose which of the bottom two were semantically closer to the top item, except that three words were presented in the word version and three pictures were presented in the picture version. In the word-picture verification task, a word was presented above a picture on the touch screen in each trial. Participants were instructed to judge whether the picture corresponded with the word by pressing "yes" or "no" on the screen. This task included 2 sets of 60 trials each. The word stimuli were identical across the two sets, but each set of the words was paired separately with a congruent picture or an incongruent picture. Only when both trials of the two sets were correct would the word stimuli be scored as accurate. The response deadline was one minute for each trial of these tasks.

As the patients were not asked to respond as quickly as possible to avoid pressure, only response accuracies were analyzed. *Z*-transformed accuracies for each task were used as the corresponding behavioral scores. We considered two types of contrasts for noun/verb behavioral measures: actions versus tool items; actions versus all object items. This specific contrast of actions versus tools was motivated by a line of hypothesis that tools are semantically closer than other types of objects to actions in that a core dimension of conceptual representation of tools are its manipulation properties (Bird, Howard, & Franklin, 2000; Mahon et al., 2007).

2.2.3. Image acquisition and preprocessing

Structural and functional imaging data were collected using a 1.5 T GE SIGNA EXCITE scanner at the China Rehabilitation Research Center. During resting-state functional images scanning, participants were instructed to keep still with their eyes closed. The 3D MPRAGE T1-weighted images were obtained in the sagittal plane with the parameters: TR = 1226 ms, TE = 4.2 ms, flip angle = 15°, voxel size = 0.49 × 0.49 × 0.70 mm^3, FOV = 250 × 250 mm^2, and slice number = 248. Two identical sequences of 3D T1 images were collected and averaged to improve the signal-to-noise ratio during

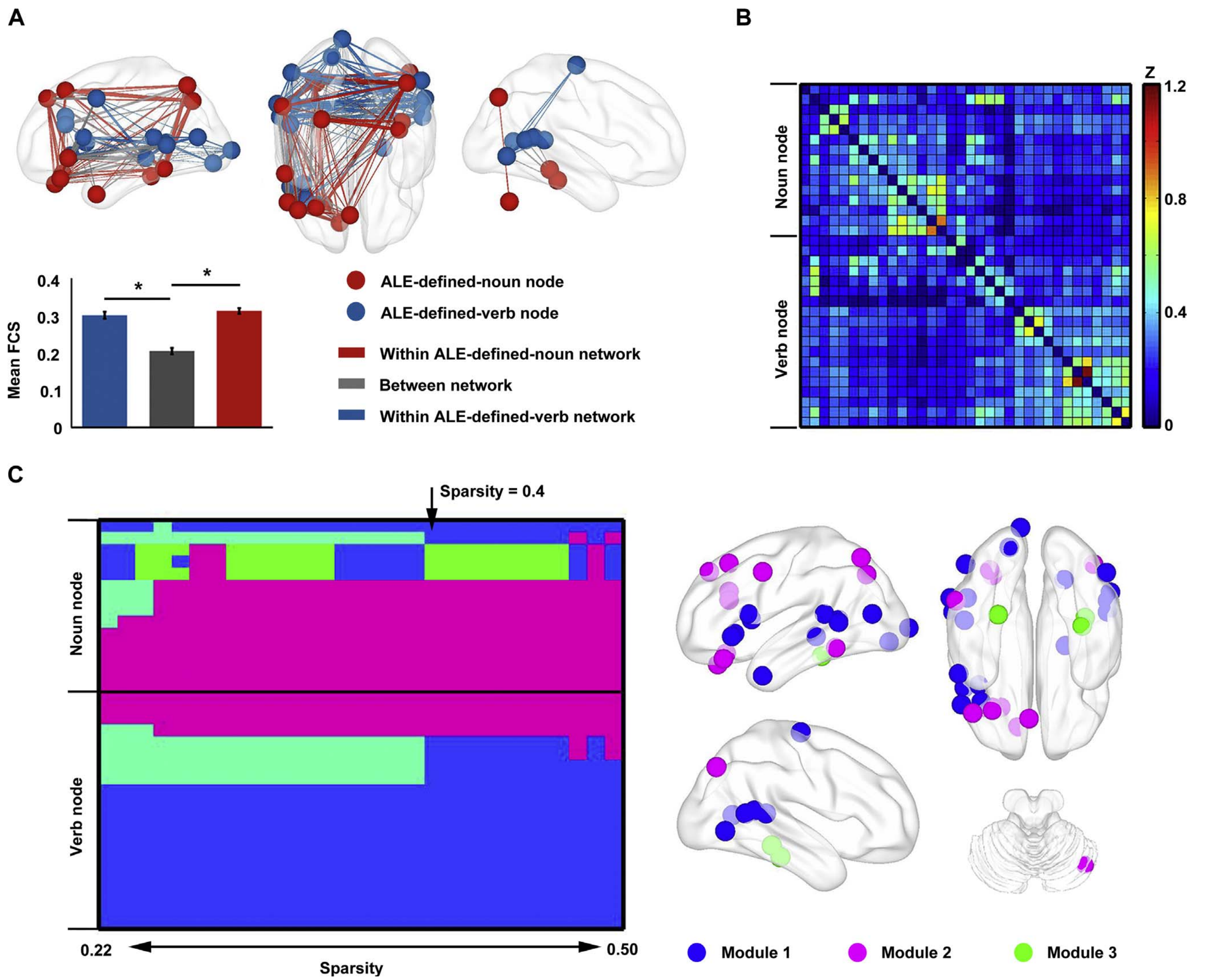

Fig. 2. Patient information and results of Experiment 2. (A) Patient lesion distribution map, with the *n* value of each voxel denoting the number of patients with the lesion. (B) Illustrations of the picture associative matching task. (C) Scatter plots of the partial correlation between relative mean FCS for verb- and noun-functional networks and relative verb and noun behavioral performance in the picture associative matching task after controlling for age, years of education, total lesion volume, and the relative nodal damage. ALE-defined networks: verb- and noun-functional networks that were constructed by ALE meta-analyses results; GTA-defined networks: verb- and noun-functional networks that were constructed by graph-theoretical modularity analysis results of Experiment 1.

analysis. The resting-state functional images were acquired using an EPI sequence along the AC–PC line with the following parameters: TR = 2000 ms, TE = 40 ms, flip angle = 90°, slice thickness = 4 mm, slice gap = 1 mm, slice in-place resolution = 3.3 × 3.3 mm^2, FOV = 210 × 210 mm^2, slice number = 28, and volume number = 120. Another T1-weighted images, which had same slice locations with the functional images on the axial plane (TR = 3071 ms, TE = 9.6 ms, inversion time (TI) = 2000ms, flip angle = 90°, slice thickness = 5 mm, slice gap = 0, FOV = 250 × 250 mm^2, slice number = 28), were acquired to co-register the functional images onto the 3D MPRAGE images. The FLAIR T2 images on the axial plane (TR = 8002 ms, TE = 127.57 ms, TI = 2000 ms, flip angle = 90°, slice thickness = 5 mm, voxel size = 0.49 × 0.49 × 5.00 mm^3, FOV = 250 × 250 mm^2, slice number = 28) were collected as visual reference for lesion drawing.

Functional MRI image data were preprocessed using the following procedures. First, time points were deleted (the first 10 volumes), and slice timing and head motion corrections (no participant exhibited head motion of >3 mm maximum translation or 3° rotation) were performed. The second scan of 3D T1 images were co-registered to the first scan of 3D T1 images and then were averaged with the first scan of 3D T1 images. Next, the functional images were co-registered to the averaged 3D T1 images via their axial plan T1-weighted images which have same slices with the functional images. This procedure was different from that performed for the healthy participants, whose functional images were co-registered to their 3D T1 images directly, due to failures in co-register between the functional and 3D T1 images. The above procedures were implemented by an in-house software program based on SPM8 (available at http://www.fil.ion.ucl.ac.uk/spm). We used the ANTS software package (Advanced Normalization Tools, available at http://picsl.upenn.edu/software/ants/) to normalize the 3D T1 images from native space to Talairach space and extract the affine transformation matrix between the native and Talairach spaces for each subjects, and used ANTS to extract the affine transformation matrix between Talairach and MNI spaces. Using these two affine transformation matrixes, functional images were normalized to the MNI spaces. The remaining steps were completed by DPARSF, including liner trend removing, band-pass filtering (0.01–0.1 Hz) and spatial smoothing (6 mm FWHM Gaussian kernel). Nuisance covariates regression was treated in the same way as the data in Experiment 1.

For the 3D T1 images, we first co-registered each of the two sequences on the same native space and then averaged them. The FLAIR T2 images were co-registered and resliced to the native space of the averaged 3D images. Lesions were manually drawn by two trained personnel on the averaged 3D T1 image slice by slice with visual reference to the FLAIR T2 images for each patient. The lesion description was finally transformed into the MNI space. More details can be obtained from our previously research (Han et al., 2013).

2.2.4. Partial correlations between relative FCS and relative behavioral score

To test the extent to which the difference in terms of the integrity of the noun- and verb-functional networks could account for the potential noun/verb behavioral dissociations, we carried out a partial correlation analysis between the relative FCS of the two networks and the relative of the behavior scores on each noun and verb task, with the total lesion volume (i.e., total number of damaged voxels across the whole brain), age, and years of education as covariates. The relative noun/verb FCS for each patient was computed by subtracting the average FCS within the noun-functional network from the average FCS within the verb-functional network. The relative behavioral score for each patient on each task was calculated by subtracting the noun behavior score (*z*-transformed accuracy) from the verb behavior score.

2.2.5. Controlling for the effects of nodal lesions

To assess whether the effects of the functional connectivity within each network on behavior are fully attributable to the extent of lesion to the relevant nodes, we performed further correlation analyses between the relative noun/verb FCS and the relative noun/verb behavioral scores, including the relative extent of the anatomical damage for the nodes in the two networks as an additional covariate. For each patient, the extent of nodal lesions for each network was calculated by averaging the percentage of voxels with lesion each node within the network. The relative nodal lesion for the two networks was calculated by subtracting the extent of nodal lesions of the noun-functional network from the nodal lesions of the verb-functional network.

2.2.6. Validation analyses

Similar to Experiment 1, we carried out validation analyses with global signal removal and additional head motion data treatment. Furthermore, because the physiological basis of fMRI signal for voxels with lesion is unclear, we conducted analysis excluding each patient's damaged voxels from the RSFC analyses.

Global signal removal. To test whether our results were reliable across different preprocessing procedures, we performed the same analyses using data with global signal regression, using preprocessing procedures same to those in Experiment 1.

Head motion. Similar to Experiment 1, we performed an additional 'scrubbing' procedure during preprocessing for the patients group to further deal with the potential head motion confound, using procedures identical to those of Experiment 1. Seven patients were excluded for not having enough remaining time points (<90 volumes out of 110 total time points; i.e., <3 min) and the data of 81 patients entered analyses after scrubbing.

Exclude damaged voxels. We performed a further validation analyses to exclude the damaged voxels within ALE-defined-verb and noun nodes for each patient. There were 41 patients had no lesion in all nodes. We first used this sub-group to validate our main results of Experiment 2. For the other patients, we excluded their damaged voxels within each node one by one. If all of voxels within a node were damaged, we would exclude this node or set the FCS from this node as zero. Results of both analyses were presented.

3. Results

3.1. Experiment 1: Characterizing the intrinsic functional network organization of verb- and noun-preferential regions in healthy subjects

3.1.1. Node definition results

We carried out ALE meta-analyses based on 22 imaging studies where verb processing and noun processing were contrasted across tasks, including 20 studies where stronger verb activations were observed and 11 where stronger noun activations were observed (Table 1). As presented in Fig. 1B (thresholded at whole brain FDR corrected $P < 0.05$, volume > 50 mm^3), brain regions that are consistently activated more strongly for verbs, i.e., ALE-defined-verb nodes, across the 20 studies include the bilateral superior temporal gyrus (STG), left middle temporal gyrus (MTG), left inferior frontal gyrus (IFG), left insular, bilateral precentral gyrus, left middle occipital gyrus (MOG), left middle frontal gyrus (MFG), left postcentral gyrus, left lingual gyrus, right inferior temporal gyrus (ITG) and right posterior cingulate. Brain regions showing consistent noun-preference activation across the 11 studies, i.e., ALE-defined-noun nodes, were the bilateral parahippocampal gyrus (PHG), bilateral precuneus, left superior parietal lobule (SPL), left IFG, left MTG, left medial frontal gyrus, left ITG, left MFG, left SFG, and right cerebellar tonsil. The peaks were extracted from the ALE probability maps to form spheres of radius 4 mm. One of the verb-preference peaks (coordinates: −10, −42, 80) was excluded because it was located outside the pre-defined gray matter mask. In this manner, we identified 19 ALE-defined-verb nodes and 15 ALE-defined-noun nodes (see details in Table 2 and Fig. 1C).

3.1.2. FCS among nodes within- and between-classes

We computed FCS among all the ALE-defined-verb and noun nodes using the healthy group dataset (N = 144). The functional connectivity pattern was shown in Fig. 3A. The FCS values were significantly higher for connections among the ALE-defined-verb nodes [$t(143) = 24.52$, $P < 0.0001$] and among the ALE-defined-noun nodes [$t(143) = 18.51$, $P < 0.0001$] in comparison to those FCS values for connections between the ALE-defined-noun nodes and the ALE-defined-verb nodes (Fig. 3A). These results indicate that the nodes that are more strongly activated by verb tasks are more tightly functionally connected with each other in resting-state, so do those more strongly activated by noun tasks.

3.1.3. Modularity analysis results

Again using the healthy group dataset, we applied graph-theoretical analysis (GTA) – modularity analysis (Newman, 2006) – to detect whether the regions showing class-preference activation indeed have intrinsic functional architecture in a data-driven manner. The graph matrix used for the modularity analyses is presented in Fig. 3B. The modularity results for sparsity thresholds ranging from 0.22 to 0.50 in increments of 0.01 are presented in Fig. 3C, indicating that these nodes are significantly organized into 3 segregated functional modules that are relative stable across sparsity thresholds ranging from 0.40 to 0.47. The right part of Fig. 3C represents the three modules ($Q = 0.30$, indicating significant modular structure; Zscore = 13.82) at sparsity threshold of 0.40. Regions of one module (blue) predominantly (89%, 16/18) corresponded to the ALE-defined-verb nodes, while the majority of nodes of another module (magenta, 77%, 10/13) corresponded to ALE-defined-noun nodes. We thus labeled the blue module as a GTA-defined-verb network and the magenta module as a GTA-defined-noun network. These results confirm that these nodes showing different preferences for nouns or verbs in terms of activation indeed tend to be intrinsically organized into dissociable components.

3.1.4. Validation results

The results remained largely stable across validation analyses.

A different (retest) dataset. Validation results of the Experiment 1

Table 2
Detailed information of the 19 ALE-defined-verb nodes and 15 ALE-defined-noun nodes identified by coordinate-based meta-analyses over 22 fMRI studies contrasting verb and noun activations. The coordinates are in MNI space.

Label	Coordinates			Region
	x	y	z	
ALE-defined-verb nodes				
1	−48	−50	8	Left superior temporal gyrus
2	−60	−50	6	Left middle temporal gyrus
3	−58	−40	12	Left superior temporal gyrus
4	−50	14	12	Left inferior frontal gyrus
5	−40	12	8	Left insular
6	−38	24	−2	Left insular
7	−54	4	42	Left precentral gyrus
8	−54	−74	12	Left middle occipital gyrus
9	−36	28	22	Left middle frontal gyrus
10	−30	28	28	Left middle frontal gyrus
11	52	−48	12	Right superior temporal gyrus
12	54	−54	10	Right superior temporal gyrus
13	52	−40	10	Right superior temporal gyrus
14	−50	−34	−4	Left middle temporal gyrus
15	22	−16	66	Right precentral gyrus
16	56	−68	−2	Right inferior temporal gyrus
17	−18	−86	−8	Left lingual gyrus
18	−10	−100	2	Left lingual gyrus
19	21	−63	9	Right posterior cingulate
ALE-defined-noun nodes				
1	−26	−38	−18	Left parahippocampal gyrus
2	−32	−70	40	Left precuneus
3	−30	−66	52	Left superior parietal lobule
4	−44	32	−20	Left inferior frontal gyrus
5	−52	26	−4	Left inferior frontal gyrus
6	42	−74	42	Right precuneus
7	−54	4	−32	Left middle temporal gyrus
8	34	−30	−20	Right parahippocampal gyrus
9	40	−66	−36	Right cerebellar tonsil
10	−4	36	−24	Left medial frontal gyrus
11	−30	30	−16	Left inferior fontal gyrus
12	−56	−48	−12	Left inferior temporal gyrus
13	−24	28	48	Left middle frontal gyrus
14	36	−36	−12	Right parahippocampal gyrus
15	−12	42	42	Left superior frontal gyrus

using the retest dataset (N = 55) are presented in Supplementary Fig. S1A. We again found that the mean within-network FCS were significantly higher than the between-network FCS [ALE-defined-verb network: $t(54) = 13.34$; $P < 0.0001$; ALE-defined-noun network: $t(54) = 13.96$; $P < 0.0001$]. The right part of Supplementary Fig. S1A showed that the whole network was subdivided into two components, which well corresponded to the ALE-defined-verb/noun networks (sparsity = 0.41, $Q = 0.26$; Zscore = 13.17).

Global signal removal. With global signal regressed out from the main dataset, the validation results are largely stable (Supplementary Fig. S1B). We again found that the average within-network FCS was significantly higher than the between-networks FCS [ALE-defined-verb network: $t(143) = 26.49$, $P < 0.0001$; ALE-defined-noun network: $t(143) = 24.55$, $P < 0.0001$]. For the modularity analysis, now after the global signal removal, more than half of the FCSs in the correlation matrix are negative and few of the positive FCSs did reach the corrected significance level. We chose the sparsity range 0.17–0.40, thresholding from the lowest for a fully-connected graph to that included positive correlations at $P < 0.01$ (uncorrected). The modularity result patterns held up well: The nodes were divided into two modules that largely corresponded with the ALE-defined networks (Supplementary Fig. S1B, right; sparsity = 0.37, $Q = 0.37$; Zscore = 8.11).

Head motion. Using the main data with addiction 'scrubbing' procedure during preprocessing, the result patterns remained stable (Supplementary Fig. S1C): The mean within-network FCS was significantly higher than the between-network FCS [ALE-defined-verb network: $t(141) = 24.34$; $P < 0.0001$; ALE-defined-noun network: $t(141) = 18.83$; $P < 0.0001$]. The modularity-analysis showed that the overall system was divided into three modules identical to the main results reported above (Supplementary Fig. S1C, right: sparsity = 0.42, $Q = 0.28$; Zscore = 16.11). This modular pattern was stable across a range of sparsity thresholds from 0.41 to 0.46.

3.2. Experiment 2: Testing the relationship between functional network integrity and behavioral deficits in patients

3.2.1. Partial correlations between relative noun/verb FCS and relative noun/verb behavioral score

The raw behavioral performance is presented in the Supplementary Table S4. The mean FCS within the noun-functional network across the 88 patients was 0.153 (SD = 0.092), and within the verb-functional network was 0.137 (SD = 0.090).

Based on the results of Experiment 1 that the two ways of constructing the verb and noun-functional networks – on the basis of the ALE results and on the basis of the modularity analyses – are largely consistent with certain differences, we considered networks with these two methods in parallel. Within each method, two types of contrasts for the noun versus verb behavioral performances were measured: actions versus tool items and actions versus various objects items.

Relationship between ALE-defined-noun/verb network FCS and noun/verb performance. We first considered the mean FCS among the ALE-defined-verb nodes and the ALE-defined-noun nodes for each patient. When using the action versus tool contrast for the noun/verb behavioral comparison, there was significant positive correlation between the relative FCS and the relative behavioral score on the picture associate matching task, controlling for total lesion volume, age, and years of education (partial $r = 0.306$, $P = 0.004$). The correlations between relative FCS and the relative behavioral scores on the other three tasks (oral picture naming, word associative matching, and word-picture verification) were not significant (Table 3, $Ps > 0.066$). When using action versus various objects for the noun/verb comparison, the same pattern was obtained: The positive correlation between relative FCS and relative behavior score were found for the picture associative task (partial $r = 0.262$, $P = 0.016$) but not for the other tasks (Table 3, $Ps > 0.183$). That is, if a patient had a relatively stronger FCS within the verb network, he or she tended to be relatively better at performing the picture associative matching task for verbs than nouns, and vice versa.

Relationship between GTA-defined-noun/verb network FCS and noun/verb performance. When examining the networks based on the GTA-defined networks from Experiment 1, again significant positive correlation between relative noun/verb FCS and relative noun/verb behavior score was found for the picture associative matching task: When the contrast between actions and tools was used as the relative noun/verb behavioral performance score, partial $r = 0.369$, $P = 0.001$; When the contrast between actions and various objects was used as the relative noun/verb performance score, partial $r = 0.355$, $P = 0.001$ (Table 3). Interestingly, these correlation coefficients are significantly higher than the ones obtained using the ALE-defined networks (actions versus tools: $t(85) = 7.400$, $P < 0.001$); actions versus all objects: $t(85) = 7.969$, $P < 0.001$). For the other three noun/verb tasks (oral picture naming, word associative matching, and word-picture verification), no significant positive correlation was observed between the relative noun/verb FCS and the relative noun/verb behavioral scores. That is, the association between the FCS and nonverbal comprehension behavioral performance for nouns and verbs is stable across the two ways of network construction.

3.2.2. Controlling for the impact of nodal damage to each network

We assessed whether the observed association between noun/verb network FCS and comprehension performances is fully attributable to effects of lesion on the corresponding network nodes, that is, whether

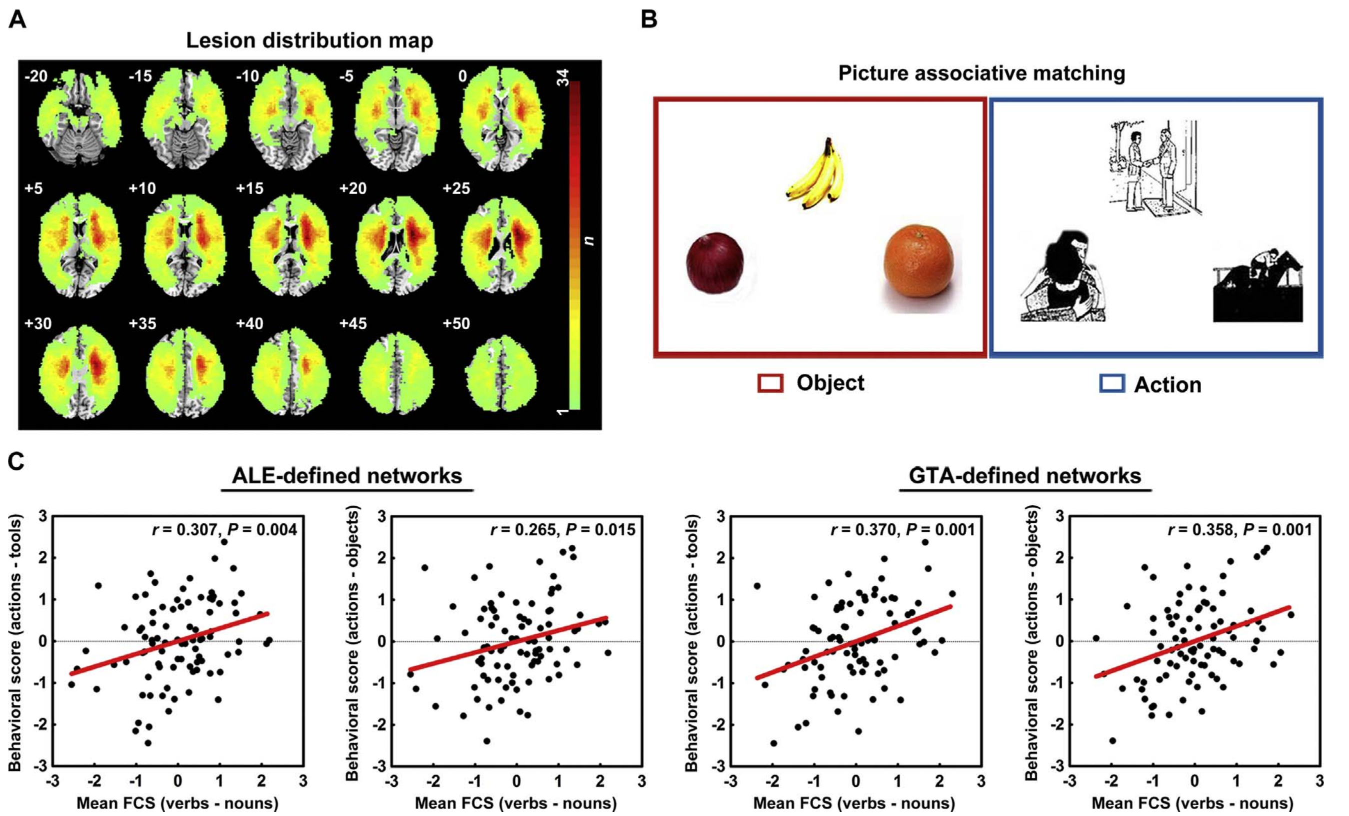

Fig. 3. Results of Experiment 1: The intrinsic network organization of the ALE-defined-noun and verb nodes in the healthy population. (A) Upper panel: The functional connectivity pattern of ALE-defined-verb and noun networks at the sparsity threshold of 0.4. Lower panel: Comparison of the average FCS within and between these networks. Error bars represent the SEM. *: $P < 0.0001$. (B) Graph matrix used in the modularity analysis. (C) Left: the assignments of areal nodes into subgraphs (colors) across a range of sparsity thresholds from 0.22 to 0.50 in 0.01 steps by modularity analyses. Right: subgraph at sparsity threshold of 0.40 is shown for the areal nodes ($Q = 0.30$; Zscore = 13.82).

the integrity of the synchronization among the networks has effects for behavior beyond the damage of the constituent grey matter regions. We did this by further computing the partial correlation between relative noun/verb FCS and relative noun/verb behavioral scores, including the relative extent of the anatomical damage for the nodes in the two networks as an additional covariate. Again both the ALE-defined networks and the GTA-defined networks were considered in parallel in this control analysis.

Results of the ALE-defined networks. For the ALE-defined networks, after controlling for the extent of lesion to the corresponding nodes in each network, the positive relationship between the relative noun/verb FCS and the relative noun/verb performances remained significant in the picture associative matching task (Fig. 2C & Table 3): Using the contrast of actions versus tools as the relative noun/verb behavioral measures: partial $r = 0.307$, $P = 0.004$; Using the contrast actions versus various objects as the relative noun/verb behavioral measure, partial $r = 0.265$, $P = 0.015$. That is, the effect of FCS for these two networks in predicting the nonverbal comprehension ability is not to be fully explained by the lesion of the nodes involved. But rather, the integrity of intrinsic communication capacity within the network has additional effects. No relationships were found for other tasks.

Results for GTA-defined networks. The same pattern as above was observed when we considered the GTA-defined networks. Significant positive correlations between relative noun/verb FCS and relative noun/verb behavior score were found for the picture associative matching task: Using the actions versus tools contrast as the noun/verb relative performance measures, partial $r = 0.370$, $P = 0.001$; Using the actions versus various objects contrast as the noun/verb measures, partial $r = 0.358$, $P = 0.001$ (see Fig. 2C & Table 3). Again the partial correlation were significantly stronger in the GTA-defined networks

Table 3
Partial correlation coefficients between the relative mean FCS of verb- and noun-functional networks and the relative verb and noun behavioral performance in each task.

Verb/noun behavioral comparison	Network construction	Correlation coefficient			
		Picture associative matching	Word associative matching	Word-picture verification	Oral picture naming
Covariates: age, years of education, and total lesion volume					
Actions vs. tools	ALE-defined networks	0.306 (*0.004*)	−0.201 (*0.066*)	−0.121 (*0.271*)	0.063 (*0.566*)
	GTA-defined networks	0.369 (*0.001*)	−0.217 (*0.046*)	0.004 (*0.974*)	−0.037 (*0.739*)
Actions vs. objects	ALE-defined networks	0.262 (*0.016*)	−0.146 (*0.183*)	−0.019 (*0.860*)	0.010 (*0.924*)
	GTA-defined networks	0.355 (*0.001*)	−0.097 (*0.376*)	0.069 (*0.528*)	−0.031 (*0.778*)
Covariates: age, years of education, total lesion volume, and nodal damage					
Actions vs. tools	ALE-defined networks	0.307 (*0.004*)	−0.202 (*0.065*)	−0.108 (*0.327*)	0.071 (*0.522*)
	GTA-defined networks	0.370 (*0.001*)	−0.219 (*0.045*)	0.022 (*0.841*)	−0.029 (*0.791*)
Actions vs. objects	ALE-defined networks	0.265 (*0.015*)	−0.143 (*0.194*)	−0.010 (*0.931*)	0.009 (*0.936*)
	GTA-defined networks	0.358 (*0.001*)	−0.094 (*0.394*)	0.081 (*0.462*)	−0.033 (*0.766*)

than in the ALE-defined networks [actions versus tools contrast $t(85) = 7.370$, $P < 0.001$; actions versus objects contrast $t(85) = 7.918$, $P < 0.001$].

3.2.3. Validation results

The overall results pattern remained stable across validation approaches. Given that the ALE-defined and GTA-defined noun- and verb-networks converged well in the main results, we here report validation results for ALE-defined networks.

Global signal removal. The partial correlation between the relative noun/verb FCS and the relative noun/verb behavioral score in the picture associate matching task was significant for the actions versus various objects contrast ($r = 0.221$, $P = 0.042$), and was no longer significant for the actions versus tools contrast ($r = 0.175$, $P = 0.110$). After controlling for the effects of nodal lesions within the networks, the partial r was 0.177 ($P = 0.107$) in the actions versus tools contrast and was 0.231 ($P = 0.035$) in the actions versus various objects contrast. Details are shown in Supplementary Table S5.

Head motion. The results of the validation of data following the 'scrubbing' procedure during preprocessing are very similar to our main results. Significant positive correlations were found for the picture associative matching task (Supplementary Table S5): The partial correlation between relative noun/verb FCS and relative noun/verb behavioral score in the actions versus tools contrast was 0.312 ($P = 0.005$) and in the actions versus various objects contrast was 0.264 ($P = 0.020$). After controlling for the effect of nodal lesions in each network, the partial r was 0.311 ($P = 0.006$) in the actions versus tools contrast and 0.265 ($P = 0.020$) in the actions versus various objects contrast.

Excluding damaged voxels. We first performed analyses including only the 41 patients who had no lesion in any node. Similar to the main analyses results, significant positive correlation between relative noun/verb FCS and relative noun/verb behavioral score was observed for the picture associative matching task in the actions versus tools contrast (partial $r = 0.353$, $P = 0.030$). We then performed analyses including all patients, while excluding the damaged voxels within the nodes for each patient, if there were any. If all voxels in a node were damaged, we excluded this node or set the FCS from this node as zero. When excluding nodes with no voxel left, the correlation between the relative noun/verb FCS and the relative noun/verb behavioral score in the picture associate matching task was significant for the actions versus tools contrast (partial $r = 0.229$, $P = 0.035$); When setting the FCS from nodes with no voxel left to zero, the partial r was 0.286 ($P = 0.008$) in the actions versus tools contrast.

4. Discussion

With two experiments we examined the neural underpinning for the dissociation of noun-object and verb-action processing from the network perspective. We first established in the healthy population that the regions consistently showing preferential activation to the same class are intrinsically connected with each other more strongly during the resting-state, forming word-class (and/or conceptual-class) specific intrinsic functional networks. Then in patients with brain damage, we found that the extent to which the two networks' functional integrity differed, measured by the mean FCS difference, significantly associated with how different the behavioral performances are on the object and action nonverbal comprehension abilities. That is, if a patient has weaker within-verb-network FCS relative to within-noun-network FCS, he or she is more likely to suffer from more severe deficit in nonverbal comprehension of actions compared to objects. These two experiments, together, revealed the functional network basis of noun/verb (object/action) dissociation previously established in the aphasia and neuroimaging field.

While the regions that are commonly activated by a class of stimuli are often referred to as a network for the class, we here showed that even at the resting-state without the task engagement, the word-class (and/or conceptual-class) specific regions are tightly connected, providing new aspect of mechanism for the neural integrative basis of noun-object or verb-action processing. Such correspondence between task-driven activation pattern and the intrinsic functional connectivity pattern during the resting-state extends the previous reports about the similar correspondence in auditory, action execution, language and memory processes (Calhoun, Kiehl, & Pearlson, 2008; Smith et al., 2009) to dissociable structures within a cognitive system, i.e., comprehension to object and action stimuli. The correlations of spontaneous BOLD fluctuations across regions are likely to be caused by their repeated co-activation during everyday activities due to Hebbian mechanisms (Hebb, 1949). Note that the correspondence is not perfect. In the spontaneous data-driven modularity analyses, three ALE-defined-verb nodes [left precentral gyrus (−54, 4, 42) and left MFG (−36, 28, 22; −30, 28, 28)] and two ALE-defined-noun nodes [left IFG (−52, 26, −4) and left anterior middle temporal gyrus (−54, 4, −32)] were consistently classified into the other module across different validation results. Interestingly, these are nodes whose functions tended to be controversial. In particular, the left inferior frontal gyrus has been suggested to be modulated by processing demand (Vigliocco et al., 2011) and high-frequency power increases during both verb and noun generation have been found here using electrocorticography recording (Conner, Chen, Pieters, & Tandon, 2014; Crepaldi et al., 2013). For the anterior middle temporal gyrus node, its lesion is associated with naming impairments for both nouns and verbs (Glosser & Donofrio, 2001). Experiment 2 showed that the FCS for the GTA-defined-networks had stronger association with behavioral performances than the ALE-defined networks, indicating that categorizing these nodes according to the modularity analyses may more accurately reflect their functions.

The dissociable intrinsic functional networks have direct cognitive relevance, as illustrated by the patients' data in Experiment 2, where the disturbance of these networks associated with the corresponding behavior. Importantly, such effects were not to be fully attributed to the damage of the constituent brain regions – the strength of the connectivity within the system has its unique effects beyond the regional lesion measures. Could the association between the network connectivity strength difference and the word class behavioral difference be explained by the potential confounding psycholinguistic properties? Although stimuli of various categories in the current Experiment 2 did not differ by word frequency or shallow orthographic/phonological variables (see Section 2), and that the class-specific regions in the target networks were obtained by meta-analysis of a large set of fMRI studies with varying stimulus properties, there are still dimensions along which the two word/conceptual classes may differ (e.g., imageability, concreteness, familiarity, valence and arousal). The difficulty in matching these variables is mainly due to the stimulus limitation of picture naming and matching tasks. It is unclear what types of psycholinguistic property are supported by the network synchronization of these networks. Worth specific mentioning is a psycholinguistic property specific to the Chinese stimuli used here – Chinese words are rich in compounding and we focused on the whole words' class properties. It has been reported that the compound constituents play an effect in compound production in Chinese aphasic patients (Bates et al., 1991), yet later studies have revealed that the whole word property is more prominent in both aphasic and healthy subjects word naming (Bi et al., 2007; Janssen, Bi, & Caramazza, 2008). As stated in the Introduction, given the difficulty in teasing apart these variables, the cognitive origins of noun/verb dissociations have been a long-standing debate, with proposals including that nouns and verbs dissociate on multiple levels (semantic, grammatical, and lexical, Laiacona & Caramazza, 2004), or that the noun/verb dissociations can all be explained by semantic variables (Vigliocco et al., 2011). A number of studies have attempted to dissociate between conceptual and grammatical classes and shown that there is no dissociation from grammatical class only (Barber, Kousta, Otten, & Vigliocco, 2010; Bedny, Dravida, & Saxe, 2014;

Moseley & Pulvermüller, 2014). It is beyond the scope of the current paper to pinpoint the cognitive origin of the noun-object and verb-action differences.

The point here is that how the observed dissociable noun/verb (or object/action) functional network framework reconciles the seeming controversies regarding the lesion profiles relating to the noun/verb (object/action) dissociations in the neuropsychological literature. While a general frontal-temporal dichotomy hypothesis was proposed (Damasio & Tranel, 1993), important exceptions have been documented. Aggujaro et al. (2006) reported that lesions covered different brain areas in different verb-impaired patients, including the left frontal operculum, the medio-temporal region and the occipito-temporal junction; Mätzig, Druks, Masterson, and Vigliocco (2009) reviewed 27 lesion studies reporting large differences (30%+) between verb- or noun-selective deficits in a picture naming task and observed large variations in lesion profiles. These lesion profiles differences for noun-object selective cases or verb-action selective cases can be readily reconciled within our network findings. These distributed lesion patterns for each class actually fell well within the intrinsic verb-/noun- (action-/object-) functional networks. The whole verb-/action- or noun-/object- functional networks, including not only the nodes, but also the connections among these nodes, together support the processing of the corresponding word class. In other words, the noun/verb (object/action) dissociation behavioral patterns can only be predicted by taking into consideration the complex network pattern as a whole rather than any single or combinations of lesion sites in a univariate manner. Different lesion sites in two patients may actually affect the network integrity to similar degree; yet two patients with similar lesion site (e.g. temporo-patietal areas) may implicate disruptions of connections within different functional networks to different degrees, leading to different behavioral profiles. These findings corroborate the recent findings of associating network integrity with neurological and psychiatric disorders (Lo et al., 2010; Wang et al., 2013), highlighting the need for the network-based approach for neuropsychological studies.

Our findings, by themselves, do not inform us how exactly the information is represented, processed, and integrated within the noun-/object- and verb-/action- functional networks. Nonetheless, combing the previous findings about the functional roles of these constituent regions and the patterns that they are connected together, new hypotheses can be developed. For instance, for the noun/object network, the strongest functional connectivity was found linking the precuneus/SPL with the bilateral PHG, the left ITG, and the IFG/MFG. For the verb/action network, the strongest functional connectivity was found linking the MTG/STG with the left IFG/insula and the left MOG. One possible scenario is that the regions processing semantic knowledge, centered around the precuneus/SPL for nouns-objects and MTG/STG for verbs-actions link with sub-regions within IFG regions for syntactic-related processing. Of course, the functions of the specific functional connections for these conceptual and word classes are to be explicitly tested.

One intriguing result is that in patients the connectivity strength for the class-specific networks significantly associated with behavioral performances only on the nonverbal comprehension task (picture associative matching) and not with performances on verbal comprehension (word associative matching, word-picture verification) or verbal production (oral picture naming). While the studies used in our ALE meta-analyses covered a range of tasks (Table 1), including picture naming and verbal semantic tasks, it is still possible that the noun/verb (object/action) dissociable functional networks pinpointed here correspond to one of these components shared by these tasks, i.e., semantic processing. However, this possibility does not readily explain our current finding of positive effects for only picture associative matching and not the other tasks, as deficits in semantic processing would also affect the other tasks (e.g., oral picture naming), which clearly involve the semantic processes and were the primary tasks used to define the noun/verb regions of interest in the first place. One possibility for the negative results for the verbal noun/verb tasks is the following. Patients performances are determined not only by the semantic processing integrity but also the other cognitive components these tasks entail, such as lexical access for production or visual word recognition, which either did not distinguish between nouns-objects or verbs-actions or the dissociative neural bases are not fully captured by the networks identified here. That is, some of the variance of the noun-/object- or verb-/action-behavioral deficits on these tasks may originate from cognitive processes that are supported by systems outside of the target networks of interest here, and thus overshadowed the noun/verb (object/action) dissociations being predicted from the target network integrity, which primarily function for semantic processing. Replication studies that consolidate these correlation results between brain network property and behavioral pattern are desired.

A few important methodological issues warrant considerations. First, the nodes we used to derive the functional network come from those showing differential activation in the two word classes. Those that are comparably activated by the two classes were not included. As a consequence, the networks may not constituent the “full” networks for noun-object or verb-action processing, which presumably include also elements where the two classes do not dissociate. We in fact also considered such regions by using the contrast noun versus baseline and verb versus baseline in the ALE analyses, which generated widely distributed in frontal and temporal gyrus for the two classes which were largely indistinguishable. Modularity analyses on these regions showed that they tended to form modules that had no correspondence to the class effects in the task activation analyses. Second, with the development of human connectomic research, various graph measures have been established to quantify the network information processing efficiency, including, for instance, global efficiency or clustering coefficient, which measure the information flow and integration of network (Rubinov & Sporns, 2010). Given that the two networks identified here were relatively small, containing fewer than 20 nodes each, we adopted a simple measure – the mean of FCS. Future studies are desired to test more specifically the mechanisms of noun-object/verb-action processing relating to these observed networks and to examine different network characteristics.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2017.08.009.

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