

Predicting the Brain Activation Pattern Associated With the Propositional Content of a Sentence: Modeling Neural Representations of Events and States

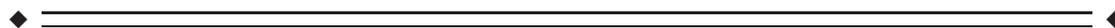
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Abstract: Even though much has recently been learned about the neural representation of individual concepts and categories, neuroimaging research is only beginning to reveal how more complex thoughts, such as event and state descriptions, are neurally represented. We present a predictive computational theory of the neural representations of individual events and states as they are described in 240 sentences. Regression models were trained to determine the mapping between 42 neurally plausible semantic features (NPSFs) and thematic roles of the concepts of a proposition and the fMRI activation patterns of various cortical regions that process different types of information. Given a semantic characterization of the content of a sentence that is new to the model, the model can reliably predict the resulting neural signature, or, given an observed neural signature of a new sentence, the model can predict its semantic content. The models were also reliably generalizable across participants. This computational model provides an account of the brain representation of a complex yet fundamental unit of thought, namely, the conceptual content of a proposition. In addition to characterizing a sentence representation at the level of the semantic and thematic features of its component concepts, factor analysis was used to develop a higher level characterization of a sentence, specifying the general type of event representation that the sentence evokes (e.g., a social interaction versus a change of physical state) and the voxel locations most strongly associated with each of the factors. *Hum Brain Mapp* 38:4865–4881, 2017. © 2017 Wiley Periodicals, Inc.

Key words: fMRI; multiconcept propositions; predictive modeling; neural representations; concept representations



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INTRODUCTION

Although individual concepts may be the fundamental elements of thought, the generativity and complexity of human thought stem from the ability to combine *multiple* concepts into propositions. Functional neuroimaging approaches have provided remarkable insights concerning the neural representations of individual concepts [Anderson et al., 2014; Bauer and Just, 2015; Coutanche and Thompson-Schill, 2015; Ghio et al., 2016; Huth et al., 2012; Just et al., 2010; Mason and Just, 2016; Mitchell et al., 2008; Peelen and Caramazza, 2012; Pereira et al., 2011; Shinkarova et al., 2011; Wang et al., 2013] and segments of stories [Huth et al., 2016; Wehbe et al., 2014], interconcept relations [Frankland and Greene, 2015; Wang et al., 2016], or combined concepts [Baron and Osherson, 2011]. But characterizing the neural representations of more complex thoughts, such as event and state descriptions, has remained a considerable challenge.

This article develops a computational account of the mapping between the concepts of a proposition describing an event or state and the neural representation that it evokes. The major advance of this study is to characterize the neural representation of events and states as they are described by sentences, by developing a predictive, bidirectional mapping between the conceptual content of a sentence and the corresponding brain activation pattern. In this article, we describe a computational model that can predict the neural representation of 240 different propositions that describe events or states with reasonable accuracy and with reliable capture of the gist of the proposition.

The initial approach taken here is that the neural representation of a sentence is composed of the neural representations of its component concepts and the roles those concepts play in the thematic structure of the sentence. Each word concept in a sentence can be characterized in terms of a set of neurally plausible semantic features (NPSFs) and in terms of the concepts' thematic role in the sentence or event. The NPSFs are intended to correspond to various brain subsystems, such as the motor system representation of how one interacts with a concrete object, or the perceptual system's representation of the perceptual properties of the object. The main analytic technique that is used here to determine the mapping between semantic features and neural activation patterns is multiple regression modeling. Once the mapping is determined in a large subset of the data, it can then be used to make predictions in the remaining independent subset.

The neural representation of the concepts of a sentence or proposition must be expressed within the brain's organizational system or ontology that categorizes and relates a large number of different concepts. We make an initial attempt at specifying this neurally based organizational system, by developing 42 NPSFs that provide a starting point for a neurally motivated feature representational system. These features are considered neurally plausible

based on previous findings concerning the neural representations of various types of semantic knowledge. For example, some subsets of these features code perceptual [Kanwisher et al., 1997; Martin, 2007; Oliver and Thompson-Schill, 2003], motor [Hauk et al., 2004; Pulvermüller et al., 2005], and affect-related [Baucom et al., 2012; Chikazoe et al., 2014; Kassam et al., 2013] features of an entity; one other subset codes different aspects of human activity in society [Iacoboni et al., 2004; Spitzer et al., 2007]; and one other subset codes properties pertaining to time or space [Fernandino et al., 2016; Kranjec and Chatterjee, 2010; Lai and Desai, 2016].

This study develops a model that relates such semantic features of concepts to the activation level of prespecified clusters of voxels. The model extends the general approach to all of the concepts in a proposition, and also takes into account the thematic role of each concept. Given the semantic and thematic characterization of the component word concepts of a proposition, the model can predict the activation pattern the reading of the corresponding sentence will evoke.

The 42 NPSFs were coded in binary form, as applicable or not applicable to each concept. The types of information the NPSFs coded included the perceptual and affective characteristics of an entity (10 NPSFs coded such features, such as man-made, size, color, temperature, positive affective valence, and high affective arousal), animate beings (person, human-group, animal), and time and space properties (e.g., unenclosed setting, change of location). For example, a concept such as the noun *judge* was coded with the following NPSFs: person, social norms, knowledge, and communication. The general assumption was that individual NPSFs could be related to activation levels in particular clusters of voxels.

In addition to relating individual concepts to the activation patterns they evoked, the model assumes that the neural signatures of the concepts in a sentence are sensitive to the roles they play in the proposition's argument structure. The current model incorporates a thematic role component [Fillmore, 1967] to account for context-dependent, propositional-level semantics. Thus each content word is also coded in terms of its thematic role in the sentence such as agent or patient.

The predictive ability of these NPSFs and thematic features can be compared with other accounts provided by semantic vector representations of concepts [Fellbaum, 1998; Landauer and Dumais, 1997; Niles and Pease, 2001] that do not take neural organization into account. Semantic vector representations are based on a word's distributional properties in a large language corpus, indicating a word's co-occurrence patterns with other words. A word such as *judge* might be characterized in terms of its co-occurrence with other items such as *jury* or *decide*. Latent Semantic Analysis (LSA) [Landauer and Dumais, 1997] is a prominent example of a semantic vector representational approach. It is possible to construct a predictive model of

the neural representations of concepts and sentences based on the semantic vector representations of the concepts. In the context of this article, semantic vector representations provide a point of comparison to NPSFs.

In addition to characterizing a sentence representation at the level of the semantic and thematic features of its component concepts, we developed an additional characterization of a sentence at a coarser level of granularity that specifies the general type of thought that the sentence evokes (e.g., the thought of a social interaction versus a physical change of state). The main analytic technique that was used to determine these coarser dimensions of representation was factor analysis applied to the sentence activation data, to identify the emerging meaning dimensions that characterize sentence representations. This facet of the analysis was data-driven (rather than driven by hypothesis); the resulting clustering of sentences with similar activation patterns indicated that they shared coarse underlying semantic dimensions. This coarser level of analysis plays three roles in this study. It identifies the 4 main types of meaning dimensions that underlie the set of 240 stimulus sentences. It identifies the main regions of brain activation that correspond to the processing of the 240 sentences. And it indicates the correlation between each of the 42 NPSFs and the 4 main meaning dimensions.

One methodological challenge presented by the study of the neural representations of sentences was to overcome fMRI's convolution of the signals from temporally adjacent stimuli, in this case, the successive words of a sentence. Previous studies of the neural processing of a story modeled the text in terms of semantically arbitrary segments determined by image acquisition segments [Huth et al., 2016; Wehbe et al., 2014]. The current approach of modeling a proposition and its component concepts uses the brain image that occurs at the end of the reading of a sentence. Our preliminary findings showed that this image contained the neural representation of all the word concepts in the sentence; thus there was no attempt to segment the observed fMRI signal evoked by a sentence into arbitrary time intervals. To obtain an estimate of the neural representation of an individual word concept, the end-of-sentence brain images of the several sentences that contained the target concept were averaged, on the assumption that the images of other words are averaged out. The resulting estimates of the neural representations of concepts provide a robust basis for developing a mapping between semantic representations and brain activation patterns.

This study thus has two main goals. The main goal was to develop a mapping between a semantic characterization of a sentence (based on the individual word concepts in the sentence and their thematic roles) and the resulting brain activation pattern that occurs when the sentence is read. The mapping can then be used to predict the activation pattern of an entirely new sentence containing new words, simply based on its semantic characterization.

TABLE I. Examples of stimulus sentences

The journalist interviewed the judge.
The angry activist broke the chair.
The flood damaged the hospital.
The happy child found the dime.
The witness shouted during the trial.
The jury listened to the famous businessman.
The young author spoke to the editor.
The judge met the mayor.
The restaurant was loud at night.
The window was dusty.

Furthermore, the mapping that is developed in the model is bidirectional, such that it is also possible to predict the semantic properties of the word concepts in a new sentence, given the activation pattern that the sentence evokes. Closely related to the main goal was an assessment of the similarity across participants of the mapping between semantic features and neural representations. It is possible that every participant has a systematic mapping between semantic features and activation patterns, but this mapping could be similar or dissimilar across participants.

The second main goal of this study was to characterize the broad semantic dimensions that underlie the activation of sentences that describe simple events and states, obtained using factor analysis of the activation patterns that accompany a large number of sentences. The emerging factors provide a characterization of the neural organization of semantics at a coarser grain size than individual semantic features.

METHODS

Participants

Seven healthy, right-handed, native English-speaking adults (mean age = 25, range = 20–35, two males) from the Carnegie Mellon community gave written informed consent approved by the Carnegie Mellon Institutional Review Board.

Stimuli and Procedures

The 240 stimulus sentences, generated by Glasgow et al. [2016] described primarily events but also some states, with each sentence containing a mean of 3.3 content words (range = 2–5) and a total of 242 unique words. Examples of stimulus sentences are shown in Table I and the full set of stimulus sentences is presented in Supporting Information, Table S1. The component concepts of the sentences were chosen to be representative of general human knowledge (objects, human roles, actions, activities, attributes, places, and time). All sentences were literal, used active voice and past tense. A word appeared on average in 3.3

TABLE II. The 42 neurally plausible semantic features (NPSFs)

Category ^a	Feature	Definition	Example stimuli
Perceptual and affective characteristics of an entity	Man-made	Objects or settings made by humans	Bicycle, desk, newspaper, church
	Natural	Objects or activities occurring in nature	Flower, flood, island
	Inanimate	Nonliving object	Ball, coffee, window
	Visual perception	Visual perceptual properties	Big, blue, empty, new, shiny
	Size	Physical volume or size	Big, heavy, long, small
	Color	Self-explanatory	Black, blue, green, red, white
	Temperature	Related to temperature	Sun, summer, winter, cold, hot
	Positive affective valence	Self-explanatory	Celebrate, laugh, vacation, happy
	Negative affective valence	Self-explanatory	Destroy, fear, terrorist, dangerous, sick
High affective arousal	Self-explanatory	Celebrate, shout, hurricane, angry	
Animate beings	Person	A human being	Boy, doctor, farmer, pilot, voter
	Animal	An animal or anatomy of animals	Bird, dog, duck, feather, horse
	Human-group	More than one human being	Team, couple, family, mob, council
Time and space	Settings	Place or temporal settings	Lake, church, park, night, hotel
	Unenclosed	An environment without shelter or enclosure	Beach, lake, field, island, street
	Location	Actions or events that imply spatial settings	Meeting, visit, stay, live
	Shelter	Being enclosed, indoors is a salient feature; opposite of unenclosed	Car, hotel, school, hospital, store
	Change of location	Self-explanatory	Approach, hike, throw, car, run
	Event	Self-explanatory	Dinner, protest, trial, vacation
Human activity type	Time-related	Related to a time period or timing	Morning, night, spring, summer, end
	Violence/conflict	Involving aggression and those who commit it	Army, guard, soldier, terrorist
	Health	Related to improving or threatening health	Medicine, doctor, patient, victim, hospital
	Eating/drinking	Self-explanatory	Drink, eat, dinner, corn, restaurant
	Communication	Medium of communication	Listen, speak, newspaper, author, reporter
	Sports	Related to recreation or competitive physical activities	Play, soccer, baseball, bicycle, team
	Technology	Related to technology or technical skills	Computer, television, engineer, scientist
	Money	Related to financial activities or economics	Buy, cash, banker, expensive, wealthy
	Arts and literature	Objects, actions or professions related to humanities, arts, literature	Actor, author, artist, theatre, draw
	Social norms	Related to laws and authority structure	Trial, criminal, lawyer, court, prison
Social action or state	Governance	Related to civics, politics, dominance	Debate, protest, army, mayor, embassy
	Intellectual	Requiring, gaining, or providing knowledge or expertise	Plan, read, computer, engineer, school
	Transfer of possession	Transaction (giving/receiving); change of ownership	Give, steal, take, buy
Social action or state	Social interaction	Interaction between two or more subjects	Interview, negotiate, party, lonely
	Social support	Providing social support is a salient feature	Help, family, minister, parent

TABLE II. (continued).

Category ^a	Feature	Definition	Example stimuli
Physical action or state	Physical action	Self-explanatory	Kick, throw, play, walk, march
	Change of physical state	Self-explanatory	Destroy, fix, grow, break
	Physical impact	Two subjects or objects coming in contact with each other	Break, destroy, drop, kick
Mental action or state	Mental action	Requiring cognitive processes; occurring internally	Liked, plan, want, teacher, clever
	Perceptual action	Self-explanatory	Listen, watch, read, witness
	Emotion	Emotional state or action	Fear, laugh, like, happy
Abstractness	Abstract	Detached from sensory or motor properties; low imagability	Plan, want, clever
Part of speech	Attribute	Adjectives	Aggressive, blue, shiny, sick

^aThe grouping into categories is included here to facilitate description but was not used in the modeling.

sentences (range = 1–7). There were 45 words that appeared only in a single sentence.

The sentences were presented 4 times each over 4 days of scans. This slow event-related design allowed acquisition of reliable single-trial neural signatures of individual sentences. The stimulus onset asynchrony between sentences was 12 s (5 s of sentence reading + 7 s fixation). The details of the stimulus presentation timing are described in Supporting Information. This general experimental paradigm and choice of parameters has been applied in many studies on neural representations of various types of concepts [Just et al., 2010; Mason & Just, 2016; Shinkareva et al., 2011; Wang et al., 2013].

Data were collected using a Siemens Verio 3 T MRI scanner at the Scientific Imaging and Brain Research Center at Carnegie Mellon University. Functional images were acquired using a gradient echo EPI pulse sequence with TR = 1000 ms, TE = 25 ms and a 60° flip angle. Twenty 5-mm-thick, AC-PC aligned slices were imaged with a gap of 1 mm between slices. The acquisition matrix was 64 × 64 with 3.125 × 3.125 × 6 mm³ voxels.

Data Preprocessing

Whole cortex fMRI data were corrected for slice timing, head motion, linear trend, low-frequency trends (by applying a high-pass temporal filter at 0.005Hz), and normalized into MNI space using SPM8 (Wellcome Department of Cognitive Neurology, London). Further analyses were performed using in-house scripts written in Matlab7 (Mathworks, MA, USA).

In the processing of the fMRI data for each presentation of a sentence, the percent signal change (PSC) relative to a baseline was computed at each voxel in the brain image. The baseline activation level was measured during and averaged over sixteen 17 s fixation conditions. The baseline measurement started at 4 s after each fixation presentation onset to account for the hemodynamic response delay. The fMRI data to assess sentence reading consisted

of the mean of 5 brain images, collected 1 s apart from each other, the first starting at 7 s from sentence onset. The temporal window for the sentence data analysis was chosen based on pilot investigations. The temporal window within which the neural signatures of *all* the content words in a simple sentence, regardless of their serial position in the sentence, was located in time *after* the entire sentence had been read (as shown in Supporting Information, Fig. S1). The PSC was then normalized to a mean of 0 and variance of 1 across voxels within each image, to equate the overall intensities across scans.

Neurally Plausible Semantic Features

The mapping between the semantics of a sentence’s conceptual content and its neural signature is presumed to be mediated by a layer of semantic features, enabling the prediction of the activation of a new sentence based on its semantic content. A set of 42 neurally plausible semantic features (NPSF) was developed to both characterize a semantic property of some of the 242 unique corpus words and to also correspond to a known or plausible neural processing mechanism. These binary features were defined for each of the 242 word concepts in the corpus, where a coding of 1 indicated that the feature was applicable to the word concept. The coding was performed by two raters with disagreements adjudicated by a third rater. Each word was coded by taking into account the meaning of the word in all of the stimulus sentences in which it appeared, and coding it the same way in the various sentences in which it appeared. The NPSF definitions and sample concepts pertaining to each NPSF are shown in Table II. Table III shows the NPSF coding of several example word concepts.

Thematic Role Variables That Characterize the Sentence-Level Role of Concepts

In addition to the NPSF feature set, six additional variables were coded indicating the sentence-level role of each

TABLE III. Examples of NPSF coding of content word concepts

Word	NPSF features
Interview	Social, Mental action, Knowledge, Communication, Abstraction
Walk	Physical action, Change of location
Hurricane	Event, Change of physical state, Health, Natural, Negative affective valence, High affective arousal
Cellphone	Social action, Communication, Man-made, Inanimate
Judge	Social norms, Knowledge, Communication, Person
Clever	Attribute, Mental action, Knowledge, Positive affective valence, Abstraction

concept: main verb, agent or experiencer, patient or recipient, predicate of a copular sentence (*The window was dusty*), modifier (*The angry activist broke the chair*), and complement in adjunct and propositional phrase, including direction, location, and time (*The restaurant was loud at night*). These variables covered all the roles that occurred in the stimulus sentences. Thus, each word concept in a sentence was coded not only with respect to the applicability of the 42 NPSFs but also with respect to the 6 thematic roles (indicating which one of the 6 roles is applicable). If a given word played a different thematic role in different sentences then its thematic role would be coded differently. The generative model can thus predict different neural activity patterns for the same words in different roles. This model has the capability of being expanded to incorporate more thematic roles and different types of sentence roles (such as negation).

Factor Analysis

To evaluate the data-driven dimensions of neural sentence representation and identify the brain locations associated with these dimensions, factor analysis (FA) methods were applied.

The main FA was performed on data of the 3 participants with the highest preliminary sentence prediction accuracy when using 300 most stable voxels anywhere in the brain. A set of 600 voxels was selected for each participant, based on the stability of their activation profiles over sentences across 4 presentations. Voxel stability refers to responding similarly to the set of items in the training set across multiple presentations of the set, that is, displaying a repeatable semantic tuning curve. Fifty to sixty voxels were selected from each of bilateral frontal, temporal, parietal, fusiform, and occipital lobes and 40 voxels were selected from cingulate cortex. A sentence was then characterized by a mean image across 4 presentations in the selected voxels. A two-level hierarchical exploratory factor analysis was applied to the activation data for the 3 participants. The first-level FA was applied to the activation

profiles of 600 voxels over the 240 sentences within participants, resulting in 7 factors underlying the voxel activation profiles per participant. The second-level FA was performed on these 21 factors to further aggregate the neural dimensions over participants. The first 5 factors of the second-level FA explained 37% of the variation. These factors formed the group-level characterization of the main dimensions that underlie the activations.

Each of the second-level factors was associated with a set of voxels, by tracing back each second-level factor to the first-level factors with factor loadings $>|0.4|$. For each of the identified contributing factors, contributing voxels with a factor loading $>|0.4|$ were selected. The resulting clusters with a minimum of 5 contributing voxels were identified as the brain locations associated with the second-level factors. To account for the variability of representations across participants, each cluster was approximated by applying an algorithm that grows a cluster by one voxel in all directions.

Model Training and Prediction of Neural Activity (Activation-Predicting Model)

Given the semantic content of a sentence, the goal was to predict the neural activation pattern that the reading of the sentence would evoke. The neural activation was limited to the brain locations discovered using FA. The procedure used a cross-validation protocol that leaves one sentence out as the test data in each fold, so that every sentence is tested once after all the iterations of training-test assignment. The training and test sets are always kept independent during the model training and prediction.

The activation data that characterized each sentence reading was the mean percent signal change over a 5 s interval acquired *after* sentence reading (sentences lasted a mean of 1.4 s), starting at 7 s from sentence onset (see Supporting Information for details of presentation).

The normalized PSC images of 240 sentences with 4 presentations were partitioned into training and test set in each cross-validation fold. The data from one test sentence (including all 4 times it was presented) were left out from the model's training set. Using only the data in the training set, brain images corresponding to each content word were constructed by averaging the PSCs of all the training sentences that contain that content word.

The data that were used to train the regression model were the means of the images corresponding to the sentences in the training set that contained the same content words manifesting the same roles. The voxels that were used for training and testing were the selected stable voxels within the regions identified by a factor analysis (see Supporting Information for specifics of the voxel selection procedure). It is important to note that the factor locations that were used in the modeling of a given participant *always excluded* all of the data from that participant. Specifically, brain locations identified by the FA based on the 3

participants with the highest prediction accuracies were used to perform the sentence decoding of the 4 remaining participants. For decoding of these 3 high-accuracy participants, three additional FAs were performed following the same procedure except for replacing the participant being classified with the fourth best participant's data.

A kernel ridge regression model [Hastie et al., 2009] was trained to map the relations between the activation patterns from selected representative voxels and intermediate semantic features of words. The learned weights specified the contributions of each of the semantic features to the activation of a voxel. The trained models from the selected voxels were then used to predict the neural signatures of all 351 role-specific words, given the corresponding semantic features.

The predicted brain activity pattern associated with each of the 240 sentences was the mean of the activity associated with its component words at certain thematic roles, without any activation information from the target sentence. In each cross-validation fold, all four presentations of the test sentence were left out of the training set, and the left-out data were used for testing. The four presentations of the test sentence were averaged to minimize noise. Only the voxels selected based on the training set were considered in the analysis. The left-out (observed) image of the test sentence was compared to each of the 240 predicted sentence images, in terms of cosine similarity. The performance of the prediction was assessed by the normalized rank, or rank accuracy, of the similarity of the predicted test sentence in the list of 240 alternatives.

The statistical significance of the prediction accuracy was determined based on the null distribution generated by a 10^5 -iteration random permutation of data, so that the number of cross-validation folds, number of test items per fold, and number of classes were controlled.

The methods used for the meaning-predicting model used the same framework and are reported in Supporting Information.

Cross-Participant Prediction of Neural Representation of Sentences

Interparticipant commonality of sentence representation was assessed by training a model on the mapping from the NPSF features to brain images using the fMRI data from all but one participant, and then predicting the brain activity of the left-out participant. The specific methods applied were the same as in the within-participant activation-predicting model, except for the method of voxel selection. For the data of the participants in the training set, representative voxels were selected based on their stability of activation at the sentence level. The cross-participant stability was defined as follows: for each of the 6 training participants, the response profiles of word concepts at each voxel were averaged across 4 presentations. The cross-participant stability was the mean pairwise profile similarity between participants. Only voxels within the prespecified factor

locations identified using data of the three most accurate participants in the training set were considered. The same set of representative voxels was then used to characterize the data of the test participant.

The Model's Capture of Event Semantics: Behavioral Judgment of Event Similarity

Human judgments of the similarity of pairs of sentences were crowdsourced using Amazon Mechanical Turk (MT, www.mturk.com) in accordance with the Carnegie Mellon Institutional Review Boards. The sentence stimuli were 195 noncopula sentences that described events, omitting the 45 copula sentences (e.g., *The flower was yellow*), to limit the number of pairs to 18915. These pairs of sentences were organized in 195 groups of 97 pairs of sentences, arranged in different groupings for different MT workers.

Because the vast majority of the sentences were semantically dissimilar, each MT worker was instructed to select only 1 pair of sentences describing the most similar pair of events within each group of 97 pairs, resulting in 195 pairs of sentences judged as similar. Among the sentence pairs judged as most similar, there were 18 pairs of sentences that were selected by three out of the four MT workers.

Alternative Semantic Representations

Linguists and psychologists have proposed several different types of semantic representations of individual concepts that unlike NPSFs, were not intended to be related to brain function. The ability of four vector-space characterizations of the 242 word concepts was compared to the NPSFs' account of the fMRI data. These vector-space representations characterize a word's meaning based on its co-occurrence with other words in large corpus. These four alternatives included GloVe vectors for word representation (300 dimensions) [Pennington et al., 2014], doc VSM and dep VSM (a documents-based and a dependencies-based vector space model, respectively, 1000 dimensions each) [Fyshe et al., 2013], and Latent Semantic Analysis (LSA, 308 dimensions) [Landauer and Dumais, 1997]. The vector used to represent a sentence was the mean of the vectors representing the individual word concepts. The analyses reported below assessed the accuracy of each of these representational approaches in predicting brain activation patterns associated with comprehending a sentence, in comparison with the accuracy of the NPSFs' account.

RESULTS

Predicting Neural Signatures of New Events From Their Semantic Content

Activation prediction

The neural representation evoked by the reading of an individual sentence was reliably predicted based on its

semantic and thematic content. Given the word-level semantic (NPSF) and thematic features of the content words of a left-out sentence, the model can predict the activation pattern of a sentence that is new to the model with a mean rank accuracy of 0.86 among 240 alternatives, where chance is 0.50. The analyses associated with this finding are described in more detail below.

The semantic-feature-to-fMRI mapping was learned by training on the data from 239 sentences using a kernel ridge regression model [Hastie et al., 2009], while the image of the 240th sentence was left out for testing the accuracy of the prediction in each cross-validation fold. A mapping from the 42 neurally plausible semantic features and 6 thematic role variables to the activations in selected voxels in preidentified brain regions was learned using all the concepts in the 239 training sentences. The *a priori* regions were clusters with high factor loadings on any of the main dimensions revealed by factor analysis of the activation data of other participants (as described below). The neural signatures of all of the component content words of the test sentence were predicted using their NPSF values and thematic roles and applying the learned mapping. The predicted neural signature of a sentence was the mean of the predicted signatures of its component words. To assess the model's prediction accuracy for a given test sentence, the observed activation pattern of the test sentence was compared for similarity to the predicted activation patterns of all 240 sentences (using the cosine measure of similarity). The accuracy measure was the normalized rank of the similarity of the test sentence's predicted activation pattern, among the 240 predictions, to its actual activation pattern. This procedure iterated through 240 cross-validation folds, testing each sentence once. At the group level (where the fMRI images of all 7 participants were averaged), the mean rank accuracy for the 240 sentence predictions was 0.86, as shown in Figure 1, significantly different from chance ($P < 10^{-5}$).

While the rank accuracy provides a measure of how distinct the predicted neural signature of a sentence is from those of other sentences, it is indifferent to the *absolute* similarity between the observed and the model-predicted neural signatures. To assess the absolute similarity, cosine similarity between the actual and predicted signatures was computed over the voxels being modeled. The mean observation-prediction similarity over sentences was 0.42, significantly different from chance ($P < 10^{-5}$). To estimate the ceiling that this similarity measure can reach given the noise in the current data, the similarity between the images of the same sentences as observed in different presentations was computed. The mean image of two presentations was compared with the mean image of the other two presentations by exhausting all possible combinations of presentation pairs when all the other parameters were controlled. This measure of observation-observation similarity results in a mean of 0.58. Thus, the mean absolute similarity of 0.42 between the observed and the model-

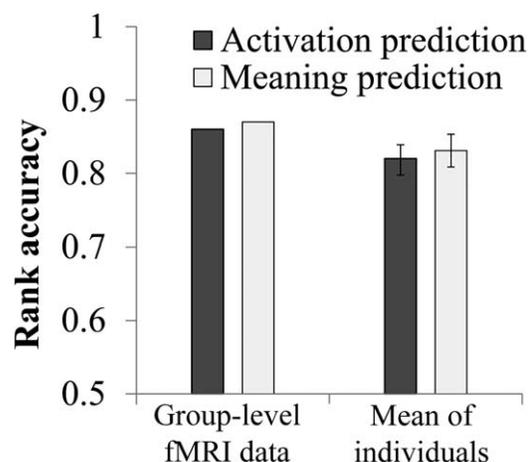


Figure 1.

Rank accuracy of identifying the 240 sentences using the activation-predicting model or the meaning-predicting model. Error bars indicate standard deviations. The rank accuracy for each participant individually was significantly above chance level (the critical value of the rank accuracy being significantly different from chance level at $P = 10^{-5}$ is 0.58 based on random permutation tests).

predicted neural signatures of the 240 sentences captures more than two-thirds of the maximum possible similarity of 0.58.

When the model was implemented at the level of each individual participant, the mean rank accuracy of the predictions across participants was 0.82 (range = 0.79–0.84), as shown in Supporting Information, Table S2). Aggregating the fMRI data over participants apparently reduces the noise and provides a more accurate mapping (mean rank accuracy of .86, described above). The remaining analyses were performed at the individual level unless otherwise specified.

Although the model above was trained without any direct information about the activation associated with the test sentence, a word in the test sentence could have occurred in other sentences in the training set. To test the model's predictive ability in the absence of any such information, a second classifier was trained only on sentences that did not contain any of the words in the test sentence (resulting in a meaning training set size of 229 sentences), thus excluding all activation levels associated with any of the word concepts in the test sentence. The resulting accuracy of the sentence prediction decreased only marginally, remaining at a mean rank accuracy of 0.81 over participants (range = 0.78–0.83). Thus, the sentence prediction accuracies are primarily based on the mapping between brain activation patterns and semantic and thematic features, rather than on the mapping to observed activation patterns of particular word concepts. In addition, this analysis establishes the model's ability to predict activation for the previously unseen words.

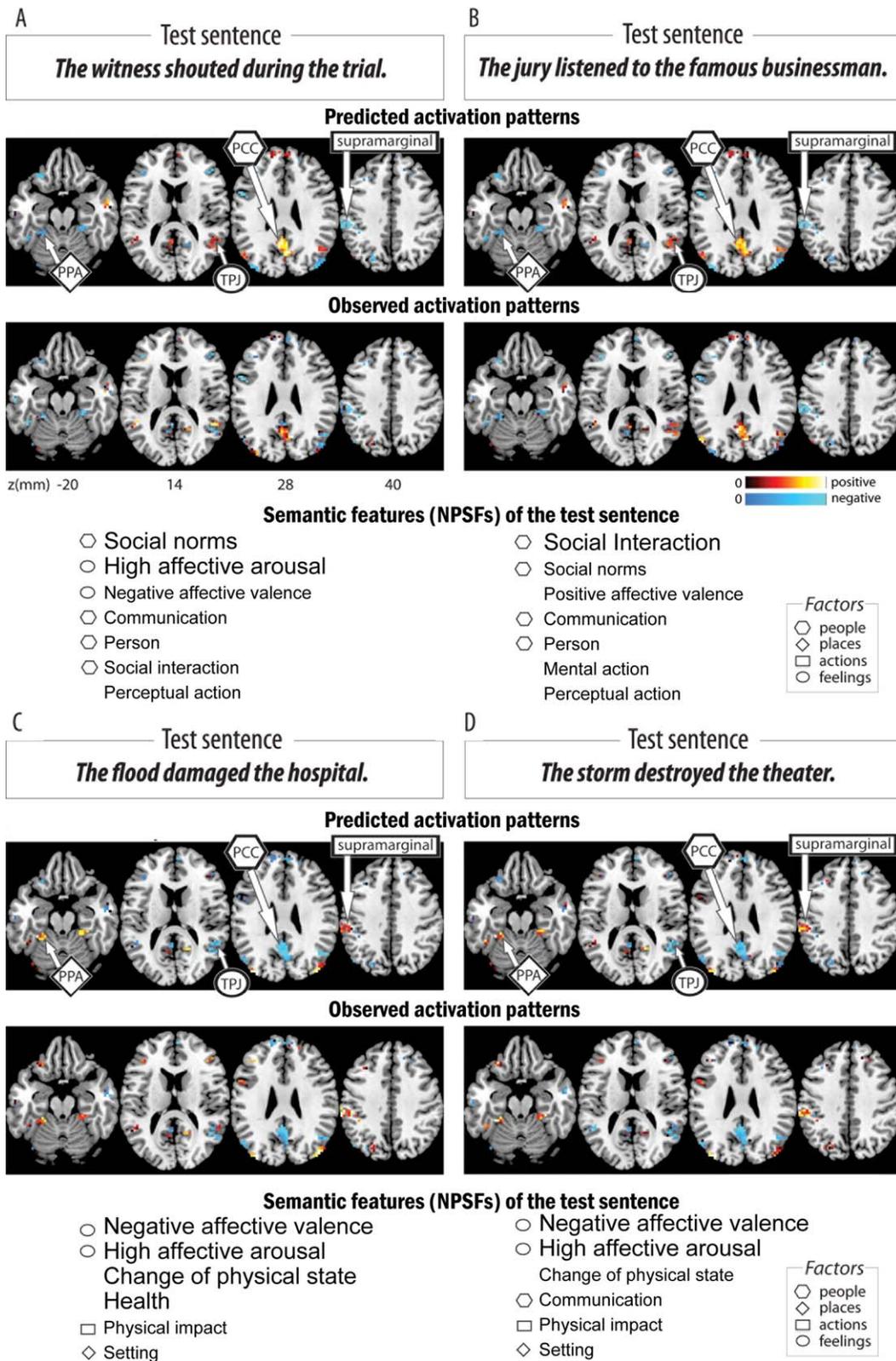


Figure 2.

Predicted and observed activation patterns and semantic features (NPSFs) for two pairs of sentences (sentences A and B in the first panel, sentences C and D in the second panel), displaying the similarity between the model-predicted (upper row) and observed (lower row) activation patterns for each of the sentences. See text for quantitative measures of similarity. Also note the similarities between the two sentences within each pair (columns A and B and columns C and D) in terms of their predicted

activation, observed activation, and semantic features (NPSFs). The geometric symbols (hexagon, diamond, rectangle, and ellipse) pointing to voxel clusters and adjoining the test sentence semantic features (NPSFs) correspond to locations of voxels clusters with high factor loadings on the large-scale semantic factors of *people*, *places*, *actions* (and their consequences), and *feelings*, respectively (Fig. 4C). The font size of the NPSFs indicates their mean values averaged across the content words of the sentence.

TABLE IV. Normalized rank of the 18 behaviorally judged most similar pairs of sentences with respect to the model’s similarity measure. Each row indicates a pair. The pairs are ordered by their rank in the model’s similarity prediction

Sentence 1	Sentence 2	Rank
The editor drank tea at dinner.	The lawyer drank coffee.	1.00
The artist hiked along the mountain.	The tourist hiked through the forest.	0.99
The activist listened to the tired victim.	The policeman interviewed the young victim.	0.99
The fish lived in the river.	The duck lived at the lake.	0.99
The council read the agreement.	The policeman read the newspaper.	0.98
The dangerous criminal stole the television.	The terrorist stole the car.	0.97
The witness shouted during the trial.	The jury listened to the famous businessman.	0.97
The angry lawyer left the office.	The tired jury left the court.	0.94
The witness went to the trial.	The witness spoke to the lawyer.	0.93
The wealthy politician liked coffee.	The lawyer drank coffee.	0.92
The accident damaged the yellow car.	The accident destroyed the empty lab.	0.91
The flood damaged the hospital.	The soldier delivered the medicine during the flood.	0.89
The boy threw the baseball over the fence.	The boy kicked the stone along the street.	0.89
The young girl played soccer.	The happy girl played in the forest.	0.87
The yellow bird flew over the field.	The girl saw the small bird.	0.78
The tourist found a bird in the theater.	The man saw the fish in the river.	0.41
The author kicked the desk.	The horse kicked the fence.	0.33
The couple read on the beach.	The cloud blocked the sun.	0.21
Mean		0.83

Meaning prediction

The mapping in the other direction, decoding semantic content from activation patterns, yielded a similar outcome. Given an unlabeled fMRI image evoked by the reading of a test sentence, the activation-to-features mapping model was trained on the data from the other 239 sentences and used to predict a vector of the NPSF semantic features of the test sentence. For example, given only the activation associated with the sentence *The witness shouted during the trial*, the model predicts that the sentence contained the following nonzero NPSFs, ordered in terms of their relative weights: negative affective valence, human group, communication, high affective

arousal, person, social action, mental action, social norms, and perceptual. The accuracy measure assessed the similarity of the actual (coded) vector of NPSFs to the predicted vector, relative to its similarity to the predicted vectors of all 240 sentences. The group-level and individual-level models produced a rank accuracy of 0.87 and mean rank accuracy of 0.83 (range 0.80–0.87), respectively, very similar to the activation-predicting model (Supporting Information, Table S2). For brevity, further analyses were performed using the activation-predicting model at the individual participant level, unless otherwise specified.

The Model’s Capture of Event Semantics

The model’s confusion errors and the decoding outcome of the meaning-predicting model indicated that it was capturing the semantics of the events described by the sentences. The activation predictions of sentences describing similar types of events—such as *The flood damaged the hospital* and *The storm destroyed the theater*—were similar to each other, as Figure 2 illustrates. The model characterizes similar events similarly even when the specific words and concepts of the sentences are dissimilar.

To systematically assess how well the model captured such event similarities, the model’s measure of event similarity was compared to independent human judgments of sentence meaning similarity for the 18,915 pairs of sentences formed by only the 195 out of the 240 sentences that described events. The model-based intersentence similarity was measured by the mean pairwise similarity of the predicted activation patterns across individual participants. The 18 pairs of sentences that were judged to be most

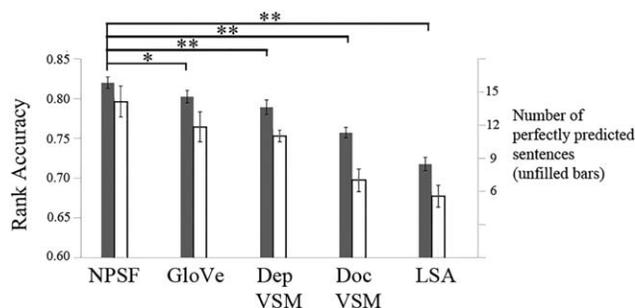


Figure 3.

Comparison of sentence activation prediction accuracies using different types of predicting semantic features. Error bars indicate standard errors. The *P* values indicate the comparison between the mean rank accuracy using each of the four alternatives versus the NPSF-based model in paired-sample *t* tests over 7 participants. **Two-tailed *P* < 0.01; *two-tailed *P* < 0.05.

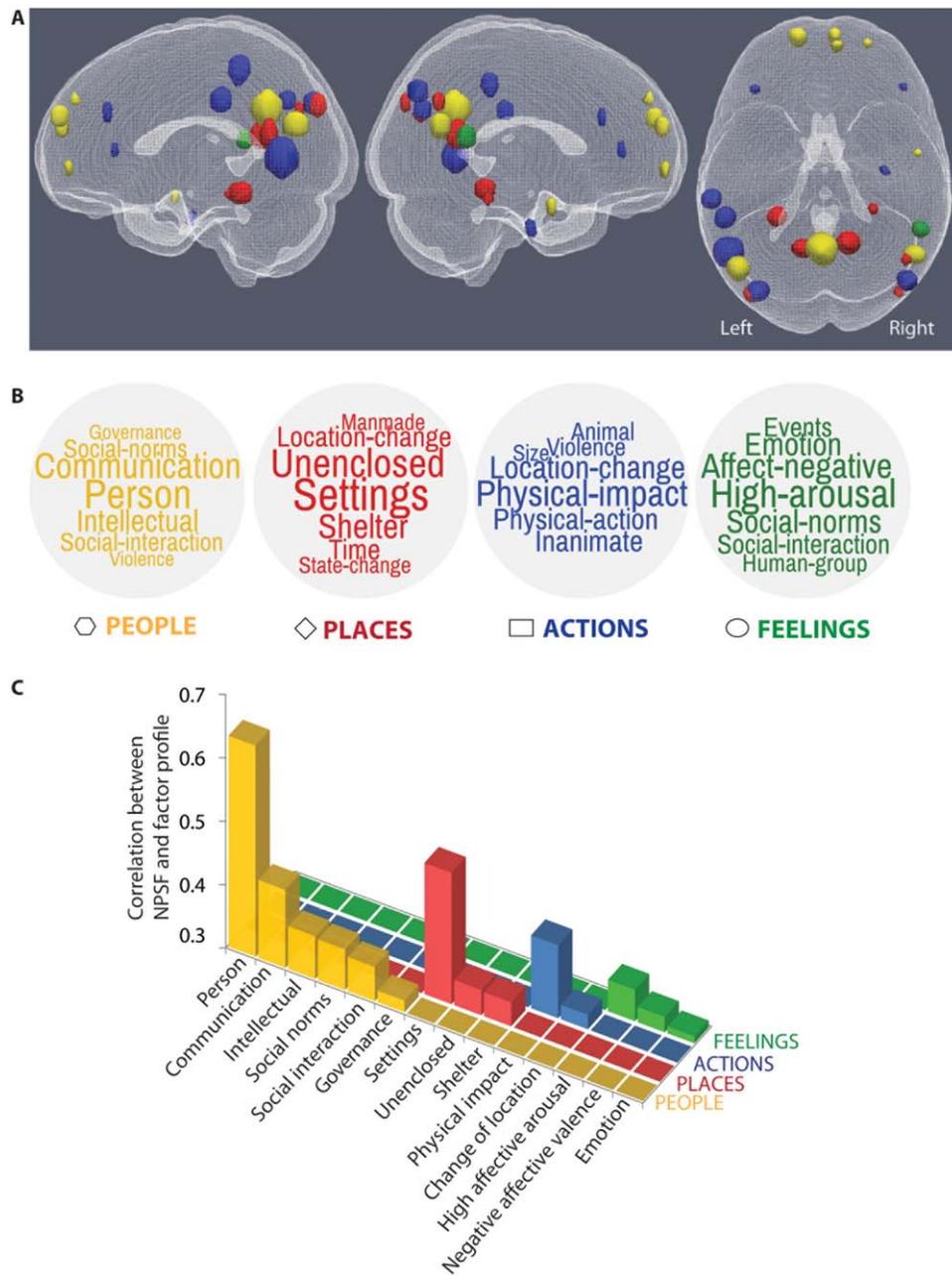


Figure 4.

Relations between brain locations, large-scale semantic factors underlying sentence representations, and neurally plausible semantic features (NPSFs) of concepts. (A) Brain regions associated with the four large-scale semantic factors: people (yellow), places (red), actions and their consequences (blue), and feelings (green). Details of the region locations are shown in Supporting Information, Table S3. (B) Word clouds associated with each large-scale semantic factor. The clouds are formed using the 7

neurally plausible semantic features most associated with each factor to illustrate some of the main meaning components of each factor. (C) NPSFs that correlate with at least one factor with $r > 0.3$ ($P < 0.0001$). The pairwise correlations are computed between each NPSF and the factor scores over sentences. The NPSF for a sentence is computed as the mean of the NPSFs of all the concepts in the sentence.

similar by the human raters had a mean rank accuracy of 0.83 in the list of sentence pairs ranked by model-predicted similarity, as shown in Table IV. This high consistency between the human judgment and the model-based neural similarity measures demonstrates that the model captures the core meaning of events at a level of abstraction higher than the meanings of the individual words.

Comparing NPSFs With Other Semantic Representations

The prediction performance of the models above was based on the mapping between the neural signatures of concepts and a postulated layer of meaning elements, namely, the neurally plausible semantic features (NPSFs). Four alternative semantic characterizations of the sentence content were compared to the NPSFs' account. These alternatives, all based on semantic vector space models, use features derived from word co-occurrence norms in text corpora: GloVe vectors for word representation [Pennington et al., 2014], a documents-based and a dependencies-based vector space model (doc VSM and dep VSM) [Fyshe et al., 2013], and LSA [Landauer and Dumais, 1997]. The NPSF features performed reliably better than any of the other feature sets in this comparison, as shown in Figure 3. Dimensionality as an intrinsic attribute of each vector space model might be responsible for the accuracy differences. Nevertheless, the decoding performance provides a pragmatic test of the information content that can be explained by these features. The corpus-based, automatically generated vector representations also produced accounts that were very reliably above chance level, demonstrating the robustness of the general approach using alternative semantic characterizations.

Commonality of Neural Representations of Sentences Across Individuals

To determine whether the brain activation pattern for a given sentence was similar across people, a model that predicted brain activation patterns from semantic features was trained on the data of all but one participant, and tested on the data of the left-out participant. The mean accuracy of the activation-predicting model in the left-out participant's brain based on the neural representations of other 6 people was 0.77 (range = 0.72–0.79). This finding indicates a considerable degree of cross-individual commonality in the neural representation of sentences, and in the pattern of associations between the semantic and neural elements.

Thematic Role Representation: Distinguishing Agent and Patient Roles in Reversible Sentences

The concepts that filled the agent and patient roles in many of the stimulus sentences made the thematic role

assignment unambiguous, such as *The happy child found the dime*. When the thematic role variables were omitted from the model, the accuracy of sentence prediction decreased slightly and significantly from a mean of 0.82–0.80 (paired-sample $t_6 = 8.4$, $P < 0.001$). An ancillary study was run using sentences whose agent and patient concepts were reversible (e.g., *The rabbit punches the monkey*), to determine how accurately the thematic roles of each concept could be decoded and whether any additional locations of brain activation came to light (the methods are described in Supporting Information). The main finding was that the agent and patient roles of the two animal concepts could be reliably decoded from the neural representation with a mean accuracy of 0.80 across five participants, demonstrating the decodability of this level of information from the structure of a sentence, independently of the conceptual content of the role fillers [Frankland and Greene, 2015]. Furthermore, the voxels used in this decoding included 17 clusters, 13 of which were within or adjacent to the regions identified in the main study (Supporting Information, Fig. S2). The remaining 4 clusters were in spatially distinct regions in the precuneus, right amygdala, left anterior middle temporal lobe, and the right precentral gyrus (circled in Supporting Information, Fig. S2). Without these 4 additional clusters, the accuracy of identifying the thematic roles in the ancillary study decreased to 0.75, but remained reliably above chance ($P < 0.05$).

The contribution of the ancillary study is to identify additional regions for representing the thematic organization of a sentence when this organization has to be inferred from the sentence structure. Activation in the amygdala has been shown to be mediated by superior temporal cortex; the activation patterns in this region differentiate pairs of reversible sentences [Frankland & Greene, 2015]. The precuneus cluster has been found to be sensitive to violation of social expectations [Berthoz et al., 2006; Petrini et al., 2014], suggesting its role in interpreting the interconcept relations from a perspective of social norms. A related account of the regions involved in thematic role processing emerges from studies of aphasia [Thompson and Meltzer-Asscher, 2014].

Underlying Large-Scale Dimensions of Neural Representation of Sentences and Their Brain Locations

To determine the nature of the meaning dimensions of the neural representation of the stimulus sentences at a more molar level than NPSFs, a two-level hierarchical factor analysis [Just et al., 2014] was applied to the activation data. There were four main factors or semantic dimensions that emerged, that characterized the neural organization of the sentence representation. These factors can be interpreted as (1) *people and social interactions*, (2) *spatial and temporal settings*, (3) *actions (and affected objects)*, and (4) *feelings*. These interpretations are based in large

part on the NPSF semantic features and sentences that were most associated with each factor (Supporting Information). For example, the factor scores of the first factor correlated with the semantic features of *Person* (0.63), *Communication* (0.42), *Intellectual* (0.37), and so forth. Sentences such as *The young author spoke to the editor* and *The judge met the mayor* had high scores on this factor. Thus, this factor was interpreted as representing people and social interactions. The factor analysis also identifies the voxels that have the highest factor loadings for each factor (Supporting Information, Table S3).

A condensed account of the relation between brain locations, large-scale semantic dimensions, and concept-level NPSFs is depicted in Figure 4. Each main dimension is described by a cloud of semantic features (Fig. 4B), which are color-mapped to their corresponding brain locations (Fig. 4A). Each NPSF tends to be correlated well with only one of the dimensions (Fig. 4C).

This factor analysis interpretably organizes the main meaning dimensions that characterize the 240 sentences in this stimulus set, relates the emerging factors to the NPSFs, and identifies the brain locations (factor-related voxel clusters) that can be used to instantiate the mapping between the semantic features (NPSFs) of concepts and the resulting activation patterns.

DISCUSSION

The main contribution of this article is the integrated, computational account of the relation between the semantic content of a sentence and the brain activation pattern evoked by the reading of the sentence. The integration applies to several facets of the account. First, the model integrates over the multiple concepts in a sentence to predict the activation of the sentence as a whole. Second, the model also takes into consideration the thematic structure that integrates the roles that the concepts play in the sentence. Third, the model integrates over a wide range of 42 neurally plausible semantic features of different types, from concrete perceptual and motor features of an object (that can be thought of as embodied) to social and abstract features of actions that have much less connection to concrete properties. Many previous studies have reported the correspondence between only a handful of features and brain activation patterns (e.g., Fernando et al., 2016; Just et al., 2010), but this study relates activation to many different types of semantic features. Fourth, the model integrates the account of the activation attributable to the 42 concept-level features to the larger-scale dimensions of meaning that emerged from the factor analysis of the activation patterns of the sentences. In all four senses, the current model provides a more integrated, larger scale account of the brain activation associated with concept and sentence meaning. Moreover, it provides a point of departure for future studies of the

neural representation of complex thoughts composed of multiple components.

Although sentences are not merely the sum of their parts, this study shows the extent to which a linear combination of thematically coded concept representations is able to characterize the neural representation of simple sentences. We note moreover, that the quantities being added are estimates of word concept representations *as they occur in context*, rather than in isolation. The addends that were used to generate sentence representations may be sentence-context-sensitive. Elsewhere, we demonstrate systematic interactions or context effects among the NPSFs of the concepts of a proposition [Just et al., 2017, under review].

The NPSFs provide a basis of prediction of sentence activation in terms of the co-activation of various brain subsystems that have characteristic processing specializations. The NPSFs were developed with these specializations in mind, and they result in more accurate predictions of sentence activation patterns than do feature sets derived from language-based corpora. Moreover, the NPSF-based characterization can be expanded to include additional types of concepts and, if needed, additional neural systems. That is, this general approach has the potential of extensibility to any number of concepts and simple sentences constructed from the concepts.

The theory-driven NPSFs and the data-driven neural dimensions (factors) derived from the factor analysis of the sentence activations provide accounts at two levels of granularity. The factors provide an account at a coarser, higher level that specifies the general type of thought associated with a simple sentence (e.g., the thought of an action and its consequences). The NPSFs provide an account at a finer level that specifies the properties of each of the concepts in the proposition (e.g., a change of location of an object). Together these two levels of account suggest that the generativity of conceptual and propositional representation is enabled by the possible combinatorial space of these fundamental neural components and their values.

The initial success of the modeling using neurally plausible features suggests that the building blocks for constructing complex thoughts are shaped by neural systems rather than by lexicographic considerations. This approach predicts that the neural dimensions of concept representation might be universal across languages, as studies are beginning to suggest [Yang et al., 2017]. In this perspective, the concepts in each language would be underpinned by some subset of a universal set of NPSFs. The predictive modeling of the neural signatures of new concepts in a variety of dissimilar languages is a possible way to test the hypotheses reflected by these neurally plausible semantic features, in contrast to hypotheses based on models that are blind to neural capabilities.

This study demonstrates the possibility of modeling the neural representation of semantic information beyond the

single-word level by taking into consideration the role of a concept in a proposition. Although only six roles present in the current stimulus set were implemented in the model, it could be expanded to incorporate more elaborated thematic roles. Furthermore, computationally, the model has the potential to identify neural signatures of other aspects of sentence meaning, such as negation, tense, syntactic roles of concepts, and so forth. Future studies may use this approach to test more complex compositional semantic representations.

Direction of Prediction

The regression modeling enables the prediction of brain activity of a sentence and the comparably accurate prediction of the sentence semantics. Given the main scientific goal of understanding the process and representation that the brain generates during sentence comprehension, the corresponding direction is predicting the activation from knowledge of the sentence, as was implemented in previous studies [Huth et al., 2016; Mitchell et al., 2008; Wehbe et al., 2014]. However, the other direction of decoding semantics from activations provides a more intuitive assessment of the model's success, constituting a "mindreading" capability. There is an immediate, human-readable assessment of how unfaithful or faithful the prediction is to the actual sentence. The two directions of mapping serve different purposes, and their comparable accuracies speak to the robustness of the general approach.

In summary, the new findings and the accompanying theoretical account provide an initial explanation of how complex meaning is neurally represented. It presents an initial mapping between brain activity and that part of the mind that represents events and states as described by sentences.

Large-Scale Semantic Dimensions and Brain Locations Emerging From Factor Analysis of Sentence Activation Patterns

The activation profiles of many regions identified in the factor analysis (Fig. 4A and Supporting Information, Table S3) are consistent with previous findings of the role of these regions in semantic knowledge representation, such as right anterior temporal lobe for semantic knowledge of people [Gesierich et al., 2012], fusiform gyrus for representing objects [Martin, 2007], parahippocampal areas for representing places [Epstein and Kanwisher, 1998], and so forth. Moreover, the response profiles of several other regions suggest that reading of simple sentences that describe events and states also involve various non-language-specific neural systems associated with the processing of social, affective, motor, and visual properties of events, as discussed below.

People

One of the large-scale dimensions emerging from the factor analysis assigned high scores to sentences describing people and social interactions. The location of the largest factor-related cluster (posterior cingulate cortex and the adjacent precuneus region) is known for its role in episodic memory and being a signature of the default mode network [Cavanna and Trimble, 2006; Gusnard and Raichle, 2001], and it has also been found to activate during social sharing of emotions versus processing emotion alone [Wagner et al., 2015], and during thinking about intentional versus physical causality [Ouden et al., 2005]. Similarly, the medial prefrontal cortex has been associated with social and moral reasoning [Moll et al., 2005; Van Overwalle, 2011]. The left superior frontal gyrus has been associated with reasoning about social contracts [Fiddick et al., 2005], social comparison [Dvash et al., 2010], and found to be part of a theory of mind network [Wolf et al., 2010]. In other words, processing social content during the reading of sentences also involves a neural network for social processing. This factor is correlated with the NPSFs of person, communication, social norms, and social interaction, as shown in Figure 4C.

Places (spatial and temporal settings)

The sentences with high scores on this factor included most of the sentences that described a scene rather than an event (e.g., *The restaurant was loud at night*). The brain regions associated with this factor include the parahippocampal area, and the posterior cingulate cortices, which have been linked to viewing scenes and representing semantic knowledge of shelters [Henderson et al., 2008; Just et al., 2010]. The cluster in the right angular gyrus has been associated with accurate temporal memory [Jenkins and Ranganath, 2010] and retrieval of learned ordinal movement sequences [Bengtsson et al., 2004], suggesting its role in the representation of time-related concepts. This factor is correlated with the NPSFs of setting, openness (nonenclosure), and shelter (enclosure), as shown in Figure 4C.

Actions (and affected objects)

Sentences that included main verbs such as *break* or *kick* had high scores on this factor. The cluster associated with this factor in the middle frontal gyrus has been associated with motor imagery [Szameitat et al., 2007] and retrieval of visually or haptically encoded objects [Stock et al., 2008]. This factor was correlated with the NPSFs of physical impact and change of location, as shown in Figure 4C.

Feelings

The right temporoparietal junction, which is known for its role in representing belief of others [Saxe and

Powell, 2006], has been found to activate for processing fear-inducing pictures [Stark et al., 2007] and fearful body expressions [Grèzes et al., 2007]. Moreover, this region has been found to represent various emotions by the appraisal-related features—such as expectedness, fairness, and so forth—of affective events [Skerry and Saxe, 2015]. The right inferior frontal gyrus has been associated with recognizing visually presented objects with negative valence [Kensinger and Schacter, 2007]. This factor was correlated with the NPSFs of high affective arousal and negative affective valence, as shown in Figure 4C.

In summary, the factor analysis yields broad semantic dimensions that characterize the events and states in the 240 stimulus sentences. The brain locations associated with the each of the factors suggest that the brain structures that are activated in the processing of various aspects of everyday life events also encode the corresponding semantic information. The factors can be construed as higher order dimensions that subsume relevant NPSFs.

Generalizability Across Individuals

The generalizability of the findings is first demonstrated when individual participants' data are modeled independently. The ability to predict and decode a new sentence was present for every one of the seven participants with high accuracies. When individual participant's data are modeled, the reliability of the results is assessed not in terms of the number of participants, but in terms of the large number of stimulus items (240 sentences). The model was further tested for its generality across people: a model trained on the data of all but one participant is able to reliably predict the neural signature of the left-out participant. This result indicates the generalizability of the neural representations across individuals. The fact that a small number of participants are sufficient to build a cross-participant model suggests the consistency of the effect.

Study Limitations and Implications

One limitation is that despite the large number of stimulus sentences examined, the admixture of narrative and descriptive sentences is limited in its structure and content. Sentences can provide far wider types of information and they can have far wider syntactic forms than those examined here. The set of NPSFs would certainly have to be expanded to code all possible sentences, but perhaps their number would asymptote at a few hundred. More complex syntactic processing would evoke more activation, but the neural representations of the concepts involved may not be affected by the syntactic complexity of the sentence. Although the specific account provided by the model is thus limited to the types of sentences examined in the study, the general principles may well be

extensible to the neural representation of concepts in any sentence.

Another limitation is that the factor analysis produced dimensions with reasonable interpretations, but the interpretations were not put to a rigorous test. It should be possible to independently assess the large-scale underlying dimensions of a sentence and thus predict its factor scores on the 4 factors. Furthermore, the outcome of the factor analysis here was limited to the sample of 240 stimulus sentences. It is likely that a much larger sample of sentence types would yield additional factors, which could also be independently assessed and tested for predictive ability.

The study was also limited to the processing of visually presented sentences, and the neural signature at the end of the reading of a sentence contained the representations of all of the component concepts in the sentence. If the sentences were presented in the auditory modality, it is possible the neural signature at the end of the listening to a sentence might not be the optimal decoding window for all of the component concepts in the sentence.

Despite its limitations, the study opens new avenues of inquiry concerning the neural representation of complex inputs. For example, the model described here can predict the activation patterns evoked by the reading of translation-equivalent sentences in another language [Yang et al., 2017]. Not only can the model be extended to different languages, but it may also extend to different media of communication: the neural representation of a short video depicting a simple event might also be characterized by using the methods developed here. A broader avenue of extension might be the characterization of the full neurally based ontology that organizes information in a human brain, regardless of the form of the input. The full potential of fMRI has yet to be realized as it is applied to the representation of increasingly complex information.

SUMMARY

This study leads to an initial theoretical and computational account of the neural representation of the propositional content of event-describing and state-describing sentences. The main contribution is the predictive bidirectional mapping between the neurosemantic properties of concepts and the neural signatures that characterize how the brain represents events and states described by simple sentences.

The novelty of the approach mainly lies in the mapping that incorporates neurally driven properties of concepts and sentences, the roles concepts play in a proposition, and identification of an end-of-sentence neural signature of the semantics of all the component concepts of the proposition. The findings indicate the following: (1) The neural representation of an event or state-describing proposition entails brain subsystems specialized in representing

particular semantic information that can be characterized by a set of neurally plausible semantic features. (2) It is possible to reliably predict sentence-level brain activity from this set of specialized neural bases and the knowledge of the semantic properties of the component words of a sentence and their inter-relations. (3) It is also possible to decode the semantic properties of the concepts in a sentence from the observed activation patterns. (4) The neural representation of the meaning of events and states is largely common across individuals.

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Supporting Information

Predicting the brain activation pattern associated with the propositional content of
a sentence: modeling neural representations of events and states

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Methods details for main study

Stimulus presentation parameters. On each day of a one-hour scan, participants read 60 of the sentences that were presented a total of 4 times in 4 blocks of randomly permuted orders of the sentences. The stimulus onset asynchrony was 12 seconds for each sentence, composed of a mean sentence presentation time of 1.4 s padded out with a blank interval to a total of 5 s followed by a 7 s fixation interval. A sentence was presented one phrase at a time, with phrases cumulating from left to right on the screen. The cumulating phrase-by-phrase sentence display protocol was motivated by the patterns of eye fixations during the reading of texts [Just and Carpenter, 1980]. The presentation duration of each phrase was intended to approximate the mean gaze duration on a phrase of that length. Each phrase contained no more than one of the 242 non-adjective content words or the word *was*. Other words, such as *the*, *at*, *in*, etc. were included in a phrase when they preceded one of the content words. The presentation duration of each phrase was computed as $(300\text{ ms} \times \text{Number of "words"}) + (16\text{ ms} \times \text{Number of letters})$, where “words” referred only to the 242 content words and the word *was*. Additionally, the word *was* was presented for 200 ms rather than 300 ms. The counting of letters included all of the words except *the*. When an adjective preceded a noun, that adjective and a possible determiner were presented before the noun, and remained on the screen while the noun was presented. As the participants read each phrase, they were to think of the intrinsic properties of the referent of that phrase, and integrate the referent into the context of the evolving sentence. The goal of this instruction was to encourage engagement and attention of the participant. The participant was instructed to think of the same properties each time the sentence was presented. After the last phrase of the sentence had been presented, a blank interval was presented to pad out the total duration of the sentence presentation to 5000 ms, during which the participants were allowed to

finish their thoughts on the sentence. The blank interval was followed by a 7 sec fixation cross (the letter X) presented in the center of the screen, during the presentation of which the participant were instructed to relax and clear their mind.

Long fixation periods to obtain baseline activation measures. At the beginning and end of each sentence presentation block, a fixation cross (the letter X) was presented for 17 seconds during which participants were asked to relax and clear their mind.

Before the actual experiment, participants were taught to perform the task in a mock scanner for 6 minutes using stimulus materials with no overlap with the test sentences.

Selection of features/voxels for regression modeling. From within the regions specified by the factor analysis, voxels were selected for training and prediction based on their stability. From each of the factor-related regions, 5 to 100 voxels with the highest stability were selected, and the predictions for these voxels were compared to the test data. Voxel stability refers to responding similarly to the set of words in the training set across multiple presentations of the set, i.e. displaying a repeatable semantic tuning curve. The number of selected voxels in each cluster was determined by:

$$K(c) = \begin{cases} 5, & c \leq 50 \\ 10, & 50 < c \leq 150 \\ 20, & 150 < c \leq 300 \\ 50, & 300 < c \leq 600 \\ 100, & c > 600 \end{cases}$$

where K was the number of selected voxels and c was the number of voxels in a cluster.

The voxel selection was based on only the training data in each cross validation fold and then applied to the test data.

Predicting the NPSF semantic features of a sentence from its neural activity patterns (meaning-predicting model)

The same theoretical framework that was implemented in the activation-predicting model can also be applied in the reverse direction, to predict (decode) the underlying semantic features of a given fMRI image obtained during the comprehension of a sentence. Once trained, the model can predict the semantic feature values of an unknown sentence based on its observed fMRI images. The accuracy measure was the normalized rank of the similarity of the test sentence's actual NPSF feature vector to its predicted vector among the 240 alternatives, where the actual features of a sentence were the mean of the human-coded feature values of its content words. The rank accuracy was computed based on the relative similarity of the predicted feature vector to the actual vector of the test sentence, among the 240 alternatives.

Ancillary study on decoding thematic roles in reversible sentences

Experimental paradigm and procedure. Functional images were acquired while participants read reversible *Agent-verb-patient* sentences and judged the consistency of the events described by the sentence and a following video clip. The main condition consisted of 4 pairs of reversible sentences, where 2 animal characters (*monkey* or *rabbit*) were the agents or patients, and 4 actions (*kick*, *pat*, *punch*, and *push*) were the main verb. To prevent participants from encoding the thematic role of only one animal and inferring the identity of the other animal, a third filler character (*wolf*) performed and received 2 actions from the other animals. On each trial, a sentence was presented one word at a time, with words accumulating on the screen. The word

onset asynchrony within a sentence was 400 ms, and the sentence presentation was followed by a 3800 ms blank interval, followed by a 4-s fixation cross (the letter X).

To require participants to encode the thematic role information, they were asked to judge whether the sentence matched or mismatched an immediately subsequent event depicted in a 3-s animation video clip (programmed using Alice 3, alice.org). The video depicted one animal character performing a physical action on another animal character. Participants indicated their response by pressing a same or different button on a response apparatus during a 2-s response period. Finally a 6-s fixation period was presented at which point the participants were asked to relax and clear their mind. The sentences were presented 4 times in 4 presentation blocks. The left-right positions of the characters in the videos were balanced across the presentations. In one of the four presentations of each sentence (distributed across the blocks), the event in the video was inconsistent with the sentence. In half of the cases in which the sentence and videos were inconsistent with each other, the sentence mis-stated the agent-patient relation; for the other half, the sentence used an incorrect verb. Additionally there were 6 blocks of 17-s fixation periods distributed over the scans to obtain the baseline measures, as in the main experiment.

Participants. Five healthy, right-handed native English-speaking adults (3 females) from the Carnegie Mellon community participated and gave written informed consent approved by the Carnegie Mellon Institutional Review Boards.

fMRI imaging protocol and ***data preprocessing*** procedures were the same as the main experiment.

Decoding thematic relations. The analysis assessed the degree to which the thematic role associated with each character in the sentence could be decoded. In each cross-validation fold, two logistic regression classifiers, one per character, were trained to associate the fMRI

signatures of the sentence with one of the two agent-patient role assignments. The training data of a classifier were the activation patterns evoked by events that involved the given character in the role of either the agent or the patient. To ensure that the decodability was not due to low level visual properties, activation data in the occipital lobe, defined by Automated Anatomical Labeling [Tzourio-Mazoyer et al., 2002], were excluded from consideration. Posthoc examination of the voxel locations showed that the selected voxels were not located in visual perceptual areas in the ventral temporal gyrus (Figure S2). Voxels used to train the classifier were 120 non-occipital voxels with the most stable activation profiles over the sentences in the training set. The stability of a voxel was measured by the mean of the pairwise correlations between its activation profiles over the sentences across the 4 presentations. The locations of the stable voxels used in the thematic role decoding were aggregated across participants. The clusters with more than 5 voxels are shown in Figure S2. The trained classifier for a character was applied to the activation patterns of the left-out test sentence to predict the thematic role of that character. The significance of the accuracy being different from chance level was tested against a null distribution generated by an 10000-iteration random permutation.

Supporting results

Underlying large-scale dimensions of neural representation of sentence contents and their brain locations

We briefly describe each factor's associated locations and semantic features. The *people* factor assigned high factor scores to sentences that describe people and their interactions (e.g. *The young author spoke to the editor, The judge met the mayor*). The scores of this factor had a positive correlation with NPSFs that coded *Person* (0.63), *Communication* (0.42), *Intellectual* (0.37), etc. (Figure 4C). The brain locations associated with this factor included posterior

cingulate cortex, the right superior orbitofrontal cortex, and other frontal and bilateral temporal areas.

The *places* factor underpinned the activation of sentences describing scenes or buildings (e.g. *The bridge survived the flood, The student walked along the long hall*). The factor scores were positively correlated with NPSFs that coded *Settings* (0.51), *Unenclosed* (0.34), etc., and the brain locations included typical shelter factor locations [Just et al., 2010] – bilateral parahippocampal place areas, precuneus, and middle occipital gyri.

The *actions (and affected objects)* factor underpinned sentences that included transitive verbs such as *break, kick* (e.g. *The child broke the glass in the restaurant*) and low scores for less active and physical events, associated with verbs like *interview, leave, and work*. The factor scores were positively correlated with NPSFs that coded *Physical impact* (0.42) and *Change of location* (0.32), and the corresponding brain locations were mostly left-lateralized and included posterior temporal and inferior parietal regions.

The *feelings* factor underpinned sentences that conveyed information about emotions, particularly negative valence, assigning high factor scores to sentences containing words such as *fear, danger, shout, survive, angry, criminal*. The factor scores were positively correlated with NPSFs that coded *High affective arousal* (0.35), *Negative affective valence* (0.32), etc. The corresponding brain locations included the right TPJ.

In addition, the factor analysis also identified a non-semantic, perceptual factor reflecting sentence length, which did not contribute to the sentence prediction. The correlation between the factor scores for this factor and number of letters in the sentence was 0.76. The associated brain regions include bilateral occipital poles and fusiform gyri, areas previously associated with word length effects [Just et al., 2010]. The sentence prediction accuracy did not benefit from the

sentence length factor. When all the brain regions associated with this factor were removed from the mapping performed on the aggregated data, the mean prediction accuracy numerically increased from 0.86 to 0.87, and the number of sentences with accuracy of 1 increased from 16 to 18. Thus, it was the characterization of the semantic properties of sentences that drove the accurate prediction.

Predicting brain activation patterns of individual word concepts in sentence contexts

A key stepping stone to successful prediction of the sentence activation was the accurate prediction of the activation patterns associated with the individual word concepts in the sentence. An assessment of this approach was performed by comparing the predicted activation pattern for a concept with the mean image of that concept across sentences. Specifically, the observed activation pattern for each of the 242 words was estimated as the mean image of all the sentences containing that word. Each word appeared on average in 3.3 sentences (range = 1 - 7). There were 45 words that appeared only in a single sentence.

Each of the observed word images was left out of the training of the regression model, and was then used for testing in a cross-validation fold. The regression model was trained to map from the NPSFs of the words to the estimated brain activation patterns in the same approach as the main analysis. The activation patterns of all candidate words, including the target word, were then predicted based on their NPSFs, and compared to the left-out test word image.

The mean rank accuracy of prediction of the word concept was 0.75 across participants, with every participant being well above chance level (critical value at $p = 10^{-5}$ level of being significantly different from chance was 0.58, determined by random permutation tests). This result establishes the utility of estimating single concept neural representations embedded in a sentence by averaging over and cancelling out the differences in contexts, and confirmed the

model's capability of prediction when it was trained in the absence of neural data associated with the prediction targets. The prediction accuracies for different semantic categories of concepts were comparable (animal: .86, event: .85, human: .80, setting: .77, object: .72, attribute: .71, verb: .70), suggesting that the sentence prediction accuracy was not driven by any single category of concept.

Temporal coincidence of sentence concept representations

To determine the optimal temporal window of the fMRI signal within which to decode the content of a sentence, several windows with different starting positions and a width of 1 s of data were examined. The sentences took on average 1.4 s to be presented. The decoding accuracy first became substantial at 7 sec after sentence onset and continued to be substantial until 9 s after sentence onset, peaking at 8 s. The optimal temporal window in terms of both its starting position and width was very similar for the words regardless of their serial position within the sentence (Figure S1). These results indicate that the neural representations of all the content words in a sentence are co-incident in time in the fMRI signal, occurring after the entire sentence has been processed.

Table S1. The 240 Stimulus Sentences (from [Glasgow et al., 2016])

- 1 The family was happy.
- 2 The politician visited the family.
- 3 The family played at the beach.
- 4 The parent bought the magazine.
- 5 The child broke the glass in the restaurant.
- 6 The parent shouted at the child.
- 7 The happy couple visited the embassy.
- 8 The wealthy couple left the theater.
- 9 The parent visited the school.
- 10 The happy child found the dime.
- 11 The child gave the flower to the artist.
- 12 The soldier crossed the field.
- 13 The commander listened to the soldier.
- 14 The horse walked through the green field.
- 15 The girl saw a horse in the park.
- 16 The engineer walked in the peaceful park.
- 17 The flower was yellow.
- 18 The yellow bird flew over the field.
- 19 The old doctor walked through the hospital.
- 20 The wealthy author walked into the office.
- 21 The dog broke the television.
- 22 The street was empty at night.
- 23 The street was dark.
- 24 The banker watched the peaceful protest.
- 25 The voter went to the protest.
- 26 The protest was loud.
- 27 The politician watched the trial.
- 28 The reporter spoke to the loud mob.
- 29 The mayor negotiated with the mob.
- 30 The mob was dangerous.
- 31 The wealthy politician liked coffee.
- 32 The young author spoke to the editor.
- 33 The scientist spoke to the student.
- 34 The scientist watched the duck.
- 35 The witness went to the trial.
- 36 The witness spoke to the lawyer.
- 37 The witness shouted during the trial.
- 38 The jury watched the witness.
- 39 The victim feared the criminal.
- 40 The engineer gave a book to the student.

- 41 The magazine was in the car.
- 42 The diplomat negotiated at the embassy.
- 43 The diplomat shouted at the soldier.
- 44 The mayor listened to the voter.
- 45 The famous diplomat left the hospital.
- 46 The patient survived.
- 47 The tired patient slept in the dark hospital.
- 48 The author kicked the desk.
- 49 The tourist went to the restaurant.
- 50 The woman left the restaurant after the storm.
- 51 The restaurant was loud at night.
- 52 The artist liked chicken.
- 53 The diplomat was wealthy.
- 54 The mayor dropped the glass.
- 55 The injured horse slept at night.
- 56 The young girl played soccer.
- 57 The girl saw the small bird.
- 58 The tourist found a bird in the theater.
- 59 The school was famous.
- 60 The magazine was yellow.
- 61 The accident damaged the yellow car.
- 62 The activist listened to the tired victim.
- 63 The aggressive team took the baseball.
- 64 The angry child threw the book.
- 65 The artist kicked the football.
- 66 The banker bought the expensive boat.
- 67 The banker drank cold water.
- 68 The banker was injured in the accident.
- 69 The baseball broke the window.
- 70 The baseball was in the office.
- 71 The beach was empty.
- 72 The bridge survived the flood.
- 73 The businessman watched soccer.
- 74 The car approached the river.
- 75 The cloud was white.
- 76 The computer was new.
- 77 The computer was on the desk.
- 78 The couple read on the beach.
- 79 The criminal put the book on the desk.
- 80 The criminal wanted cash.
- 81 The dangerous criminal stole the television.
- 82 The dime was new.
- 83 The doctor bought the used boat.

- 84 The doctor stole the book.
- 85 The dog drank water.
- 86 The dog ran in the park.
- 87 The door was blue.
- 88 The driver wanted cold tea.
- 89 The duck was aggressive.
- 90 The editor drank tea at dinner.
- 91 The feather was blue.
- 92 The flood was dangerous.
- 93 The green duck slept under the tree.
- 94 The judge lost the dime.
- 95 The lawyer was friendly.
- 96 The man lost the ticket to soccer.
- 97 The medicine was on the table.
- 98 The old man threw the stone into the lake.
- 99 The policeman interviewed the young victim.
- 100 The reporter ate at the new restaurant.
- 101 The reporter interviewed the dangerous terrorist.
- 102 The school was empty during the summer.
- 103 The small church was near the school.
- 104 The soldier kicked the door.
- 105 The storm was powerful.
- 106 The teacher used the computer.
- 107 The teacher visited the beach in summer.
- 108 The teacher worked at the new school.
- 109 The team celebrated.
- 110 The team lost the football in the forest.
- 111 The team played soccer in spring.
- 112 The terrorist stole the car.
- 113 The ticket was on the red desk.
- 114 The tourist was friendly.
- 115 The tree was green.
- 116 The used book was on the table.
- 117 The white feather was under the tree.
- 118 The yellow dog approached the friendly teacher.
- 119 The young policeman walked to the theater.
- 120 The young student read at the desk.
- 121 The activist dropped the new cellphone.
- 122 The activist marched at the trial.
- 123 The angry activist broke the chair.
- 124 The angry lawyer left the office.
- 125 The army built the small hospital.
- 126 The artist drew the river.

- 127 The artist found the red ball.
- 128 The artist hiked along the mountain.
- 129 The artist shouted in the hotel.
- 130 The author interviewed the scientist after the flood.
- 131 The big horse drank from the lake.
- 132 The bird was red.
- 133 The boat crossed the small lake.
- 134 The boy threw the baseball over the fence.
- 135 The cellphone was black.
- 136 The chicken was expensive at the restaurant.
- 137 The cloud blocked the sun.
- 138 The commander ate chicken at dinner.
- 139 The commander negotiated with the council.
- 140 The commander opened the heavy door.
- 141 The council feared the protest.
- 142 The council read the agreement.
- 143 The diplomat bought the aggressive dog.
- 144 The dog ate the egg.
- 145 The duck flew.
- 146 The editor carried the magazine to the meeting.
- 147 The editor gave cash to the driver.
- 148 The expensive camera was in the lab.
- 149 The farmer liked soccer.
- 150 The fish lived in the river.
- 151 The flood damaged the hospital.
- 152 The girl dropped the shiny dime.
- 153 The green car crossed the bridge.
- 154 The happy girl played in the forest.
- 155 The horse kicked the fence.
- 156 The hurricane damaged the boat.
- 157 The jury listened to the famous businessman.
- 158 The lawyer drank coffee.
- 159 The man saw the dead mouse.
- 160 The man saw the fish in the river.
- 161 The mob approached the embassy.
- 162 The old farmer ate at the expensive hotel.
- 163 The old judge saw the dark cloud.
- 164 The parent took the cellphone.
- 165 The policeman arrested the angry driver.
- 166 The red plane flew through the cloud.
- 167 The reporter met the angry doctor.
- 168 The small boy feared the storm.
- 169 The soldier arrested the injured activist.

170 The soldier delivered the medicine during the flood.
171 The storm ended during the morning.
172 The teacher broke the small camera.
173 The tourist ate bread on vacation.
174 The trial ended in spring.
175 The vacation was peaceful.
176 The wealthy farmer fed the horse.
177 The woman bought medicine at the store.
178 The woman took the flower from the field.
179 The worker fixed the door at the church.
180 The young engineer worked in the office.
181 The accident destroyed the empty lab.
182 The actor gave the football to the team.
183 The army marched past the school.
184 The bicycle blocked the green door.
185 The bird landed on the bridge.
186 The boy held the football.
187 The boy kicked the stone along the street.
188 The businessman laughed in the theater.
189 The businessman lost the computer at the airport.
190 The businessman slept on the expensive bed.
191 The child held the soft feather.
192 The clever scientist worked at the lab.
193 The coffee was hot.
194 The company delivered the computer.
195 The corn grew in spring.
196 The couple laughed at dinner.
197 The couple planned the vacation.
198 The doctor helped the injured policeman.
199 The duck lived at the lake.
200 The dusty feather landed on the highway.
201 The editor damaged the bicycle.
202 The egg was blue.
203 The engineer built the computer.
204 The family survived the powerful hurricane.
205 The glass was cold.
206 The guard opened the window.
207 The guard slept near the door.
208 The journalist interviewed the judge.
209 The judge met the mayor.
210 The judge stayed at the hotel during the vacation.
211 The lonely patient listened to the loud television.
212 The man read the newspaper in church.

- 213 The minister found cash at the airport.
- 214 The minister lost the spiritual magazine.
- 215 The minister spoke to the injured patient.
- 216 The minister visited the prison.
- 217 The mob damaged the hotel.
- 218 The mouse ran into the forest.
- 219 The parent watched the sick child.
- 220 The park was empty in winter.
- 221 The patient put the medicine in the cabinet.
- 222 The pilot was friendly.
- 223 The policeman read the newspaper.
- 224 The politician celebrated at the hotel.
- 225 The priest approached the lonely family.
- 226 The red pencil was on the desk.
- 227 The reporter interviewed the politician during the debate.
- 228 The reporter wrote about the trial.
- 229 The storm destroyed the theater.
- 230 The student planned the protest.
- 231 The student walked along the long hall.
- 232 The summer was hot.
- 233 The tired jury left the court.
- 234 The tired lawyer visited the island.
- 235 The tourist hiked through the forest.
- 236 The tree grew in the park.
- 237 The voter read about the election.
- 238 The wealthy family celebrated at the party.
- 239 The window was dusty.
- 240 The woman helped the sick tourist.

Table S2. Mean rank accuracy of identifying 240 sentences using the activation-predicting model or the meaning-predicting model at a group level (with data aggregated over participants) and for individual participants. The rank accuracies and number of perfectly predicted sentences of all participants were significantly above chance level. The critical value of the individual rank accuracy being significantly different from chance level is 0.54 at $p = 0.05$ level, and 0.59 at $p = 0.000001$ level; the critical value of the number of items being predicted with 100% accuracy is 1.99 at $p = 0.05$ level and 7.99 at $p = 0.000001$ level (determined by 10^7 -iteration random permutation tests).

	Activation-predicting Model		Meaning-predicting Model	
	Accuracy	Number of perfectly predicted sentences	Accuracy	Number of perfectly predicted sentences
Data aggregated over participants	0.86	16	0.87	15
Individual participants				
1	0.84	19	0.87	19
2	0.84	16	0.84	10
3	0.83	17	0.84	7
4	0.81	15	0.83	8
5	0.81	12	0.80	2
6	0.81	8	0.84	11
7	0.79	12	0.80	3
Mean	0.82	14.14	0.83	8.57

Table S3. Brain locations associated with the four large-scale semantic factors identified by factor analysis. Clusters with at least 10 voxels are shown on the brain template in Figure 4A.

Factor	Center location	MNI coordinates			Radius (mm)	Number of voxels
		x	y	z		
People and social interactions	PCC/precuneus	-1	-56	30	10.5	212
	L superior frontal gyrus	-15	59	25	7.1	22
	Superior medial frontal gyrus	5	61	20	6.7	39
	Superior medial frontal gyrus	9	53	34	6.3	17
	R superior orbitofrontal cortex	26	59	-3	5.6	20
	L middle temporal gyrus	-48	-68	20	8.6	51
	R middle temporal gyrus	51	-61	19	7.9	88
	R ATL	57	-4	-22	5	27
	Temporal_Mid_L	-61	-18	-21	4.2	7
	Frontal_Sup_R	17	36	45	3.2	7
	Frontal_Mid_L	-30	30	45	4.2	6
	Temporal_Mid_R	62	-14	-21	4.4	5
	Temporal_Sup_L	-49	-46	16	3.6	5
	Occipital_Sup_L	-26	-74	38	4	5
Frontal_Mid_L	-31	19	54	3.9	5	
Spatial and temporal settings	L PPA	-28	-41	-16	7.7	65
	R PPA	29	-36	-20	6	52
	L PCC	-12	-57	16	7.8	46
	R PCC	14	-54	15	8.7	76
	L middle occipital gyrus	-39	-81	29	7.3	34
	R middle occipital gyrus	41	-80	31	5.6	14
	R angular gyrus	45	-63	31	5.3	11
	Precuneus	-6	-71	55	6	9
Temporal_Mid_R	57	-2	-22	3.9	6	

Table S3 continued

	L middle frontal gyrus	-37	30	27	7.2	11
	L supramarginal gyrus	-60	-30	32	8.4	17
	L inferior parietal gyrus	-52	-39	47	7.9	14
	R angular gyrus	45	-73	36	7.8	16
	L middle temporal gyrus	-54	-60	2	10.8	61
Actions and objects	L middle occipital gyrus	-35	-79	30	8.2	17
	Right IFG	46	37	7	4.7	14
	Fusiform_R	40	-14	-35	4.3	10
	Precentral_L	-52	10	32	3.8	5
	Fusiform_L	-42	-53	-19	3.3	5
	Frontal_Inf_Orb_L	-31	32	-18	3.7	5
	Parietal_Inf_L	-44	-37	36	4.1	5
Feelings	R TPJ	54	-47	12	7.2	17
	Frontal_Inf_Tri_R	46	33	7	3.7	7

Note: PCC = posterior cingulate cortex, ATL = anterior temporal lobe, PPA = parahippocampal place area, TPJ = temporoparietal junction

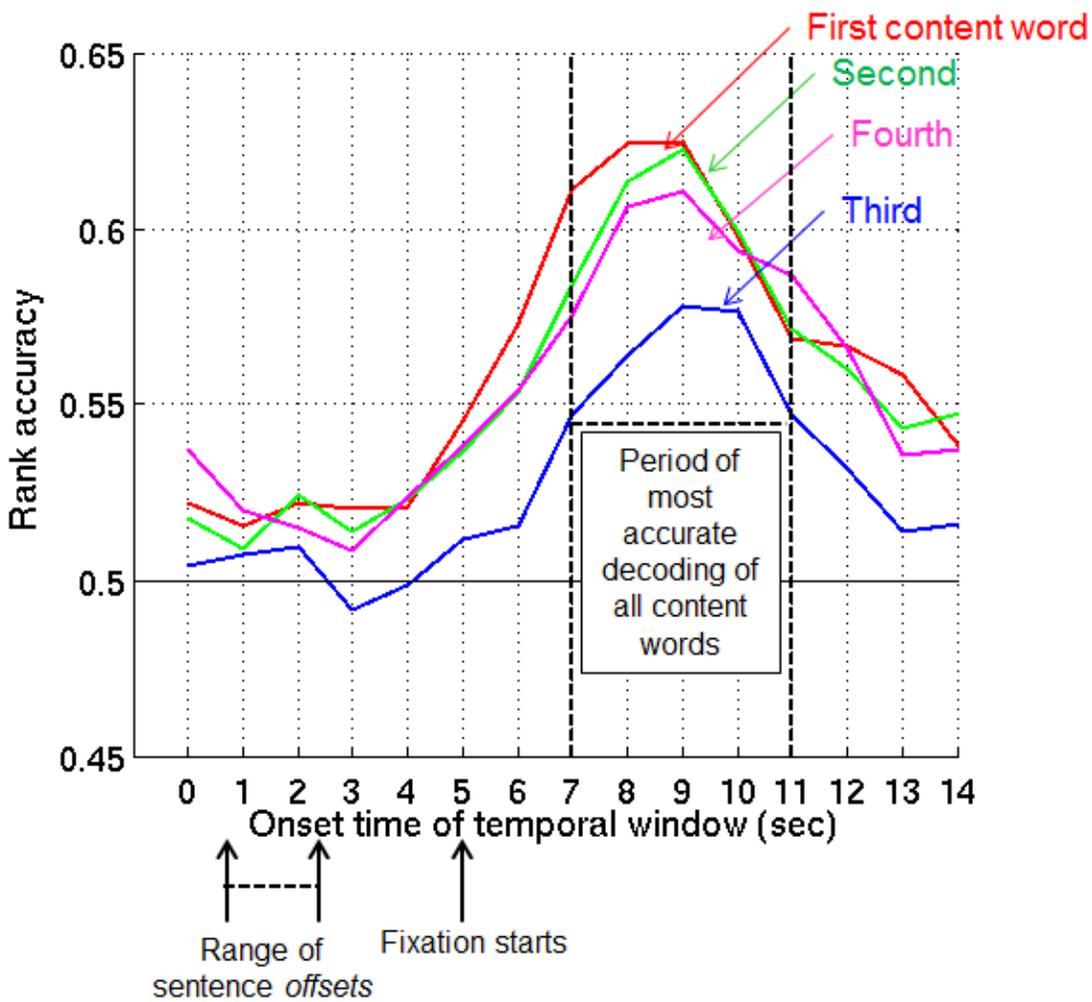


Figure S1. The accuracies of predicting activation patterns of words that occurred at four different serial positions in the sentence (4 colored curves) all peaked in the same temporal decoding window.

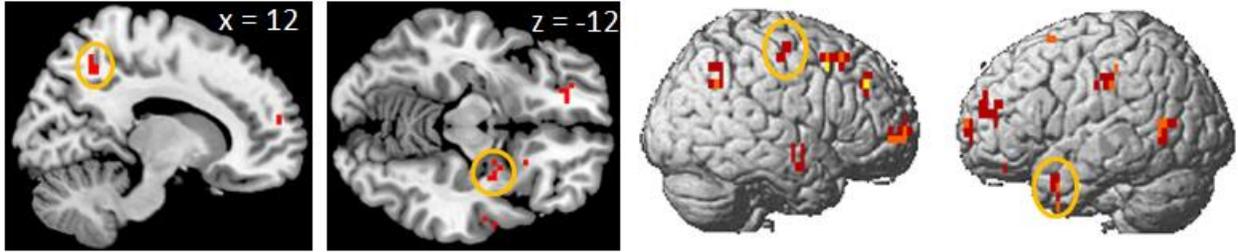


Figure S2. Brain locations that encode thematic role information. The circled clusters in the precuneus (MNI coordinates: 12, -54, 46), right amygdala (22, -3, -15), right precentral gyrus (41, -15, 52) and left ATL (-40, 6, -38) are spatially distinct from those identified in the main study (Table S3).

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