The Neural Basis of Semantic Prediction in Sentence Comprehension

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Abstract

■ Although prediction plays an important role in language comprehension, its precise neural basis remains unclear. This fMRI study investigated whether and how semantic-category-specific and common cerebral areas are recruited in predictive semantic processing during sentence comprehension. We manipulated the semantic constraint of sentence contexts, upon which a tool-related, a building-related, or no specific category of noun is highly predictable. This noun-predictability effect was measured not only over the target nouns but also over their preceding transitive verbs. Both before and after the appearance of target nouns, left anterior supramarginal gyrus was specifically activated for tool-related nouns and left parahippocampal place area was activated specifically for building-related nouns. The semantic-category common areas included a subset of left inferior frontal gyrus during the anticipation of incoming target nouns (activity enhancement for high predictability) and included a wide spread of areas (bilateral inferior frontal gyrus, left superior/middle temporal gyrus, left medial pFC, and left TPJ) during the integration of actually perceived nouns (activity reduction for high predictability). These results indicated that the human brain recruits fine divisions of cortical areas to distinguish different semantic categories of predicted words, and anticipatory semantic processing relies, at least partially, on top–down prediction conducted in higher-level cortical areas. ■

INTRODUCTION

Predictive processing is a basic principle of brain function. During cognitive activities in general and language comprehension in particular, the human brain has been argued to continuously anticipate upcoming inputs with top–down predictions based on available information. Such predictions potentially facilitate the processing of newly available bottom–up input by reducing the processing demand of this input when it confirms predictions (e.g., Clark, 2013; Kok, Jehee, & De Lange, 2012; Friston, 2005, 2010; Engel, Fries, & Singer, 2001; for language processing, see Kuperberg & Jaeger, 2016; Pickering & Garrod, 2013; Hickok, 2012; Federmeier, 2007). Predictive processing, therefore, consists of at least two processes: anticipatory processing of forthcoming information before its onset (anticipatory process or predictive process) and integration of top–down predictions with new bottom–up input (prediction resolution; e.g., Bonhage, Mueller, Friederici, & Fiebach, 2015; Dikker & Pylkkänen, 2013). These two processes are believed to be tightly related and support each other, with one process tending to be predominant over the other as a function of the specific processing situations. Until now, the existing studies on predictive language processing are mainly associated with the integration processing of the actually perceived words. Although some studies provided evidence for the anticipatory nature of language processing, the brain areas and the precise neural mechanisms involved in anticipatory language processing remain unclear. This study focused on the neural basis of semantic prediction in sentence comprehension and was interested in the semantic-category-specific and common cerebral areas underlying predictive processing as well as prediction resolution.

The Neural Evidences of Predictive Language Processing

A few neuroimaging studies have attempted to investigate the cortical areas associated with semantic prediction. An fMRI study conducted by Weber and colleagues observed reduced activity in the left anterior superior/middle temporal cortex to a highly predictable word after it actually appeared in a word context (Weber, Lau, Stillerman, & Kuperberg, 2016). Two magnetoencephalography (MEG) studies further examined the neural basis underlying the anticipatory processing of an incoming word, in which increased, rather than decreased, activity was observed in the strongly constraining condition. Specifically, one study observed increased activity in the left middle temporal, ventromedial prefrontal, and visual cortices before a highly predictable target word appeared in a picture context (Dikker & Pylkkänen, 2013), and another study found enhanced activity in the left middle temporal

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gyrus (MTG) in response to highly predictive adjectives before the target nouns (Fruchter, Linzen, Westerlund, & Marantz, 2015). Although these two MEG studies paid attention to the anticipatory process of prediction, they both used word pairs or picture–word pairs as materials. Their results, consequently, could not directly generalize to real sentence comprehension, as semantic prediction in sentence comprehension involves not only the retrieval or priming of semantic associations but also the binding of multiple elements into a coherent meaning representation (e.g., Hagoort, 2005, 2013).

Some studies further explored the neural areas underlying predictive processing in sentence or discourse comprehension. Early fMRI studies mainly examined the integration processing of the actually presented target words and found that increases of target word predictability (realized by a strong sentence-context constraint) were associated with decreases of hemodynamic activity in the inferior frontal and middle/superior temporal regions (e.g., Schuster, Hawelka, Hutzler, Kronbichler, & Richlan, 2016; Obleser & Kotz, 2010). Subsequent studies began to employ a novel paradigm or new data analysis method to examine the anticipatory process of language prediction. For example, Bonhage et al. (2015) presented participants with partial sentences without the final highly predictable target word. By combining eye tracking and fMRI techniques, they found that several temporal–parietal and subcortical areas showed increased activity for anticipatory processing based on lexical–semantic information (compared to that based on syntactic information; Bonhage et al., 2015). An MEG study, with the help of representational similarity analysis, further found that, before the onset of the highly predictable target words in sentence contexts, the spatial–temporal patterns of brain activity were more similar when these target words were the same word than when they were different words. This finding was considered to provide neural evidence for anticipatory lexical processing (Wang, Kuperberg, & Jensen, 2018). An fMRI study conducted by Willems, Frank, Nijhof, Hagoort, and Van den Bosch (2016) examined the brain areas associated with the "entropy" and "surprisal" (indices derived from a linguistic computational model) of words in natural discourse. They found that when entropy was low (highly predictive of upcoming words), hemodynamic activity increased in brain areas including the left middle frontal gyrus, right inferior frontal gyrus, left inferior parietal lobule, and left SMA, whereas when surprisal value was low (high predictability of the actually presented words given preceding contexts), hemodynamic activity decreased in areas such as the inferior frontal sulcus, left inferior temporal sulcus, and bilateral superior temporal gyrus (Willems et al., 2016). With the help of source localization analysis, some MEG or EEG studies also showed that highly predictive sentence fragments (compared to the less predictive ones) led to neural activation increases in temporal and parahippocampal cortices (e.g., Maess, Mamashli, Obleser, Helle, & Friederici, 2016) before the presentation of target words.

These sentence or discourse comprehension studies, from different points of view, provided neural evidence for the anticipatory nature of lexical/semantic processing during on-line language comprehension. The process they examined, in fact, is more related to lexical/semantic anticipation in general or more focused on the difference between semantic, syntactic, and phonological processing. With regard to semantic processing itself, the detailed semantic content (e.g., specific semantic categories) of anticipatory language processing, and especially the precise composition of its underlying brain network, is still not completely clear.

For the neural basis of semantic processing or meaning comprehension, there are increasing evidences indicating that the cortical semantic network may have fine divisions (or dissociable neural systems) being specialized for processing different semantic categories (Lin et al., 2018; Huth, De Heer, Griffiths, Theunissen, & Gallant, 2016; Mahon & Caramazza, 2003). For example, the representation/processing of tool often selectively activated subregions of the left posterior MTG (pMTG) and left anterior supramarginal gyrus (ant-SMG; Gallivan, Mclean, Valyear, & Culham, 2013; Mahon et al., 2007; for reviews, see Lewis, 2006), whereas the representation/processing of building/scene often selectively activated subregions of the left posterior parahippocampal gyrus, called parahippocampal place area (PPA; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998). The above evidences for the semantic-specific cortical subdivisions mainly came from studies with isolated words/pictures as materials or from sentence/discourse comprehension studies that focused on the integration processing of the actually presented information. Recently, some EEG studies further found that the semantic-category-specific neural dissociation may also occur during predictive language processing, as indicated by the comparisons of sentence fragments predicting different categories of words: The dorsal or ventral region of the motor–neural system was preactivated depending on the body–part relationship of the action-related word/sound (Grisoni, Mille, & Pulvermüller, 2017); the visual or sensorimotor cortical regions were specifically preactivated for animal- and tool-related words (Grisoni, Tomasello, & Pulvermüller, 2020). Although Grisoni and colleagues' studies provided new insight into the mechanisms of semantic prediction, the category-specific neural dissociation they observed during anticipatory processing was not reported in the same comparison (e.g., animal vs. tool nouns) at the actual encounter of these nouns, thus leaving the functional significance and generality of the category-specific neural preactivation remaining to be examined. The neural dissociation of different semantic categories of words before their actual appearance in sentences would not only provide more direct evidence for the anticipatory nature of semantic processing but also help us to further understand the precise neural basis of semantic processing in sentence/discourse comprehension.

The first aim of this study was to examine whether, during sentence comprehension, the human brain is able to recruit dissociable brain areas to anticipate different categories of semantic information, by using an fMRI technique and distinguishing tool- and building-related target nouns and by taking a comprehensive look at the processes of predictive processing and prediction resolution.

The Neural Mechanisms by Which the Human Brain Works to Realize Semantic Prediction

Besides the semantic category-specific cerebral areas, the brain areas that are recruited in the predictive processing of incoming semantic information irrespective their specific categories (common semantic prediction) are also important for our understanding of language comprehension. The activation/deactivation working pattern of these common brain areas is closely related to the cognitive and neural mechanisms of prediction.

The predictive coding account (Friston, 2005, 2010; Rao & Ballard, 1999), a neurobiologically informed theory of brain function, describes a model of predictive processing in which each level of the neural hierarchy (except the lowest level) is engaged in predicting the responses at the next lower level via feedback connections, whereas only the prediction error (difference between the predicted and actually perceived activities) propagates through the remainder of the processing hierarchy via feedforward connections. In this theory, predictive processing is considered to be an active process in the sense of top–down preactivation. Some researchers (Rao & Ballard, 1999) further suggest that this functional hierarchy is organized across cortical areas, with the relatively higher hierarchical levels of processing being attributed to higher-level cortical areas.

According to the predictive coding account (Rao & Ballard, 1999), the core cortical areas that underlie common semantic prediction in language comprehension are at least in part located in the relatively higher-level cortical areas, with these higher-level areas engaged in top–down predictive processing and the possible semantic-category-specific cortical preactivation (such as the tool-related left pMTG and ant-SMG or building-related left PPA) being the downstream consequence of this top–down prediction. One of the candidate higher-level cortical areas is the subregion of the left inferior frontal gyrus (IFG), given that this cortical region has already been considered to be one of core areas associated with sentence/discourse comprehension and found to be involved in top–down controlled semantic processing (such as semantic retrieval/selection or semantic binding; Hagoort, 2005, 2013; Friederici, 2002, 2011).

Furthermore, the predictive coding account implies that the higher-level cortical areas that support top–down common semantic prediction are possible to lead to increased hemodynamic activity in the highly predictive (vs. less predictive) condition. The reason is that, to make predictions in the highly predictive context, the corresponding cortical areas need to be kept in an active state, whereas predictions are less likely to be made in the less predictive context because of insufficient evidence (e.g., Linderholm, 2002). Until now, some studies have already found that, during sentence or discourse comprehension, hemodynamic activity in a range of cortical regions (including the left IFG) decreased for the integration processing of the actually perceived highly (vs. less) predictable words (e.g., Schuster et al., 2016; Weber et al., 2016; Obleser & Kotz, 2010), which is consistent with the suppressed feedforward propagation of confirmed predictions. The neural activity patterns underlying anticipatory semantic processing, however, remain to be examined further.

As mentioned earlier, the existing studies on predictive language processing have already observed a wide spread of brain areas (such as the left MTG, left IFG, left SMA) participating in predictive lexical/semantic processing (e.g., Grisoni et al., 2020; Maess et al., 2016; Willems et al., 2016; Bonhage et al., 2015; Fruchter et al., 2015; Dikker & Pylkkänen, 2013). The cortical areas revealed by these studies were, however, inconsistent with each other. More importantly, most of these neuroimaging studies did not strictly control the specific semantic category of predicted information or collapsed the different semantic categories (e.g., animal and tool categories) together when comparing the highly predictive with less-predictive sentence frames during cortical source localization (e.g., Grisoni et al., 2020). The existing results, therefore, are not able to clarify whether the activation of the above brain areas was more associated with the preactivation of a very specific type of semantic information or mainly driven by top–down predictive processing of incoming semantic information irrespective of their specific categories.

The second goal of this study was to explore, during sentence comprehension, what are the core brain regions underlying common semantic anticipation and how these semantic category–common brain areas work to support predictive semantic processing.

This Study

To answer these experimental questions, the fMRI technique was used in this study, and participants were asked to read Mandarin Chinese sentences for comprehension. Each sentence includes a target critical noun and a transitive verb immediately preceding this noun. We manipulated the semantic constraint of the sentence context, so that the critical noun at the end of each sentence is either highly or weakly predictable; meanwhile, two kinds of strong-constraint sentence context were created, upon which the highly predictable critical noun is associated with either tool- or building-related semantic category (WEAK, STRtool, or STRbuilding). Given the low time resolution of fMRI, during the presentation of each sentence, we set a time delay between the critical nouns and the preceding transitive verbs. The delayed presentation of the critical nouns experimentally mimicked natural situations in which someone is waiting for the answer from his or her partner. We measured both the anticipatory processing of the critical noun over its preceding transitive verb and the integration of the critical noun after its actual appearance (see Methods section for the detailed description).

If the human brain is able to perform anticipatory semantic processing and recruit distinct cortical areas to do so, the brain region specifically associated with tool- or building-related representation/processing would show neural dissociations between the two strong-constraint conditions before the onset of the target nouns. By searching for the brain regions that would show semantic prediction effect in both the STRtool and STRbuilding conditions compared to the WEAK condition, we would discover the core brain areas underlying common semantic prediction.

At the critical verbs, according to the predictive coding account, the semantic category–common cortical areas are possible to display hemodynamic activity increases in the strong-constraint condition (STRtool > WEAK, STRbuilding > WEAK) because of top–down anticipatory processing conducted in this condition (as explained earlier), and this cortical activation increase may be in part observed in the relatively higher-level cortical areas, such as the left IFG. In contrast, if the human brain conducted predictive processing even in the very weakly constraining (and consequently resource-demanding) context, or if the human brain only integrated the current verbs with preceding contextual information and conducted anticipatory processing in neither the weak-constraint nor strong-constraint conditions, decreased rather than increased neural activity would be observed in the strong-constraint (vs. weak-constraint) conditions; the reason is that the critical verbs themselves are relatively more predictable in the two strong-constraint conditions (see Methods section for the predictability of the critical verb) and are consequently easier to be integrated.

During the integration processing of the actually perceived target nouns (at the critical nouns), the semantic category–common cortical areas are expected to show decreased hemodynamic activity in the two strong-constraint (STRtool/STRbuilding vs. weak-constraint) condition, indicating the suppressed feedforward propagation of confirmed prediction.

In addition, although the predictive coding account emphasizes hierarchical message passing in the neural hierarchy, it does not deny the possibility of lateral interaction with information at the same neural hierarchy level (e.g., activation being driven or inhibited by information at the same level; e.g., Friston, 2010; Rao & Ballard, 1999). The meaning of lateral interaction was also explained when the predictive coding framework was used to account for language comprehension. It was assumed that semantic information preactivation in language comprehension is supported both by hierarchical top–down prediction and by activation spreading such as priming stemming from lingering mental representation at the same representation level (Kuperberg & Jaeger, 2016). For the present results, a negative correlation is likely to be observed between the verb and noun semantic-constraint effect in the relatively higher-level cortical areas (e.g., the left IFG), if the semantic preactivation in the situation of this study was predominately driven by top–down controlled predictive processing, whereas such correlation is less likely to be observed if the semantic preactivation is primarily driven by lateral message parsing or by both top–down prediction and lateral interaction.

METHODS

Participants

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established before data analysis, all manipulations, and all measures in the study. Sample size was determined according to other studies investigating the neural basis of predictive language processing (Bonhage et al., 2015) and tool/building-related processing (Mahon et al., 2007; Downing et al., 2006), with relatively more participants recruited in this study.

Twenty-eight right-handed young adults were paid to participate in the experiment, with normal or corrected-to-normal vision and without psychiatric or neurological problems. All participants gave written informed consent. The study was approved by the ethics committee of the Institute of Psychology, Chinese Academic of Sciences. The data of two participants were not successfully recorded, because one participant did not complete the experiment and there was a technical problem for the other participant. For the remaining 26 participants whose data were successfully recorded, one participant was deleted from further analysis because of extremely poor coverage in the functional images due to excessive head movements, and three participants were removed because the accuracy rate of behavioral results was below 75%. These inclusion/exclusion criteria were established before data analysis. Therefore, data of the remaining 22 participants (11 women; mean age = 22.56 years, ranging between 19 and 25 years old) were included in the final statistical analysis of the fMRI data.

Stimuli

Twenty-nine sets of Mandarin Chinese sentences were used as experimental stimuli. We manipulated the semantic constraint of the sentence context, with each set of stimuli including three versions: “strong-constraint, tool” (STRtool), “strong-constraint, building” (STRbuilding), and “weak-constraint” (WEAK). Specifically, the experimental sentences in both the STRtool and STRbuilding versions have a highly constraining semantic context, upon which a tool-related noun or a building-related noun is highly predicted; the experimental sentences in the WEAK version, however, have a weakly constraining semantic context. Each experimental sentence included a critical noun at the sentence-final position, with this noun always being the best completion of the preceding context; moreover, the critical noun in the WEAK condition is always an inanimate noun, which is neither building related nor tool related. Taken together, this resulted in a one-factor design, with the factor Semantic constraint including three levels: STRtool, STRbuilding, vs. WEAK (see Table 1 for example stimuli).

The syntactic structure of the experimental sentences was kept constant across the three conditions. Each experimental sentence includes two subclauses, with the first one setting a communication background (called CONTEXTs throughout the article; e.g., “Xiaoqi wanted to put the nail into the wall,…”) and the second one consisting of a pronoun, a transitive verb, and a critical noun (e.g., “…he found a hammer”). The transitive verb (e.g., “found”) preceding the critical noun in each sentence is the critical verb, which, combined with the preceding context, plays a very important role in triggering the generation of the hypothesized candidate representations of the forthcoming critical noun (e.g., “a hammer”), as it is the predicate of the sentence and needs a noun argument to complete its meaning and to form a complete predicate–argument structure (Kroeger, 2004; for the detailed reasons, see Li, Ren, Zheng, & Chen, 2020; Li, Zhang, Xia, & Swaab, 2017).

To validate the degree of predictability of the critical nouns, two cloze probability (CP) tests were conducted by presenting the sentence until the word immediately preceding the critical verbs (Test 1; e.g., “Minmin wanted to clip a piece of chemical…”) or until the critical verbs (Test 2; e.g., “Minmin wanted to clip a piece of chemical, and she found…”). Thirty-two participants, who did not participate in the fMRI experiment, finished the two distinct CP tests, with 16 participants in each test. The participants were instructed to complete the frames with the first event that came to mind and that would make the sentence meaningful. We measured not only the lexical predictability of the upcoming critical nouns themselves (i.e., the CP of a particular word) but also the semantic predictability of these nouns (i.e., the CP of all of the words that contain the same semantic feature, such as tool relatedness or building relatedness; see Table 2 for detailed values). One-way ANOVAs revealed a significant main effect of Semantic constraint for both Test 1 and Test 2—$F(2, 56) = 16.69$, $p < .001$; $F(2, 56) = 441.25$, $p < .001$; $F(2, 56) = 16.69$, $p < .001$; and $F(2, 56) = 693.92$, $p < .001$ for “critical-noun predictability of Test 1,” “critical-noun predictability of Test 2,” “semantic predictability of Test 1,” and “semantic predictability of Test 2,” respectively—because of the fact that, for both lexical predictability and semantic predictability, the CP values in the two strong-constraint conditions were all significantly higher than that in the weak-constraint condition (all ps $< .001$), and the difference between the two strong-constraint conditions reached significance for neither Test 1 nor Test 2 (all ps $> .13$). Moreover, for both critical-noun predictability and semantic predictability, paired t tests with difference score (STRtool minus $\text{WEAK}_{\text{best completion}}$ or STRbuilding minus $\text{WEAK}_{\text{best completion}}$) as the dependent factor showed a significant difference between Test 1 and Test 2 (with all ts ≥ 8.65, all ps $< .001$), indicating that, in the two strong-constraint conditions, the semantic predictability of upcoming nouns increased significantly after the critical verb was presented. Therefore, the CP

Table 1. Illustrations for the Experimental Materials in the Strong- and Weak-Constraint Conditions

Conditions	*Example Sentences*	
Strong-tool	小齐想在墙上钉钉子，	他“找到了”锤子。
	Xiaoqi wanted to put the nail into the wall, and he “found” a hammer.	
Strong-building	小齐想去买一束玫瑰，	他“找到了”花店。
	Xiaoqi wanted to buy a bunch of roses, and he “found” a florist’s shop.	
Weak	小齐想多帮助其他人，	他“找到了”试题。
	Xiaoqi wanted to do more to help others, and he “found” the test paper.	

The underlined words are the critical nouns; the words in quotes are the critical verbs immediately preceding the critical nouns. The period from the onset of the critical verb to the onset of the critical noun provides us an opportunity to examine the anticipatory processing of the forthcoming critical nouns; the period starting from the onset of the critical noun reflects integration between contextual predictions and the new bottom–up input after the critical noun has appeared.

Table 2. CP of the Critical Nouns (or Other Completed Words) in the Three Experimental Conditions

Conditions		Preceding Verb (Test 1) *M*	Preceding Verb (Test 1) *SD*	Preceding Noun (Test 2) *M*	Preceding Noun (Test 2) *SD*
Tool	CP of critical nouns	42.46%	18.63%	85.13%	11.13%
	CP of all tool-nouns	49.35%	18.48%	90.95%	8.93%
	CP of “pronoun + verb”	15.19%	13.17%	N.A.	N.A.
Building	CP of critical nouns	34.91%	20.49%	80.82%	8.67%
	CP of all building-nouns	42.03%	22.22%	85.99%	8.78%
	CP of “pronoun + verb”	16.38%	10.75%	N.A.	N.A.
Weak constraint	CP of best completion	20.04%	11.5%	22.63%	6.97%
	CP of all tool-nouns	2.16%	5.35%	5.17%	9.01%
	CP of all building-nouns	1.72%	4.39%	7.97%	10.55%
	CP of “pronoun + verb”	7.54%	8.94%	N.A.	N.A.

“Critical nouns” indicate the critical nouns used in the experimental sentences of corresponding experimental condition, “tool-nouns” indicate all of the completed nouns that belong to the tool category, and “building-nouns” indicate all of the completed nouns that belong to the building category. In addition, “CP of pronoun + verb” indicates the averaged CP of the critical verbs and the pronouns immediately preceding these verbs. “N.A.” indicates that the corresponding CP value is not applicable, as the pronoun and verb have already been presented at the ‘Preceding Noun’ position. For the weak-constraint condition, the critical nouns were the best completion in Test 2.

pretests confirmed that our manipulation of semantic constraint was successful and that the critical verbs indeed played an important role in triggering the generation of the hypothesized semantic features of forthcoming critical nouns.

In addition, the CP of the critical verbs and that of the pronouns immediately preceding these verbs were calculated from the Test 1 mentioned above, and then the average values of these two types of CP (CP of “pronoun + verb”) were obtained (see Table 2 for detailed values). One-way ANOVAs, with CP of “pronoun + verb” as the dependent factor, resulted in a significant main effect of Semantic constraint, $F(2, 56) = 7.91$, $p < .001$, because of the fact that CP of “pronoun + verb” of the WEAK condition was significantly smaller than that of the STRtool or STRbuilding condition (all ps $< .028$). These results indicated that the critical verbs and the immediately preceding pronouns were relatively highly predictable in the two strong-constraint conditions relative to the weak-constraint condition.

To validate that the tool nouns indeed refer to tools, 16 participants, who did not participate in the fMRI experiment and other pretests, were asked to rate the operability and imageability of the critical nouns on a 7-point scale (from 1 to 7). The larger the score, the more operable or imageable the nouns were. For both operability and imageability scores, one-way ANOVAs revealed a significant main effect of Semantic constraint, $F(2, 56) = 284.70$, $p < .001$, and $F(2, 56) = 22.83$, $p < .001$, for operability and imageability, respectively. Further comparisons showed (with p values of the pairwise comparisons being corrected by Bonferroni method) that, as seen from Figure 1A, the operability of tool-nouns ($M = 6.47$, $SD = 0.31$) was significantly higher than that of building-nouns ($M = 2.25$, $SD = 0.37$) and nouns in the weak-constraint condition ($M = 4.87$, $SD = 1.15$; all ps $< .001$), whereas the operability of building-nouns was lower than that in the WEAK condition ($p < .001$); meanwhile, the imageability of tool-nouns ($M = 6.63$, $SD = 0.17$) was also higher relative to that of building-nouns ($M = 5.59$, $SD = 0.46$) and nouns in the weak-constraint condition ($M = 5.88$, $SD = 0.85$; ps $< .001$). These results indicated that the manipulation of tool-nouns was successful. In addition, the fact that the operability of building-nouns was significantly lower than that of tool-nouns and less-predictable nouns (in the WEAK condition) was in line with the semantic features of buildings.

We also controlled the word frequency (M [SD] = 1.70 [0.59], 2.00 [0.70], and 2.01 [0.79]) and number of strokes (M (SD) = 19.62 [8.42], 18.79 [6.64], and 20.52 [5.23]) of the critical nouns in the STRtool, STRbuilding, and WEAK conditions (see Figure 1B). The result of the ANOVAs demonstrated that the main effects of Semantic constraint reached significance for neither word frequency nor the number of strokes (all ps $> .07$).

Procedure

Sentences were projected onto a screen in white 20-point font, and participants were instructed to read each

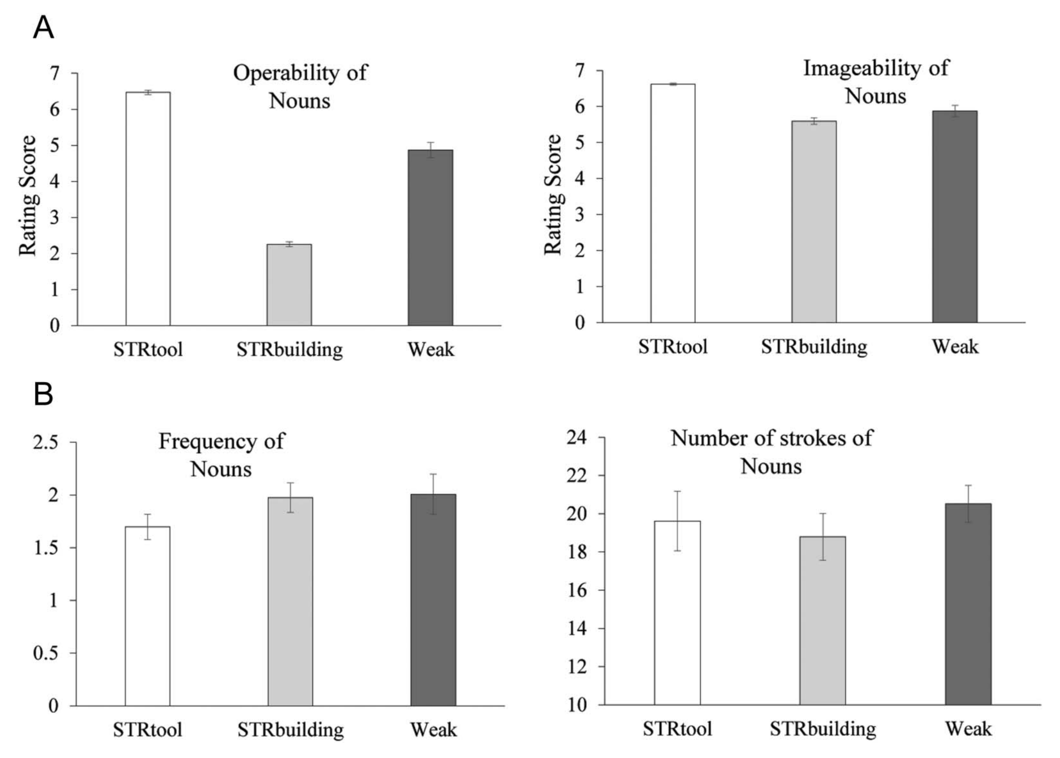


Figure 1. The characteristics (i.e., operability, imageability, word frequency, and number of strokes) of the critical nouns in sentences.

sentence for comprehension. Each trial began with a fixation cross, presented at the center of the screen for 1000 msec. The first part of each sentence (i.e., the first subclause, which was accompanied by a comma; e.g., "Xiaoqi wanted to put the nail into the wall,") was presented for 3000 msec, and the second part (i.e., the pronoun and the critical verb in the second subclause; e.g., "he found") was presented for 1000 msec. Finally, the third part (i.e., the critical noun in the second subclause, which was accompanied by a full stop; e.g., "a hammer.") was presented for 1000 msec. The first part set a communication background, consequently being named as CONTEXTs here; the second part included the pronouns and the critical verbs, hence being named as VERBs; and during the presentation of the third part, participants were conducting integration processing of the actually perceived critical noun, with this part being named as NOUNs. Uniformly distributed variable jitters of 3–7 sec were introduced between CONTEXTs and VERBs, between VERBs and NOUNs, and between NOUNs and the following trial. This manipulation ensured that BOLD responses to one event were not contaminated with a BOLD response to the previous stimulus.

We applied an event-related fMRI design. Twenty-nine sets of experimental sentences (87 experimental sentences in total) and 21 filler sentences were allocated to three runs. In each run, the sentences coming from three experimental conditions and the filter sentences were presented to the participants in a pseudorandom order. Importantly, for all of the 29 sets of experimental sentences (29 × 3) included in the final data analysis, none of the sentences (or critical nouns) had been presented before in this experiment, which excludes the possibility of anticipatory lexical processing driven by repeated presentation. In addition, except for the 87 experimental sentences mentioned above, seven sets of sentences were presented one more time (i.e., being presented twice), with this second presentation being not modeled in the three experimental conditions during data analysis.

For 18 sentences in all of the filler materials, each one included a semantically incongruent word, with one third of the filter sentences having a STRtool context, another one third of them having a STRbuilding context, and the others having a weak-constraint context. To ensure that participants indeed read the sentences for comprehension, they were asked to press a button if any word was found to be semantically incongruent with the current sentence context. After a brief practice session, the trials were presented in three runs of approximately 16 min each, separated by brief resting stages.

fMRI Data Acquisition

A GE Discovery MR750 3-T scanner was used for this study. A high-resolution structural image was obtained using a 3-D spoiled gradient recall pulse sequence with the following parameters: echo time = minimum full, inversion time = 450 msec, field of view = 256 mm × 256 mm, flip angle = 12°, matrix size = 256 × 256, voxel size = 1 ×

1 × 1 mm, slice number = 192 slices, and slice thickness = 1 mm.

BOLD fMRI was obtained using a gradient-echo EPI sequence: repetition time = 2000 msec, echo time = 30 msec, field of view = 224 mm × 224 mm, flip angle = 90°, matrix size = 64 × 64, voxel size = 3.5 × 3.5 × 3.5 mm, number of slices = 33, and slice thickness = 3.5 mm.

fMRI Analysis

Preprocessing of the MRI data was performed using DPARSF (Yan & Zang, 2010, rfmri.org/DPARSF). After removing the first five volumes of each block for steady state magnetization, the functional images were slice-time corrected and realigned to the mid volume in the time series to correct for head motion. Then, the functional images were coregistered to anatomical images for each participant. The anatomical images were segmented into gray and white matter, and the spatial normalization parameters acquired during this step were used to normalize the functional images. Finally, spatial smoothing was performed using an isotropic 6-mm FWHM Gaussian kernel.

Whole-brain Analysis

The whole-brain analysis was conducted using SPM12 (Statistical Parametric Mapping, Wellcome Trust Center for Neuroimaging; www.fil.ion.ucl.ac.uk/spm/). We examined three phases of brain activities. The VERBs phase of brain activities (activities induced during the processing of the critical verbs in the second subclause) provided us an opportunity to examine the brain areas that support the anticipatory processing of the critical nouns, whereas the NOUNs phase of activities (activities induced during the processing of the critical nouns of the second subclause) could enable us to examine the brain areas underlying the integration processing of the actually perceived critical nouns. The CONTEXTs phase of cortical activities (activities induced during the processing of the first subclause) could tell us which cerebral areas had already been activated/deactivated before the onset of the critical verbs, hence providing us an opportunity to examine the nature of the cortical activations observed at the VERBs phase of processing (see the following paragraphs). That is, the contextual activations themselves are not the main interest of this study, as the potentially confounding factors were not strictly matched across the three experimental conditions over the position of CONTEXTs. Importantly, as did by Bonhage et al. (2015), we modeled the prediction as a short event (duration = 1 sec) instead of the whole delay, as anticipatory processing was not expected to take place over the entire VERBs interval and given that we wanted to avoid any maintenance-related brain activation.

First-level Analysis

For the first-level analysis, a generalized linear model was constructed to model the CONTEXTs phase (time-locked to the onset of the first subclause, duration = 3 sec), the VERBs phase (time-locked to the onset of the critical verb part, duration = 1 sec), and the NOUNs phase (time-locked to the critical noun, duration = 1 sec). Each of the three phases included four regressors, which described activities in the three experimental conditions (STRtool, STRbuilding, and WEAK) and filler sentences, respectively. Moreover, six motion parameters were included in the generalized linear model as regressors of no interest.

Planned first-level t contrasts were performed on two aims. First, to examine the specific brain areas recruited in selectively predicting a tool-related word and predicting a building-related word, we directly contrasted STRtool to STRbuilding conditions (Contrast 1). Brain areas specialized for building prediction should display an increased hemodynamic activity in Contrast 1a (STRbuilding > STRtool), whereas brain regions specialized for tool prediction should show increased activity in Contrast 1b (STRtool > STRbuilding). Furthermore, we compared the semantic-category-specific activations at the VERBs phase with those at the CONTEXTs phase, by conducting the [VERB (STRbuilding-versus-STRtool) versus CONTEXT (STRbuilding versus STRtool)] contrast. If the semantic-category-specific predictions/activations result from effortfully combining the verb meaning with preceding context, but not purely from spreading activation of the context words, these activations should be significantly stronger at the VERBs phase compared to the CONTEXTs phase.

Second, to reveal common brain areas recruited in predictive processing of different categories of semantic information, Contrast 2 (STRbuilding vs. WEAK) and Contrast 3 (STRtool vs. WEAK) were conducted. These common brain areas should show the same pattern of activation/deactivation in Contrast 2 and Contrast 3.

1) Contrast 1:
   Contrast 1a: STRbuilding > STRtool:
   [STRbuilding regressors (Contrast Value 1) versus STRtool regressors (contrast value − 1)].
   or Contrast 1b: STRtool > STRbuilding
   [STRtool regressors (Contrast Value 1) versus STRbuilding regressors (contrast value − 1)]
2) Contrast 2: STRbuilding versus WEAK
   [STRbuilding regressors (Contrast Value 1) versus WEAK regressors (contrast value − 1)]
3) Contrast 3: STRtool versus WEAK
   [STRtool regressors (Contrast Value 1) versus WEAK regressors (contrast value − 1)].

Second-level Analysis

We first examined the main effect of Semantic constraint (STRtool, STRbuilding, and WEAK) by taking the images of each of the three experimental conditions to the second level of analysis and conducting the one-way within-participant ANOVA. These analyses were performed for each phase of processing (CONTEXTs, VERBs, and NOUNs) separately.

Then, a random-effects analysis was performed by entering all participants' first-level contrasts (Contrast 1, Contrast 2, and Contrast 3) into a one-sample t test, which was conducted for each processing phase (CONTEXTs, VERBs, and NOUNs) and each t-contrast type separately. Finally, we performed a global conjunction analysis of the two t test maps ("STRbuilding vs. WEAK" ∩ "STRtool vs. WEAK") to find the core cortical areas that support common semantic prediction independently of the semantic category of the predicted words. Note that all of these second-level t test analyses were masked by the significant clusters of the one-way ANOVA, as the planned comparisons are contingent on observing first a significant effect of one-way ANOVA.

We reported whole-brain effects at a voxel-level threshold of $p < .001$ (Eklund, Nichols, & Knutsson, 2016) and a cluster-level FWE-corrected (using cluster-level FWE correction implemented in SPM12) threshold of $p < .05$.

ROI Analysis

Given that whole-brain analyses are necessarily conservative because of the correction for multiple comparisons, we additionally supplemented the whole-brain analysis with ROI analyses. Meanwhile, the ROI analysis can further verify the findings (e.g., semantic-category-specific cortical activations) of our whole-brain analysis, as these ROIs have already been found by previous studies to be specifically associated with building- or tool-related processing. We selected four ROIs as seeds, with mask of each seed being created by taking a 6-mm sphere around the peak coordinates.

For each of the four preselected ROIs, signal changes in the three conditions (STRtool, STRbuilding, and WEAK) during the scans were extracted for each participant. A one-way ANOVA was conducted to compare the activities between the three conditions: STRtool, STRbuilding, and WEAK. If the main effect reached significance, follow-up paired t tests were conducted to examine the differences between each two conditions (resulting in three pairwise comparisons); for the paired t tests, multiple comparisons were corrected by using the Bonferroni method by a factor of 12 (3 comparisons multiplied by 4 ROIs), with corrected p values being reported. In line with the whole-brain analysis, if the ROI t tests showed significant cortical semantic-category-specific activations (STRtool vs. STRbuilding), further ANOVAs were performed to examine whether the tool- or building-specific activations at the VERBs region were significantly stronger than those at the CONTEXTs region, with Region (VERB vs. CONTEXT) and Condition (STRbuilding vs. STRtool) as independent factors.

For the ROI analysis, first, to distinguish the specific regions associated with tool-related semantic representation/processing, subregions of the left pMTG and left ant-SMG were chosen, as parts of these two areas have been reported by previous studies to participate in tool-related processing (Gallivan et al., 2013; Mahon et al., 2007; Lewis, 2006; Grossman et al., 2002; Chao, Haxby, & Martin, 1999; Perani, Schnur, Tettamanti, Cappa, & Fazio, 1999). Montreal Neurological Institute (MNI) coordinates of these two ROIs were defined by using the search term "tool" on Neurosynth software (a software for automatic meta-analysis; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) and extracting the peaks of the activated areas (values retrieved on February 10, 2021): left pMTG (MNI coordinates: −52, −60, −2) and left ant-SMG (MNI coordinates: −60, −30, 42).

Second, subregions of PPA have been demonstrated to be specifically related to scene and building processing (e.g., Downing et al., 2006; Peelen & Downing, 2005; Epstein & Kanwisher, 1998); thus, we also selected the left PPA as an ROI. As we defined the ROIs above, the Neurosynth software (Yarkoni et al., 2011) and the search term "building" or "scene" were used; this search, however, resulted in no result (2021/02/10). Then, following the approach applied in the study by Downing et al. (2006), we defined the coordinates of the building/scene-processing-related PPA based on previously reported anatomical locations and mean coordinate: left PPA (MNI coordinates: −27, −44, −9; converted from the averaged Talairach coordinates "−28, −39, −6" in Epstein & Kanwisher, 1998, and "−23, −44, −9" in Peelen & Downing, 2005, by using the tal2icbm_spm function; Lancaster et al., 2007).

Finally, to examine the possible contribution of the relatively higher-level cortical areas in common semantic anticipation at the VERBs region, we also define an ROI (i.e., subregion of the left IFG) that has been found to be correlated with top–down controlled processing of semantic information. The MNI coordinates of this ROI were defined by using the search term "semantics" on Neurosynth software and extracting the peak of the activated IFG (values retrieved on 2021/02/10): left IFG (MNI coordinates: −42, 32, 16). The term "semantics" was used here because the resulting cortical activation was associated with the retrieval (e.g., James & Gauthier, 2004) or generation (by combing multiple words; e.g., Schell, Zaccarella, & Friederici, 2017) of semantics, which is closely related to predictive semantic processing.

The ROIs specifically associated with tool representation/processing were the left pMTG (−52, −60, −2) and left ant-SMG (−60, −30, 42).

The ROI specifically associated with building representation/processing was the left posterior parahippocampal gyrus (left PPA; −27, −44, −9).

The ROI associated with top–down controlled semantic binding was the left IFG (−42, 32, 16).

RESULTS

Behavioral Results

The 22 participants who were included in the final statistical analysis had an average accuracy rate of 91.6% (*SD* = 7.6%; i.e., successfully detecting the semantically incongruent sentences), indicating that they were attentive and able to judge whether the final word was semantically congruent in the context of the trial.

fMRI Results

Results Time-locked to the CONTEXTs

The whole-brain analysis showed that neither the STRbuilding > STRtool comparison nor the STRtool > STRbuilding comparison resulted in significant activations. The strong-constraint condition (compared to the weak-constraint condition) led to increased activity in the left IFG (extending to the middle frontal gyrus), left superior parietal lobe, and bilateral fusiform gyrus (extending to the inferior occipital gyrus), which reached significance for the STRbuilding > WEAK and STRtool > WEAK comparisons as well as conjunction analysis of these two comparisons. In addition, the left PPA showed increased activity in the STRbuilding > WEAK contrast (see Figure 2 and Table 3).

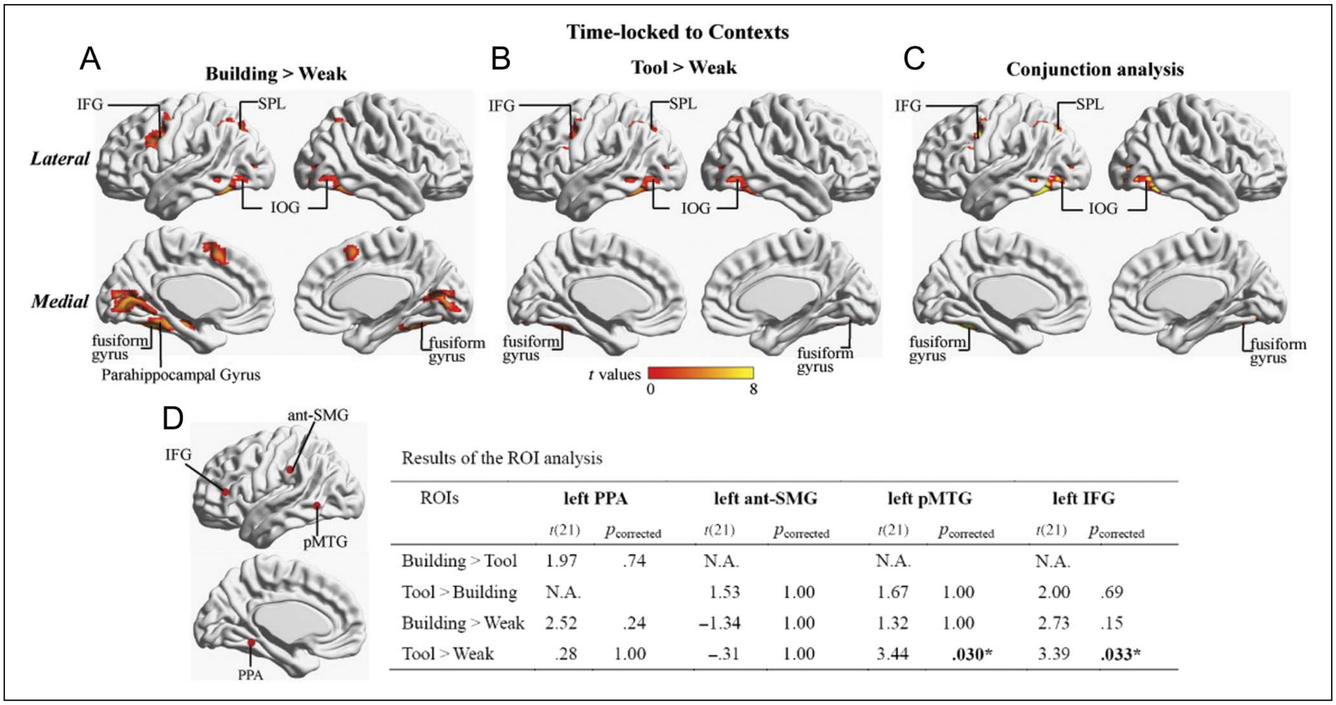
For the ROI analysis, only for the pMTG cortical region, the one-way ANOVAs showed a significant main effect of Semantic constraint for the pMTG, $F(2, 42) = 5.02$, $p = .012$, $\eta^2 = .19$, and IFG, $F(2, 42) = 8.74$, $p < .005$, $\eta^2 = .29$, regions. The subsequent *t* tests demonstrated that both the left pMTG and left IFG displayed a significantly increased activity in the STRtool > WEAK contrast (see Figure 2D).

Results Time-locked to the Critical Verbs

The whole-brain analysis revealed that the left PPA displayed increased activity in the STRbuilding condition compared to both STRtool (STRbuilding > STRtool) and WEAK (STRbuilding > WEAK) conditions, whereas the STRtool > STRbuilding comparison resulted in no significant cluster (see Figure 3 and Table 4).

For the ROI analysis of the verbs, one-way ANOVAs revealed a significant main effect of Semantic constraint for all of the four ROIs: $F(2, 42) = 11.99$, $p < .001$, $\eta^2 = .36$; $F(2, 42) = 4.66$, $p = .017$, $\eta^2 = .18$; $F(2, 42) = 5.73$, $p < .01$, $\eta^2 = .21$; and $F(2, 42) = 8.44$, $p < .001$, $\eta^2 = .29$, for the left PPA, left ant-SMG, left pMTG, and left IFG, respectively. The subsequent *t* tests demonstrated that the left PPA (ROI associated with scene/building processing) displayed significant activity increases in the STRbuilding > STRtool contrast, whereas the left ant-SMG (ROI associated with tool processing) showed significant activity increases in the STRtool > STRbuilding contrast (see Figure 3C). Meanwhile, the left IFG demonstrated increased activity in both the STRbuilding > WEAK and STRtool > WEAK contrasts. The left pMTG did not show a significant activity in the follow-up *t* tests.

For the ROIs that displayed a significant activity difference in the STRbuilding-versus-STRtool contrast, further ANOVA was conducted to examine whether the tool- or



Results of the ROI analysis

ROIs	left PPA		left ant-SMG		left pMTG		left IFG	
	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$
Building > Tool	1.97	.74	N.A.		N.A.		N.A.	
Tool > Building	N.A.		1.53	1.00	1.67	1.00	2.00	.69
Building > Weak	2.52	.24	−1.34	1.00	1.32	1.00	2.73	.15
Tool > Weak	.28	1.00	−.31	1.00	3.44	**.030***	3.39	**.033***

Figure 2. fMRI Activation pattern resulting from analysis time-locked to the contexts (first subclause of the sentence). (A–C) Results coming from the whole-brain analysis. (D) Results coming from the ROI analysis, with *p* values being corrected by Bonferroni method by a factor of 12. SPL = superior parietal lobe; IOG = inferior occipital gyrus.

Table 3. Activation Clusters and Increased Activation Peaks for the Whole-Brain Analysis Time-locked to the CONTEXTs

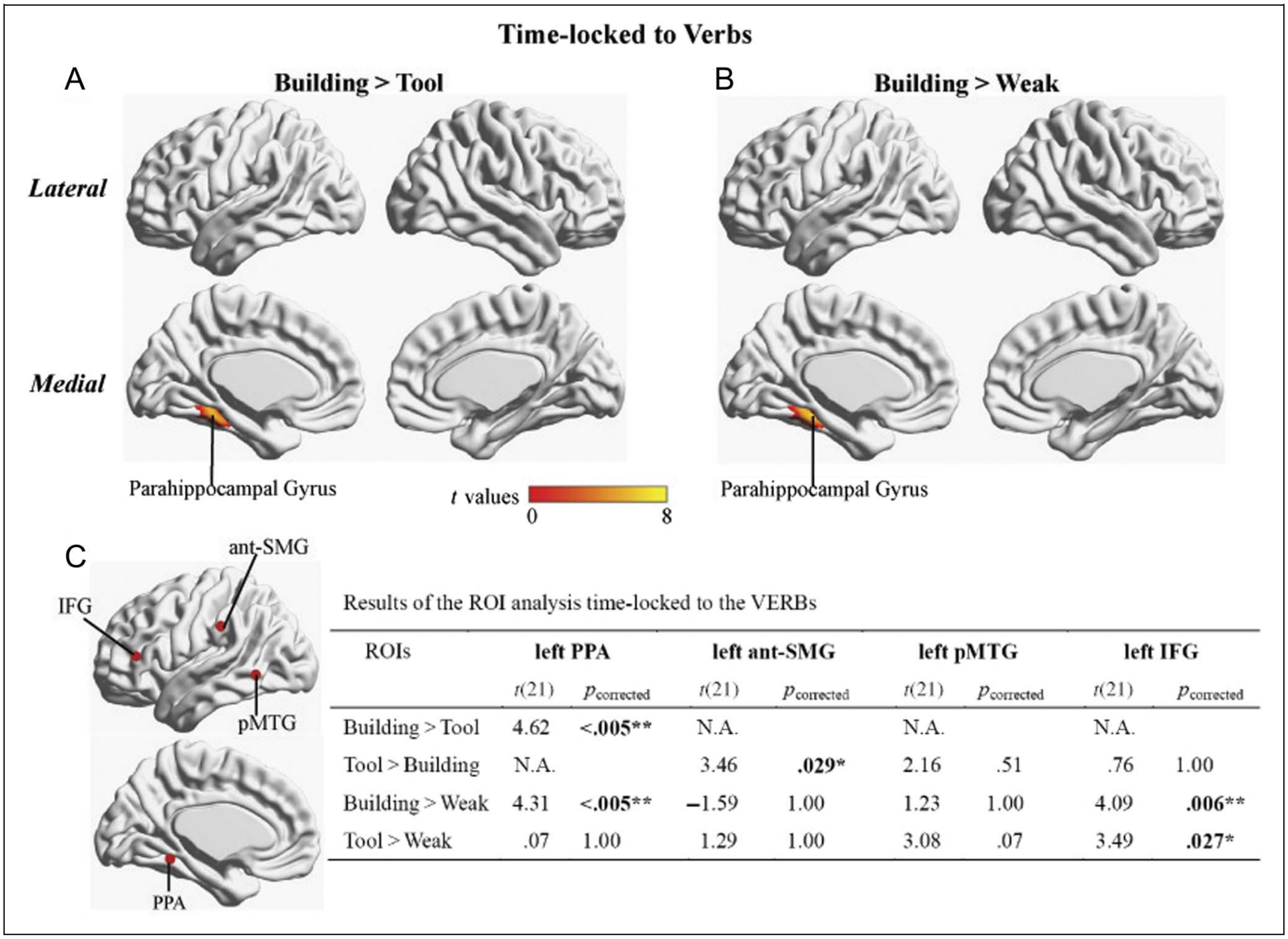
Contrast	*Region of the Peak Voxel*	*Cluster Size (Voxels)*	*MNI Coordinates*			*Peak t Value*
Areas specifically recruited in the representation/processing of buildings						
B > T	*ns*					
Areas specifically recruited in the representation/processing of tools						
T > B	*ns*					
Areas associated with the "STRbuilding-versus-WEAK" or "STRtool-versus-WEAK" contrast						
B > Weak	L inferior/middle frontal gyrus	207	−42	9	30	6.64
	L superior parietal lobe	170	−27	−54	42	6.78
	L fusiform gyrus/inferior occipital gyrus/parahippocampal gyrus	402	−36	−45	−21	7.44
	L lingual gyrus/calcarine	307	−6	−78	3	5.71
	R superior parietal lobe	57	30	−54	45	8.08
	R fusiform gyrus/inferior occipital gyrus	273	39	−63	−9	7.58
T > Weak	L inferior/middle frontal gyrus	138	−39	−3	42	6.67
	L superior parietal lobe	82	−24	−51	42	7.15
	L fusiform gyrus/inferior occipital gyrus	278	−30	−84	−9	6.76
	R fusiform gyrus/inferior occipital gyrus	165	45	−57	−15	5.66
Weak > B	*ns*					
Weak > T	*ns*					
Areas associated with common semantic processing						
(conjunction analysis of A "B > WEAK" and "T > WEAK")						
Strong > Weak	L inferior/middle frontal gyrus	127	−48	9	30	25.67
	L superior parietal lobe	80	−27	−51	45	24.31
	L fusiform gyrus/inferior occipital gyrus	227	−36	−78	−3	30.03
	R fusiform gyrus/inferior occipital gyrus	153	27	−81	−6	27.16

"B" indicates the strong-constraint semantic context from which a building-related noun is expected, "T" indicates the strong-constraint semantic context from which a tool-related noun is expected, and "Weak" indicates the weak-constraint semantic context.

building-specific activations at the VERBs region were significantly stronger than those at the CONTEXTs region, with Region (VERB vs. CONTEXT) and Condition (STRbuilding vs. STRtool) as independent factors. The results showed that, for both the left PPA and left ant-SMG, there was a significant interaction between Region and Condition, $F(1, 21) = 13.81, p < .001, \eta^2 = .40$, and $F(1, 21) = 9.67, p < .005, \eta^2 = .32$, indicating that the semantic-category-specific PPA/ant-SMG activations were significantly stronger at the VERBs region compared to those at the CONTEXTs region.

Results Time-locked to the Critical Nouns

The whole-brain analysis showed that, first, the STRbuilding condition (vs. STRtool) evoked increased activity in the bilateral PPA, whereas the STRtool condition (vs. STRbuilding) led to increased activity in the ant-SMG



Results of the ROI analysis time-locked to the VERBs

ROIs	left PPA		left ant-SMG		left pMTG		left IFG	
	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$
Building > Tool	4.62	**<.005****	N.A.		N.A.		N.A.	
Tool > Building	N.A.		3.46	**.029***	2.16	.51	.76	1.00
Building > Weak	4.31	**<.005****	−1.59	1.00	1.23	1.00	4.09	**.006****
Tool > Weak	.07	1.00	1.29	1.00	3.08	.07	3.49	**.027***

Figure 3. fMRI Activation pattern resulting from analysis time-locked to the critical verbs (anticipatory process of semantic prediction). (A, B) Results coming from the whole-brain analysis. (C) Results coming from the ROI analysis, with p values being corrected by Bonferroni method by a factor of 12.

and opercularis part of the left IFG. Meanwhile, the STRbuilding condition (compared to the STRtool) additionally evoked increased activity in the left IFG, left medial prefrontal gyrus (extending to the superior frontal gyrus), left anterior superior/middle temporal gyrus [S/MTG], and left TPJ. Second, for both the two contrasts (STRtool vs. WEAK and STRbuilding vs. WEAK) and the conjunction analysis of these two contrasts ("STRtool vs. WEAK" ∩ "STRbuilding vs. WEAK"), a range of areas displayed decreased activity in the strong-constraint conditions compared to the weak-constraint condition, including the left IFG (extending to the middle frontal gyrus), the left medial pFC (mPFC) and superior frontal gyrus, the right IFG, the left S/MTG (consisting of both the anterior and central parts), and the left TPJ (see Figure 4 and Table 5).

For the ROI analysis, the one-way ANOVAs resulted in a significant main effect of Semantic constraint: $F(2, 42) = 9.57, p < .001, \eta^2 = .32$; $F(2, 42) = 14.93, p < .001, \eta^2 = .42$; and $F(2, 42) = 9.24, p < .001, \eta^2 = .31$, for the left PPA, left ant-SMG, and left pMTG, respectively. Further t test analyses found that hemodynamic activity of the left PPA (ROI associated with scene/building processing) significantly increased in the STRbuilding > STRtool contrast, whereas the left ant-SMG (ROI associated with tool processing) showed significant activity increases in the STRtool > STRbuilding contrast. The left pMTG displayed significant activity increases in the STRtool > WEAK contrast and marginally significant activity increases in the STRtool > STRbuilding contrast. The left IFG showed significant activation in none of the three contrasts (STRtool vs. STRbuilding, STRtool vs. WEAK, and STRbuilding vs. WEAK; see Figure 4F).

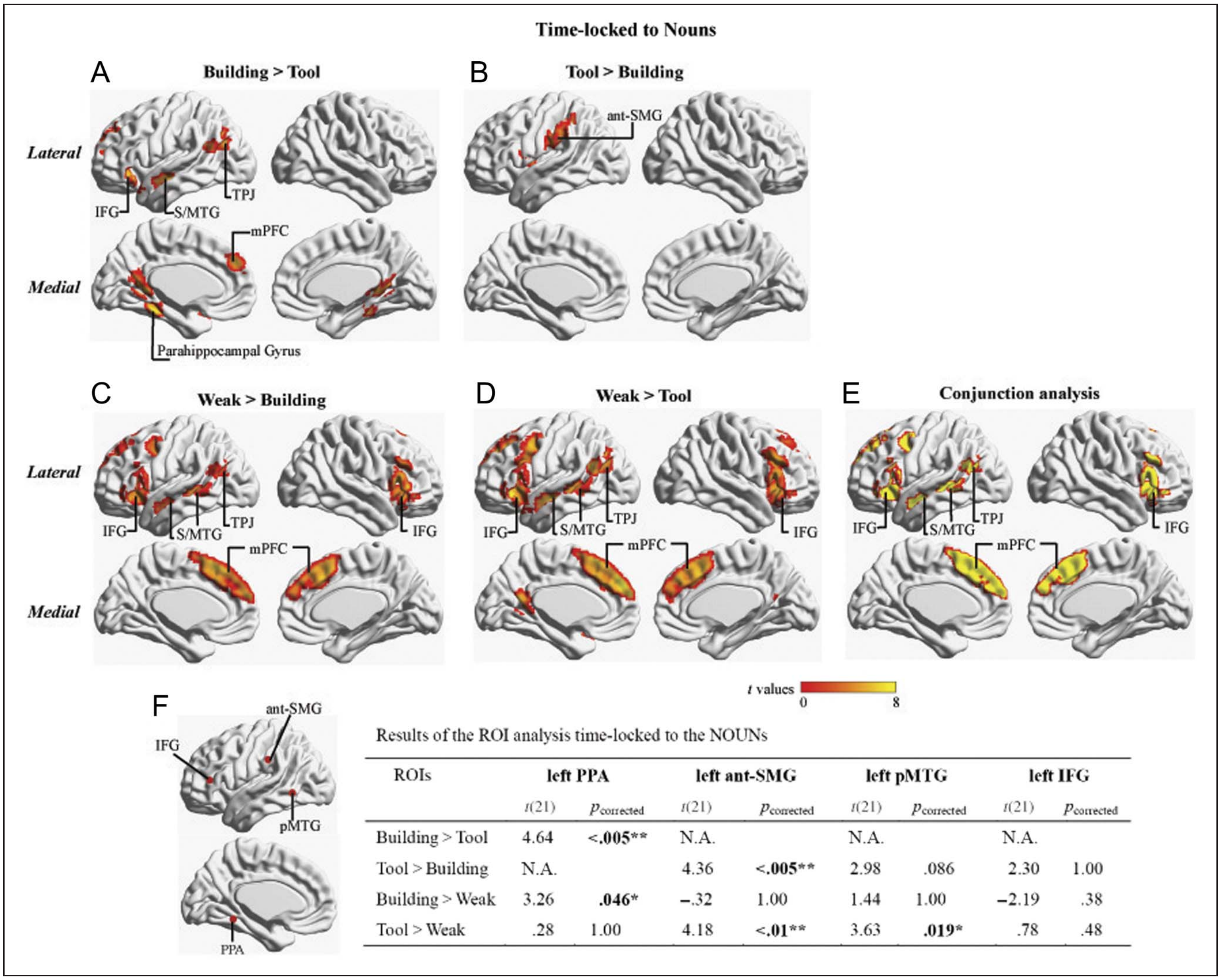
Correlation between the Verb and Noun Semantic-Constraint Effect in the Left IFG

The strong-constraint condition (STRbuilding and STRtool), compared to the weak-constraint condition, induced increased left IFG activity at the critical verbs but decreased left IFG activity at the critical nouns. We

Table 4. Activation Clusters and Increased Activation Peaks for the Whole-Brain Analysis Time-locked to the Critical VERBs

Contrast	*Region of the Peak Voxel*	*Cluster Size (Voxels)*	*MNI Coordinates*			*Peak t Value*
Areas specifically recruited in the representation/processing of buildings						
B > T	L parahippocampal gyrus (PPA)	89	−30	−42	−12	6.06
Areas specifically recruited in the representation/processing of tools						
T > B	*ns*					
Areas associated with the "STRbuilding-versus-WEAK" or "STRtool-versus-WEAK" contrast						
B > Weak	L parahippocampal gyrus (PPA)	99	−33	−39	−15	6.80
T > Weak	*ns*					
Weak > B	*ns*					
Weak > T	*ns*					

"B" indicates the strong-constraint semantic context from which a building-related noun is expected, "T" indicates the strong-constraint semantic context from which a tool-related noun is expected, and "Weak" indicates the weak-constraint semantic context.



Results of the ROI analysis time-locked to the NOUNs

ROIs	left PPA		left ant-SMG		left pMTG		left IFG	
	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$	$t(21)$	$p_{\text{corrected}}$
Building > Tool	4.64	**<.005****	N.A.		N.A.		N.A.	
Tool > Building	N.A.		4.36	**<.005****	2.98	.086	2.30	1.00
Building > Weak	3.26	**.046***	−.32	1.00	1.44	1.00	−2.19	.38
Tool > Weak	.28	1.00	4.18	**<.01****	3.63	**.019***	.78	.48

Figure 4. fMRI Activation pattern resulting from analysis time-locked to the critical nouns (integration process of semantic prediction). (A–E) Results coming from the whole-brain analysis. (F) Results coming from the ROI analysis, with p values being corrected by Bonferroni method by a factor of 12.

Table 5. Activation Clusters and Increased Activation Peaks for the Whole-Brain Analysis Time-locked to the Critical NOUNs

Contrast	*Region of the Peak Voxel*	*Cluster (Voxels)*	*MNI Coordinates*			*Peak t Value*
Areas specifically associated with the representation/processing of buildings						
B > T	L parahippocampal gyrus (PPA)	137	−24	−36	−15	8.23
	L IFG	111	−42	30	−9	7.01
	L medial prefrontal gyrus/superior frontal gyrus	149	−12	48	30	7.36
	L anterior S/MTG	97	−51	−12	−18	7.42
	L TPJ	136	−42	−72	24	6.31
	R parahippocampal gyrus (PPA)	55	24	−33	−18	6.80
Areas specifically associated with the representation/processing of tools						
T > B	L inferior parietal lobe/supramarginal gyrus	124	−60	−33	30	5.59
	L inferior parietal lobe	62	−42	−42	45	4.70
	L IFG (opercularis)	66	−51	3	15	4.98
Areas associated with the "WEAK-versus-STRbuilding" or "WEAK-versus-STRtool" contrast						
Weak > B	L IFG (triangularis)	357	−48	24	−3	6.52
	L middle frontal gyrus	79	−39	3	54	5.83
	L medial prefrontal gyrus/superior frontal gyrus	859	−12	42	45	7.16
	L anterior S/MTG	57	−54	−6	−21	5.34
	L central S/MTG	111	−51	−39	−3	5.79
	L TPJ	97	−45	−57	21	5.37
	R IFG (triangularis)	456	60	18	9	7.15
Weak > T	L IFG (triangularis)	773	−48	33	−6	10.08
	Extending to the anterior middle temporal gyrus		−54	−9	−18	8.13
	L middle frontal gyrus	156	−51	−36	−3	5.84
	L medial prefrontal gyrus/superior frontal gyrus	1090	−12	36	48	11.24
	L central S/MTG	156	−51	−33	−3	6.06
	L TPJ	217	−48	−57	21	7.37
	R IFG (triangularis)	576	42	36	−6	6.79

further examined the relationship between the verb and noun semantic-constraint effect in the left IFG.

We, first, defined the subregion of interest in the left IFG areas (IFG_ROI). At the critical verbs, the IFG_ROI was the same as the one we used in an earlier ROI analysis (i.e., a 6-mm sphere around the MNI coordinates "−42, 32, 16"). At the critical nouns, two IFG_ROIs were defined, with one being the left IFG that showed significant activation in our conjunction analysis at nouns ($\text{IFG}_{\text{wholeCluster}}$) and the one being the Brodmann's areas (BAs) 44 and 45 regions of the left IFG (defined using the WFU PickAtlas toolbox; Maldjian, Laurienti, Kraft, & Burdette, 2003) that displayed significant activation in our conjunction analysis at nouns ($\text{IFG}_{\text{BA44/45}}$; "left BA 44/45" ∩ "left IFG cluster activated at noun conjunction analysis"), as these subregions are considered to play an important role in semantic language processing (e.g., Friederici, 2011; Lauro, Tettamanti, Cappa, & Papagno, 2008; Hagoort, 2005). Second, for each IFG_ROI, the signal changes were extracted for each condition and each participant, and then the semantic constraint effect was calculated ([STRtool + STRbuilding] 0.5-WEAK).

Table 5. *(continued)*

Contrast	*Region of the Peak Voxel*	*Cluster (Voxels)*	*MNI Coordinates*			*Peak t Value*
Areas associated with common semantic integration						
(conjunction analysis of A "WEAK > B" and "WEAK > T")						
Weak > Strong	L IFG (triangularis)	337	−48	33	−6	56.01
	L middle frontal gyrus	78	−39	3	51	47.04
	L medial prefrontal gyrus/superior frontal gyrus	832	−18	30	51	30.87
	L anterior S/MTG	57	−54	−6	−18	39.90
	L central S/MTG	99	−51	−36	−3	31.85
	L TPJ	97	−45	−57	21	36.90
	R IFG (triangularis)	420	48	27	27	25.75

"B" indicates the strong-constraint semantic context from which a building-related noun is expected, "T" indicates the strong-constraint semantic context from which a tool-related noun is expected, and "Weak" indicates the weak-constraint semantic context.

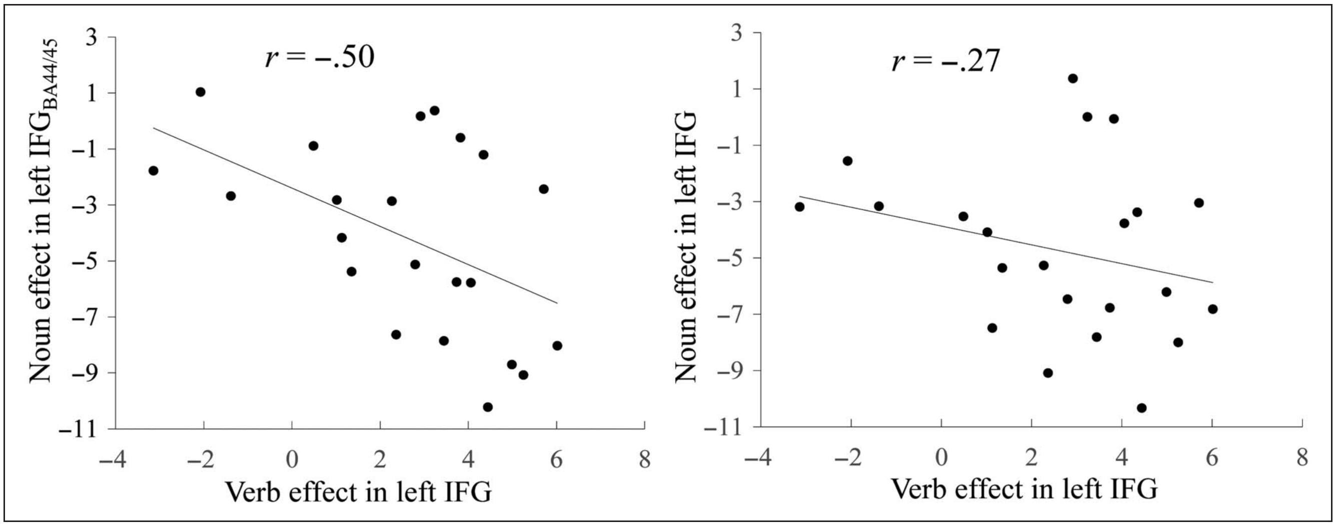


Figure 5. Results of correlation analyses. (A) Significant negative correlation between VERB semantic-constraint effect (in the left IFG_ROI) and NOUN semantic-constraint effect in the left $IFG_{BA44/45}$. (B) The relationship between VERB semantic-constraint effect (in the left IFG_ROI) and NOUN semantic-constraint effect in the left $IFG_{wholeCluster}$.

We performed two-tailed Pearson correlations between the semantic constraint effects at the critical verbs and critical nouns, which were conducted for the two IFG_ROIs at nouns ($IFG_{wholeCluster}$ and $IFG_{BA44/45}$) separately, with p values being Bonferroni corrected by a factor of 2. We found that, for $IFG_{BA44/45}$, the more the left IFG activity increased (strong vs. weak) at the verbs, the more the left IFG activity decreased (strong vs. weak) at the incoming target nouns ($r = -.50$, $p_{corrected} = .038$); for the $IFG_{wholeCluster}$, no significant correlation was found between the verb and noun semantic-constraint effects ($r = -.27$, $p_{corrected} = .45$; Figure 5).

DISCUSSION

This fMRI study examined whether and how the human brain recruits the semantic-category-specific and common cerebral areas to support semantic prediction in sentence comprehension. The major results we found are discussed below. First, distinct brain areas were recruited in the processing of different categories of semantic information both before and after their actual appearance in sentences. Second, a common brain network was found to support the integration processing of the actually perceived target nouns, which included the bilateral IFG, left mPFC, left S/MTG, and left TPJ, with these cortical areas displaying decreased activity in the strong-constraint condition compared to the weak-constraint condition. Finally, during the anticipatory processing of forthcoming nouns, a subset of the left IFG showed increased activity in the strong-constraint (vs. weak-constraint) condition, irrespective of the semantic category of the nouns. These results are discussed in detail below.

Dissociable Neural Regions Specifically Responding to Different Categories of Semantic Information during Sentence Comprehension

One aim of this study was to examine whether the human brain recruits dissociable neural systems to support the anticipatory processing of different categories of semantic information. The whole-brain and ROI analyses, taken together, showed that, not only at the highly predictable critical nouns themselves but also at the critical verbs preceding these nouns, the left PPA area displayed activity enhancement specifically to the STRbuilding condition (STRbuilding > STRtool), whereas the left ant-SMG area displayed activity enhancement specifically to the STRtool condition (STRtool > STRbuilding). It was unlikely that such dissociation of brain areas was driven by lexical property difference unrelated to high-level semantic categories. The reason was that unrelated lexical properties, such as lexical frequency and number of strokes, of the critical nouns were comparable across the three experimental conditions (STRbuilding, STRtool, and WEAK); the critical verbs preceding these nouns were also the same across the three conditions. In fact, the only major difference between the STRtool and STRbuilding conditions was the semantic category (tool vs. building) of the highly predictable target nouns. Meanwhile, an subset of the left PPA has already been found to be specifically associated with building processing (Downing et al., 2006; Epstein et al., 1999; Epstein & Kanwisher, 1998), whereas a subset of the left ant-SMG has already been found to respond distinctly to tool-related processing (Gallivan et al., 2013; Mahon et al., 2007; for review, see Lewis, 2006). Given the above reasons, we feel safe to argue that, both before and after the actual appearance of the target nouns in sentences, the human brain is able to recruit distinct brain areas to support the processing of different categories of semantic information to reach language comprehension.

The building-specific (left PPA) and tool-specific (left ant-SMG) cortical activations observed at the VERBs (before the onset of the target nouns) were significantly stronger than those at the preceding CONTEXTs region of sentences, as indicated by the significant interaction between Condition (STRbuilding vs. STRtool) and Region (VERBs vs. CONTEXTs) for activities of both the left PPA and left ant-SMG. Moreover, neither the building-specific left PPA nor the tool-specific left ant-SMG was found to show significant activation at the CONTEXTs region of sentences, as indicated by the direct comparison between the STRbuilding and STRtool conditions. By taking a comprehensive look at the results, we argued that the semantic-category-specific activations at the critical verbs are not purely because of the retention of already activated information (during the processing of preceding contexts) in working memory but (at least in part) come from the consequence of binding these verbs with their context into a coherent representation. That is, the presence of the critical verbs triggered the combination process to anticipate the semantic content of incoming words, which is in line with the findings of previous ERP studies (Li et al., 2017, 2020).

The neural dissociation of different categories of semantic information became even stronger after the critical nouns appeared in the sentences, as this dissociation was observed in both the whole-brain and ROI analyses, which indicated that the meaning conveyed by these nouns was activated more sufficiently after their actual appearance. In addition, note that we found that, for the tool-specific cortical areas, the left ant-SMG displayed activity enhancement specifically to the STRtool condition (compared to STRbuilding) during both predictive processing and prediction resolution, whereas the pMTG demonstrated a trend of specific activity enhancement to STRtool condition only after the actual presentation of the target nouns. This might be because of the potential different roles of pMTG and ant-SMG in representing tool-related semantics. The existing studies showed that the left pMTG has a prominent role in representing lexical knowledge and visual perceptual features of tools and tool-related actions (Kellenbach, Brett, & Patterson, 2003; Damasio et al., 2001; Chao et al., 1999), whereas the left ant-SMG appears to be more involved in representing the functional meaning of tool-related actions (e.g., grasping/manipulating tools) and in the planning and preparation of movements (Lewis, 2006; Chaminade, Meltzoff, & Decety, 2005; Moll et al., 2000). That is, although both the left pMTG and left ant-SMG are associated with the functional action knowledge of tool, the former is possibly more correlated with lexical and visual perceptual information. In line with these interpretations, the left pMTG, but not the ant-SMG, was consistently found to be activated when participants read isolated words depicting tools (a task more directly related to the lexical processing of tool nouns; Grossman et al., 2002; Phillips, Noppeney, Humphreys, & Price, 2002; Moore & Price, 1999; for a review, see Lewis, 2006). In contrast, in this study, the tool-related nouns are embedded in sentences whose comprehension involves the retrieval and usage of the functional action meaning of tools; it might be that, at the critical verbs, action semantics, but not lexical and perceptual features, were preactivated, hence only the left ant-SMG being specifically activated at these verbs. Despite the specific activation of only the ant-SMG area, it is worth stressing that the present results demonstrated that, during sentence comprehension, before the actual appearance of the target nouns, dissociable cortical regions were recruited selectively in the processing of different categories of semantic information. This category-specific neural dissociation may be related to the successful processing and representation of the corresponding semantic information.

Overall, consistent with the existing neural imaging studies that demonstrated predictive lexical or semantic processing (e.g., Wang et al., 2018; Willems et al., 2016; Fruchter et al., 2015), the semantic-category-specific neural dissociation observed at the transitive verbs of our study indicates that semantic features of upcoming words can be preactivated before their actual appearance in the sentence/discourse context. In fact, previous studies have already found that the human brain has dissociable neural systems being specialized for the processing of different types of semantic categories (e.g., for isolated word/picture processing in Mahon et al., 2007, and Caramazza & Mahon, 2003; general discourse processing in Huth et al., 2016). The preactivation of semantic-category-specific brain regions has also been shown in some recent studies (Grisoni et al., 2017, 2020), as mentioned in the Introduction section. The present results not only are in line with the previous findings but also extend the semantic-category-specific neural dissociation to further more semantic categories. Moreover, this study, by using a high-spatial-resolution fMRI technique, further demonstrates that the subdivisions of cortical semantic network play an important and selective role in both predictive processing and prediction resolution, with the same pattern of neural dissociation (in terms of the main cortical regions and activation/deactivation direction) being involved in these two processes of language comprehension.

The Core Brain Areas Underlying Common Semantic Prediction

First, during the integration processing of the highly predictable target nouns after their actual appearance, widely distributed brain areas were found by this study to support common semantic prediction, as these areas were observed to show significant activity reduction in both the tool-related and building-related strong-constraint conditions (compared to the weak-constraint condition). These common brain areas included not only the bilateral IFG and left S/MTG, which have already been found to be core areas supporting semantic processing (e.g., Hagoort, 2005, 2013; Friederici, 2012; Binder, Desai, Graves, & Conant, 2009), but also other areas such as the left mPFC and left TPJ. Moreover, these cortical areas covered both the anterior and central subsets of the left S/MTG. The above cortical activity reduction (in both building < weak and tool < weak comparisons) is less likely to be driven by unrelated lexical property differences. As described in the Methods section, neither the lexical frequency nor the number of strokes of the critical nouns displayed a significant difference across the three conditions; although the operability (or imageability) of the less-predictable nouns is lower than that of the tool-related nouns, it was higher than (or showed no difference compared to) that of the building-related nouns, which would not lead to the same pattern of cortical activation across the building < weak and tool < weak comparisons. A more reasonable interpretation of the category–common activity reduction is that the semantic integration of these tool- or building-related target nouns was facilitated by preceding sentence contexts, as the only major similarity between the tool and building nouns is that they are both highly predictable than the nouns in the weak-constraint condition.

Specifically, the core language areas, such as the bilateral IFG and left S/MTG, were observed to show activity reduction during the integration processing of the highly predictable nouns. As introduced before, the IFG (specifically the left IFG) has already been considered to be associated with the top–down modulated semantic processing, such as semantic retrieving/selecting (e.g., Thompson-Schill, D'Esposito, & Kan, 1999) or binding (Hagoort, 2005, 2013); the left S/MTG has also been considered to be involved in semantic storage/retrieval (Hagoort, 2005, 2013) or combination (e.g., Friederici, 2012) process. The activity decreases of the left IFG and S/MTG observed in this study suggested that, when processing the highly predictable target nouns, semantic operation processes (such as top–down and bottom–up retrieval of relevant semantic information, suppression of irrelevant information, or binding of related information to form a coherent interpretation) were facilitated by a preceding strong-constraint sentence context. That is, further semantic matching of the predicted information was suppressed (Friston, 2010; Rao & Ballard, 1999). In addition, the left mPFC (extending into the superior frontal cortex) and left TPJ also showed activity reduction to the highly predictable target nouns. Left mPFC and left TPJ have been found to be related to the theory-of-mind process (e.g., see Mar, 2011, and Molenberghs, Johnson, Henry, & Mattingley, 2016, for meta-analyses). The left mPFC and TPJ activity reduction observed in this study, therefore, suggested that the integration process of semantic prediction may involve the mental inference brain areas, with activity in these brain areas being facilitated in the strong-constraint condition. The hemodynamic activity reduction to highly predictable nouns observed in our study is consistent with the findings of previous studies (e.g., Schuster et al., 2016; Weber et al., 2016; Obleser & Kotz, 2010).

Note that, at the critical nouns, the building > tool contrast also showed significant cortical activation in multiple cortical areas (including the left IFG, S/MTG, TPJ, and mPFC) as well as the building-specific PPA. In this study, the lexical/semantic predictability, the number of strokes, and the lexical frequency of the critical nouns all did not show a significant difference between the STRbuilding and STRtool conditions. The cortical activity increases in the STRbuilding (vs. STRtool) condition might be because of the fact that the imageability of the building-related nouns used in our study is lower than that of the tool-related nouns, as previous studies have already shown that abstract nouns with lower imageability tend to induce greater activation in the left temporal and inferior frontal cortex (Hoffman, Binney, & Lambon Ralph, 2015; Sabsevitz, Medler, Sei De Nberg, & Binder, 2005).

Second, at the critical verbs before the onset of the target nouns (anticipatory phase), a subset of the left IFG was found to display activity enhancement in both the STRtool and STRbuilding conditions (compared to the weak-constraint condition), as indicated by the ROI analysis. In our study, the critical verbs and the pronouns immediately preceding these verbs were the same across the three experimental conditions; meanwhile, these verbs and pronouns have a relatively higher level of predictability in the two strong-constraint conditions compared to the weak-constraint condition. The highly predictable words, during sentence or discourse comprehension, have already been found to lead to decreased neural activity (e.g., Schuster et al., 2016; Weber et al., 2016; Obleser & Kotz, 2010). At the encounter of the critical verbs in this study, if the processors were purely engaged in integrating the current words into the preceding sentence context, the strong-constraint condition (vs. weak-constraint) would lead to reduced rather than enhanced hemodynamic activity in the left IFG, which was not consistent with the present result. Instead, the present result is consistent with the expectation of the top–down prediction hypothesis of the predictive coding account (e.g., Rao & Ballard, 1999), as generating top–down prediction needs the corresponding higher-level cortical areas to be activated and is also considered to be metabolically costly (Kuperberg & Jaeger, 2016), hence hemodynamic cortical activity increasing in the highly predictive condition. Given the above reasons, we argued that the IFG activity enhancement observed at the verbs of our study is more likely to be associated with generating the lexical–semantic features of forthcoming critical nouns. That is, a subset of the left IFG is likely to be (at least part of) the core brain area supporting common anticipatory semantic processing during language comprehension.

In addition, a negative correlation was observed between the verb and noun semantic-constraint effects (strong vs. weak constraint) in the left IFG, indicating that the more the IFG activity increased (stronger prediction) at the verbs before noun presentation, the more the IFG activity decreased (greater suppression of confirmed prediction) at the subsequent nouns. This correlation reached significance only when the noun semantic-constraint effect was restricted to the BA 44/45 regions. Although the correlation effect observed in this study is not very strong and needs to be examined further, it is in line with the previous findings that there was a negative correlation between verb and noun N400 effects (strong vs. weak constraint) (Grisoni et al., 2020; Maess et al., 2016). The negative correlation of the verb–noun semantic constraint effects in the left IFG of our study provides additional evidence for our argument that the left IFG activity enhancement during the verb period is associated with the top–down prediction of upcoming nouns.

The existing studies have already found that neural activity in the temporal or frontal lobe, such as the MTG and IFG, increases for the highly predictable words before their actual appearance (e.g., Grisoni et al., 2017, 2020; Willems et al., 2016; Fruchter et al., 2015; Dikker & Pylkkänen, 2013). The left IFG activity enhancement observed at the verbs of this study is generally in line with the previous findings. This study also provides new insights on the neural mechanisms of semantic prediction by showing that the left IFG activity enhancement at the anticipatory phase is not because of the preactivation of a very specific type of semantic information but instead is associated with top–down predictive processing of incoming semantic information irrespective of their specific categories. In addition, the present result further found that the subset of the left IFG that was activated during predictive semantic processing did not display significant activity variation during prediction solution, which indicates that, during language comprehension, the left IFG may have partially dissociable subregions to specifically support predictive processing and prediction resolution.

Third, at the CONTEXTs, several cortical areas (including the left IFG, left SPL, and bilateral fusiform gyrus) displayed activity increases in the strong-constraint conditions (compared to the weak-constrain condition). For the CONTEXTs, not only the contextual constraint but also the contextual words themselves were different across the strong- and weak-constraint conditions. The properties of these contextual words were not strictly controlled, as this study is mainly interested in the results at the critical-verb and critical-noun periods. The activity enhancement effect observed at the CONTEXTs might be related to multiple factors, such as the easiness of lexical processing and follow-up context integration as well as possibly existing anticipatory processing.

The Neural Mechanisms by Which the Human Brain Works to Perform Predictive Semantic Processing in Sentence Comprehension

As mentioned in the Introduction, the predictive coding account proposes that each level of the neural hierarchy attempts to predict the activity at lower levels, and only unpredicted activity (prediction error) at the relatively lower level propagates through the remainder of the processing hierarchy via feedforward connection (Friston, 2005, 2010; Rao & Ballard, 1999). At the encounter of the critical target nouns in this study, the neural activity reduction for the highly predictable nouns in the semantic category–common brain areas (including the left IFG) is line with the assumption regarding the suppressed feedforward propagation of confirmed prediction. Interestingly, this study further found that, different from the semantic category–common areas, the category-specific cortical areas (such as the tool-specific ant-SMG/pMTG and building-specific PPA) displayed increased rather than decreased hemodynamic activity to the highly (vs. less) predictable target nouns. This activity enhancement in the category-specific brain regions for the predicted nouns might reflect the relatively better representation of corresponding semantic information, because of the consequence of preactivation at the preceding verbs and integration processing at the current nouns.

During the anticipatory processing of incoming target nouns (at verbs) in this study, a subset of the higher-level left IFG is found to participate in the predictive processing of incoming lexical–semantic information irrespective of their specific categories. Meanwhile, the relatively lower-level cortical areas displayed dissociable hemodynamic activity enhancement specifically to the corresponding semantic category (e.g., ant-SMG activation specifically for tools and PPA activation specifically for buildings). It is possible that the semantic category–common IFG region (subset of the left IFG) plays an important role in generating top–down predictions, whereas the category-specific brain regions reflect the downstream consequence of the predictive processing conducted in higher-level left IFG. This functional detachment along the cortical hierarchy is consistent with the top–down prediction assumption of the predictive coding account (Rao & Ballard, 1999). Overall, this study not only provides supporting evidence for the predictive coding account but also further demonstrates how the semantic-category-specific and common areas in the cortical hierarchy network work together to support predictive semantic processing and prediction resolution in language comprehension.

Limitation of This Study

Note that, to distinguish the anticipatory and integration processes of semantic prediction, we set a time delay between the first and second subclauses and also between the transitive verb and the critical noun in the second subclause. Although we used such an experimental paradigm to simulate the situations in which someone is waiting for the answer from his or her partner, the relatively long time delay between the transitive verb and the critical noun is still different from that in daily reading comprehension. This long time delay might enable processors to conduct conscious anticipatory processing (Ferreira & Chantavarin, 2018). Despite this speculation, in this study, the neural dissociation of different categories of semantic information observed at the verbs is less likely to be confounded by conscious anticipation induced by the long time delay, as the prediction process was modulated as a short event instead of the whole delay (see also Bonhage et al., 2015). Nevertheless, further studies need to be conducted in other more natural paradigms to validate whether the finding of this study is able to generalize to other language comprehension situations.

Conclusion

To summarize, this study revealed the semantic-category-specific and common brain areas supporting predictive semantic processing and their underlying working mechanisms in language comprehension. Specifically, dissociable cortical areas displayed activity enhancement specifically to different semantic categories of nouns (e.g., ant-SMG for tool-nouns and PPA for building-nouns) both before and after their actual appearance in sentences, indicating the preactivation and resulting representation of the category-specific information. Moreover, a common brain network was found to participate in semantic prediction regardless of the semantic category of the target nouns. During the integration processing of the actually perceived nouns, this common brain network (including the bilateral IFG, left S/MTG, left mPFC, and left TPJ) was found to display decreased hemodynamic activity in the high-prediction condition, indicating reduced further matching of the predicted information (the facilitating effect of semantic prediction). During the anticipatory processing of forthcoming target nouns, the common brain area (i.e., subset of the left IFG) showed increased hemodynamic activity in the highly predictive sentence context, suggesting that predictive semantic processing relies on top–down prediction conducted in higher-level cortical areas. These results not only provide direct neural evidence for the anticipatory nature of semantic processing but also deepen our understanding of the precise neural basis and working mechanisms of semantic processing in sentence comprehension.

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Data Availability

The data set containing the 29 sets of experimental stimuli, the results of the first- and second-level analyses, and the analysis code are available for public download at the following link: data.mendeley.com/datasets/gfvc9crsjv/draft?a=3d8bf568-4f13-4792-8629-2b74072b1850.

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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