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The Role of the Left Inferior Frontal Gyrus in Implicit Semantic Competition and Selection: An Event-Related fMRI Study

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Abstract

Recent research suggests that the left inferior frontal gyrus (LIFG) plays a role in selecting semantic information from among competing alternatives. A key question remains as to whether the LIFG is engaged by the selection of semantic information only or by increased semantic competition in and of itself, especially when such competition is implicit in nature. Ambiguous words presented in a lexical context provide a means of examining whether the LIFG is recruited under conditions when contextual cues constrain selection to only the meaning appropriate to the context (e.g., *coin-mint-money*) or under conditions of increased competition when contextual cues do not allow for the resolution to a particular meaning (e.g., *candy-mint-money*). In this event-related fMRI study, an implicit task was used in which subjects made lexical (i.e., word/nonword) decisions on the third stimulus of auditorily-presented triplets in conditions where the lexical context either promoted resolution toward a particular ambiguous word meaning or enhanced the competition among ambiguous word meanings. LIFG activation was observed when the context allowed for the resolution of competition and hence the selection of one meaning (e.g., *coin-mint-money*) but failed to emerge when competition between the meanings of an ambiguous word was unresolved by the context (e.g., *candy-mint-money*). In the latter case, there was a pattern of reduced activation in frontal, temporal and parietal areas. These findings demonstrate that selection or resolution of competition as opposed to increased semantic competition alone engages the LIFG. Moreover, they extend previous work in showing that the LIFG is recruited even in cases where the selection of meaning takes place implicitly.

Keywords

fMRI; left inferior frontal gyrus; left superior temporal gyrus; semantic ambiguity; semantic competition; semantic selection

1. Introduction

Much current research has focused on the neural systems underlying the ability to attend to one stimulus in the face of multiple competing stimuli (for a recent review, see Kan & Thompson-Schill, 2004a). One prime example of this process occurs during language

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comprehension, where competition takes place at multiple levels of the grammar (e.g., phonetic, phonological, lexical-semantic and syntactic) and must be quickly resolved by the language processing system in order for the intended message to be understood. The goal of the present investigation is to examine the neural substrates of competition and selection during lexical-semantic processing.

Recent neuroimaging evidence suggests that the left inferior prefrontal cortex (LIPFC) may be critically involved in semantic processing. This evidence comes out of research showing that, in addition to posterior brain regions of the left hemisphere, frontal areas also contribute to certain aspects of processing word meaning (Devlin, Matthews, & Rushworth, 2003; Gabrieli et al., 1996; Gabrieli, Poldrack, & Desmond, 1998; Gitelman, Nobre, Sonty, Parrish, & Mesulam, 2005; Poldrack et al., 1999; Roskies, Fiez, Balota, Raichle, & Petersen, 2001). In fact, current theorizing about the LIPFC suggests that this region may play a key role in functions such as the controlled retrieval of semantic knowledge (Badre & Wagner, 2004; Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Gold & Buckner, 2002; Gold, Balota, Kirchoff, & Buckner, 2005; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001), the manipulation of semantic knowledge in explicit tasks (Spitzer et al., 1996), and crucially the selection of semantic information among competing alternatives (Kan & Thompson-Schill, 2004a, b; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill et al., 1998, 2002).

Of primary importance to the present work is the proposal put forth by Thompson-Schill and colleagues (Kan & Thompson-Schill, 2004a, b; Thompson-Schill et al., 1997, 1998, 1999, 2002) that the LIPFC is engaged in the selection of meaning from competing alternatives. Evidence for this hypothesis was originally derived from Thompson-Schill et al. (1997), who, in an fMRI study, varied the demands placed on selection (i.e., high versus low) across three different semantic tasks. In the generation task, subjects covertly generated a verb in response to a visually presented noun which had either many associated verb responses (high selection) or few associated responses (low selection). In the classification task, subjects classified pictures of common objects according to a specific attribute of the object (high selection) or the basic level object name (low selection). Finally, in the comparison task, subjects made comparisons of a target word to several probe words and then decided which probe was most similar in terms of specific attributes (high selection) or global similarity (low selection). In all cases, in the high selection condition, retrieval of object-specific semantic knowledge made available both task-relevant semantic information and task-irrelevant semantic information, such as inappropriate associations or irrelevant features of the object. In contrast, in the low selection condition, all of the retrieved semantic information was task-relevant, either in generating the most dominant association, identifying the name of the object or making a global similarity judgment. Crucially, when comparing the high versus low selection conditions across all three tasks, Thompson-Schill et al. found increased activation in the LIPFC, specifically in the left inferior frontal gyrus (LIFG), for the high selection condition. This result was argued as evidence that this region plays a critical role in the selection of relevant semantic information in the presence of competing information.

While Thompson-Schill et al. (1997) associate LIFG activation with selection, their results are also consistent with an account where increased competition leads to LIFG activation. On the one hand, the high selection condition is also one of high competition, where many semantic properties are accessed and compete for selection. On the other hand, the low selection condition is one of low competition, where few semantic properties are retrieved and compete for selection. Thus, the LIFG activation observed by Thompson-Schill et al. may be due to either increased competition occurring prior to selection or resolution of the competition itself (i.e., selection).

An ideal test case of these alternative interpretations is that of semantically ambiguous words (e.g., *mint: candy/money*), where single lexical items share multiple unrelated meanings. In the psycholinguistic literature, it has been shown that all meanings of an ambiguous word are initially activated and compete for selection, at least for a brief period of time (Onifer & Swinney, 1981; Swinney, 1979). Selection is eventually accomplished by using contextual cues, if available, to constrain the choice to only the meaning appropriate to the specific context (Simpson, 1994). In other words, only one meaning is integrated into the surrounding context and selected for processing. These findings have direct relevance to Thompson-Schill et al.'s proposal, as either competition among multiple unrelated meanings of ambiguous words or integration and ultimate selection of one meaning may recruit left frontal regions, in particular the LIFG.

The results from recent fMRI studies on semantic ambiguity suggest that the LIFG responds to the *resolution* of competition and not simply to the presence of competition inherent in ambiguous words (Chan et al., 2004; Copland et al., 2003; Hoenig & Scheef, 2005; Mason & Just, 2007; Rodd, Davis, & Johnsrude, 2005; Zemleni, Renken, Hoeks, Hoogduin, & Stowe, 2007). In particular, if LIFG activation were merely an index of semantic competition inherent in the stimulus, then ambiguous words outside of a context (i.e., where resolution or selection of a particular meaning cannot take place) should elicit activation in left frontal areas. Findings of two recent studies are inconsistent with this claim (Chan et al., 2004; Copland et al., 2003). In one study, Chan et al. (2004) found that ambiguous words (relative to unambiguous words) yielded increased activation in left mid-superior rather than left inferior frontal regions. Moreover, the only LIFG activation observed in this study was for unambiguous words. In another study, Copland et al. (2003) found *decreased* activation in the LIFG when subordinate (i.e., less frequent) meanings, presumably involving increased competition, were primed. Thus, semantic competition inherent in ambiguous words does not seem to in and of itself engage the LIFG. Rather, having to resolve this competition (i.e., by integrating and selecting one meaning of an ambiguous word) appears to recruit the LIFG.

There are a series of studies that are consistent with the view that the IFG is recruited in processing ambiguous words when meaning competition is resolved (Hoenig & Scheef, 2005; Mason & Just, 2007; Rodd et al., 2005; Zemleni et al., 2007). In one study, Rodd et al. (2005) investigated the role of sentence context in resolving semantic ambiguity by comparing neural responses to sentences containing ambiguity (e.g., *There were dates and pears in the fruit bowl*; ambiguous words underlined for emphasis) and those without ambiguity (e.g., *There was beer and cider on the kitchen shelf*). In one experiment, subjects decided whether a probe word presented after each sentence was related to the meaning of the sentence, whereas in the second experiment, subjects simply listened to the sentences. In both cases, Rodd et al. found increased neural activation in bilateral IFG for ambiguous relative to unambiguous sentences. Taken together, these findings suggest that the LIFG is recruited when the meaning of an ambiguous word is integrated within a sentence context and hence when a particular meaning of an ambiguous word is selected.

The goal of the present study was to further investigate the neural substrates of semantic competition and selection using an event-related fMRI paradigm. In contrast to previous studies which have for the most part used explicit tasks, the current study used an implicit task with semantic ambiguity (e.g., *mint: candy/money*) to examine whether LIFG activation was modulated by competition and/or selection during semantic processing. A semantic priming paradigm was employed, in which subjects were required to make a lexical (i.e., word/nonword) decision on the third stimulus of auditorily-presented triplets in conditions where the lexical context either promoted selection of and resolution toward a particular ambiguous word meaning or enhanced the competition among ambiguous word meanings. In the concordant condition (e.g., *coin-mint-money*), both flanking words were related to the same

meaning of the middle ambiguous word. Although the middle stimulus was semantically ambiguous, the flanking words reduced competition between the ambiguous word meanings and allowed for one meaning to be integrated and ultimately selected. In the discordant condition (e.g., *candy-mint-money*), the flanking words were related to different meanings of the ambiguous word. Thus, the context in which the ambiguous word occurred did not allow for integration and ultimate selection of a particular meaning to take place. In the neutral condition (e.g., *gown-mint-money*), only the final word was related to a particular meaning of the ambiguous word, reducing competition and favoring selection of one meaning but to a lesser extent than the concordant condition. Finally, in the unrelated condition (e.g., *cake-rat-money*), which served as a baseline against which all other conditions were compared to determine the amount of priming, all three words were semantically unrelated. If the LIFG is engaged primarily when the context allows for the resolution toward and hence integration and selection of a particular meaning, then increased activation in this region should be observed in the concordant condition and to a lesser extent the neutral condition relative to the unrelated condition. In contrast, if the LIFG is engaged by competition, then increased activation in this region should be observed in the discordant condition relative to the unrelated condition.

Note that these predictions are different from what one might expect based on previous neuroimaging studies of semantic priming, where related conditions often show decreased neural activation relative to unrelated conditions (Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Rissman, Eliassen, & Blumstein, 2003; Wheatley, Weisberg, Beauchamp, & Martin, 2005; Wible et al., 2006). In contrast to previous studies which used unambiguous word pairs, the present study employed ambiguous word triplets. Processing of these triplets invokes higher-level meaning integration and selection processes (i.e., one meaning must be integrated across a lexical context and ultimately selected), which are not involved in processing unambiguous word pairs. It is therefore highly likely that neural activation patterns in the current study will differ from the patterns previously shown in semantic priming studies using word pairs.

2. Results

Behavioral Data – Pilot Study

Mean RTs for each subject per condition were initially computed after errors and outliers were removed. Outliers were defined as those values greater than 1800 ms, and greater or less than 2 standard deviations from each subjects' mean per condition. A total of 132 responses (6.3% of the data; 34 errors and 98 outliers) were removed prior to conducting the data analysis. Repeated-measures ANOVAs, with the factor of Condition (concordant, discordant, neutral, unrelated), were conducted on the RT and accuracy data (see Table 1). With respect to the RT data, a significant main effect of Condition was observed [$F(3, 42) = 19.55, p < .0001$]. According to Bonferroni-adjusted pairwise comparisons ($p < .05$), RTs in the concordant condition were significantly faster than those in the discordant and unrelated conditions and marginally faster than those in the neutral condition ($p = .087$). In addition, RTs in the neutral condition were significantly faster than those in the discordant and unrelated conditions. RTs in the discordant condition were no different than those in the unrelated condition. With respect to the accuracy data, the main effect of Condition was not significant [$F(3, 42) = 2.15, p = .11$], indicating that subjects' accuracy was similar across the conditions.

Behavioral Data – fMRI Study

Mean RTs for each subject per condition were initially computed after errors and outliers were removed. Outliers were defined as those values greater than 1800 ms, and greater or less than 2 standard deviations from each subjects' mean per condition. A total of 201 responses (9.6% of the data; 90 errors and 111 outliers) were removed prior to conducting the data analysis.

Repeated-measures ANOVAs, with the factor of Condition (concordant, discordant, neutral, unrelated), were conducted on the RT and accuracy data (see Table 2). With respect to the RT data, a significant main effect of Condition was observed [$F(3, 42) = 11.44, p < .0001$]. According to Bonferroni adjusted pairwise comparisons ($p < .05$), RTs in the concordant condition were significantly faster than those in the discordant, neutral and unrelated conditions. RTs in the discordant condition were no different than those in the unrelated condition. With respect to the accuracy data, the main effect of Condition was not significant [$F(3, 42) = 1.95, p = .14$], indicating that subjects' accuracy was similar across the conditions.

Planned Comparisons

Clusters activated at a corrected threshold of $p < .05$ are presented in Table 3. The discussion below will focus on the following planned comparisons: concordant versus unrelated, discordant versus unrelated, neutral versus unrelated, concordant versus discordant, concordant versus neutral, and discordant versus neutral.

Concordant versus Unrelated

A number of significantly activated clusters were found for the contrast of concordant versus unrelated trials. Specifically, three clusters emerged in which there was greater activation in the concordant condition compared to the unrelated condition. The largest of these was a cluster in the posterior portion of the left STG (BA 22), which extended primarily into the left middle temporal gyrus (see Figure 1A left panel). Somewhat smaller clusters were found in the anterior portion (pars triangularis/pars orbitalis, BA 45/47) of the LIFG (see Figure 1A) and the right superior frontal gyrus (SFG; BA 8). For the LIFG cluster, 47% of the voxels were located in pars triangularis (BA 45) and 42% of the voxels in pars orbitalis (BA 47).

In addition, four clusters were found in which there was greater activation for the unrelated than the concordant condition. These clusters emerged in the following areas: the left paracentral lobule (BA 5/7), the left thalamus (medial dorsolateral nucleus), the right superior parietal gyrus (BA 7) and the right fusiform gyrus (BA 37).

Since LIFG activation was predicted to distinguish among our main hypotheses, we directly compared activation across the various conditions in the above-mentioned cluster. To this end, a functional region of interest (ROI) analysis was computed on the percent signal change values obtained for the LIFG cluster (60 voxels). Results are shown in Figure 2. Percent signal change values were entered into a one-way repeated measures ANOVA with Condition (concordant, discordant, neutral, unrelated) as the within-subjects factor. The main effect of Condition was significant [$F(3, 42) = 6.35, p < .001$]. According to Bonferroni adjusted pairwise comparisons ($p < .05$), there was, as expected, a significant difference between the concordant and unrelated conditions. No other comparisons were significant. However, because of the highly conservative nature of the Bonferroni correction, an uncorrected analysis was also conducted to uncover any additional differences. In this less conservative analysis, there was significantly greater activation in both the discordant ($p = .033$) and neutral ($p = .029$) conditions compared to the unrelated condition. In addition, the difference between the concordant and discordant conditions approached significance ($p = .078$).

Discordant versus Unrelated

A comparison of the discordant and unrelated conditions yielded several clusters which were statistically more active for unrelated than discordant trials. These regions included the right SFG (BA 6), the right middle frontal gyrus (MFG; BA 8), the left precentral gyrus (BA 4/6) and the postcentral gyrus bilaterally (BA 40/42). No significant clusters emerged in which there was greater activation for discordant than unrelated trials.

Neutral versus Unrelated

When neutral trials were compared to unrelated trials, a large number of clusters emerged in which there was greater activation for the unrelated than the neutral condition. Among the frontal areas, clusters in the left SFG (BA 10), the left insula and the right MFG (BA 9) were more active for the unrelated than the neutral condition. In the temporal cortex, the only significant cluster to emerge was in the left fusiform gyrus (BA 37). In addition, a number of clusters were found in the parietal cortex (all bilateral), including the postcentral gyrus (BA 3/40), the precuneus (BA 7) and the cingulate gyrus (BA 24/31). Two clusters in the right occipital cortex were also reliably more active for unrelated than neutral trials. These included the right cuneus (BA 18) and the right middle occipital gyrus (BA 19). No regions showed more activation for the neutral compared to the unrelated condition.

Concordant versus Discordant

A comparison of the concordant and discordant conditions yielded two clusters which were reliably more active for concordant than discordant trials. These clusters were centered in the left hemisphere, specifically in the left insula and the left STG (BA 22; see Figure 1B). The left STG cluster was located in the posterior portion of the gyrus, neighboring on the supramarginal gyrus and the angular gyrus (Figure 1B left panel) while the left insula cluster, in close proximity to the LIFG, extended primarily along the STG (Figure 1B right panel). No clusters were found to show more activation for discordant compared to concordant trials.

Concordant versus Neutral

When concordant and neutral trials were compared, two clusters were found to be more active for the concordant than the neutral condition. The largest cluster centered on the right subcallosal gyrus, whereas the other cluster centered on the left STG (BA 22; see Figure 1C), which again was restricted to the posterior extent, in close proximity to the supramarginal gyrus. No regions exhibited greater activation for neutral than concordant trials.

Discordant versus Neutral

When the discordant and neutral conditions were compared, one significant cluster emerged in which there was more activation for discordant than neutral trials. This cluster was centered in the left precuneus (BA 31). No clusters emerged in which there was greater activation for the neutral than the discordant condition.

3. Discussion

Behavioral Findings

Similar to previous results (Hagoort, 1993; Milberg, Blumstein, & Dworetzky, 1987; Schvaneveldt, Meyer, & Becker, 1976), RTs in the concordant condition were faster than those in all other conditions. This finding indicates that when the lexical context allows for the resolution of ambiguity and the selection of one meaning, fewer computational resources are required. In contrast, RTs in the discordant condition, where subjects had to switch from the preferred (i.e., dominant) meaning of the ambiguous word to the less-preferred (i.e., subordinate) meaning, were much slower and crucially showed no semantic priming, as indicated by a lack of difference in RTs between the discordant and unrelated conditions. The fact that priming was lost in the discordant condition suggests that selection processes failed in the discordant triplets, and that neither the subordinate nor dominant meaning of the ambiguous word was selected. It should be noted that, as expected, the above-mentioned effects only emerged in the RT data and not in the accuracy data. The lack of accuracy effects is consistent with previous work using the triplet priming paradigm (Hagoort, 1993; Milberg et al., 1987; Schvaneveldt et al., 1976).

An unexpected aspect of the behavioral results was that RTs in the neutral condition were no different than those in the discordant condition. Given that there was a difference between these two conditions in the pilot study, this result was somewhat surprising. Particularly noteworthy was that subjects in the fMRI experiment made the most errors in the neutral condition, whereas subjects in the pilot study made the most errors in the discordant and unrelated conditions, a more expected pattern. It is possible that in the fMRI experiment, the larger number of errors in the neutral condition reduced the data contributing to the RT analysis (which used only correct responses) allowing a few scores to artificially increase the mean RT latencies.

Neuroimaging Findings

The main goal of the present study was to explore whether the LIFG is engaged by increased semantic competition per se or by the resolution of such competition (i.e., integration and selection of a meaning). The present findings suggest that the presence of competition alone, as in the discordant condition, is not sufficient to produce increased LIFG activation. Relative to the unrelated condition, the discordant condition showed *reduced* activation in frontal and parietal areas, including the right SFG, right MFG, left precentral gyrus, and the bilateral postcentral gyrus. Nonetheless, the results are consistent with the hypothesis that LIFG activation is driven by semantic selection. Activation of the LIFG and neighboring regions (left insula) was only observed in cases where selection of a particular meaning of the ambiguous word could take place. Specifically, the LIFG showed greater activation for the concordant than the unrelated condition. Crucially, this contrast is the only one where the lexical context allows for the resolution of competition and the selection of one meaning. With respect to the neutral condition, although the cluster analysis did not reveal increased left frontal activation, results of the ROI analysis showed that activation in the neutral condition fell between that of the concordant and discordant conditions. Although not all conditions were significantly different from each other, the neutral condition showed greater activation than the discordant condition and less activation than the concordant condition (i.e., concordant > neutral > discordant). This data provides evidence that the lexical context of the neutral condition allowed for resolution or meaning selection to take place, although not to the same extent as in the concordant condition. Meaning integration and eventual resolution could have been more difficult or incomplete in the neutral condition because of the presence of the initial word that was unrelated in meaning to the ambiguous word. Of further importance, when comparing the concordant and neutral conditions, where selection could be argued to take place in either case, no LIFG activation was observed.

It may at first seem surprising that the concordant condition showed greater neural activation than the other conditions, given the many studies on repetition and semantic priming which have found reduced neural activation associated with behavioral priming, often referred to as repetition suppression (Buckner, Koutstaal, Schacter, & Rosen, 2000; Demb et al., 1995; Gabrieli et al., 1996; Raichle et al., 1994). Based on these studies, one might have expected that the concordant condition would exhibit the least amount of neural activation. However, there are now several studies which have found increased activation (i.e., repetition enhancement) associated with semantic priming (Copland, de Zubicaray, McMahon, & Eastburn, 2007; Kotz, Cappa, von Kramon, & Friederici, 2002; Raposo, Moss, Stamatakis, & Tyler, 2006; Rossell, Bullmore, Williams, & David, 2001; Rossell, Price, & Nobre, 2003). Interestingly, in a recent study with ambiguous word stimuli similar to those used in the present experiment, Copland et al. (2007), using a long 1000 ms ISI, found increased neural activation in the LIFG for pairs related to the dominant meaning of an ambiguous word. They argued that this increased neural activation reflected successful semantic integration of the target with the ambiguous prime (i.e., selection of a particular meaning). Although the ISI in the current study was shorter (100 ms), at least 1000 ms had elapsed before subjects made a lexical decision on the third stimulus of each triplet. Following the argument put forth by Copland et al. (2007),

it may be that meaning integration and selection processes underlie the increased activation observed in the concordant condition.

While increased neural activation was associated with semantic priming in the concordant condition, there is some evidence from the present study for reduced activation associated with semantic priming. Although previous studies have examined semantic priming using stimulus pairs rather than triplets, comparison of the activation patterns in the neutral and unrelated conditions provides a means of assessing potential semantic priming effects. Although the first stimulus in these conditions is semantically unrelated to the following two stimuli, the last two stimuli are either semantically related (neutral condition) or semantically unrelated (unrelated condition). Thus, the neutral condition is most similar to the related conditions of previous fMRI studies, in which pairs of semantically-related words (e.g., *dog-cat*) have typically been used as stimuli. Relative to the unrelated condition, the neutral condition showed reduced activation in a large number of cortical sites, most notably the left SFG, left insula, right MFG, right inferior temporal gyrus (ITG) and the postcentral gyrus, precuneus and cingulate bilaterally. The finding of reduced neural activation for the neutral condition of the current study replicates what has been observed in a number of previous studies (Copland et al., 2003; Giesbrecht, Camblin, & Swaab, 2004; Matsumoto et al., 2005; Rissman et al., 2003; Tivarus, Ibinson, Hillier, Schmalbrock, & Beversdorf, 2006; Wheatley et al., 2005; Wible et al., 2006). Moreover, the areas in which these reductions were observed overlap highly with those previously noted, including frontal (superior, middle, and inferior) and temporal (superior, middle, and inferior) regions as well as the cingulate cortex.

Returning to our discussion of the role of the LIFG, results of the current study are consistent with the work of Thompson-Schill and colleagues (Kan & Thompson-Schill, 2004a, b; Thompson-Schill et al., 1997, 1998, 1999, 2002). As such, the findings provide further evidence for a role of the LIFG in performing selection in the face of competing semantic information. The present data extends the Thompson-Schill findings by showing that LIFG activation is observed only under conditions where one of the multiple meanings of an ambiguous word can be ultimately integrated and selected. By contrast, LIFG activation does not emerge under conditions where both meanings are competing with each other but where the context does not allow for the resolution and hence selection of one meaning. Importantly, these findings also demonstrate that LIFG activation can be observed even in cases where selection is assumed to take place implicitly. In Thompson-Schill's previous work, explicit tasks were used. Thus, subjects were required to evaluate the semantic properties of the stimuli, and as a result, were highly aware of the dimension along which the stimuli were competing. In fact, the selection of a response crucially hinged on the explicit manipulation of the semantic attributes of the stimuli. By comparison, the implicit lexical decision task used in the current study, though presumably tapping lexical-semantic representations, did not require explicit evaluation of semantic knowledge, as it was irrelevant to making a word/nonword decision.

There is no disputing that access to semantic knowledge occurs with the lexical decision task. Semantic priming is consistently observed for both ambiguous and unambiguous words in behavioral studies using this task. Moreover, previous neuroimaging studies investigating semantic priming using a lexical decision task have found activation in semantic processing areas, including the left STG and less consistently the LIFG (Matsumoto et al., 2005; Rissman et al., 2003; Wible et al., 2006). In sum, the present findings add to the growing literature emphasizing a role for the LIFG in semantic selection. Moreover, these data indicate that the LIFG is also engaged in cases of implicit semantic selection (see also Bilenko, Grindrod, Myers, & Blumstein, in press).

Additional support for the idea that the principal function of the LIFG is to perform selection comes from findings of recent neuropsychological studies of patients who have left frontal

brain damage including the LIFG (Bedny, Hulbert, & Thompson-Schill, 2007; Metzler, 2001; Milberg et al., 1987). These studies are particularly relevant as many of them have employed the same paradigm as the one used in the current fMRI study. For instance, Milberg et al. (1987) have shown that Broca's aphasic patients exhibit no semantic priming in a behavioral version of the current experiment. Specifically, these patients show no significant difference between RTs in the concordant, discordant, neutral, and unrelated conditions. By comparison, age-matched control subjects show the expected garden-path (i.e., reduced) priming effect in the discordant condition and larger priming effects in both the concordant and neutral conditions. More recently, Bedny et al. (2007) have shown that patients who have lesions confined to the LIFG do not exhibit the typical RT difference between the concordant and discordant conditions (i.e., faster RTs in the concordant condition relative to the discordant condition). This pattern of performance is in stark contrast to that of the two control groups, age-matched individuals and patients with lesions to frontal regions other than the LIFG, both of whom produce faster RTs to trials in the concordant condition. The common theme across these studies is that patients with LIFG damage seem to lose the RT advantage in the concordant condition, which results in a loss of semantic priming or RTs in the concordant condition being no faster than those in the discordant condition. Combined with the present neuroimaging data, these findings point to a critical role of the LIFG in selecting ambiguous word meanings.

Indeed, there is no question that the LIFG is recruited in selecting contextually-appropriate meanings of ambiguous words. Several recent fMRI studies of the processing of ambiguous words in sentence contexts have shown increased LIFG activation when ambiguity is resolved by the sentence context. In particular, both Zemplini et al. (2007) and Mason and Just (2007) showed increased activation in a bilateral network including the LIFG when the meaning of an ambiguous word presented early in the sentence was resolved at the end of the sentence toward the subordinate (i.e., less frequent) meaning of the ambiguous word.

Finally, the results of this study confirm the importance of the left STG in semantic processing. While no a priori assumptions were made regarding activation in the left STG, it is interesting that this region was consistently activated across all comparisons involving the concordant condition. Given that the left STG has been implicated across a wide range of semantic tasks in previous neuroimaging studies (e.g., Price, Moore, Humphreys, & Wise, 1997; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996), it is not surprising that activation was observed in this area.

4. Conclusion

Results of the present study suggest that the LIFG is not recruited simply by the presence of competition inherent in ambiguous words, but rather that it is recruited only when the competition is resolved by the context and hence when selection of a particular meaning takes place. While the present data lend further support to the hypothesis that the LIFG contributes to the selection of semantic information from among competing alternatives, they also extend this proposal to cases where selection takes place implicitly.

5. Methods

Participants

Fifteen native speakers of English (8 females; aged 19–29 years, mean = 22 ± 3.1 years) participated in the study. All participants were strongly right-handed, as confirmed by the administration of the Edinburgh Handedness Inventory (Oldfield, 1971). Informed consent was obtained in a manner approved by the Human Subjects Committees of Brown University and Memorial Hospital of Rhode Island. All participants were familiarized with the scanner, the

fMRI procedure and the experimental task before the study began. In addition, participants received monetary compensation for their time and effort.

Task Design

On each experimental trial, participants listened to three stimuli presented in succession (see Figure 3 for an illustration of the task and the Appendix for a full list of stimuli). Within a trial, each stimulus was separated by a 100 ms interstimulus interval (ISI). All trials were jittered in increments of 905 ms (= TR/4), as determined by a design optimization algorithm (Dale, 1999). This method resulted in seven distinct trial onset asynchrony (TOA) values, ranging from 3620 to 9050 (in 905-ms steps). Participants were required to make a yes/no decision as to whether the third stimulus of each triplet was a word or not (i.e., lexical decision). They were to indicate their response by pressing one of two buttons as quickly and accurately as possible using their right hand.

Materials

The experimental materials were 35 ambiguous words with a highly dominant meaning. The degree of dominance of the stimuli (> 85%, mean frequency: 93%) was determined from available norms in which frequency counts for the various meanings of ambiguous words were provided (Twilley, Dixon, Taylor, & Clark, 1994). In these norms, dominance was computed by asking subjects to give an associate of a particular word and percent response related to a particular meaning was determined. Semantic associates of the dominant and subordinate meanings of the stimuli were taken from Nelson, McEvoy, and Schreiber (1998). For each ambiguous word, the following conditions were constructed: concordant (e.g., *coin-mint-money*), discordant (e.g., *candy-mint-money*), neutral (e.g., *gown-mint-money*) and unrelated (e.g., *cake-rat-money*). The ambiguous words were always resolved toward the subordinate (i.e., less preferred) meaning. In the concordant condition, both associates were consistent with the subordinate meaning. Hence, the lexical context presumably reduced competition between the meanings of the ambiguous word and allowed for the resolution and ultimate selection of one meaning appropriate to the context. In the discordant condition, a garden-path effect was created, such that the initial presentation of a dominant-meaning associate followed by the related ambiguous word required a switch from the preferred to the less preferred interpretation with the presentation of the subordinate-meaning related target word. In this case, the lexical context led to increased competition between the two meanings and did not allow for the selection of one meaning. In the neutral condition, the first word was unrelated to either meaning of the middle ambiguous word, while the target word was related to the subordinate meaning. Thus, the lexical context in this condition reduced competition, although not to the same extent as in the concordant condition, and allowed for resolution and ultimate selection of the contextually-appropriate subordinate meaning. Finally, in the unrelated condition, which served as a baseline, none of the words were related. Across conditions, the first words of each triplet were matched in terms of lexical frequency, as confirmed by a non-significant ANOVA [$F(3, 102) = .235$, ns]. The unambiguous middle word in the unrelated condition was also matched for frequency with the ambiguous word that occurred in all other conditions [$t(34) = .699$, ns]. In addition, an equal number of filler trials were constructed, half of which contained an ambiguous word and the other half, an unambiguous word. These trials all ended in a pronounceable nonword, which was matched to the word targets for duration [$t(34) = .383$, ns].

Five stimulus sets containing seven stimuli from each condition were created such that the same ambiguous word was not repeated within a set. Trials within each set were pseudo-randomized, with the restriction that no more than three word or nonword targets were presented in succession. All stimuli were recorded by a male speaker of American English and

digitized at a sampling rate of 22050 Hz directly into a Dell desktop computer using the Brown Lab Interactive Speech System (BLISS) software (Mertus, 2000).

Pilot Study

The experiment was initially piloted on a separate groups of participants ($n = 15$) who did not take part in the fMRI study. Materials and procedures were identical to those employed in the fMRI study with the exception that the stimuli were not presented in a jittered manner. The pilot study was conducted to establish that semantic priming effects were indeed modulated by the various conditions in which the ambiguous words were presented.

Data Acquisition

Auditory stimuli were presented through MR-compatible headphones (Resonance Technologies, Inc.). Participants performed 280 experimental trials over the course of five 6-minute event-related fMRI runs. Trials from a particular condition were distributed evenly across the runs. The order of the trial types within each run was fixed. Order of the runs was counterbalanced across subjects, such that each subject received a unique order. This permutation was done to ensure that each subject had an equal chance of initially receiving an ambiguous word in any one of the four experimental conditions, rather than each subject always receiving the same ambiguous word in the same condition first. Participants' reaction time (RT) and accuracy were recorded by a Dell laptop computer. RT was recorded from the onset of the third stimulus. Mapping of the button (left/right) and response (yes/no) was counterbalanced across subjects. In addition, all subjects completed a practice test of 10 trials during acquisition of the MPRAGE dataset.

Scanning was performed on a 1.5T Siemens scanner using a standard whole-head coil. Each session began with the acquisition of a high-resolution MPRAGE anatomical sequence (TR = 1900 ms, TE = 4.15 ms, TI = 1100 ms, 1-mm isotropic voxels, 256 mm field of view). Functional data were acquired using a gradient-echo echo-planer pulse sequence (TR = 3620 ms, TE = 38 ms, 45 axial slices, $3 \times 3 \times 3$ mm, 103 volumes per run).

fMRI Data Analysis

Image preprocessing and statistical analyses were performed using AFNI (Cox, 1996; <http://afni.nimh.nih.gov/afni>). For the functional data, the first 4 volumes of each run were discarded to ensure that steady state magnetization was reached. The remaining data were corrected for differences in timing of slice acquisition, followed by a six-parameter rigid-body transformation for motion correction (Cox & Jesmanowicz, 1999). Structural and functional volumes were spatially normalized to Talairach and Tournoux (1988) space. In addition, functional volumes were spatially smoothed with a 6-mm Gaussian filter (FWHM).

Statistical analyses were performed using the general linear model in AFNI. The fMRI time series data were convolved with a canonical hemodynamic response function (HRF). The resulting functions were used as covariates in the general linear model. The model included separate covariates for each of six different trial types: correctly performed trials from the five experimental conditions (i.e., concordant, discordant, neutral, unrelated, nonword) and trials in which participants were incorrect (i.e., word errors, nonword errors). Covariates consisting of the six realignment parameters (three rotational, three translational) from each session were also included in the model to remove any residual movement-related variance. The raw fit coefficients output by the model were converted to percent signal change by dividing the coefficient from each voxel by the baseline for that voxel (i.e., mean for that voxel across the entire experiment).

The percent change values for each condition (excluding the two error conditions) and each participant were entered into a two-way, mixed-factor ANOVA, with stimulus condition as the fixed factor and participant as the random factor. Six planned contrasts were then carried out: concordant versus discordant, concordant versus neutral, concordant versus unrelated, discordant versus neutral, discordant versus unrelated and neutral versus unrelated. A voxel-level threshold of $p < .025$ and a cluster-level threshold of 51 contiguous 3 mm^3 voxels were adopted, which, on the basis of Monte Carlo simulations, yielded a corrected threshold of $p < .05$. The atlases used to locate anatomical structures were the Anatomy Toolbox atlases (Amunts et al., 1999; Eickhoff et al., 2005).

In addition to the above-mentioned statistical analyses, Region of Interest (ROI) analyses were performed on left frontal areas (LIFG and neighboring regions) where significant clusters emerged. For each ROI, percent signal change values were obtained for each subject and experimental condition (concordant, discordant, neutral, unrelated). A repeated-measures analysis of variance (ANOVA) was performed on subject and condition means for each ROI.

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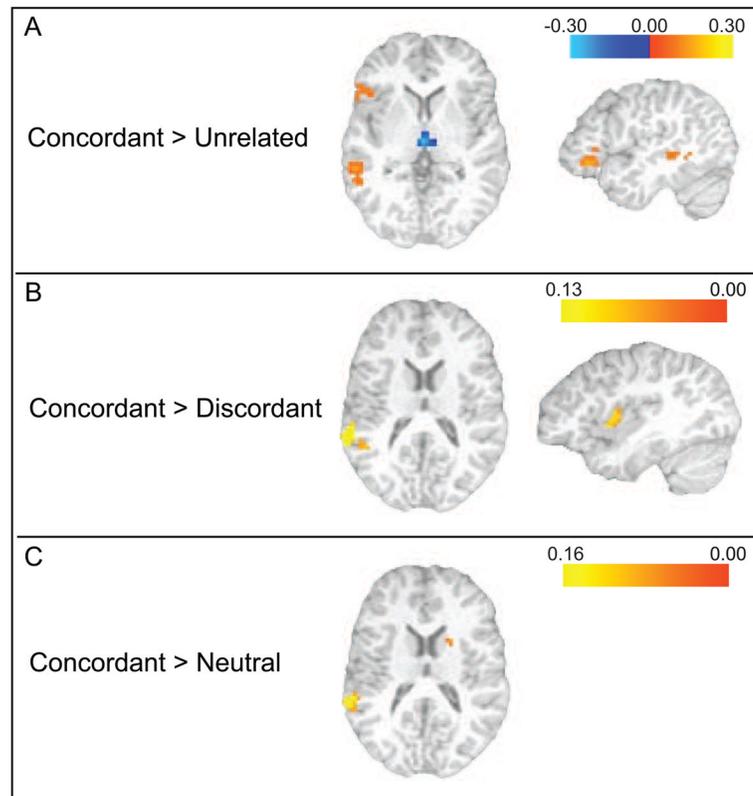


Figure 1.

A) Concordant more active than unrelated condition. Left panel: The locations of the left inferior frontal gyrus and left superior temporal gyrus clusters in an axial slice ($z = 5$). Right panel: The location of the left inferior frontal gyrus cluster in a sagittal slice ($x = -46$). B) Concordant more active than discordant condition. Left panel: The location of the left superior temporal gyrus cluster in an axial slice ($z = 17$). Right panel: The location of the left insula cluster in a sagittal slice ($x = -37$). C) Concordant more active than neutral condition. The location of the left superior temporal gyrus cluster in an axial slice ($z = 17$).

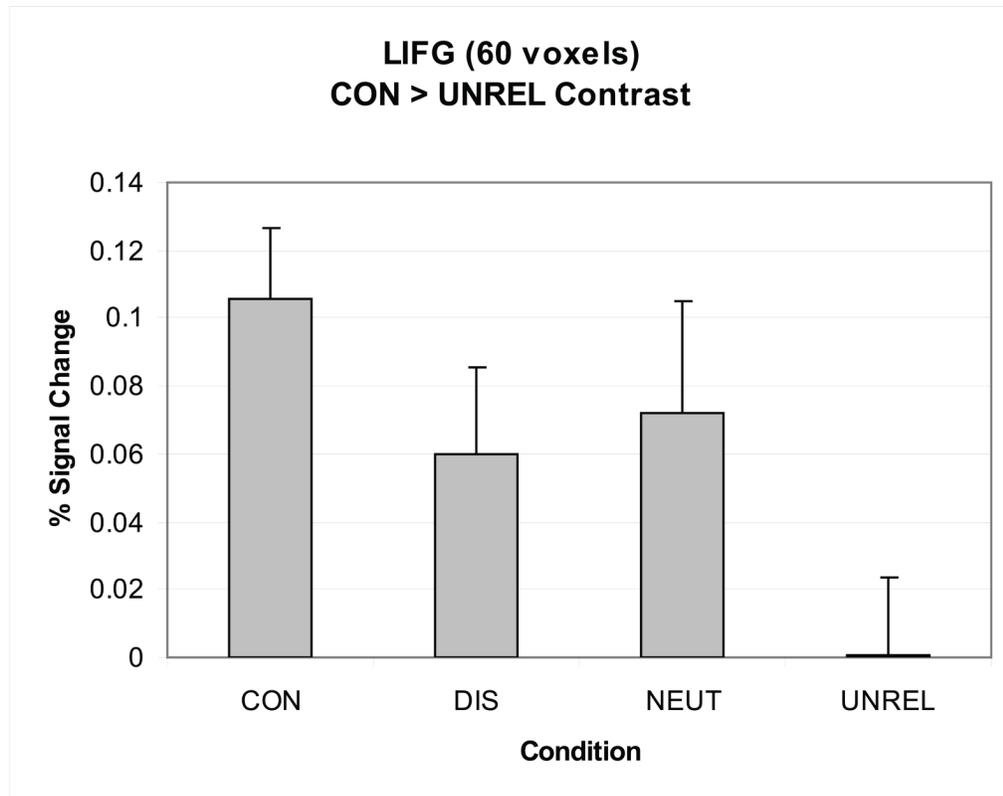


Figure 2. Results of the ROI analysis. Mean percent signal change for each experimental condition extracted from the LIFG cluster from the contrast of the concordant and unrelated conditions.

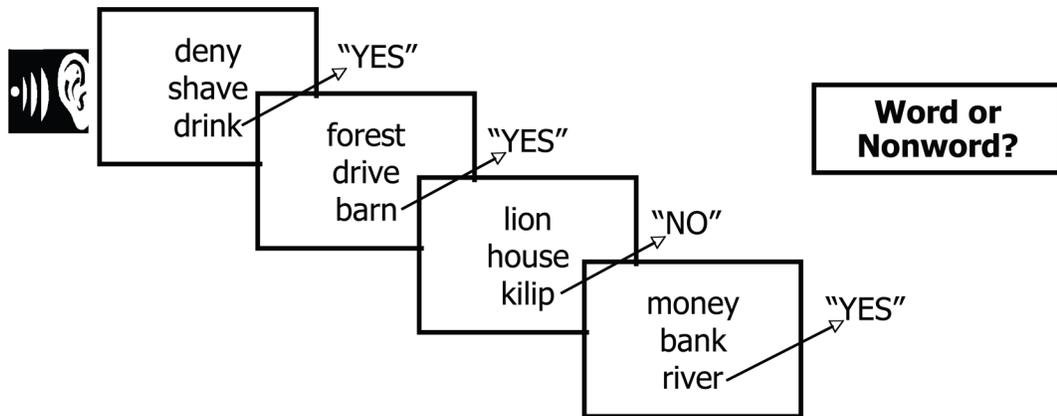


Figure 3. The triplet priming task. Within a trial, each stimulus was auditorily presented with 100 ms between stimuli. Subjects made a lexical (i.e., word/nonword) decision on the third stimulus.

Table 1

Behavioral data from the pilot study (n = 15). Mean RT (ms) and mean accuracy (% correct) with standard deviations (SD) for all experimental conditions

| | Concordant | Discordant | Neutral | Unrelated |
|-----------|-------------------|-------------------|----------------|------------------|
| RT | 794 | 846 | 813 | 837 |
| SD | (70) | (69) | (58) | (63) |
| % Correct | 99.4 | 97.5 | 98.9 | 97.7 |
| SD | (1.2) | (4.0) | (2.4) | (2.2) |

Table 2

Behavioral data from the fMRI study (n = 15). Mean RT (ms) and mean accuracy (% correct) with standard deviations (SD) for all experimental conditions

| | Concordant | Discordant | Neutral | Unrelated |
|-----------|-------------------|-------------------|----------------|------------------|
| RT | 828 | 878 | 862 | 881 |
| SD | (112) | (140) | (120) | (122) |
| % Correct | 97.0 | 95.2 | 94.5 | 96.2 |
| SD | (3.8) | (6.0) | (6.4) | (2.8) |

Table 3
Areas exhibiting significant activation differences in planned comparisons, thresholded at voxel level $p < .025$, cluster level $p < .05$ (\geq 51 contiguous voxels)

| Condition | Region | # Voxels | BA | x | y | z | t-value |
|-------------------------|----------|----------|-------|-----|-----|------|---------|
| Concordant > Discordant | Frontal | 64 | - | -37 | 2 | 8 | 4.19 |
| | Temporal | 84 | 22 | -58 | -37 | 17 | 3.79 |
| | Frontal | 70 | 34 | 17 | -13 | 5 | 2.75 |
| | Temporal | 67 | 22 | -58 | -40 | 17 | 4.26 |
| Concordant > Unrelated | Frontal | 60 | 45/47 | -46 | 29 | -4 | 3.59 |
| | | | | | | | |
| Unrelated > Concordant | Temporal | 68 | 8 | 5 | 41 | 47 | 2.67 |
| | Temporal | 72 | 22 | -55 | -37 | 5 | 5.15 |
| | Temporal | 51 | 37 | 29 | -52 | -10 | 3.22 |
| | Parietal | 135 | 5/7 | -1 | -46 | 59 | 2.56 |
| Discordant > Neutral | | 102 | 7 | 32 | -52 | 56 | 3.58 |
| | n/a | 56 | - | -1 | -16 | 2 | 3.44 |
| | Parietal | 51 | 31 | -1 | -67 | 23 | 3.09 |
| | Frontal | 214 | 6 | 2 | 2 | 65 | 2.73 |
| Unrelated > Discordant | | 71 | 8 | 32 | 29 | 41 | 3.13 |
| | Parietal | 66 | 4/6 | -37 | -16 | 62 | 3.17 |
| | | 230 | 40 | -64 | -22 | 17 | 4.10 |
| | | 55 | 42 | 62 | -13 | 14 | 3.26 |
| Unrelated > Neutral | Frontal | 61 | 10 | -10 | 59 | 5 | 2.45 |
| | | 98 | - | -40 | -19 | 11 | 4.29 |
| | | 84 | 9 | 32 | 38 | 35 | 4.72 |
| | Temporal | 75 | 37 | 26 | -52 | -10 | 3.22 |
| Temporal | Parietal | 121 | 40 | -64 | -25 | 17 | 3.46 |
| | | 106 | 7 | -10 | -79 | 44 | 3.11 |
| | | 77 | 7 | -4 | -49 | 44 | 3.94 |
| | | 62 | 24 | -1 | 2 | 35 | 3.46 |
| Occipital | | 52 | 7 | 20 | -67 | 50 | 3.11 |
| | | 99 | 31 | 5 | -34 | 44 | 3.57 |
| | | 76 | 3 | 59 | -22 | 38 | 3.23 |
| | | 51 | 18 | 2 | -70 | 20 | 3.33 |
| | 68 | 19 | 41 | -76 | 20 | 2.53 | |

Note. Coordinates, indicating the maximum intensity voxel for each cluster, are in Talairach and Tournoux space. L = left, R = Right.

BA = Brodmann's area.

| Homonym | Concordant | Appendix Discordant | Neutral | Unrelated |
|---------|-------------------------|------------------------|-----------------------|----------------------|
| arms | weapons-arms-guns | legs-arms-guns | motors-arms-guns | shelters-towns-guns |
| ball | music-ball-dance | round-ball-dance | window-ball-dance | market-blood-dance |
| bank | shore-bank-river | cash-bank-river | throat-bank-river | troop-wash-river |
| bluff | cliff-bluff-hill | fake-bluff-hill | wool-bluff-hill | duke-script-hill |
| boil | sore-boil-blister | kettle-boil-blister | robe-boil-blister | tin-wipe-blister |
| calf | leg-calf-muscle | baby-calf-muscle | song-calf-muscle | mouth-vine-muscle |
| duck | crouch-duck-avoid | goose-duck-avoid | choke-duck-avoid | scan-frown-avoid |
| fast | famine-fast-starve | swift-fast-starve | sofa-fast-starve | canal-loan-starve |
| fleet | nimble-fleet-swift | ship-fleet-swift | festive-fleet-swift | potent-tub-swift |
| hamper | impede-hamper-stop | laundry-hamper-stop | refine-hamper-stop | sever-treasure-stop |
| hide | skin-hide-cow | mask-hide-cow | tube-hide-cow | fruit-drug-cow |
| jam | traffic-jam-stuck | grape-jam-stuck | credit-jam-stuck | talent-cab-stuck |
| jar | jolt-jar-shake | lid-jar-shake | moan-jar-shake | sob-dot-shake |
| loaf | laze-loaf-relax | bread-loaf-relax | tint-loaf-relax | stomp-drape-relax |
| mint | coin-mint-money | candy-mint-money | gown-mint-money | cake-rat-money |
| net | gain-net-worth | fish-net-worth | farm-net-worth | dog-chill-worth |
| page | summon-page-call | paper-page-call | distort-page-call | detach-swing-call |
| pen | pig-pen-cage | ink-pen-cage | choir-pen-cage | lamb-map-cage |
| prune | bush-prune-cut | fruit-prune-cut | tent-prune-cut | wrist-pave-cut |
| racket | loud-racket-noise | tennis-racket-noise | shy-racket-noise | ripe-luggage-noise |
| rank | smell-rank-odor | captain-rank-odor | stone-rank-odor | knee-proud-odor |
| rash | careless-rash-hasty | skin-rash-hasty | vacant-rash-hasty | sticky-dense-hasty |
| riddle | puncture-riddle-bullets | joke-riddle-bullets | invert-riddle-bullets | dilate-query-bullets |
| sage | smart-sage-wise | spice-sage-wise | stiff-sage-wise | brave-blank-wise |
| sock | slap-sock-hit | shoe-sock-hit | dwelt-sock-hit | knit-mock-hit |
| sound | secure-sound-sturdy | noise-sound-sturdy | formal-sound-sturdy | busy-friend-sturdy |
| staple | bread-staple-food | attach-staple-food | bride-staple-food | bench-riot-food |
| steep | simmer-steep-brew | slope-steep-brew | torture-steep-brew | defy-gaze-brew |
| story | level-story-floor | fiction-story-floor | mother-story-floor | method-nature-floor |
| strand | island-strand-alone | string-strand-alone | product-strand-alone | pressure-boast-alone |
| strip | narrow-strip-paper | undress-strip-paper | constant-strip-paper | quiet-bind-paper |
| tire | yawn-tire-weary | flat-tire-weary | bake-tire-weary | glide-shout-weary |
| toast | honor-toast-drink | butter-toast-drink | destroy-toast-drink | deny-shave-drink |
| toll | bell-toll-church | fee-toll-church | soup-toll-church | pie-bid-church |
| top | spin-top-toy | bottom-top-toy | bite-top-toy | bless-dark-toy |