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## Context-dependent interpretation of words: Evidence for interactive neural processes

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The meaning of a word usually depends on the context in which it occurs. This study investigated the neural mechanisms involved in computing word meanings that change as a function of syntactic context. Current semantic processing theories suggest that word meanings are retrieved from diverse cortical regions storing sensory-motor and other types of semantic information and are further integrated with context in left inferior frontal gyrus (LIFG). Our fMRI data indicate that brain activity in an area sensitive to motion and action semantics – the posterior middle temporal gyrus (PMTG) – is modulated by a word's syntactic context. Ambiguous words such as *bowl* were presented in minimal disambiguating contexts indicating object (*the bowl*) or action (*to bowl*) meanings and were compared to low-ambiguity controls. Ambiguous words elicited more activity than low-ambiguity controls in LIFG and various meaning-related areas such as PMTG. Critically, ambiguous words also elicited more activity in *to*-contexts than *the*-contexts in PMTG and LIFG, suggesting that contextual integration strengthened the action meaning in both areas. The pattern of results suggests that the activation of lexical information in PMTG was sensitive to contextual disambiguating information and that processing context-dependent meanings may involve interactions between frontal and posterior areas.

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### Introduction

Neuroimaging methods have been extensively used to study how the brain represents and processes the meanings of words (e.g., Thompson-Schill, 2003; Martin and Chao, 2001; Damasio et al., 2004). Most research has addressed the brain areas and circuits that are activated in processing different types of isolated words. For example, words for animals and artefacts (e.g., *cow*, *knife*) produce systematically different patterns of activation (Chao et al., 1999; Moore and Price, 1999; Perani et al., 1999b). This research indicates that word meanings are repre-

sented in a distributed network involving sensory, motor, individual-specific, and other types of information (Martin and Chao, 2001).

An interesting property of words, however, is that their meanings are highly context-dependent. In fact, most English words are ambiguous: they have multiple meanings that vary in how much they overlap. Many words have multiple semantically unrelated meanings (e.g., *watch*: a time piece, to look; *rose*: a flower, past tense of *rise*); others have multiple semantically related senses (e.g., *twist an ankle* vs. *twist the truth*); and some have both (e.g., one of the meanings of *rose* is the name of both a flower and a related color). Even the meaning of a seemingly unambiguous word such as *piano* depends on the context in which it occurs: *moving a piano* brings to mind different concepts than *playing a piano*; the fact that cats have fur is relevant to understanding *pet the cat* whereas having claws is relevant to *scratched by the cat* (Tabossi, 1988). Thus, meanings are not fixed entries or lists of attributes; they are dynamically computed each time a word is encountered. Determining the meanings of words requires *combinatorial* processing: using different sources of information (prior knowledge, context) to converge on an interpretation. This fundamental aspect of language processing poses a complex problem insofar as each word's meaning depends in part on the meanings of other words whose meanings are themselves also context-dependent in varying degrees.

Our goal in this study was to examine the brain mechanisms and circuits underlying such context-dependent combinatorial processes. We examined a common type of lexical ambiguity that allowed us to assess the effects of different contexts on comprehending the same word. Most content words in English such as *hammer* or *bowl* can be used as either nouns or verbs and thus require contextual information to be correctly interpreted as object (*he wants the hammer*) or action (*he wants to hammer*). The alternative meanings are from different grammatical and conceptual categories (noun-object, verb-action) and thus clearly disambiguated by minimal contexts such as *the* and *to*. Behavioral studies have shown that elements of both common meanings of such words are transiently activated, even in strongly

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disambiguating contexts such as *I bought a bowl*. For example ambiguous words automatically prime target words that are semantically related to either meaning early in processing (Swinney, 1979; Tanenhaus et al., 1979; Federmeier et al., 2000). Selection of the contextually appropriate meaning via top-down contextual influences then occurs within about 200 ms (see Simpson, 1994 for review). fMRI does not have sufficient temporal resolution to examine rapid changes over this short time window. However, it does provide a way to examine how a word's context modulates brain activity.

Subjects in an event-related design were presented with phrases referring to tools and manipulable objects and actions performed with such objects. Highly ambiguous words such as *hammer* or *bowl* were presented in a noun context (*the hammer, the bowl*) or in a verb context (*to hammer, to bowl*). These conditions were compared to similar phrases containing words that are minimally ambiguous because they have a single dominant interpretation (e.g., *the dagger, to sharpen*; see Table 1). Whereas combination with the context was required to interpret the high-ambiguity words as an object or an action, it was not required for low-ambiguity words. Hence the comparison between high- and low-ambiguity conditions provides a way to isolate ambiguity-specific activity, including multiple semantic associations and the combinatorial processes by which context disambiguates interpretation. Moreover, the comparison between the noun and verb contexts of the same words provides a way to isolate the brain activity that is modulated by linguistic context, a factor previously unexplored in fMRI studies of ambiguity. Unlike previous sentential studies of ambiguity (e.g., Rodd et al., 2005), the use of minimal two-word combinations from a restricted semantic domain reduces both variability in meaning driven activity and the influence of other factors such as working memory demands and other types of linguistic analyses (e.g., thematic role assignment).

Current word processing models suggest that reading or producing a word consistently implicates a distributed network of

brain regions associated with distinct functions. Beyond brain regions decoding orthographic or auditory word forms (see Hickok and Poeppel, 2004; Price, 2000), lexical semantic sensory-motor attributes are stored and activated in distributed networks of cortical regions organized around sensory-motor systems (Martin and Chao, 2001; Damasio et al., 2004; Pulvermüller, 1999, 2001). These semantic attributes are claimed to be subsequently integrated for further manipulation in frontal areas such as left inferior frontal gyrus (LIFG), an area associated with a variety of semantic and integrative functions (Thompson-Schill, 2003; Gabrieli et al., 1998; Martin and Chao, 2001; Hagoort, 2005). Because the roles of LIFG and the semantic sensory-motor areas associated with our stimuli have been extensively investigated, we build upon previous research to further explore the relationship between these regions.

Words referring to tools and manipulable objects such as *hammer* automatically activate sensory-motor aspects of tool use in regions also implicated in perceiving, imagining, executing and planning actions with tools (Martin and Chao, 2001; Chao and Martin, 2000; Kellenbach et al., 2003; Beauchamp et al., 2002; Johnson-Frey et al., 2005). Such regions include two areas encoding motor schemas for interacting with objects – the intraparietal sulcus (IPS) and ventral premotor cortex (PMv) (cf. Binkofski et al., 1998; Grafton et al., 1997; Gerlach et al., 2002; Noppeney et al., 2005) – and the posterior middle temporal gyrus (PMTG), an area anterior to motion perception area V5/MT, which is sensitive to motion aspects of tool use and actions (Chao et al., 1999). Although PMTG has also been argued to perform more general semantic processes in sentence comprehension (e.g., Kuperberg et al., 2003; Baumgaertner et al., 2002), systematic investigations comparing a variety of visual and word stimuli have consistently showed its engagement in processing stimuli implying motions such as actions and tools (Kable et al., 2002, 2005; Tyler et al., 2003; Beauchamp et al., 2002, 2003). PMTG has also been shown to play a causal role in representations of actions as demonstrated by lesion studies (Tranel et al., 2003) and to be more sensitive to verbs than nouns as verbs tend to imply motion more than ordinary nouns (Perani et al., 1999a; Damasio et al., 2001; Kable et al., 2002; see also Fiez et al., 1996; Tranel et al., 2005).

LIFG in turn has been associated with at least two integrative functions. Sentence processing studies have proposed that LIFG, particularly its posterior portion, processes syntactic structures and serial-order based representations (Caplan et al., 1998; Dapretto and Bookheimer, 1999; Friederici et al., 2003; Keller et al., 2001). Semantic processing studies in contrast have proposed that the anterior portion of LIFG is responsible for the controlled retrieval and selection of appropriate semantic information among competing alternatives on the bases of contextual information (Thompson-Schill et al., 1997; Wagner et al., 2001). The strength of the response in LIFG is sensitive to the number of competing alternatives and the amount of semantic information it receives (see Badre and Wagner, 2002; Thompson-Schill et al., 2005 for reviews). Demands on LIFG thus vary as a function of whether task-relevant semantic knowledge can be accessed through bottom-up retrieval. When automatic access is insufficient due to the presence of prepotent competing representations, LIFG's selection or regulatory processes play a central role in guiding the processing of meaning stored in posterior cortex (Badre and Wagner, 2002).

Table 1  
Examples of stimulus phrases in each condition

	High-ambiguity word	Low-ambiguity word	
Noun context	the bowl	the tray	
	the sling	the leash	
	the brush	the blade	
	the hook	the pliers	
	the handcuff	the hatchet	
	the fork	the rod	
	the skewer	the chisel	
	the rake	the spade	
	the ring	the hoop	
	the clip	the jug	
	the stick	the rope	
	Verb context	to bowl	to dig
		to sling	to knead
to brush		to untie	
to hook		to sift	
to handcuff		to fasten	
to fork		to flog	
to skewer		to unlock	
to rake		to slay	
to ring		to bind	
to clip		to pluck	
to stick		to wipe	

This account of the role of LIFG in semantic processes is consistent with previous studies using stimuli similar to those used in the present research. Highly ambiguous words and sentence structures have been shown to elicit a stronger response in LIFG than less ambiguous words and structures, due to competition between alternatives, which requires the inhibition of inappropriate interpretations (Mason et al., 2003; Rodd et al., 2005; Chan et al., 2004). Moreover, the process of settling on an action meaning (e.g., *sharpen*) also elicits a stronger neural response in LIFG than settling on a noun meaning (e.g., *knife*; Perani et al., 1999a; Damasio and Tranel, 1993; Shapiro et al., 2005). Verbs involve more complex selection or retrieval processes than nouns because verbs carry additional morphological, syntactic and semantic information (concerning, e.g., the kinds of nouns that occur with them; Tyler et al., 2004; Thompson-Schill et al., 2005).

Given these facts, we examined two alternative hypotheses about the relation between semantic sensory–motor areas and processes in LIFG. The *activation–selection* hypothesis posits that ambiguous words such as *hammer* will automatically elicit semantic attributes associated with both common meanings regardless of context, consistent with earlier behavioral studies (Simpson, 1994). Regulatory or selection mechanisms in LIFG would then strengthen contextually appropriate information and inhibit inappropriate information, thus determining the appropriate object or action interpretation. This view predicts that PMTG, IPS and PMv should show an ambiguity effect (more semantic activation for high-ambiguity words than low-ambiguity words) but not a context effect (greater semantic activation for words in verb contexts compared to the same words in noun contexts). Although PMTG may be more responsive to low-ambiguity verbs compared to low-ambiguity nouns due to its previous sensitivity to actions compared to objects (Perani et al., 1999a; Damasio et al., 2001; Kable et al., 2002, 2005), PMTG should not show a context effect for high-ambiguity items. In contrast, LIFG should exhibit both an ambiguity effect (because it receives greater input from high-ambiguity words) and a context effect (because of its role in selection and controlled processes and its greater sensitivity to verbs than nouns). Thus, this hypothesis suggests a feedforward, activate–decide model in which areas representing sensory–motor semantics “propose” and LIFG “disposes.”

The *interactive* hypothesis in contrast suggests that mechanisms in LIFG take place within a process involving possible collaboration or feedback interactions between areas. Specifically, activation in semantic sensory–motor areas may also be modulated by contextual information (in addition to ambiguity) and thus differ for *to hammer* vs. *the hammer*, as expected for LIFG. Of the semantic areas discussed so far, PMTG is more likely to show a context effect given its previous sensitivity to actions compared to objects (Perani et al., 1999a; Damasio et al., 2001; Kable et al., 2002). The interactive hypothesis is thus consistent with low-ambiguity verb phrases such as *to sharpen* producing greater activity in PMTG than low-ambiguity noun phrases such as *the dagger* solely in virtue of their respective lexical meanings (action vs. object). The critical prediction, however, is that the same pattern should be obtained when the action interpretation can only be determined via combinatorial processing, as in the high-ambiguity condition. Thus, *to hammer* (and other stimuli of this type) should produce greater activation than *the hammer* in PMTG. This outcome would suggest that

contextual information strengthens the activation of action-related motion attributes in PMTG and that the contextually appropriate interpretation is determined via feedback or interaction between PMTG and LIFG, rather than via a strictly feedforward activation–selection process.

## Methods

### Materials

Forty high-ambiguity words were each matched for frequency and character length with two low-ambiguity words that have dominant uses as noun and verb respectively (see Table 1). The high-ambiguity words were equibased, i.e., they had similarly frequent object and action interpretations (noun and verb uses) in English (according to the 20 million words Cobuild corpus, cf. Sinclair, 1995). Log<sub>10</sub> frequencies reported were computed from the total frequency in the corpus. The mean log frequency for noun and verb uses of high-ambiguity words was 3.24 and 3.19, respectively, and the mean of their low-ambiguity matches was 3.22 for nouns and 3.22 for verbs. Comparisons of these log frequencies across all these conditions were not significant ( $t < 1$ ). The mean log frequency difference between noun and verb uses of high-ambiguity words was .26. Most low-ambiguity words only have one attested use in the corpus, except for 19 words (out of 80) that had a low frequency alternative (the mean log frequency difference between the high and low frequency alternative of these 19 cases was 1.16). The full list of stimulus words can be accessed at <http://www-users.york.ac.uk/~spg500/stim.pdf>.

Nouns or noun uses referred to manipulable objects, except for two cases that nevertheless involved motion (*train*, *boat*). Verbs and verb uses mostly referred to actions with or upon objects, except for a few cases that, for lack of better frequency matched stimuli, only involved body motion (*dart*, *clap*, *kneel*). One half of the high-ambiguity words (=20) had related meanings in their noun and verb uses as in *hammer*, where the action implies the object. The other half had unrelated meanings or sometimes both related and unrelated ones, as in *clip*. This relatedness grouping did not yield any significant difference in our analyses so that all high-ambiguity words were grouped together. Because number of senses can also affect the richness of the semantic representation activated (Rodd et al., 2002), we computed the number of senses for each stimulus word according to the most common senses listed in two dictionaries (Encarta World English Dictionary, New Oxford American Dictionary, cf. Rooney, 1999; McKean, 2005). The mean number of senses for high-ambiguity words was 7.8, including both object and action senses, whereas low-ambiguity words such as *chisel*, *pliers*, *knit* and *squirt* had an average of 2.78 senses per word. Among high-ambiguity words, noun uses had an average of 4 senses, whereas verb uses had an average of 3.8 senses.

As shown in Table 1, words were presented in a noun or a verb phrasal context. Each of the stimulus phrases was paired with a general world knowledge question about the meaning of the phrase that participants had to answer throughout the experiment. These questions (one per trial) guaranteed that stimulus phrases were read for meaning. The questions referred to properties of objects such as their typical uses, places or physical characteristics (e.g., *for eating?*, *found in kitchens?*, *is hollow?*), or to properties of events

(e.g., *done to eggs?*, *done with yarn?*) or were short dictionary-like definitions (e.g., for phrases like *to lock* or *the clutch*, the questions may be *to secure?* or *a car part?*). Half of the questions were false and half were true.

### Design and procedure

Seventeen right-handed native English speakers (9 males and 8 females), students at the University of Wisconsin-Madison, participated in this study. Each participant saw all stimulus conditions in an event-related design. The order of presentation was counterbalanced across subjects by rotating the first and second half of the stimulus list to minimize possible word repetition effects, although the interpretation of the phrase was never the same. Thus, nine subjects saw an ambiguous word in a noun context first (e.g., *the bowl*), before its verb context (*to bowl*), whereas eight subjects saw the stimuli in the opposite order. All items were randomly assigned a location in the stimulus list, provided that the first and second presentation of a high-ambiguity word occurred in different halves of the list.

For each trial, participants first saw a short phrase such as *the hammer* presented for 1000 ms that was replaced by a black background. 3000 ms later, they were asked a general world knowledge question about the denotation of the phrase just read (e.g., *used by people?*), which also lasted 1000 ms. There were 13 s of inter-trial interval with a fixation cross on the screen. Participants were instructed to remain alert throughout the experiment and keep the meaning of the stimulus phrase in mind until the question appeared so that they could answer it as quickly as possible by pressing a button on a button box. Trials were presented in 8 blocks of 6 min 20 s and each block encompassed 20 trials. Each scanning session began with 20 s of dummy gradient and RF pulses to achieve steady state tissue magnetization.

### fMRI data acquisition and image analyses

Whole-brain images were acquired with a 3 T scanner (GE Signa VH/I). High resolution T1-weighted images (30 sagittal slices, .9375 mm × .9375 mm × 5 mm) were obtained for all participants, and a gradient echo, echoplanar sequence (TR=2000 ms, TE=50 ms) was used to acquire data sensitive to the blood oxygen level dependent (BOLD) signal within a 64 × 64 matrix (30 sagittal slices coplanar with the T1 acquisition, 3.75 mm × 3.75 mm × 5 mm).

All data processing was performed with VoxBo software. Pre-processing entailed image reconstruction, slice-acquisition correction, realignment and notch filtering to remove frequencies above .29 Hz and below .02 Hz. The principle of the fMRI time series analysis was to model the fMRI signal changes evoked by each stimulus presentation epoch with covariates comprised of BOLD hemodynamic response functions (HRF) shifted along the timeline of the task to represent the trial's discrete epochs (Zarahn et al., 1997). The least-squares solution of the GLM of the fMRI time series data yielded parameter estimates that were associated with each covariate of interest. Empirically derived stock HRFs (stored with VoxBo software and obtained from averages across different subjects and experiments) were placed at time 0 s and time 4 s to model the expected BOLD response evoked by the two epochs of the trial (the stimulus phrase and the question). Because the smoothness of the fMRI response to neural activity allows fMRI

evoked responses that arise from temporally dependent events to be resolved on the order of 4 s (Zarahn et al., 1997), this procedure allowed us to estimate the responses evoked by the stimulus phrase and by the question, separately. We only report analyses relevant to our hypotheses performed on the activity corresponding to the phrase presentation portion of the trial. There were four covariates of interest in the GLM depending on ambiguity and syntactic context (High-ambiguity-Noun context, High-ambiguity-Verb context, Low-ambiguity-Noun context and Low-ambiguity-Verb context).

Analyses were performed as region of interest (ROI)-based group analyses. Unlike some studies, fMRI data were not spatially transformed into a common atlas space. This is because our hypotheses related to very specific anatomical structures, and hand-identifying these would be more precise and more sensitive than relying on, for example, spheres of a given volume placed at particular sets of coordinates in atlas space (Brett et al., 2002; Juch et al., 2005; Swallow et al., 2003). Thus, the analyses proceeded as follows.

Relationships between conditions were tested by computing *t*-statistics for each individual subject. For each subject's data, above-threshold voxels in each ROI showing a main effect of the stimulus presentation covariate (with Bonferroni correction at  $\alpha=.05$ ) were identified. This detected all voxels that were active for the reading portion of the trial irrespective of condition. These voxels were then spatially averaged and subsequently used to calculate the *t*-values of the contrasts of each trial type vs. baseline. Baseline activity included the unmodeled portion of the trial plus the inter-trial period. Thus we calculated the contrasts [Phrase<sub>High-ambiguity-Noun context</sub> - baseline], [Phrase<sub>High-ambiguity-Verb context</sub> - baseline], [Phrase<sub>Low-ambiguity-Noun context</sub> - baseline] and [Phrase<sub>Low-ambiguity-Verb context</sub> - baseline]. *t*-values derived from these contrasts represented normalized indices of effect sizes for each condition relative to baseline in each ROI because the residual error term that makes up the denominator of the *t*-value is linearly related to the same scaling factor (or gain effect) that characterizes differences in overall BOLD signal intensity across scanning sessions (see Postle et al., 2000 for a detail description and justification of this procedure). These *t*-values (effect sizes) were then used as dependent variables in the random-effect group analyses reported for each ROI (Woods, 1996).

### Regions of interest

We anatomically defined the ROIs, which included areas previously identified in the literature. We drew five ROIs for each participant's brain. Because we did not have any specific prediction about how different portions of the LIFG would contribute to the processing of our stimuli (our phrases in principle include both syntactic and semantic processes) we define a region of interest in LIFG (BA44/45) including both pars triangularis and pars opercularis. This region was delimited in the inferior–superior axis by the anterior lateral fissure and the inferior frontal sulcus and in the anterior–posterior axis, by the horizontal ramus of the lateral fissure and the inferior pre-central sulcus (the ROI did not include the sulci themselves). The LIFG was thus drawn around the vertical ramus of the lateral fissure. The PMv ROI included in anterior–posterior axis, the surface between the pre-central and central sulci and in the inferior–superior axis, the surface between the sylvian fissure up to the horizontal line defined by the inferior

Table 2  
Mean Talairach coordinates across subjects in each ROI

ROI	<i>x</i>	<i>y</i>	<i>z</i>	Nearer BA
PMTG	−49	−59	2	37
LIFG	−42	18	2	45/47
IPS	−34	−46	43	40
PMv	−47	1	15	44/6
STG	−51	−41	7	22

Each cell represents the mean coordinate across subjects of each ROI's local maxima.

frontal sulcus. The intraparietal sulcus ROI included an area of about 1 cm around the sulcus, running from anterior to posterior segments. The posterior middle temporal gyrus included the area defined by the most posterior segment of BA21 and the middle segment of BA37. In the inferior–superior axis, the area was delimited by the superior and inferior temporal sulci and in the anterior–posterior axis, by the perpendicular imaginary line defined by the most posterior horizontal segment of the sylvian fissure up to the posterior continuation of the inferior temporal sulcus (according to Dumoulin et al., 2000). Upon conversion of each individual brain into MNI space, we confirmed that the PMTG so defined included the coordinates previously reported in the literature (Chao et al., 1999; Kellenbach et al., 2003). See Table 2 for spatial coordinates. Finally, the superior temporal gyrus included the posterior segment of this gyrus and had a similar extension to that of PMTG in the anterior–posterior axis. Examples of ROIs in one subject are shown in Fig. 1.

To compare our results with previous studies, each individual subject's brain was transformed into the space of the MNI template,

together with the functional activity in each ROI corresponding to the contrast of phrase presentation vs. baseline. We computed the transform from a subject's native space T1 to the T1 template provided by SPM 96b using the coregistration algorithm provided by SPM 96b, as implemented by VoxBo, and we applied the same transformation matrix to the volumes of parameter estimates resulting from the contrast of phrase presentation vs. baseline. We then located the MNI coordinates of each ROI's local maxima in each subject and averaged them across subjects. These average coordinates were automatically transformed into Talairach and Tournoux coordinates (Talairach and Tournoux, 1988) using available routines (<http://www.imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach>). These Talairach coordinates are reported in Table 2.

## Results

### Behavioral responses

92% of yes–no responses to the questions in each trial were answered correctly, confirming that participants paid attention to the task and read the phrases for meaning. There was no significant main effect of ambiguity or context in the proportion of correct responses in a repeated measures ANOVA (ambiguity:  $F(1,16) = 0.71, p = 0.41$ ; context:  $F(1,16) = 0.07, p = 0.79$ ) although there was a small interaction ( $F(1,16) = 6.9, p < 0.02$ ). This was due to the fact that correct responses were higher for low-ambiguity verbs than high-ambiguity verb contexts (0.94 vs. 0.90 proportion correct) whereas the opposite pattern was obtained for noun contexts (low-ambiguity nouns: 0.91; high-ambiguity nouns: 0.93). These small differences do not necessarily reflect difficulty associated with the context or the ambiguity manipulations per se

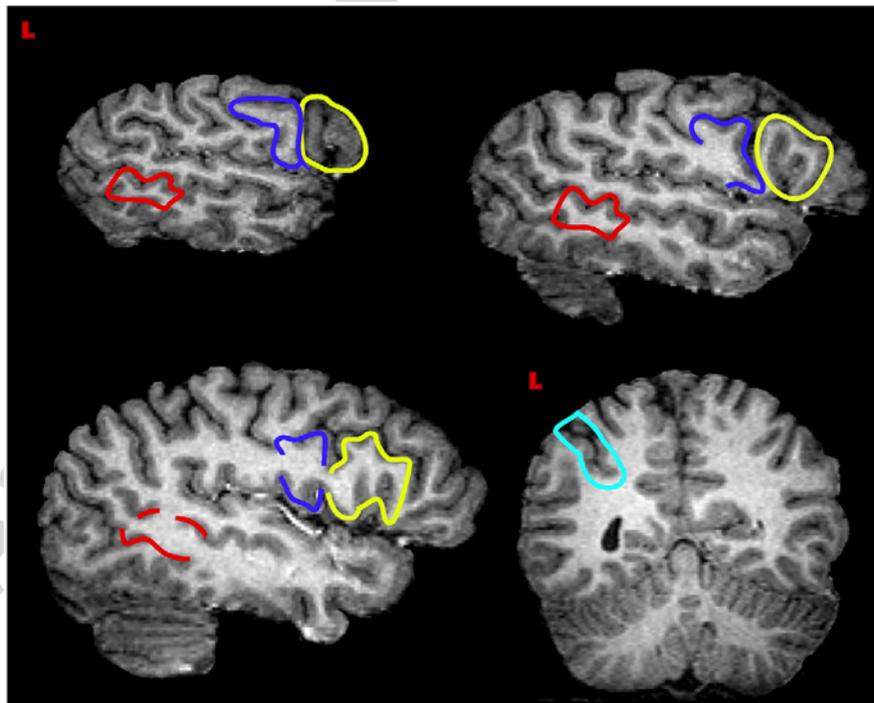


Fig. 1. Examples of region interests drawn in one subject. Three different left sagittal slices showing the posterior middle temporal gyrus in red, the ventral premotor region in blue and the inferior frontal gyrus in yellow. The coronal view shows the left intraparietal sulcus in light blue. Open lines indicate that the region was not fully filled but drawn along the lines over the gray matter.

because the questions associated with the phrases varied in difficulty and thus could have influenced responses. For example, the question *to eliminate?* after reading *to hammer* could have elicited an incorrect *yes* answer because of its semantic consistency with the preceding phrase meaning, independently of the ambiguity of the phrase.

### Imaging results

We report the main effects obtained from computing ANOVAs with subjects as random factor in each region of interest (ROI). Each analysis included Ambiguity (High vs. Low-ambiguity words) and Syntactic Context (Noun vs. Verb Context) as independent factors and participants' *t*-values (representing the effect sizes relative to baseline activity) as dependent variable. The main ROIs were PMTG, LIFG PMv and IPS (see Fig. 1); the superior temporal gyrus (STG), an area often co-activated with LIFG in language studies (Price, 2000; Keller et al., 2001), was also included to compare the predicted results in PMTG with another language-related area.

### Ventral premotor and intraparietal sulcus

In both motor-related areas (PMv and IPS), there was a main effect of Ambiguity (PMv:  $F(1,16)=5.09$ ,  $MSE=7.9$ ,  $p<0.04$ ; IPS:  $F(1,16)=4.70$ ,  $MSE=5.25$ ,  $p<0.05$ ), no effect of Syntactic Context (PMv:  $F(1,16)=3.10$ ,  $p=0.10$ ; IPS:  $F(1,16)=0.22$ ,  $p=0.64$ ) and no interaction (both  $F$  values  $<1$ ). As shown in Fig. 2, high-ambiguity words elicited more activity than low-ambiguity words regardless of context, suggesting that high-ambiguity words activated attributes associated with their alternative interpretations, consistent with earlier behavioral studies.

### Left inferior frontal gyrus

In LIFG, there was a main effect of Ambiguity ( $F(1,16)=5.43$ ,  $MSE=6.87$ ,  $p<0.04$ ), a main effect of Syntactic Context

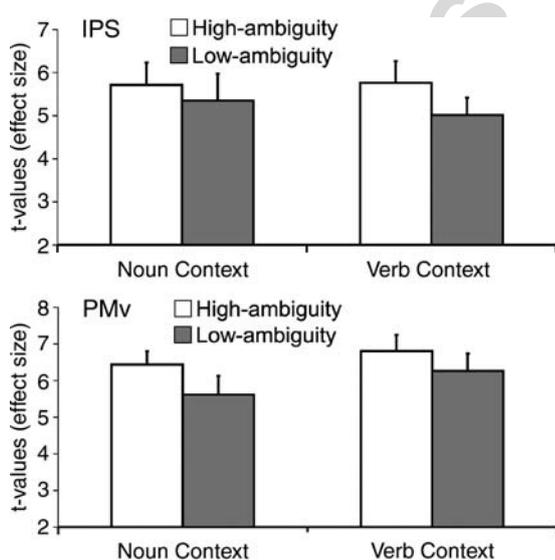


Fig. 2. Effect of lexical ambiguity and syntactic context in the intraparietal sulcus (IPS) and ventral premotor cortex (PMv). Error bars indicate standard error.

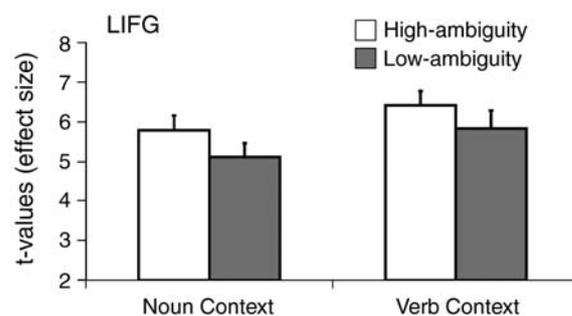


Fig. 3. Effects in left inferior frontal gyrus (LIFG) as a function of lexical ambiguity and syntactic context. Error bars indicate standard error.

( $F(1,16)=5.77$ ,  $MSE=7.79$ ,  $p<0.03$ ), and no interaction ( $F<1$ ). As shown in Fig. 3, verb contexts elicited greater activity than noun contexts, and high-ambiguity words produced greater activity than low-ambiguity words. A planned comparison between the noun and verb contexts of high-ambiguity words (e.g., *to hammer* vs. *the hammer*) was also significant ( $t(16)=1.75$ ,  $p<0.05$ , one tailed). This indicates that high-ambiguity words and verb contexts elicited more processing in LIFG, as suggested by previous studies. Note that the same word (e.g., *hammer*) elicited a greater response in the verb context than the noun context, consistent with the view that computing the action interpretation differs from computing the object interpretation, in virtue of the former being more complex (Tyler et al., 2004; Thompson-Schill et al., 2005).

### Posterior middle temporal gyrus

The pattern of activation in PMTG was very similar to that in LIFG, with a main effect of Ambiguity ( $F(1,16)=4.76$ ,  $MSE=6.07$ ,  $p<0.05$ ), a main effect of Syntactic Context ( $F(1,16)=9.41$ ,  $MSE=11.61$ ,  $p<0.008$ ) and no interaction ( $F<2$ ). Verb contexts elicited more activity than noun contexts, and high-ambiguity words elicited more activity than low-ambiguity words (Fig. 4). The planned comparison between the noun and verb context conditions for the high-ambiguity words yielded a significant difference ( $t(16)=3.25$ ,  $p<0.01$ , two tailed). Thus, this area was more responsive to actions than to object interpretations when the distinction was determined by the combination of an ambiguous word plus context.

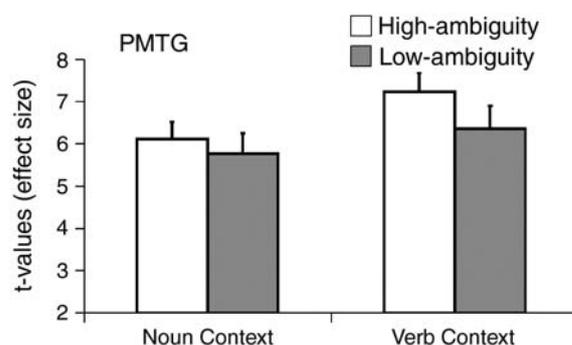


Fig. 4. Effects in posterior middle temporal gyrus (PMTG) as a function of word ambiguity and syntactic context. Error bars indicate standard error.

### Superior temporal gyrus

The analysis in the STG showed no significant effect of Ambiguity or Syntactic Context ( $F(1,16)=0.43$ ,  $p>0.5$  and  $F(1,16)=2.36$ ,  $p>0.10$ , respectively). Although STG is an area often involved in language processing (Price, 2000; Keller et al., 2001), other areas, particularly PMTG, were more sensitive to the ambiguity and context manipulations. This indicates that the effects in PMTG are rather specific and not necessarily shared with other comparable posterior areas.

### Discussion

The results indicate that LIFG and areas associated with semantic attributes including IPS, PMv and PMTG were all sensitive to the ambiguity manipulation: high-ambiguity words such as *bowl* and *hammer* in any syntactic context elicited greater brain activity than low-ambiguity words such as *dagger*. This difference can be explained by the fact that ambiguous words automatically activate elements of more than one meaning (Simpson, 1994). Stimulus phrases containing ambiguous words activated motor and motion information associated with both objects and actions, thus producing stronger activity in semantic areas. The fact that high-ambiguity phrases then elicited stronger activity in LIFG than low-ambiguity ones is consistent with previous findings in that the presence of competing bottom-up representations may engage LIFG to inhibit contextually inappropriate representations (Thompson-Schill, 2003; Wagner et al., 2001). Processing in LIFG thus may have reflected the selection or inhibition of object or action attributes as a function of fit to the syntactic context, enabling the integration of ambiguous words and context.

LIFG was also sensitive to the context manipulation: verb contexts elicited more activity than their noun counterparts, even when the same high-ambiguity word was compared across contexts (*to hammer>the hammer*). Verb forms have consistently been shown to elicit a stronger response than nouns in LIFG due to their greater complexity, and their use is impaired when this area is damaged (Perani et al., 1999a; Tyler et al., 2004; Damasio and Tranel, 1993). This outcome parallels the ambiguity effect: high-ambiguity words may require more complex processing than low-ambiguity words, and verbs more than nouns.

The most important result concerns the effects of context in PMTG. The greater sensitivity of PMTG to verb contexts compared to noun contexts, particularly for high-ambiguity words, indicates that its semantic attributes can be more or less activated as a function of context. This contrasts with motor-related areas PMv and IPS that were equally responsive to phrases with object and action interpretations, indicating that the sensory-motor attributes that they encode are similarly associated with and activated by actions involving tools/artefacts and by tools/artefacts themselves, as suggested by previous results (Oliveri et al., 2004; Chao and Martin, 2000; Grafton et al., 1997; Hauk et al., 2004). Although low-ambiguity verbs such as *sharpen* were expected to elicit more activity in PMTG than low-ambiguity nouns (*to sharpen>the dagger*) because of their lexical action meaning (Perani et al., 1999a; Kable et al., 2002), high-ambiguity words such as *bowl* or *hammer* could not have elicited a context effect for similar reasons because the same word appeared in both contexts. Rather, the data suggest that the combination of a word such as *bowl* or *hammer* with its syntactic context (*to* or *the*) was critical for PMTG to strengthen the syntactically appropriate action

meaning over the object alternative (*to bowl>the bowl*). This result indicates that PMTG received contextual disambiguating information and communicated or interacted with LIFG in computing meaning as a function of context.

These results suggest that contextual combination was implemented via interaction between LIFG and PMTG and is less consistent with an alternative scenario such that motion attributes consistent with both objects and actions were passed along to LIFG for contextual selection and integration. Beyond this observation the results are consistent with two logical possibilities: either meaning selection/retrieval mechanisms in frontal areas sent top-down information back to PMTG inhibiting the contextually inappropriate meaning (D'Esposito et al., 1999; Postle et al., 2004) or PMTG itself performed some selection-integration process supporting and interacting with LIFG.

Previous studies using ambiguous words provide partial support for the role of PMTG in retrieval of semantic knowledge and the top-down feedback alternative. Two studies using ambiguous words in sentential contexts found stronger activity in LIFG and PMTG for ambiguous conditions, although in one of these studies the posterior activity was centered in inferior temporal regions (perhaps because of the overwhelming use of noun-noun ambiguities like *dates*, which did not strongly engage action semantics) (Rodd et al., 2005; Snijders et al., 2006). Both these studies interpret the posterior activity as implementing lexical semantic processes (cf. Hickok and Poeppel, 2004) or sustained activation of lexical information. In a picture naming production study, which used stimuli more similar to the current study, the contrast between ambiguous words such as *comb* produced as nouns and those produced as verbs elicited more activity in PMTG (Tranel et al., 2005), indicating that PMTG was engaged in action representation and retrieval when no linguistic combinatorial process was engaged.

Yet many sentence processing studies have argued that the middle temporal gyrus is involved in semantic integration processes consistent with the second interpretation of the results (Friederici and Kotz, 2003; Kuperberg et al., 2003; Baumgaertner et al., 2002). Although it is possible that PMTG processes both combinatorial and lexical semantic aspects of verbs, more evidence is required. Many sentence processing results using anomalous or unexpected stimuli are consistent with an interpretation in which middle temporal activity is due to difficulty of lexical retrieval during sentence comprehension: because the sentential contexts previous to the critical manipulation may automatically activate semantically related continuations and inhibit others (cf. DeLong et al., 2005), unexpected or anomalous continuations may simply be more difficult to retrieve in such contexts (Baumgaertner et al., 2002; Kuperberg et al., 2003).

Regardless of which alternative ends up being correct, our results, together with previous findings, inform current models of language processing: they suggest that a word's context modulates activity in posterior areas encoding specific semantic attributes and that context-dependent interpretation may engender interactions or feedback mechanisms between anterior and posterior areas. This latter possibility is supported by connectivity findings showing both anatomical connections and functional correlations between inferior frontal and posterior temporal areas including PMTG (Bokde et al., 2001; Fiebach et al., 2006; Parker et al., 2005; Matsumoto et al., 2004). Our results thus join a growing body of evidence in psycholinguistics and cognitive neuroscience indicating that complex processes such as sentence comprehension

(Keller et al., 2001), single word reading (Dale et al., 2000; Price et al., 2001; Pammer et al., 2004) and semantic retrieval (Noppeney et al., 2004) depend on the interplay between co-activated areas and different types of linguistic information (MacDonald et al., 1994).

In summary, the current study provides evidence for a type of combinatorial process that is common in language comprehension and thus represents a step beyond construing the processing of word meanings as passively activating a stored representation. The study also illustrates a way to transition from studies of isolated words to studies of phrases and sentences, illustrating how techniques that have proved successful in identifying properties of words can be extended to more meaningful constituents of language.

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