Lexical Preactivation in Basic Linguistic Phrases

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Abstract

■ Many previous studies have shown that predictable words are read faster and lead to reduced neural activation, consistent with a model of reading in which words are activated in advance of being encountered. The nature of such preactivation, however, has typically been studied indirectly through its subsequent effect on word recognition. Here, we use magnetoencephalography to study the dynamics of prediction within serially presented adjective–noun phrases, beginning at the point at which the predictive information is first available to the reader. Using corpus transitional probability to estimate the predictability of a noun, we found an increase in activity in the left middle temporal gyrus in response to the presentation of highly predictive adjectives (i.e., adjectives that license a strong noun prediction). Moreover, we found that adjective predictivity and expected noun frequency interacted, such that the response to the highly predictive adjectives (e.g., *stainless*) was modulated by the frequency of the expected noun (*steel*). These results likely reflect preactivation of nouns in highly predictive contexts. The fact that the preactivation process was modulated by the frequency of the predicted item is argued to provide support for a frequency-sensitive lexicon. ■

INTRODUCTION

Top–down predictive processing is one of the fundamental principles of brain function (Bar, 2007). Using prior knowledge and contextual information, higher-order areas communicate expectations to lower areas, which then compare the received input to the predicted input. Language processing is no exception to this rule. For example, listeners move their eyes to items that are predictable from context, before the item itself has been named (Altmann & Kamide, 1999; Kamide, Altmann, & Haywood, 2003). Likewise, predictable words are read more quickly (Ehrlich & Rayner, 1981) and elicit reduced neural signals, most commonly observed as a reduction in the N400 ERP component (Kutas & Hillyard, 1984).

Predictability effects have been taken as support for the notion that likely upcoming words are at least partly preactivated in advance of being encountered (Kutas & Federmeier, 2000), although some have argued for an alternative explanation in which these effects stem from the increased ease of integrating predictable words into the preceding context (Brown & Hagoort, 1993; Norris, 1986; see Lau, Phillips, & Poeppel, 2008, for a review of the different interpretations of the N400 response). Recent empirical support for the preactivation account comes from an experiment showing a modulation in N400 effects for the English indefinite articles *a* and *an*, based on whether the context licensed a prediction for a noun that agreed with the article (e.g., *The day was breezy so the boy went outside to fly a [kite]/ *an [airplane]*; DeLong, Urbach, & Kutas, 2005). Because both indefinite articles should be equally easy to integrate into the semantic context of the sentence, the only plausible explanation for the N400 effect in this case is that participants were preactivating the representation of the upcoming noun. Similar responses have been reported for semantically vacuous agreement features in other European languages (Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005; Wicha, Moreno, & Kutas, 2003).

A separate line of evidence for lexical preactivation comes from predictability effects in early sensory responses (Kim & Lai, 2012; Dikker & Pylkkänen, 2011; Dikker, Rabagliati, & Pylkkänen, 2009). For example, Dikker and Pylkkänen (2011) presented participants with pictures, followed by words that either did or did not match the presented image. Some of the pictures were predictive of a specific word (e.g., a picture of an apple), and some were not, instead denoting a larger semantic category from which a single predictable word could not be isolated (e.g., a picture of a shopping bag full of groceries). When the strong prediction for the word *apple* generated by the presentation of a picture of an apple was violated, there was an increase in the M100, a magnetoencephalography (MEG) signal generated in visual cortex around 100 msec after stimulus presentation. Importantly, the contexts that did not afford a specific lexical prediction did not elicit a similar violation response. These findings point to a top–down modulation of visual cortex activity by lexical expectations generated in language regions (Dikker et al., 2009). In summary,

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predictability effects for semantically vacuous words, on the one hand, and top–down modulatory effects in sensory cortex, on the other hand, both provide support for the lexical preactivation account of predictability effects.

A popular model for these top–down predictability effects proposes that prediction arises directly from the organization of neurons in the cortex. Predictive coding theories propose that cortical regions contain two types of neuron populations: "expectation" neurons, which encode the representations, and "surprise" neurons, which encode the mismatch between the predicted representation and the bottom–up input (Friston, 2005). The predictive coding model makes the prediction that anticipatory processing of a stimulus should elicit neural activity in some of the same regions that are active when that same stimulus is perceived. This prediction has been increasingly supported by recent evidence (Kok, Failing, & de Lange, 2014; Egner, Monti, & Summerfield, 2010). For example, seeing an image of a face and anticipating seeing a face both activate the fusiform face area (Egner et al., 2010). One might therefore expect that anticipation of a lexical stimulus would be detectable in the same regions involved in lexical processing more generally. Indeed, a follow-up analysis of the picture–noun data set described above showed that MEG activity in temporal and occipital cortex was increased in the presence of a specific prediction (picture of an apple) before the presentation of the word (Dikker & Pylkkänen, 2013).

Predictive coding models make the additional prediction that lexical preactivation in predictive contexts will reflect the identity of the individual item being predicted. This has been demonstrated for predictive processing in earlier sensory areas. Kok, Jehee, and de Lange (2012), for example, showed that the representation of a predicted element was "sharpened," in that it became easier to decode its identity from activity in visual cortex. More recently, Kok et al. (2014) showed that patterns of activity in early visual cortex evoked by expected (but not presented) stimuli had similar feature specificity to those evoked by the stimulus itself.

Design

The goal of the current experiment is to find direct evidence for the preactivation of particular lexical items. One challenge in tackling this question lies in the fact that it is difficult to pinpoint the exact moment at which a linguistic prediction is generated. Prediction has typically been studied by varying the predictability of the last word of a sentence (Kutas & Hillyard, 1984, and many others). An issue with using this paradigm for studying preactivation is that a prediction for the last word of a sentence likely arises gradually as more and more information about the sentence is accumulated, rather than being generated in its entirety immediately before the last word of the sentence. For example, in the sentence *he loosened the tie around his neck*, much of the information that enables a reader to predict the word *neck* is likely to already be available after the word *tie*. This complication makes it difficult to temporally isolate a preactivation signal.

We departed from this classic paradigm in two respects. First, following Bemis and Pylkkänen (2011), we used simple adjective–noun phrases, such as *stainless steel*, as opposed to full sentences. Participants read the phrases while their neural activity was recorded using MEG. To ensure that they were fully engaged with the materials, they made a lexical decision on the second word of the phrase (the noun). While reading isolated phrases is undoubtedly less natural than reading full sentences, this paradigm has several advantages for our purposes. First, the sources of information used to generate the predictions are more limited, giving us better control over the nature of the prediction signal. For example, syntactic structure is kept constant across all stimuli, minimizing variation in syntactic predictions, which can affect neural responses (Linzen, Marantz, & Pylkkänen, 2013). Second, because each of the items is much shorter, we can include significantly more items than in a sentential paradigm. Finally, and most crucially, this paradigm allowed us to achieve precise control over the point in time at which a prediction can be generated: in the phrase *stainless steel*, a specific lexical prediction can be generated immediately at *stainless*. Using MEG, we can then measure neural activity before the word *steel*, giving us a direct measure of a prediction signal, rather than an indirect error response.

A second way in which our paradigm differs from classic N400 experiments is in the way predictability was operationalized. Most studies of predictability have estimated it using the cloze procedure (Taylor, 1953), a pretest in which native speakers read a sentence with a missing final word and are instructed to fill in the blank. The cloze probability of a word is defined as the proportion of participants who completed the sentence using that word. For example, if 97% of participants complete the sentence *he loosened the tie around his…* with the word *neck*, the cloze probability of the word *neck* would be .97. By contrast, here we operationalized predictability using corpus transitional probability (TP), that is, the probability of encountering a second word w_2 given that a first word w_1 has been encountered ($P(w_2|w_1)$), estimated from frequencies in the Corpus of Contemporary American English (Davies, 2009). For *stainless steel*, for example, TP is calculated as the number of times *stainless steel* appeared in the corpus divided by the total number of times *stainless* appeared in the corpus (McDonald & Shillcock, 2003). One advantage of TP over cloze probability is that, whereas cloze probability is always bounded by the number of respondents (with 100 participants, the lowest possible cloze probability is .01), TP does not have this limitation, which makes it possible to study differences between items with fairly low predictability, for example, TP = .05, and very low predictability, for example, TP = .005 (Smith & Levy, 2013).

To recapitulate, our paradigm allowed us to characterize the nature of the signal generated by the expectation of a noun. We quantified the degree to which an adjective evokes an expectation for a noun using corpus TP from the adjective to the noun.

Anatomical ROI

As mentioned above, predictive coding models suggest that expectation of a stimulus involves neural activity in the same region that processes that stimulus when it is encountered. Preactivation of a specific lexical item is therefore likely to occur in the areas that are involved in lexical access more generally. Consequently, we focused our analysis on the left middle temporal gyrus (MTG), a cortical region thought to play a central role in lexical access (Friederici, 2012; Hickok & Poeppel, 2007; Rodd, Davis, & Johnsrude, 2005; Indefrey & Levelt, 2004; Binder et al., 1997). This area has also recently been implicated in generating expectations from linguistic stimuli and matching them against perceptual stimuli (Francken, Kok, Hagoort, & De Lange, 2015).

Word Frequency

The preactivation of a word is likely to involve some of the same processes that are engaged when the word is accessed in other circumstances. One of the most reliable predictors of ease of lexical access is word frequency. Frequent words are processed faster in lexical decision experiments (Whaley, 1978; Rubenstein, Garfield, & Millikan, 1970) and during natural reading (Inhoff & Rayner, 1986). EEG experiments have found that the amplitude of the N400 is reduced for frequent words (Van Petten & Kutas, 1990; Smith & Halgren, 1987). Importantly, within the MEG literature, frequency effects have been found in the left MTG during the time window of the M350, the evoked response thought to be associated with lexical access (Solomyak & Marantz, 2010; Embick, Hackl, Schaeffer, Kelepir, & Marantz, 2001). This body of evidence leads us to predict that the preactivation of an infrequent word should be more effortful than the preactivation of a frequent one. Concretely, when an adjective is predictive of a specific noun, we expect the frequency of the expected noun to modulate MTG activity before the presentation of the noun. For example, upon recognition of the adjective *stainless*, we expect participants to preactivate the linguistic representation of the likely continuation *steel*; we therefore expect to see concomitant effects of the frequency of *steel* associated with this preactivation in the MTG. More generally, we expect to see an interaction in the MTG between adjective predictivity and the frequency of the expected noun continuation, such that as adjective predictivity increases, we are more likely to observe effects of the frequency of the most likely noun continuation. This should occur in the time window subsequent to recognition of the adjective, but before the presentation of the noun. After the presentation of the noun, we expect that frequency effects will be reduced for the more predictable items, consistent with EEG experiments that have shown that N400 frequency effects are only significant for words that appear earlier in a sentence (Van Petten & Kutas, 1990) or that are less predictable from context (Dambacher, Kliegl, Hofmann, & Jacobs, 2006).

METHODS

Materials

We first define the variables that we calculated for each phrase and then describe how the phrases were selected (partially based on those variables).

Lexical Variables

We illustrate the calculation of the lexical variables using the phrase *economic reform*. The most likely continuation of *economic* is not *reform*, but *growth*. In this case, we say that the expected noun is *growth*, and the presented noun is *reform*. We define the following variables:

- Adjective frequency: freq(*economic*)
- Adjective predictivity: TP from the adjective to its most likely noun continuation: $P(growth \mid economic)$
- Expected noun frequency: the frequency of the adjective's most likely noun continuation: freq(*growth*)
- Presented noun frequency: the frequency of the noun that was actually presented: freq(*reform*)
- Presented noun predictability: TP from the adjective to the presented noun: $P(reform \mid economic)$

Focusing on a single expected noun is clearly a simplification; most adjectives license more than one prediction. After reading the adjective *economic*, for example, participants may well predict both *growth* and *reform*. These continuations would likely be preactivated in proportion to their conditional probability (Smith & Levy, 2013; DeLong et al., 2005): Following recognition of *economic*, the noun *growth* may be activated to a greater extent than *reform*.[1] To capture this intuition, we defined a generalization of expected noun frequency that we term *weighted expected noun frequency*. This variable is a weighted average of the frequencies of the adjective's continuations, where the weights are given by the TPs of the continuations. We only considered noun continuations within phrases that met our minimum frequency requirement (i.e., 50 tokens in the corpus, corresponding to a probability of 1 in 8 million). Consequently, some of the conditional probability mass for each adjective was not assigned to any noun; we assigned this probability to a generic noun that had the average frequency of all nouns in the corpus. As an illustration, in the case of *economic* (assuming that there are only two supra-threshold noun continuations), the calculation of this variable would be given by

$$\begin{aligned}\mathrm{WF}(\textit{economic}) = {} & P(\textit{reform}|\textit{economic}) \times \mathrm{freq}(\textit{reform}) \\ & + \mathrm{P}(\textit{growth}|\textit{economic}) \times \mathrm{freq}(\textit{growth}) \\ & + (1 - P(\textit{reform}|\textit{economic}) \\ & \quad - P(\textit{growth}|\textit{economic})) \\ & \quad \times \mathrm{avgNounFreq}\end{aligned}$$

The shape of frequency effects has long been known to be approximately logarithmic (Whaley, 1978), and there is increasing evidence that this is the case for predictability effects as well (Smith & Levy, 2013). We therefore log-transformed all frequency and predictability variables before entering them into our statistical models.

Selection Criteria

A set of 474 adjective–noun phrases was obtained as follows. We first selected all sequences of two words from the Corpus of Contemporary American English (Davies, 2009) that satisfied the following conditions:

(1) The first word was tagged as an adjective at least 90% of the time, according to the automatic part-of-speech tagging included with the corpus.
(2) The second word was tagged as a noun at least 90% of the time.
(3) The sequence had a frequency of at least 50 tokens in the corpus out of ~400 million tokens in the corpus, corresponding to a probability of approximately 1 in 8 million.
(4) The length of both words was between three and nine characters.
(5) All nouns had an accuracy of at least 75% in the lexical decision data in the English Lexicon Project (this criterion was implemented to ensure that participants were likely to be familiar with the words).

Many phrases contained the same adjectives or nouns as other phrases in the selection (e.g., *high table* and *high chair*, or *black chair* and *high chair*). Whenever this was the case, we only kept the phrase in which the noun was most predictable. Because phrases with highly predictable nouns are relatively rare, this procedure maximized our coverage of the predictability range. More specifically, we first grouped the phrases by noun (e.g., *black chair* and *high chair*) and excluded all but the most predictable items; we then grouped the remaining phrases by adjective (e.g., *high table* and *high chair*) and again excluded all but the most predictable items. This process yielded a candidate set of phrases, each composed of a unique adjective and unique noun.

A side effect of this procedure was that many phrases, particularly towards the lower end of the TP range, contained nouns that were not the most predictable ones given the adjective. For example, the phrase *economic reform*, which has TP = .01, was included even though a phrase with the same adjective, *economic growth*, had higher TP (.05). This was done because *growth* occurs in *rapid growth*, which has even higher TP (.08). In our final set, the noun was the most expected continuation of the adjective in 51% of the phrases (242 of 474); in the top quartile of adjective predictivity (i.e., adjectives that had a noun continuation with TP > .10), this proportion was 77% (90 of 117). Because the phrase used when the most predicted noun was not available typically had the second highest TP among all phrases that included the adjective, the order of magnitude of the TP of the selected phrase was usually similar to that of the phrase that was excluded (median ratio of highest TP to selected TP: 2.63).

Given the candidate set of phrases, we excluded items that were clearly part of a longer phrase (e.g., *congestive heart*, which always appears in the context *congestive heart failure*) and items that are usually capitalized, which tend to be names of places or works of art (e.g., *Purple Haze*). Finally, we asked six undergraduate students to rate the phrases for familiarity and excluded phrases that five of six raters rated as unfamiliar (e.g., *logistic regression*). The final list contained 474 phrases, which are listed in the Appendix, along with their associated TP values. After sorting by TP, the noun in every other phrase was replaced with a pronounceable nonword (e.g., *academic dusporate*), obtained using Wuggy (Keuleers & Brysbaert, 2010).

Table 1 lists the descriptive statistics for key stimulus variables. Noun frequency and noun predictability (TP between adjective and noun) were correlated (r = .34),

Table 1. Descriptive Statistics for Stimulus Variables

	Adjective Frequency (log)	*Noun Frequency (log)*	*Phrase Frequency (log)*	*Adjective Predictivity (log)*	*Noun Predictability (log)*
Min	5.05	5.91	3.93	−5.36	−7.9
Max	12.88	12.68	10.77	−0.17	−0.17
Median	8.59	9.77	4.98	−3.02	−3.49
Mean	8.69	9.73	5.23	−2.91	−3.45
SD	1.43	1.27	1.05	1.00	1.37

as were adjective frequency and noun predictability ($r = -.71$). Adjective frequency was also correlated with adjective predictivity ($r = -.59$). None of the variables were strongly correlated with adjective length or noun length (all $r < .3$). The high correlation between adjective frequency and the two predictability measures is due to the fact that these quantities are mathematically related:

$$\begin{aligned} \log(\mathrm{TP}) &= \log(\mathrm{freq}(\mathit{phrase})/\mathrm{freq}(\mathit{adj})) \\ &= \log(\mathrm{freq}(\mathit{phrase})) - \log(\mathrm{freq}(\mathit{adj})) \end{aligned}$$

As mentioned above, we only selected phrases that appeared with a frequency of at least 1 per 8 million to eliminate implausible or ungrammatical phrases. This entails that log(TP) and log(freq(*adj*)) must sum to at least 3.9, and therefore, a phrase cannot simultaneously have $\log(\mathrm{TP}) = -6$ and $\log(\mathrm{freq}(\mathit{adj})) = 7$. Note that because log(freq(*phrase*)) is always positive, many combinations of values for log(TP) and log(freq(*adj*)) would still be impossible even if the frequency threshold for phrases were lifted.

Participants

Sixteen participants (nine women) from New York City participated in the experiment. All participants provided informed consent and were paid for their participation. Participants ranged in age from 19 to 45 years (median = 25.5 years). All participants were right-handed (assessed using the Edinburgh Handedness Inventory; Oldfield, 1971) and were native speakers of English with normal or corrected-to-normal vision.

Procedure

The experiment was conducted in the KIT/NYU facility at New York University. Before recording, the head shape of each participant was digitized to allow source localization and coregistration with structural MRIs. We also digitized three fiducial points (the nasion and the left and right preauricular points) and the position of five coils, placed around the participant's face. Once the participant was situated in the magnetically shielded room for the experiment, the position of these coils was localized with respect to the MEG sensors, allowing us to assess the position of the participant's head for source reconstruction. Data were recorded continuously with a 157-channel axial gradiometer (Kanazawa Institute of Technology, Kanazawa, Japan). Structural MRIs were obtained for 15 of the 16 participants; the MEG data from one participant were thus eliminated from analysis because of failure to obtain a structural MRI.

Before the experiment, participants were not given any indication of the goal of the experiment or the properties of the materials. The exact instructions were as follows: "You will read two letter strings on the screen, one at a time. If the second string is a real English word, respond with your index finger. If it is not, respond with your middle finger." Each participant saw all 474 items. The order of presentation was randomized for each participant individually. The assignment of items to conditions was fixed across participants; in other words, the same nouns were replaced with nonwords for all participants (see Materials for details). A given adjective was always presented with the same noun or nonword; for example, *stainless* was followed by *steel*, and *uncharted* was followed by the nonword *cothenent* (which replaced the predicted continuation *territory*) for all participants.

Stimuli were presented using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and projected onto a screen approximately 50 cm away from the participant. They were presented in white 30-point Courier font on a gray background. The structure of each trial was as follows. First, a fixation cross was presented in the center of the screen for 300 msec, followed by a blank screen presented for 300 msec. The adjective was then presented for 300 msec, followed again by a blank screen presented for 300 msec. Finally, the noun (or nonword) was presented for 300 msec, and participants responded to the latter stimulus by pressing a button.

Preprocessing

The preprocessing and analysis of the MEG data closely followed the procedures of Solomyak and Marantz (2009, 2010). Environmental noise was removed from the data by regressing signals recorded from three orthogonally oriented magnetometers, placed approximately 20 cm away from the recording array, against the recorded data, using the continuously adjusted least squares method (Adachi, Shimogawara, Higuchi, Haruta, & Ochiai, 2001). The data were then low-pass filtered at 40 Hz, resampled to 250 Hz to facilitate analysis, and high-pass filtered at 0.1 Hz. MEG channels in which there was no signal or excessive amounts of noise were interpolated from neighboring channels or rejected (at most three per participant). Trials in which at least one channel showed a peak-to-peak amplitude exceeding 4000 fT were rejected, as these amplitude values are likely to reflect blinks and noise artifacts (the number of rejected trials ranged from 39 to 112, mean = 77.1, median = 77; the minimum number of trials analyzed for a given participant was 362). None of the participants were excluded because of excessive trial rejections.

The MNE software package (Martinos Center MGH, Boston, MA) was used to estimate neuroelectric current strength based on the recorded magnetic field strengths using minimum *l*2 norm estimation (Dale & Sereno, 1993; Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). Current sources were modeled as three orthogonal dipoles spaced approximately 5 mm apart across the cortical surface (Dale et al., 2000), yielding approximately 2500 potential electrical sources per hemisphere. The participants' cortical surfaces were reconstructed based on their structural MRIs using Freesurfer (Martinos Center). The neuromagnetic data were coregistered with the structural MRIs using MNE by first aligning the fiducial points and then using an Iterative Closest Point algorithm to minimize the difference between the scalp and the points defining the head shape of each participant.

The forward solution was calculated for each source using a single-layer boundary element model based on the inner skull boundary. Noise covariance estimates were obtained from a 200-msec baseline period before the presentation of each adjective. Using the grand average of all trials across conditions (i.e., both Word and Nonword trials), the inverse solution was computed to determine the most likely distribution of neural activity. We utilized a free orientation analysis, in which the source orientations were unconstrained with respect to the cortical surface. The resulting source estimates were signed with a positive sign indicating an upward directionality and a negative sign indicating a downward directionality in the coordinate space defined by the head. The estimated activation was normalized into a test statistic by dividing the estimates by their predicted standard error given the noise covariance, yielding signed dynamic statistical parametric maps (dSPMs; Dale et al., 2000). The signal-to-noise ratio parameter, which controls the regularization of the estimates, was set to 1.

Regions and Time Windows of Interest

Main Analysis

ROIs were defined anatomically using the cortical parcellation performed by FreeSurfer on the basis of the Desikan–Killiany gyral atlas (Desikan et al., 2006). We selected the left MTG anatomical ROI (Figure 3A later in the paper) for the purposes of our main analysis. In this and other temporal lobe labels, the Desikan–Killiany atlas includes the gyrus along with the banks of the surrounding sulci. We defined three time windows of interest: adjective lexical access, presented noun lexical access, and preactivation of the expected noun (Figure 3B). The time windows were defined on the basis of the peaks of the M350 evoked response. This component has been argued to be associated with lexical access (Pylkkänen & Marantz, 2003) and has demonstrated sensitivity to lexical variables such as frequency (Embick et al., 2001). Lexical access of the adjective was assessed in a time window starting 100 msec before the peak of the M350 response evoked by the presentation of the adjective and ending 100 msec after the peak (concretely, 242–442 msec after adjective presentation). Likewise, lexical access of the presented noun was assessed in a 200-msec time window centered around the peak of the M350 response to the noun, which was slightly earlier than the response to the adjective (197–397 msec post-noun onset). Finally, we made the simplifying assumption that effects of lexical preactivation would be most evident after lexical access of the adjective was complete. Consequently, the preactivation time window started at the end of the adjective lexical access time window. To avoid including activity evoked by the presented noun, this time window ended at the presentation of the noun (concretely, the time window extended from 442 to 600 msec post-adjective onset) and was therefore somewhat shorter than the two other time windows. All three time windows are illustrated in Figure 3B.

Figure 3B also shows the average left MTG response to the adjective for a four-way split of adjective predictivity as well as the response to the noun for a median split of presented noun predictability. Time-varying correlations (Figure 3C–E) were generated using sliding 50-msec windows centered at [25, 75, …, 575] msec post-adjective onset or post-noun onset.

Supplemental Analyses

We conducted post hoc analyses for two additional anatomical ROIs, which roughly corresponded to significant peaks of activity in the evoked response to the adjective at 300–400 msec (Figure 1A): the left lateral OFC (LOFC; Figure 4A later in the paper) and left superior temporal gyrus (STG) anatomical ROIs. Finally, because previous investigations of predictability showed early effects at the M100 (Dikker & Pylkkänen, 2011; Dikker et al., 2009), we conducted an analysis of early predictability effects in this study, in which we examined the time window 100–200 msec post-noun onset in the MTG; we also examined 10-msec windows centered around the two candidate M100 peaks in the left cuneus anatomical ROI, corresponding to the location of visual cortex within the occipital lobe.

Exploratory Analysis of Left Hemisphere Language Regions

In addition to the main confirmatory ROI analysis, we conducted an exploratory analysis of a broad language network, covering most of the sources located within lateral cortical regions in the left frontal and left temporal lobes. Specifically, we pooled the sources within the following anatomical regions in the left hemisphere, as specified in the Desikan et al. (2006) parcellation: STG, transverse temporal gyrus, banks of the STS, MTG, inferior temporal gyrus, temporal pole, fusiform gyrus, insula,[2] inferior frontal gyrus (pars triangularis, pars opercularis, and pars orbitalis), and LOFC. The analysis was conducted for the average activity in a given source over sliding 100-msec windows centered at [50, 150, …, 550] msec post-adjective onset or post-noun onset. The resulting t maps for the variables of interest are shown in Figures 1B–E and 2B–E; see the next section for details on how those t values were obtained. The figures for the evoked responses to the adjective (Figure 1A) and the noun (Figure 2A) were generated by first morphing

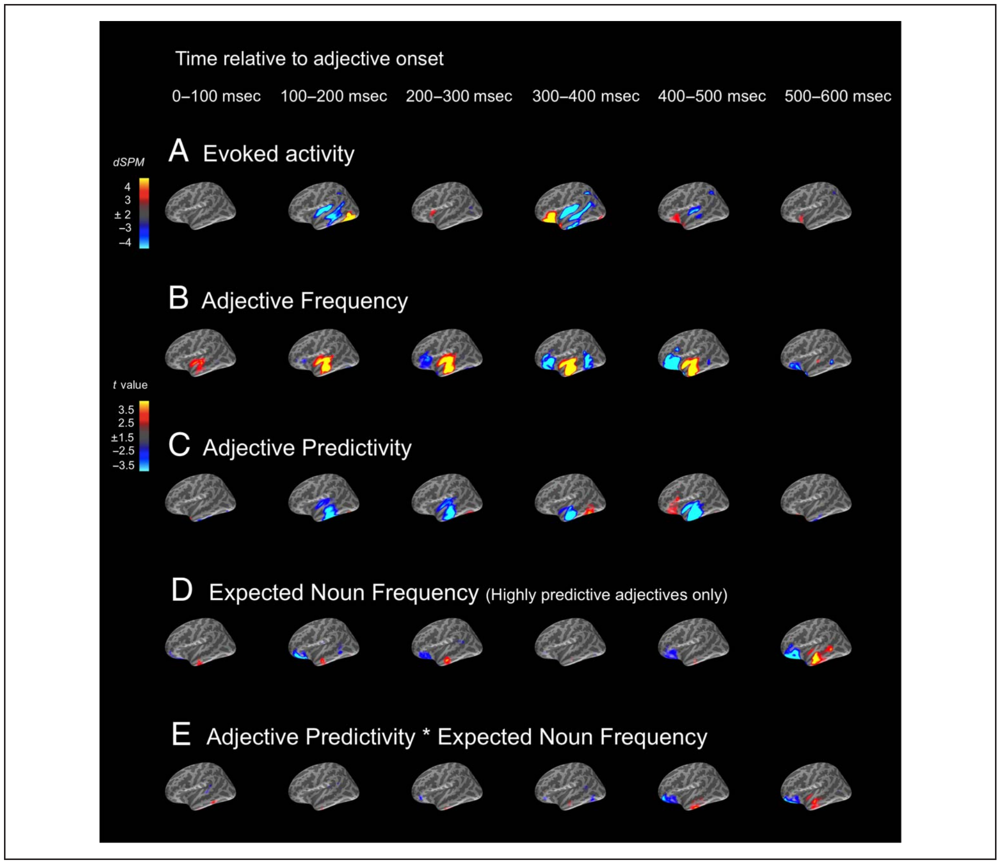


Figure 1. Neural response to the adjective in left hemisphere language areas. (A) The grand-averaged evoked response to the adjective (in dSPM units). (B) The effect of adjective frequency. (C) The effect of adjective predictivity. (D) The effect of expected noun frequency for the items in the top half of adjective predictivity (controlling for adjective frequency and adjective predictivity). (E) The interaction between adjective predictivity and expected noun frequency (controlling for adjective frequency). In B–E, the *t* values represent the results of a second-level *t* test of the within-subject β-coefficients (described more fully in the Methods section). For all images, red and yellow indicate positively signed values, and blue indicates negatively signed values.

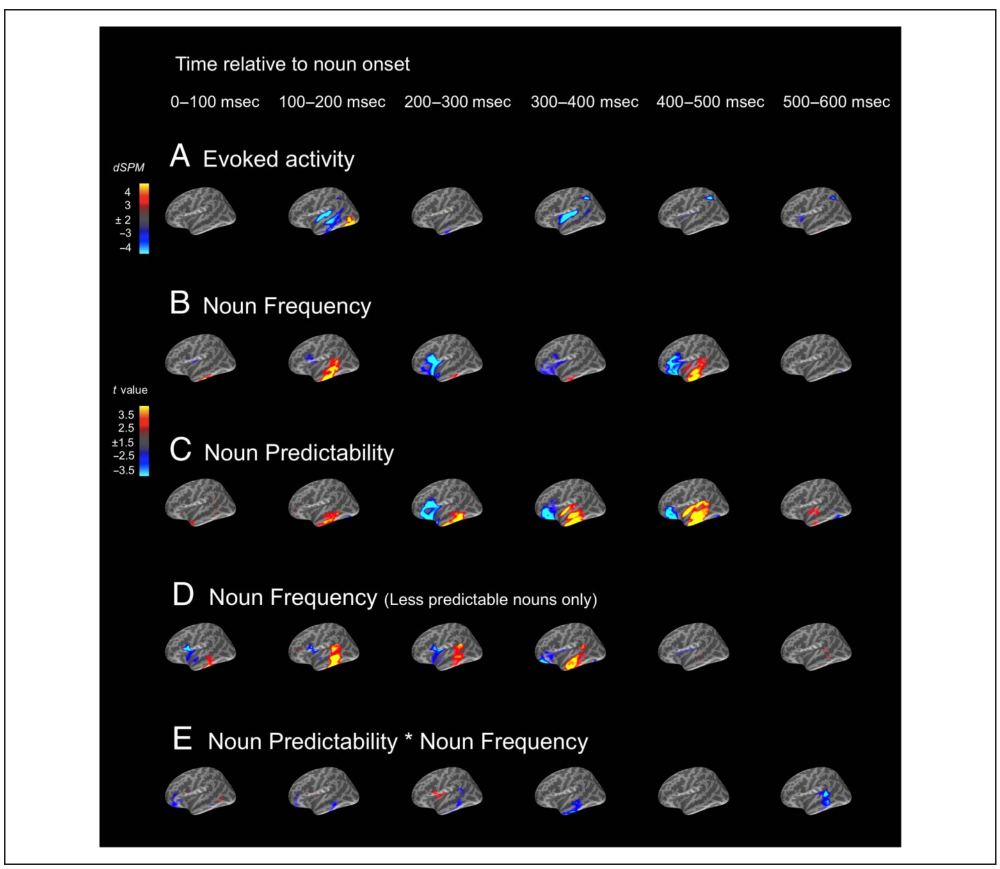


Figure 2. Neural response to the noun in left hemisphere language areas. (A) The grand-averaged evoked response to the noun (in dSPM units). (B) The effect of presented noun frequency. (C) The effect of presented noun predictability. (D) The effect of presented noun frequency for the items in the bottom half of presented noun predictability (controlling for presented noun predictability). (E) The interaction between presented noun predictability and presented noun frequency. In B–E, the *t* values represent the results of a second-level *t* test of the within-subject β-coefficients (described more fully in the Methods section). For all images, red and yellow indicate positively signed values, and blue indicates negatively signed values.

the grand-averaged activity (in dSPM units) for each participant into the neuroanatomical space of the average brain, followed by averaging across all participants; unlike the *t* maps, the evoked responses were calculated for all cortical sources within the left hemisphere.

Statistical Methodology

Behavioral Analysis

After excluding the Nonword trials, we performed a logarithmic transformation of the RTs for the Word trials, following standard practice. For each participant, we excluded trials for which the log-transformed RTs were more than 2.5 standard deviations away from the participant's mean and trials in which the RT was less than 100 msec or more than 5000 msec. We used the *lme4* package in R (Bates, Maechler, & Bolker, 2013) to fit a linear mixed-effects model with crossed random effects for participants and items. Traditional repeated-measures designs account for "random" differences across participants that are irrelevant to the experimental manipulation and therefore enable generalization of results beyond the specific group of participants used in the experiment. Just like participants, linguistic materials may also differ from one another in many ways that are irrelevant to the experimental manipulation. Mixed-effects models with crossed random effects extend the logic of repeated measures to participants and items simultaneously and enable generalization beyond both the sample of participants and the sample of items used in the experiment (Baayen, Davidson, & Bates, 2008). This model was used to predict log-transformed RTs from presented noun predictability and presented noun frequency. We used a maximal random effects structure: for items, only a random intercept, and for participants, random slopes for presented noun predictability and presented noun frequency and their interaction as well as a random intercept. Predictors were centered before being entered into the model. The reported p values are derived from likelihood ratio tests in stepwise regression.

MEG ROI Analyses

Linear mixed-effects models were fitted to the average activity in an ROI over a time window of interest, following rejection of trials with activity at least 4 standard deviations away from the mean across all trials and all participants. The linguistic variables (e.g., frequency) were entered into the models as fixed effects. A maximal random effects structure was used, with random intercepts for participants and items, as well as a random slope for the particular linguistic variable being tested in the model. Predictors were centered before being entered into the models. To obtain the p values for the main effects as well as the significance of the stepwise regressions and interaction effects, likelihood ratio tests were employed for the relevant nested linear mixed-effects models. In many cases, multiple regression was used to address correlations between stimulus variables; for example, the interaction between adjective predictivity and expected noun frequency was tested in a regression model that included adjective frequency as well (i.e., adjective frequency was controlled for).

We analyzed the adjective and the noun time windows separately. All of the trials were included in the analyses of the adjective time window, and only Word trials were included in the analyses of the noun time window (i.e., Nonword trials were excluded).

Exploratory MEG Analysis

Because it was not computationally feasible to conduct the full mixed-effects analysis for each source individually, we employed a summary statistic approach (Holmes & Friston, 1998), as follows. For a given participant's data, at each source and during each time window, we computed the β-coefficient from a linear regression model predicting the source activity (in dSPM units) as a function of the linguistic variable of interest (e.g., frequency). We then morphed the resulting maps of the β-coefficients from each participant's neuroanatomical space to the space of the average brain using seven iterative smooth steps. Because the a priori selection of the MTG anatomical ROI allowed us to establish the significance of the effects in the main analysis, we did not correct the resulting *t* maps for multiple comparisons across sources. Consequently, the *t* maps should not be used to determine the significance of the effects, but rather to verify their general spatial distribution.

RESULTS

Behavioral Results

Accuracy ranged from 95% to 99% (median = 97.9%). Mean RTs ranged from 491 to 1057 msec (median = 735 msec).

Both presented noun predictability and presented noun frequency were inversely correlated with RTs (predictability: $\beta = -.012$; frequency: $\beta = -.02$). Both variables were significant in stepwise regressions (predictability: $p = .007$; frequency: $p = .002$). The interaction between the variables did not reach significance ($\beta = -.0004, p = .88$). Adding trial number to the regression model revealed that participants became significantly slower over the course of the experiment ($\beta = .0002$, $p = .002$). This effect did not interact with either predictability or frequency (predictability: $p = .6$; frequency: $p = .8$). There is therefore no evidence that participants modified their prediction strategy over the course of the experiment. Finally, a logistic mixed-effects model showed that accuracy was marginally higher on high frequency nouns ($\beta = .3, p = .09$) and did not vary based on predictability.

Discrepancy Trials

To see whether the discrepancy between the predicted noun and the presented noun affected RTs, we conducted a separate analysis restricted to those Word trials in which the presented noun was not the most predictable continuation for the given adjective ("discrepancy trials"). The number of trials included in this analysis was roughly a quarter of the total trials in the experiment, because we eliminated all Nonword trials as well as Word trials in which the presented noun was the most predictable continuation for the adjective; thus, the statistical power for this particular analysis is lower than other analyses in this study.

As in the complete set of Word trials, higher predictability and presented noun frequency were associated with shorter RTs (frequency: $\beta = -.019, p = .004$; predictability: $\beta = -.02, p = .01$), and there was no interaction between the two ($p = .93$). There was a marginal positive effect of adjective predictivity on RTs ($\beta = .016, p = .05$), indicating that recognition of a noun is slowed down by the presence of a conflicting prediction for a different noun.

MEG Results: Evoked Response

The grand-averaged evoked responses to the adjective and the noun are shown from lateral perspectives in Figures 1A and 2A, respectively. There is widespread negative activity (shown in blue) within the left temporal lobe, particularly at 300–400 msec post-adjective onset, as well as a significant patch of positive activity (shown in red and yellow) within the left inferior frontal cortex, mostly overlapping with the LOFC ROI, at 300–400 msec post-adjective onset.

Figure 3B displays the time course of average activity within the left MTG, for the adjective and noun time windows. The second negative peak in the adjective time window (i.e., the M350 response to the adjective) occurs at a latency of roughly 350 msec post-adjective onset, whereas the second negative peak in the noun time window (i.e., the M350 response to the noun) occurs at a latency of roughly 300 msec post-noun onset.

MTG ROI Analysis

Main Effects

In the adjective lexical access time window, higher adjective frequency was associated with weaker activity in the left MTG ($t = 2.94, p = .004$; Figure 3C).[3] Higher adjective predictivity was associated with stronger activity in the same region and time window ($t = -3.74, p = .0007$).[4] Because of the high correlation between adjective frequency and adjective predictivity ($r = -.59$), we assessed the significance of each variable in a stepwise regression with the other variable. Using this procedure, only adjective predictivity remained significant ($\chi^2 = 5.96, p = .01$).

In the presented noun lexical access time window, after exclusion of the Nonword trials, higher presented noun frequency was associated with weaker left MTG activity ($t = 2.04, p = .05$). Higher presented noun predictability led to significantly weaker activity in the left MTG in the same time window ($t = 4.66, p = .0002$). In a stepwise regression, only presented noun predictability remained significant ($\chi^2 = 12.30, p = .0005$).

In summary, adjectives that license a relatively strong prediction evoked increased left MTG activity in the adjective lexical access time window; less predictable nouns evoked increased activity in the presented noun lexical access time window.

Interaction Effects

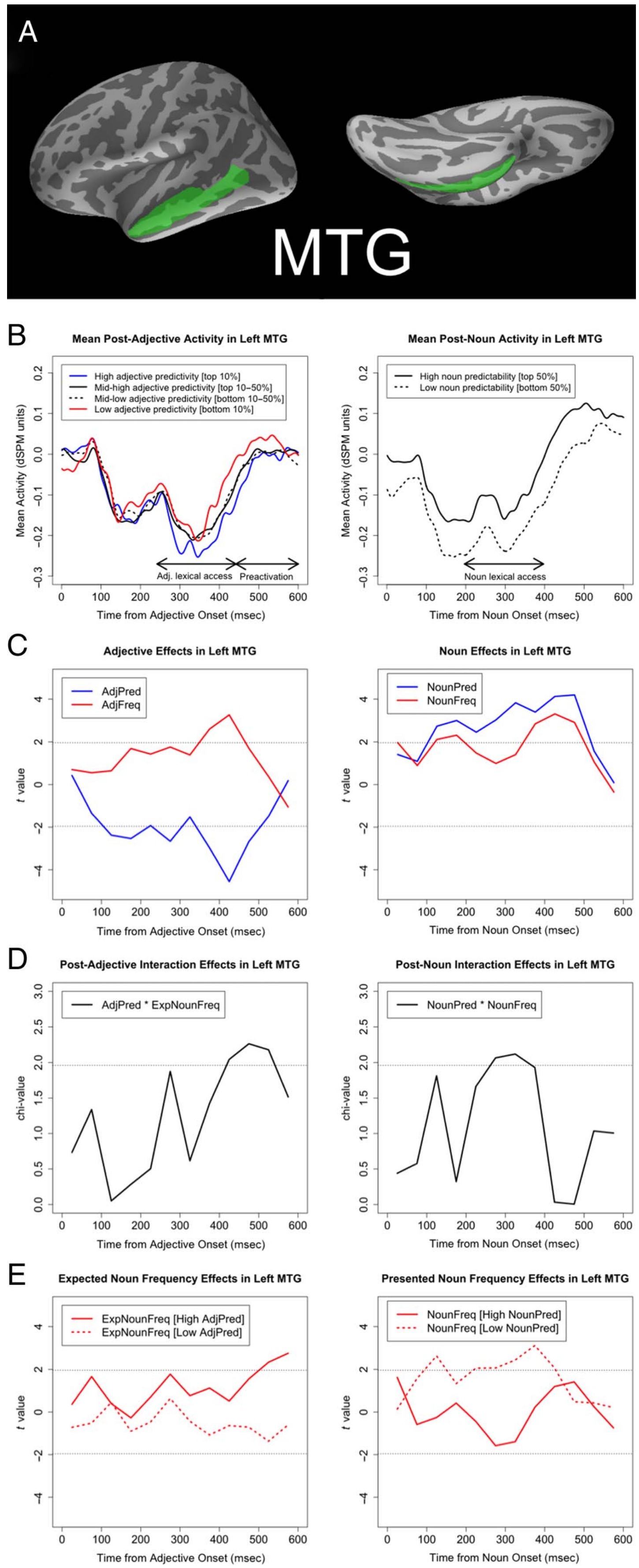
In the preactivation time window, adjective predictivity and expected noun frequency interacted in the left MTG ($\chi^2 = 5.73, p = .02$, controlling for adjective frequency; see Figure 3D). A median split on adjective predictivity (Figure 3E) indicated that this interaction was driven by the fact that higher expected noun frequency led to significantly weaker activity, but only for the items in the top half of adjective predictivity ($t = 2.43, p = .02$, controlling for both adjective frequency and adjective predictivity). Adding weighted expected noun frequency to the model increased the fit somewhat, although the difference did not reach significance ($\chi^2 = 2.29, p = .13$). The items in the bottom half of adjective predictivity showed no effect of expected noun frequency ($t = -1.08, p = .28$, controlling for adjective frequency and adjective predictivity).

In the presented noun lexical access time window, there was a significant interaction between presented noun predictability and presented noun frequency in the left MTG ($\chi^2 = 6.51, p = .01$; see Figure 3D). A median split on presented noun predictability (Figure 3E) indicated that this interaction was driven by significantly weaker activity in response to higher-frequency presented nouns, but only for the items in the bottom half of presented noun predictability ($t = 3.05, p = .006$, controlling for presented noun predictability). The items in the top half of presented noun predictability showed no effect of presented noun frequency ($t = -0.94, p = .35$, controlling for presented noun predictability).

Discrepancy Trials

We again conducted a separate analysis of Word trials in which the presented noun was not the most expected

Figure 3. Left MTG ROI analysis. (A) ROI: The MTG ROI, displayed in green on the average brain, from lateral and ventral perspectives. (B) Average activity: On the left, the average response in the MTG to the adjective for high (top 10%: blue line), mid-high (top 10–50%: solid black line), mid-low (bottom 10–50%: dotted black line), and low (bottom 10%: red line) adjective predictivity. On the right, the average response in the MTG to the noun for the top half (solid black line) and bottom half (dotted black line) of presented noun predictability. Horizontal lines with arrows indicate the time windows of interest for the ROI analyses. (C) Main effects: On the left, the effects of adjective predictivity (blue) and adjective frequency (red) during the adjective time window. On the right, the effects of presented noun predictability (blue) and presented noun frequency (red) during the noun time window. (D) Interaction effects: On the left, the interaction between adjective predictivity and expected noun frequency (controlling for adjective frequency) during the adjective time window. On the right, the interaction between presented noun predictability and presented noun frequency during the noun time window. (E) Binned analyses: On the left, the effect of expected noun frequency (controlling for adjective frequency and adjective predictivity) during the adjective time window for the top half (solid red line) and bottom half (dotted red line) of adjective predictivity. On the right, the effect of presented noun frequency (controlling for presented noun predictability) during the noun time window for the top half (solid red line) and bottom half (dotted red line) of presented noun predictability. The dotted black lines in C–E represent the level of correlation needed to reach statistical significance at $p = .05$ (uncorrected).



one. In the presented noun lexical access time window, there was no effect of adjective predictivity ($t = -0.95$, $p = .35$, controlling for presented noun predictability). We repeated the analysis in the later time window 300–500 msec, which we selected post hoc to more accurately capture the peak of the presented noun predictability effect. In this time window, higher adjective predictivity was associated with greater MTG activity ($t = -2.00$, $p = .05$, controlling for presented noun predictability); this effect did not reach significance; however, when presented noun frequency was included in the model as well ($t = -1.60$, $p = .11$). There is therefore some neural evidence for an opposing effect of a violated strong prediction, relative to the effect of presented noun predictability.

Removal of High Valence Items

Because our phrase selection process was automatic, our final set of materials included some phrases with high valence (e.g., *rectal exam*). To rule out the possibility that some of our effects were due to the presence of these high valence phrases, we manually eliminated 18 phrases (denoted with asterisks in the Appendix) that we judged to contain a high valence adjective or noun and subsequently repeated our primary MTG analyses without these items. In the adjective lexical access time window, adjective frequency ($t = 2.71$, $p = .008$) and adjective predictivity ($t = -3.66$, $p = .001$) remained significant. In the preactivation time window, there was a significant interaction of adjective predictivity and expected noun frequency ($\chi^2 = 5.97$, $p = .01$, controlling for adjective frequency); this interaction was driven by a significant effect of expected noun frequency for the items in the top half of adjective predictivity ($t = 2.78$, $p = .01$, controlling for adjective frequency and adjective predictivity).

In the presented noun lexical access time window, presented noun frequency was below significance ($t = 1.70$, $p = .10$), although presented noun predictability remained highly significant ($t = 4.15$, $p = .0006$). The interaction of presented noun frequency and presented noun predictability remained significant ($\chi^2 = 4.37$, $p = .04$), driven by a significant effect of presented noun frequency for the items in the bottom half of presented noun predictability ($t = 2.81$, $p = .01$, controlling for presented noun predictability). In summary, all of the effects in the MTG survived the removal of the high valence items, with the exception of the presented noun frequency effect, which dipped below the significance threshold.

Post hoc ROI Analyses

STG

Given the significant patch of negative activity in the left STG at 300–400 msec (Figures 1A and 2A) as well as the role of this region in the language network (e.g., Friederici, 2012), we conducted a post hoc analysis of activity in this region.

In the adjective lexical access time window, there were significant effects of adjective frequency ($t = 3.59$, $p = .002$) and adjective predictivity ($t = -2.22$, $p = .04$). Both effects were in the same direction as those found in the MTG; the frequency effect was slightly stronger, and the predictivity effect was slightly weaker than in the MTG. In the preactivation time window, there was no significant interaction between adjective predictivity and expected noun frequency ($\chi^2 = 1.93$, $p = .16$, controlling for adjective frequency). Furthermore, there was no significant effect of expected noun frequency for the items in the top half of adjective predictivity ($t = 1.08$, $p = .29$, controlling for adjective frequency and adjective predictivity).

In the presented noun lexical access time window, there was no effect of presented noun frequency ($t = 0.28$, $p = .78$), and the effect of presented noun predictability was marginally significant ($t = 1.88$, $p = .07$). There was no interaction of presented noun frequency and presented noun predictability ($\chi^2 = 0.19$, $p = .67$) and no effect of presented noun frequency for the items in the bottom half of presented noun predictability ($t = 0.80$, $p = .43$, controlling for presented noun predictability). In summary, most of the effects in this region are either similar to or weaker than the effects in the left MTG, supporting the selection of the latter region as our central ROI.

LOFC

Within the frontal lobe, the region that is traditionally associated with language processing is the left inferior frontal gyrus (IFG), which includes Broca's area (e.g., Friederici, 2012). However, the patch of positive evoked activity in the frontal lobe at 300–400 msec post-adjective onset (Figure 1A) did not localize to the IFG and instead overlaps almost entirely with the left LOFC (see Figure 4A). We therefore report a post hoc analysis of the activity in that anatomical region rather than the IFG.

The evoked response in the LOFC (Figure 4B) shows a prominent positive peak at roughly 350–400 msec following word presentation; correspondingly, the direction of the presented noun predictability effect is such that activity is more negative for the high predictability condition. Thus, the sign of the correlation with presented noun predictability is negative, as opposed to the effects in the MTG and STG, which were positive; the latter point follows from the fact that a negative correlation with a positive peak indicates a weakening of activity, whereas a negative correlation with a negative peak indicates a strengthening of activity.

In the adjective lexical access time window, higher adjective frequency was associated with weaker LOFC activity ($t = -2.56$, $p = .01$; Figure 4C), but there was no

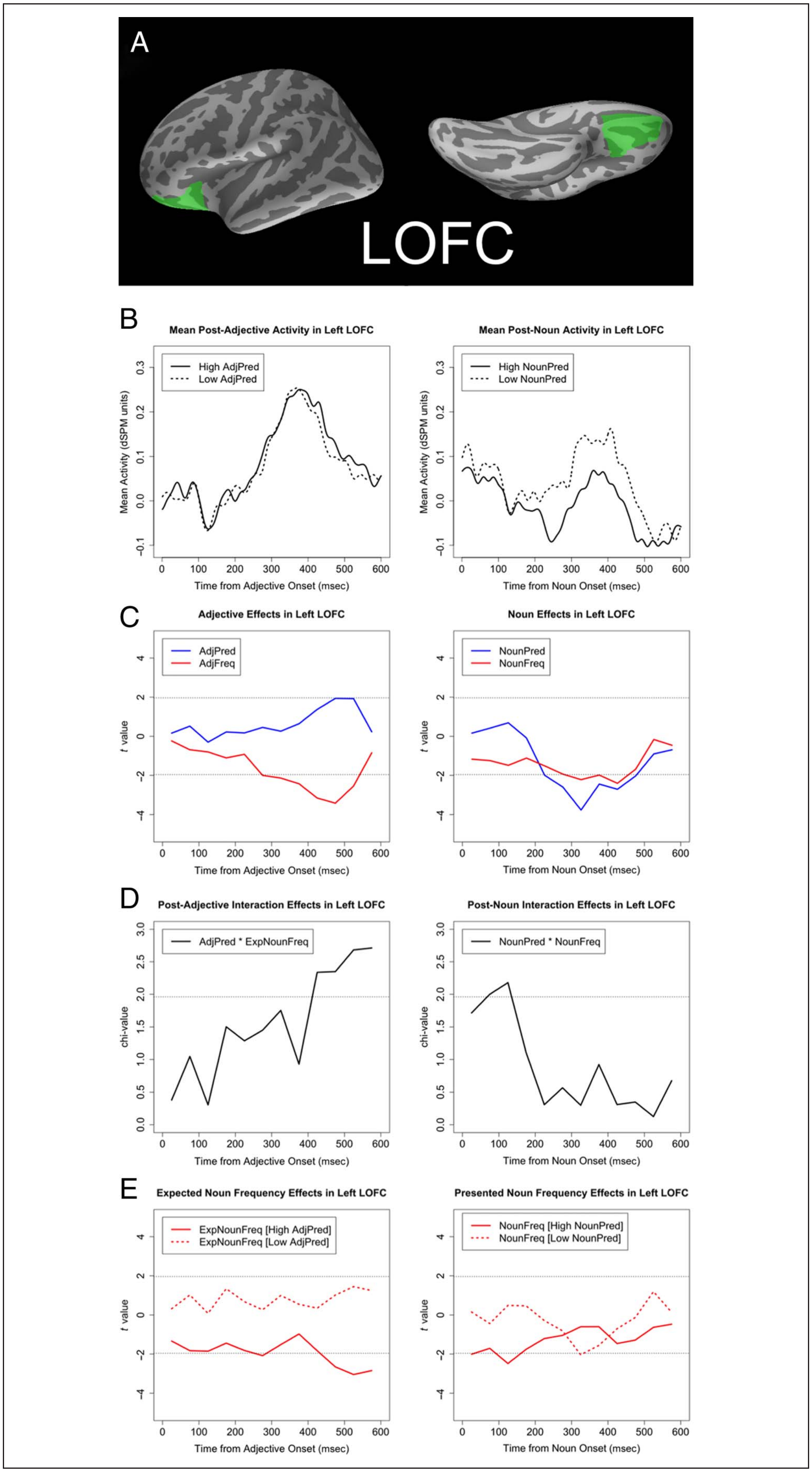


Figure 4. Left LOFC post hoc ROI analysis. (A) ROI: The LOFC ROI, displayed in green on the average brain, from lateral and ventral perspectives. (B) Average activity: On the left, the average response in the LOFC to the adjective for the top half (solid black line) and bottom half (dotted black line) of adjective predictivity. On the right, the average response in the LOFC to the noun for the top half (solid black line) and bottom half (dotted black line) of presented noun predictability. (C) Main effects: On the left, the effects of adjective predictivity (blue) and adjective frequency (red) during the adjective time window. On the right, the effects of presented noun predictability (blue) and presented noun frequency (red) during the noun time window. (D) Interaction effects: On the left, the interaction between adjective predictivity and expected noun frequency (controlling for adjective frequency) during the adjective time window. On the right, the interaction between presented noun predictability and presented noun frequency during the noun time window. (E) Binned analyses: On the left, the effect of expected noun frequency (controlling for adjective frequency and adjective predictivity) during the adjective time window for the top half (solid red line) and bottom half (dotted red line) of adjective predictivity. On the right, the effect of presented noun frequency (controlling for presented noun predictability) during the noun time window for the top half (solid red line) and bottom half (dotted red line) of presented noun predictability. The dotted black lines in C–E represent the level of correlation needed to reach statistical significance at $p = .05$ (uncorrected).

main effect of adjective predictivity ($t = 0.72, p = .48$). In the preactivation time window, there was a significant interaction of adjective predictivity and expected noun frequency ($\chi^2 = 7.19, p = .007$, controlling for adjective frequency; Figure 4D); this interaction was driven by the fact that higher expected noun frequency led to weaker activity, for the items in the top half of adjective predictivity ($t = -3.21, p = .003$, controlling for adjective frequency and adjective predictivity; Figure 4E). Adding weighted expected noun frequency to the model marginally improved the fit ($\chi^2 = 3.37, p = .07$).

In the presented noun lexical access time window, higher presented noun frequency was associated with marginally weaker LOFC activity ($t = -1.96, p = .06$; Figure 4C), and higher presented noun predictability was associated with significantly weaker activity ($t = -2.98, p = .008$). There was no interaction of presented noun frequency and presented noun predictability ($\chi^2 = 0.004, p = .95$; Figure 4D), and there was no significant effect of presented noun frequency for the items in the bottom half of presented noun predictability ($t = -1.31$, $p = .19$, controlling for presented noun predictability; Figure 4E).

In summary, most of the variables had similar effects on LOFC activity as they did on MTG activity (though with opposite signs, as discussed earlier), with the exception of the main effect of predictivity in the adjective lexical access time window and the interaction between presented noun frequency and predictability in the presented noun lexical access time window, which were found in the MTG but not the LOFC.

Early Predictability Effects

To determine whether there was an early effect of presented noun predictability in the MTG, we analyzed the time window 100–200 msec post-noun onset. This time window indeed showed a significant effect of presented noun predictability ($t = 3.29, p = .002$). Given the possibility of spillover from the earlier effect of adjective frequency in this region, we also ran a stepwise regression with adjective frequency and presented noun frequency; in this model, presented noun predictability was no longer significant ($\chi^2 = 1.22, p = .27$). However, it is difficult to interpret the latter fact in light of the high correlation of adjective frequency and presented noun predictability ($r = -.71$), which would serve to reduce the effects of each variable when present in the same model. In summary, there is somewhat inconclusive evidence for early predictability effects in the MTG after noun presentation.

The evoked activity in the left cuneus, roughly overlapping with the location of visual cortex in the occipital lobe, showed a negative peak at 76 msec, followed by a positive peak at 136 msec post-noun onset. Following the M100 analysis in Dikker and Pylkkänen (2011), we analyzed 10-msec windows centered around both peaks.[5] In addition to noun predictability, we tested for an effect of noun length to validate our selection of visual ROI (under the assumption that early visual processing should be sensitive to visual form properties, such as word length). For the time window around the earlier peak, there was no effect of presented noun predictability ($t = 0.53, p = .60$, for the time window 71–81 msec post-noun onset), but higher presented noun length was associated with stronger activity ($t = -2.52, p = .02$). For the time window around the later peak, higher presented noun predictability was associated with marginally weaker activity ($t = -1.87, p = .06$, for the time window 131–141 msec post-noun onset), and higher presented noun length was associated with stronger activity ($t = 2.74, p = .01$). In a stepwise regression with presented noun length, the effect of presented noun predictability dipped further below significance ($\chi^2 = 1.71$, $p = .19$). The evidence in our data for visual predictability effects is therefore inconclusive, although suggestive.

Exploratory Analysis of Language Areas

Figures 1 and 2 display the results of the exploratory analysis of language areas for the response to the presentation of the adjective and noun, respectively. Many of the patterns observed within the ROI results are visible in the present analysis: (i) there are positive effects of adjective frequency (Figure 1B) and presented noun frequency (Figure 2B) within the mid-anterior temporal lobe and corresponding negative effects in the LOFC, both peaking at 400–500 msec after the presentation of the each word; (ii) the effects of adjective predictivity (Figure 1C) and presented noun predictability (Figure 2C) have opposite directionalities, and in particular, there is a negative effect of adjective predictivity and a positive effect of presented noun predictability, peaking at 400–500 msec in the temporal lobe; (iii) the preactivation effect—the effect of expected noun frequency in response to the highly predictive adjectives at 500–600 msec post-adjective onset (Figure 1D)—displays a strikingly similar spatial distribution to both the earlier effect of adjective frequency at 400–500 msec post-adjective onset as well as the later effect of presented noun frequency at 400–500 msec post-noun onset; and finally, (iv) the preactivation effect peaks at 500–600 msec, although the effects of adjective frequency and adjective predictivity are no longer visible at that latency, suggesting that these effects are distinct from each other.

DISCUSSION

This study set out to characterize the neural signal corresponding to lexical preactivation. MEG activity was recorded while participants performed a lexical decision task on the second word of visually presented adjective–noun phrases (e.g., *stainless steel*). The behavioral results showed that predictable and frequent nouns were recognized faster, replicating previous results (Fischler & Bloom, 1979; Whaley, 1978; Rubenstein et al., 1970, and many others). Neurally, lexical preactivation manifested in increased activity: During the adjective time window, left MTG activity was greater for predictive adjectives (e.g., *stainless*, which is predictive of *steel*). Later, during the noun time window, left MTG activity was significantly reduced for predictable nouns (e.g., *steel*, which is a predictable continuation of *stainless*).

These results are consistent with the previously observed association of the left MTG with lexical access (Friederici, 2012; Hickok & Poeppel, 2007) as well as with the predictive coding hypothesis, according to which predictive processing modulates the same region implicated in bottom–up processing of a stimulus (Egner et al., 2010; Friston, 2005). Moreover, these results indicate that the nature of this predictive processing is such that neural activity is increased at the point at which a specific prediction is generated, whereas activity is reduced at the point at which the prediction is verified; this corroborates the findings of Dikker and Pylkkänen (2013), in which activity in a left middle temporal ROI (among other regions) was increased during the generation of a specific lexical prediction based on a presented picture and reduced when such predictions were satisfied by the presentation of the expected word.

In this study, the left MTG displayed a significant interaction between adjective predictivity and expected noun frequency in what we termed the preactivation time window (~450–600 msec post-adjective onset). This interaction was driven by a significant effect of expected noun frequency for predictive adjectives (e.g., *stainless,* which is predictive of *steel*), but not for less predictive adjectives (e.g., *important*, which is not predictive of any particular noun). Later, in what we termed the presented noun lexical access time window (~200–400 msec post-noun onset), there was a significant interaction between presented noun frequency and presented noun predictability, driven by a significant effect of presented noun frequency for less predictable nouns only (e.g., *clue* in *important clue*).

These results suggest that participants not only preactivated the likely continuations for predictive adjectives before presentation of any noun, but that this preactivation was sensitive to the frequency of the expected noun. By contrast, in the case of less predictive adjectives, participants waited until the presentation of the noun to access the appropriate lexical representation. This evidence for preactivation argues against the strong form of the integration theory of predictability effects, according to which predictable words are easier to process not because any prediction has taken place before they are read but solely because they are easier to integrate into an existing semantic representation (Norris, 1986). It is still possible that *some* of the effects of predictability can be attributed to greater ease of integration, but our results, in conjunction with form prediction effects (Dikker & Pylkkänen, 2011; DeLong et al., 2005), suggest that ease of integration cannot be the whole story (see also Smith & Levy, 2013).

The fact that a word's frequency could modulate neural activity before its presentation raises the question of how to understand such an effect within the explanatory frameworks used to understand word frequency effects more generally. Rational models of reading (Smith & Levy, 2008, 2013; Norris, 2006) emphasize the influence of predictability on word recognition. Within such a framework, readers optimize their behavior on the basis of their estimates for the likelihood of upcoming words. In the absence of context, word frequency is taken as the baseline expectation for encountering a word. Given the presentation of a high-frequency (or highly predictable) word, a reader might require less perceptual evidence to decide on its identity (Norris, 2006) or less processing time because of prior preparation (Smith & Levy, 2008). One important implication of this approach to word recognition is that unconditional word frequency should be irrelevant when a word is highly predictable from context. Consistent with this hypothesis as well as with prior EEG findings (Dambacher et al., 2006; Van Petten & Kutas, 1990), we found that the response in the MTG to a presented noun was only modulated by its frequency when the noun was a less predictable continuation of the preceding adjective. In summary, our main effects of predictability, as well as the reduction in frequency effects for predictable nouns, largely validate the rational models' emphasis on predictability as the central determinant of reading behavior.

However, although the pervasive effects of predictability indeed suggest that the rational models are on the right track, a strict interpretation of such a model proposes that frequency effects should be *entirely* accounted for by predictability (Smith & Levy, 2008), a position that is inconsistent with our finding of frequency effects for anticipated nouns before their presentation. Instead, these results suggest that frequency effects are associated with the very process of lexical access itself. Although it is not immediately obvious how to account for this phenomenon within the framework of the rational models, several prominent models within the psycholinguistic literature crucially predict this phenomenon. For example, according to Morton's (1969) Logogen model, word frequency determines the resting level of activation for a lexical item; similarly, according to Forster's (1976) Serial Search model, the lexicon is composed of frequency-ordered bins. Thus, our experiment can be seen as providing some new evidence for a long-held view within the psycholinguistic literature, in which frequency effects arise because of the architecture of the lexicon.

The language production literature suggests another intriguing interpretation of the effect of expected noun frequency. A family of recent models argues that lexical prediction employs some of the same mechanisms as language production (Dell & Chang, 2014; Federmeier, 2007; Pickering & Garrod, 2007). For example, older adults with high verbal fluency scores show stronger prediction effects than those with lower fluency scores, suggesting that predicted words may be actively generated using the language production system (Federmeier, McLennan, Ochoa, & Kutas, 2002). Frequency effects in production have been extensively documented (Strijkers, Costa, & Thierry, 2010; Kittredge, Dell, Verkuilen, & Schwartz, 2008; Jescheniak & Levelt, 1994; Oldfield & Wingfield, 1965). These effects seem to arise both at the form level and at the semantic level (Kittredge et al., 2008); information at both of these levels needs to be accessed to generate form predictions (Dikker & Pylkkänen, 2011) and semantic feature predictions (Federmeier & Kutas, 1999). The expected noun frequency effects in our experiment may therefore reflect the retrieval of the predicted concept, the retrieval of the orthographic form associated with it, or both.

Our main analysis focused on the left MTG, based on research implicating it in semantic and lexical access (Friederici, 2012). Exploratory analysis of left hemisphere language areas showed that effects generally localized to an anterior section of the temporal lobe (cf. Lau, Weber, Gramfort, Hämäläinen, & Kuperberg, 2014, who reported a similar location for the effects of lexical–semantic prediction), as well as to a portion of the inferior frontal lobe. Post hoc ROI analyses also confirmed effects of the variables of interest in regions outside the MTG: a temporal region, the STG, and a prefrontal region, the LOFC. The STG is standardly assumed to be part of the language network; the effects in that region were qualitatively similar to, though weaker than, the effects we found in the MTG. The prefrontal effects are consistent with the role of the pFC in anticipatory processing (Dikker & Pylkkänen, 2013; Bar, 2007). Somewhat unexpectedly, the prefrontal effects localized to LOFC rather than to the IFG, which is the prefrontal region more commonly associated with the language network. It is possible that the spatial distribution of the prefrontal effects may be due to a source localization error. However, a recent MEG study, using the same source space analysis methodology as this study, found effects of a semantic variable at ~300–500 msec in the LOFC (Fruchter & Marantz, 2015); moreover, a different analysis technique has localized prefrontal lexical prediction effects to ventromedial pFC (Dikker & Pylkkänen, 2013), which is closer to LOFC than to IFG. Multimodal recordings might be able to shed light on the precise localization of this effect. Finally, post hoc analysis revealed equivocal evidence for early (~100–200 msec) presented noun predictability effects within the MTG and the left cuneus, consistent with previous findings of lexical predictability effects in early sensory responses (Kim & Lai, 2012; Dikker & Pylkkänen, 2011), although the early effects reported here did not reach statistical significance when control variables were included in the regression models.

There are further aspects of our study that remain open as future avenues of investigation. We quantified the predictability of the second word in a phrase via corpus TP. It is an open question how closely this corpus measure would relate to an empirically derived cloze probability measure, the traditional stand-in for predictability (see Smith & Levy, 2011, for a comparison of sentential cloze probabilities with corpus measures of predictability). In particular, any interpretation of a TP effect confounds prediction based on raw co-occurrence statistics with prediction based on semantics and world knowledge (Frisson, Rayner, & Pickering, 2005). Although not easily distinguishable in this study, the potentially independent effects of these two sources of information could be investigated in a future study.

In this study, participants performed a lexical decision after each phrase. This task, although a useful tool to ensure that participants are paying attention to the materials, may have engaged conscious prediction strategies that are not recruited during naturalistic language comprehension (Neely, 1991). A conscious prediction strategy, developed over the course of the experiment, would likely manifest as an increased effect of predictability in later trials compared to earlier ones; such an effect was not observed. Nevertheless, it is worth investigating whether the effects reported here would generalize to a more ecologically valid paradigm, such as a passive reading task.

Finally, the primary index of preactivation in our study was the frequency of the most likely noun continuation. Clearly, there is reason to suspect that readers might predict more than a single possible continuation. A preliminary step toward addressing this possibility was taken in this study; the weighted average of the frequencies of possible continuations was shown to slightly improve the model fit relative to the frequency of the single most likely continuation, although this difference did not reach statistical significance. The latter point provides some tentative evidence in favor of a richer conceptualization of lexical preactivation. Hopefully, future work will serve to further characterize the nature of such preactivation, particularly the extent to which possible continuations are preactivated in proportion to their conditional probability given the preceding context.

Conclusion

This study used MEG to probe the neural signals that correspond to the generation of a lexical prediction, using minimal adjective–noun phrases such as *stainless steel*. We observed an increase in activity in the left MTG in response to the presentation of more highly predictive adjectives (e.g., *stainless*). Later, though still before the presentation of the noun, neural activity was modulated by the frequency of the predicted noun (*steel*). Correspondingly, when the noun was later presented, predictable nouns elicited weaker neural activity than unpredictable ones.

APPENDIX. List of Stimuli and Associated TPs (before Logarithmic Transformation)

Adjective	*Noun*	*TP*
unsalted	butter	.845
stainless	steel	.824
barbed	wire	.793
umbilical	cord	.663
iced	tea	.575
soapy	water	.539
renewable	energy	.523
pubic	hair*	.521
undivided	attention	.453
untimely	death*	.423
concerted	effort	.421
immune	system	.395
salivary	gland	.389
airtight	container	.378
soy	sauce	.372
rheumatic	fever	.355
runny	nose	.354
watchful	eye	.346
mental	health	.311
sour	cream	.307
uncharted	territory	.307
cervical	cancer*	.306
taxable	income	.303
cloudless	sky	.302
ballistic	missile	.294
unborn	child	.289
prickly	pear	.278
thankless	job	.271
soluble	fiber	.268
martial	law	.262
powdered	sugar	.260
eminent	domain	.245
high	school	.240
toothy	grin	.239
magnetic	field	.233
leaded	glass	.232
crude	oil	.224
jobless	rate	.223

APPENDIX. (*continued*)

Adjective	*Noun*	*TP*
residual	limb	.221
vast	majority	.217
bilingual	education	.214
septic	tank	.211
everyday	life	.208
rectal	exam*	.206
cellular	phone	.205
anaerobic	digestion	.203
hallowed	ground	.200
marital	status	.199
slippery	slope	.199
oncoming	traffic	.197
catalytic	converter	.193
salutary	effect	.184
habitable	zone	.184
bearded	man	.182
digestive	tract	.179
foreign	policy	.168
illicit	drug	.165
auditory	canal	.162
deviant	behavior	.161
unholy	alliance	.159
uncanny	ability	.152
allergic	reaction	.152
husky	voice	.152
wooded	area	.151
breakneck	pace	.151
pivotal	role	.150
angular	momentum	.150
abdominal	pain	.144
elective	office	.144
daunting	task	.143
incurable	disease	.141
facial	nerve	.140
saline	solution	.140
empirical	evidence	.138
impartial	spectator	.137
floppy	disk	.135
lethal	injection*	.134

APPENDIX. *(continued)*

Adjective	*Noun*	*TP*
negligent	homicide*	.131
crusty	bread	.131
electoral	college	.127
outer	space	.124
virtual	reality	.118
lifeless	body*	.116
unskilled	labor	.115
royal	family	.115
boneless	pork	.112
fictional	world	.110
humid	air	.109
custodial	parent	.108
stormy	weather	.107
evasive	action	.104
indecent	exposure	.101
sore	throat	.099
intrinsic	value	.099
unwed	mother	.098
tropical	storm	.098
bald	head	.098
timely	manner	.098
coercive	power	.097
artistic	director	.096
unmarked	car	.096
leaky	roof	.095
hind	leg	.095
domestic	violence*	.095
frontal	lobe	.094
populous	country	.093
infinite	number	.092
vicious	cycle	.091
sluggish	economy	.091
thorny	issue	.090
exclusive	interview	.089
nasal	cavity	.089
offensive	line	.089
bacterial	infection	.087
rapid	growth	.087
doctoral	degree	.086

APPENDIX. *(continued)*

Adjective	*Noun*	*TP*
undue	burden	.086
postwar	period	.084
unsolved	murder*	.083
cerebral	cortex	.082
nonprofit	group	.082
honorary	doctorate	.082
cubic	foot	.081
radial	velocity	.080
aerobic	fitness	.080
disabled	list	.079
schematic	diagram	.079
keen	interest	.078
imminent	danger	.077
glacial	ice	.075
sane	person	.075
teenage	girl	.074
periodic	table	.074
outspoken	critic	.073
minor	league	.073
lunar	surface	.073
naval	base	.072
traumatic	event	.072
unanimous	decision	.071
brisk	business	.071
utopian	vision	.071
natural	gas	.071
nominal	fee	.070
volcanic	activity	.070
bridal	gown	.069
molten	lava	.069
rightful	owner	.069
vaginal	dryness*	.069
violent	crime*	.067
literal	sense	.067
wide	variety	.066
ultimate	goal	.065
oily	skin	.065
private	sector	.065
perpetual	motion	.064

APPENDIX. *(continued)*

Adjective	*Noun*	*TP*
lanky	frame	.064
fertile	soil	.064
untreated	sewage	.063
sexual	abuse*	.063
immortal	soul	.061
regular	basis	.059
notable	exception	.057
skeletal	muscle	.056
sole	purpose	.055
gay	marriage	.055
prolific	writer	.055
pungent	odor	.055
rugged	terrain	.055
surgical	procedure	.054
miniature	golf	.054
explosive	device	.054
unequal	treatment	.053
radiant	heat	.052
spinal	column	.052
enormous	amount	.051
tentative	agreement	.051
impending	doom	.051
khaki	shirt	.051
raw	material	.050
popular	culture	.049
speedy	trial	.049
candid	camera	.049
stressful	situation	.049
bad	news	.048
temperate	climate	.048
adverse	impact	.048
funny	thing	.046
electric	mixer	.046
petite	woman	.046
sensory	input	.046
receptive	audience	.045
modernist	art	.045
primal	scene	.045
ethnic	identity	.045

APPENDIX. *(continued)*

Adjective	*Noun*	*TP*
stony	silence	.045
spectral	type	.045
discreet	distance	.044
viable	option	.044
indoor	plumbing	.043
stylistic	analysis	.043
irregular	heartbeat	.043
romantic	comedy	.043
canned	food	.042
upper	lip	.042
covert	operation	.042
dismal	failure	.041
rosy	picture	.040
unfair	advantage	.040
inaugural	ball	.040
universal	coverage	.040
awkward	position	.040
patriotic	duty	.039
sheer	size	.039
stellar	evolution	.038
unwanted	pregnancy*	.038
generic	term	.037
ample	room	.037
decisive	victory	.036
homeless	shelter	.035
earthly	paradise	.035
sizable	chunk	.035
sensual	pleasure	.035
deaf	ear	.034
muscular	strength	.034
planetary	scientist	.033
coarse	meal	.033
sweet	potato	.033
normative	sample	.033
factual	knowledge	.032
judicial	activism	.032
lifelong	friend	.031
geometric	pattern	.031
lively	debate	.031

APPENDIX. *(continued)*

Adjective	*Noun*	*TP*
barren	landscape	.031
festive	mood	.031
optimal	level	.031
orbital	debris	.030
liberal	democracy	.030
damp	cloth	.030
optical	illusion	.029
extra	money	.029
ancestral	homeland	.029
shallow	dish	.028
monthly	payment	.028
fiscal	crisis	.028
insane	asylum	.027
nervous	breakdown	.027
polite	applause	.027
biblical	text	.026
clinical	practice	.026
genetic	diversity	.026
serious	problem	.025
socialist	realism	.025
strict	liability	.025
integral	component	.025
senior	editor	.025
exact	location	.025
creamy	texture	.025
preschool	teacher	.024
main	reason	.024
glossy	magazine	.024
rigorous	training	.024
dumb	luck	.024
digital	video	.024
dietary	intake	.024
vivid	memory	.024
sleepy	town	.024
polar	cap	.024
soft	tissue	.024
linear	model	.023
drunken	driver	.023
fatal	flaw*	.023

APPENDIX. *(continued)*

Adjective	*Noun*	*TP*
reliable	source	.022
thermal	expansion	.022
broad	daylight	.022
tragic	accident	.022
upcoming	book	.022
durable	peace	.021
dental	hygiene	.021
casual	observer	.021
annual	budget	.021
dirty	laundry	.021
mere	fact	.021
static	pressure	.021
blind	date	.021
fuzzy	logic	.021
spiritual	leader	.021
vibrant	color	.021
nice	guy	.020
wild	card	.020
cardiac	output	.020
logical	extension	.020
identical	twin	.020
slim	chance	.020
free	agent	.019
incoming	freshman	.019
fresh	lemon	.019
cautious	optimism	.019
lucrative	contract	.019
potent	symbol	.019
weekly	newspaper	.019
solar	radiation	.018
endless	stream	.018
rational	choice	.018
portable	radio	.018
automatic	pilot	.018
ambitious	project	.018
eternal	damnation*	.018
civic	pride	.018
cruel	joke	.018
tall	grass	.017

APPENDIX. (*continued*)

Adjective	*Noun*	*TP*
academic	success	.017
exotic	dancer	.017
positive	attitude	.017
cultural	heritage	.017
genuine	concern	.017
ripe	tomato	.017
good	idea	.016
humble	opinion	.016
frequent	flier	.016
fair	game	.016
urgent	message	.016
full	moon	.016
seasonal	flu	.016
fierce	battle	.016
silent	auction	.016
symbolic	capital	.016
stable	condition	.016
absolute	certainty	.016
uneasy	truce	.016
informal	survey	.016
indirect	discourse	.015
jealous	rage	.015
racial	equality	.015
selective	breeding	.015
immediate	aftermath	.015
precious	commodity	.015
black	pepper	.015
joint	statement	.015
bare	chest	.014
guilty	plea	.014
useful	tool	.014
secular	humanism	.014
extreme	poverty	.014
inner	self	.014
physical	therapy	.014
spatial	scale	.014
nasty	stuff	.014
constant	reminder	.013
steep	incline	.013

APPENDIX. (*continued*)

Adjective	*Noun*	*TP*
financial	planner	.013
organic	carbon	.013
atomic	physics	.013
gentle	breeze	.013
valuable	lesson	.013
conscious	awareness	.013
aesthetic	quality	.012
distant	cousin	.012
explicit	reference	.012
dense	foliage	.012
suitable	habitat	.012
tiny	fraction	.012
economic	reform	.011
terrible	tragedy	.011
religious	belief	.011
retail	industry	.011
faithful	servant	.011
coastal	region	.011
nuclear	arsenal	.011
healthy	diet	.011
vague	notion	.011
ethical	dilemma	.011
urban	renewal	.011
neutral	hydrogen	.011
practical	advice	.011
bitter	pill	.011
stiff	neck	.010
eastern	seaboard	.010
dominant	theme	.010
original	sin	.010
dull	knife	.010
permanent	residence	.010
innocent	victim	.010
moral	theology	.010
risky	strategy	.009
personal	trainer	.009
anonymous	donor	.009
divine	creation	.009
blue	cheese	.009

APPENDIX. (*continued*)

Adjective	*Noun*	*TP*
pure	vanilla	.009
remote	corner	.009
low	profile	.009
defensive	posture	.009
narrow	path	.009
mild	recession	.009
abstract	concept	.009
empty	stomach	.009
temporary	relief	.008
northern	border	.008
brilliant	career	.008
deadly	virus*	.008
rough	patch	.008
bright	sunlight	.008
accurate	diagnosis	.008
slight	movement	.008
corporate	ladder	.008
severe	drought	.007
ongoing	dialogue	.007
honest	broker	.007
native	tongue	.007
yellow	squash	.007
visual	imagery	.007
negative	publicity	.007
elderly	gentleman	.007
regional	stability	.007
southern	accent	.007
modest	proposal	.007
emotional	intensity	.006
previous	page	.006
safe	passage	.006
medical	marijuana	.006
large	pot	.006
cheap	plastic	.006
heavy	saucepan	.006
legal	pad	.006
apparent	suicide*	.006
basic	premise	.005
formal	complaint	.005

APPENDIX. (*continued*)

Adjective	*Noun*	*TP*
recent	poll	.005
critical	acclaim	.005
efficient	method	.005
athletic	shoe	.005
angry	mob	.005
quick	trip	.005
dangerous	precedent	.005
crucial	aspect	.005
dramatic	reduction	.005
rare	occasion	.004
similar	vein	.004
common	stock	.004
creative	genius	.004
entire	universe	.004
sad	song	.004
illegal	gambling	.004
military	campaign	.004
active	volcano	.003
proper	burial	.003
strong	supporter	.003
musical	notation	.003
huge	crowd	.003
perfect	timing	.003
strange	sensation	.003
sick	bay	.003
massive	influx	.003
rural	county	.003
thin	sheet	.003
current	crop	.002
easy	prey	.002
powerful	engine	.002
famous	phrase	.002
major	obstacle	.002
expensive	jewelry	.002
quiet	dignity	.002
tough	stance	.002
local	chapter	.002
fine	mist	.002
beautiful	scenery	.002

APPENDIX. (*continued*)

Adjective	*Noun*	*TP*
modern	reader	.002
political	rhetoric	.002
young	adulthood	.001
dead	giveaway*	.001
small	intestine	.001
possible	scenario	.001
important	clue	.000

*Denotes high valence items, which were removed for the supplemental MTG analysis.

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Notes

1. Alternatively, for an individual trial, one might regard a participant as predicting only a single possible noun with a probability equal to that noun's TP; on the aggregate, however, we would nevertheless observe effects proportional to the relevant conditional probabilities.
2. Because there was no definition for the insula region within the parcellation, we obtained the region via an alternate parcellation for the average brain, which was then morphed back to each participant's neuroanatomical space.
3. Because the M350 response is negatively signed, a positive correlation indicates a weakening of activity, and a negative correlation indicates a strengthening of activity.
4. Despite the highly significant adjective predictivity effect in the main analysis (see also Figure 3C), a median split analysis failed to show a comparably robust separation between the items in the top half and bottom half of adjective predictivity. This discrepancy indicated that the continuous regression using linear mixed-effects models was a more sensitive measure of the adjective predictivity effect. Consequently, we decided to split the data into the top 10% (blue line), top 10–50% (solid black line), bottom 10–50% (dotted black line), and bottom 10% (red line) of adjective predictivity (Figure 3B), which confirmed our hypothesis. In particular, the continuous regression models are a better fit to the data than the median split, because the predictivity effect is more significant at the higher and lower ranges of adjective predictivity values, relative to the items in the middle of the distribution.
5. The latency of the M100 peak in Dikker and Pylkkänen's (2011) study was 97 msec, which is roughly midway between the two peaks observed here; we thus decided to analyze both peaks in the present data. It should be noted, however, that Dikker and Pylkkänen (2011) performed a sensor space analysis, which may yield results that are not comparable to the results of the present source space analysis.

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