Word Frequency Effects in Naturalistic Reading

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Abstract

Word frequency is a central psycholinguistic variable that accounts for substantial variance in language processing. A number of neuroimaging studies have examined frequency at a single word level, typically demonstrating a strong negative, and sometimes positive correlation between frequency and hemodynamic response. Here, 40 subjects read passages of text in an MRI scanner while their eye movements were recorded. We used fixation-related analysis to identify neural activity tied to the frequency of each fixated word. We found that negative correlations with frequency were reduced, while strong positive correlations were found in the temporal and parietal areas associated with semantics. We propose that the processing cost of low frequency words is reduced due to contextual cues. Meanings of high frequency words are more readily accessed and integrated with context resulting in enhanced processing in the semantic system. The results demonstrate similarities and differences between single word and naturalistic text processing.

The neurocognitive basis of reading has been investigated intensively, given that it is a fundamentally important acquired skill. The frequency with which words are encountered in language has a major influence on reading. High frequency words elicit shorter processing and fixation times, and exhibit lower error rates than low frequency words in reading (Monsell, 1991; Adelman et al., 2014). Word frequency (WF) also has a major influence on other psycholinguistic tasks, such as lexical decision (Schilling et al., 1998; Balota et al., 2004), picture naming (Huttenlocher and Kubicek, 1983; Hennessey and Kirsner, 1999), and auditory word comprehension (Connine et al., 1993; Benkí, 2003) and affects eye movements during reading (Inhoff and Rayner, 1986; Rayner and Duffy, 1986; Henderson and Ferreira, 1990) showing that frequency effects are not dependent on a particular type of input (e.g., verbal/nonverbal, visual/auditory) or output (e.g., overt articulation, covert reading).

Several imaging studies have examined the neural basis of frequency effects using single word stimuli. Activation for low more than high frequency words is most consistently found. For example, activation in the inferior frontal gyrus (IFG), anterior insula, and pre/supplementary motor area (SMA) are commonly found bilaterally (Fiez et al., 1999; Fiebach et al., 2002; Joubert et al., 2004; Kronbichler et al., 2004; Hauk et al., 2008; Yarkoni et al., 2008; Graves et al., 2010). This activation is generally interpreted as reflecting phonological processing (Bookheimer, 2002), but some authors have also pointed out the role of general executive processing (Graves et al., 2010). Activation in the IPS and the putative visual wordform area (VWFA; Cohen et al., 2000) is also found, the latter being interpreted as whole-word orthographic processing (Joubert et al., 2004; Kronbichler et al., 2004) or orthography-phonology mapping (Graves et al., 2010).

There are reasons to expect greater activation for high frequency words as well. The access to meaning of a high frequency word is likely to be more automatic and extensive, given repeated exposure. If access to meaning is easier for high frequency words, they can be expected to facilitate performance in semantic decision tasks, and this is exactly what is found in behavioral studies (Monsell et al., 1989; Chee et al., 2002). In general, high frequency words have richer semantic representations, where 'richness' can be measured in a number of different ways. High frequency words appear in more contexts (Adelman et al., 2006). They have stronger associative connections to other words, as suggested by the fact that that they are more likely to be produced as associates (Nelson and McEvoy, 2000). For a set of concrete words, a positive correlation between frequency and semantic neighborhood density, number of features, contextual dispersion, and number of senses was found (Pexman et al., 2008; Yap et al., 2011; Yap et al., 2012). This approach was extended to abstract words, where a positive correlation between frequency and semantic neighborhood and sensory experience ratings was found (Zdrazilova and Pexman, 2013). In a set of words that included both concrete and abstract words, Recchia and Jones (2012) found a positive correlation between frequency and the number of semantic neighbors, number of features, contextual dispersion, and number of senses. Using corpus-based representations that emphasize taxonomic (as opposed to associative) information, Reilly and Desai (2017) found a strong positive correlation between frequency and semantic neighborhood density for a set of over 9000 words spanning the concreteness spectrum. Thus, behavioral studies suggest that a high frequency word is likely to activate more features, more associated and similar concepts, and more senses. Note that while higher frequency facilitates behavioral performance, a denser semantic neighborhood need not always have a faciliatory effect. For example, Mirman and Magnuson (2008) found that processing was slower for dense near neighborhoods and faster for denser distant neighborhoods. But the fact that semantic neighborhoods facilitate or impede performance indicates that this information is activated in the first place. However, only a few imaging studies have found a positive correlation with frequency (Prabhakaran et al., 2006; Carreiras et al., 2009; Graves et al., 2010).

Here, our goal was to examine the neural effects of frequency in a naturalistic reading task. A fundamental characteristic of natural skilled reading is that it unfolds spatiotemporally under the control of the reader: Readers move their eyes actively through text in a series of fixations and saccades (Dodge, 1901; Rayner, 2009). Fixations are brief pauses during which the high-acuity fovea focuses on words, and saccades are high-velocity movements that reorient fixation. Eyetracking studies typically reveal immediate effects of a word's properties when that word is fixated, and suggest that the majority of word encoding and a good deal of higher-level language processing take place during word fixation (Rayner, 2009; Clifton et al., 2016). As words are continually fixated and integrated with the context, it is possible that the frequency of individual lexical items may have a different neural signature. We consider three competing hypotheses regarding effects of WF relative to those in single-word studies. One possibility is that frequency has effects similar to those in single-word studies, with strong negative correlations and modest or no positive correlations. A second alternative is that frequency has a relatively minor effect in a naturalistic reading task, because context plays a greater role. WF is less relevant because words are used aptly in coherent texts and are processed using contextual cues. This would suggest that naturalistic reading is not tied strongly to the properties of the fixated word. A third alternative is that positive and negative correlations with frequency are differentially affected in a naturalistic task. Lower frequency words will demand less executive resources in semantic retrieval due to the assistance provided by context. Hence, negative correlations will be minimized. On the other hand, positive correlations are expected to be due to automatic activation of a richer semantic field (e.g., greater number features, and more associated as well as similar concepts). An apt context need not reduce this activation (except the activation of multiple senses), and hence they will remain at the same level, or can even possibly be enhanced due to the context providing greater depth. Schuster et al. (2016) examined effects of frequency, as well as predictability and length, using sentence stimuli that combined fMRI and eyetracking. They found negative correlation with frequency in the left IFG, IPS, and fusiform gyrus near VWFA, with no positive correlations, supporting the first alternative.

In the present study we test these hypotheses by using simultaneously recorded eye movements and fMRI while subjects read connected passages of text. We then used fixation-related analysis of the fMRI data to identify neural activation associated with each fixated word (Henderson & Choi, 2015; Henderson, Choi, Luke, & Desai, 2015; Marsman, Renken, Velichkovsky, Hooymans, & Cornelissen, 2011; Richlan et al., 2014)(Desai et al., 2016). Fixation-related fMRI analyses were tied in a parametric manner to WF.

Methods

Participants

Forty-three right-handed subjects (13 male), aged 18-35 years (mean 21.58), were recruited from the Columbia, South Carolina community. They were all native speakers of English and reported normal or corrected-to-normal vision. All subjects gave informed consent and were screened for MRI safety, and were given $10 per hour for participation. Three subjects did not finish the experiment and were removed from analysis, one due to a technical problem with the scanner and the other two due to inattention during the experiment, leaving 40 participants for the analysis. Data from a subset of these participants has been presented elsewhere (Choi et al., 2014; Desai et al., 2016) with other analyses.

Materials

Twenty-two paragraphs, eleven from the novel *The Emperor's New Clothes* by Hans Christian Andersen, and eleven from a Nelson-Denny reading assessment practice text, were presented during the experiment. Paragraphs were edited given the limits of the MRI display, and were 49 to 66 words in length. Text was displayed in Courier New font with 4.76 characters subtending 1° of visual angle. After proper nouns and closed-class words were excluded, a total of 1312 words (420 unique words) with frequency counts were included in the analysis. Frequencies were generated from the SUBTLEXus corpus (Brysbaert & New, 2009) and were log transformed. The mean (SD) log token frequency was 3.36 (1.06) (or 1.65 (1.06) log frequency per million), number of letters 5.88 (2.12), number of syllables 1.74 (0.89), and concreteness 3.02 (1.08).

Apparatus

Stimuli were presented using an Avotec Silent Vision 6011 projector in its native resolution (1024×768) at a refresh rate of 60 Hz. Eye-movements were recorded via an SR Research Eyelink 1000 long-range MRI eyetracker sampling at 1000Hz. Viewing was binocular and eye-movements were recorded from one eye.

Procedure

Text appeared in paragraph form and participants were instructed to read silently as they would normally read a novel. A wide (quadruple) line spacing was used for the ease of fixation assignment. Each paragraph was presented for 12s. Paragraphs were presented in a constant order to maintain passage coherence. Each run included 11 paragraphs as well as 33 filler trials in which participants completed three non-reading tasks (Choi et al., 2014). Fillers were randomly presented between paragraphs. An ITI of 6s was inserted before each trial (paragraph or filler). Each functional run lasted about 14 min.

Eye-movement Data Acquisition. In the scanner, a thirteen-point calibration procedure was administrated before each functional run to map eye position to screen coordinates. Successful calibration required average error less than .49° and maximum error less than .99°. A fixation cross was presented on the screen before each trial, with the first word in the text appearing at that location. Eye movements were recorded throughout each functional run.

fMRI Data Acquisition. MR data were collected on a Siemens Medical Systems 3T Trio. A 3D T1-weighted "MPRAGE" RF-spoiled rapid flash scan in the sagittal plane, and a T2/PD-weighted multi-slice axial 2D dual Fast Turbo spin-echo scan in the axial plane was used. The multi-echo whole brain T1 scans had 1mm isotropic voxel size and sufficient field of view to cover from the top of the head to the neck with the following protocol parameters: TR=2530ms, TE1=1.74ms, TE2=3.6ms, TE3=5.46ms, TE4=7.32ms, flip angle=7°. All functional runs were acquired using gradient echo, echo-planar images with the following protocol parameters: TR=1850ms, TE=30ms, flip angle=75°. Volumes were consisted of thirty-four 3 mm slices with transversal orientation. Each volume covered the whole brain with FOV=208mm and 64X64 matrix, resulting in 3.3×3.3×3 mm^3 voxel size.

fMRI Analysis. The AFNI software package (Cox, 1996) was used for image analysis. Within-subject analysis involved slice timing correction, spatial co-registration (Cox and Jesmanowicz, 1999) and registration of functional images to the anatomy (Saad et al., 2009). Voxel-wise multiple linear regression was performed with the program 3dREMLfit, using reference functions representing each condition convolved with a standard hemodynamic response function. Reference functions representing the six motion parameters were included as covariates of no interest. In addition, the signal extracted from CSF was also included as noise covariates of no interest. A binary regressor coding the onset of all fixations (including on those words not used in the WF analysis) was also used.

To examine the effects of WF, an amplitude-modulated (parametric) regressor was used that contained the onset times (from the onset of each run) of each first fixation and the frequency of the fixated word. There are multiple fixations within each TR. We take advantage of the fact that the timings of the fixations within each TR, as well as the frequencies of the fixated words within each TR, vary from TR to TR. This variation, combined with the large number of TRs, provides sufficient power to extract information from the low temporal resolution fMRI data based on the high temporal resolution eye-tracking data. The ideal hemodynamic response resulting from this regressor was subsampled to match the time resolution of EPI images.

The individual statistical maps and the anatomical scans were projected into standard stereotaxic space (Talairach and Tournoux, 1988) and smoothed with a Gaussian filter of 5 mm FWHM. In a random effects analysis, group maps were created by comparing activations against a constant value of 0. The group maps were thresholded at voxelwise $p < 0.005$ and corrected for multiple comparisons by removing clusters with below-threshold size (1399 mm^3) to achieve a mapwise corrected $\alpha < 0.05$. Using the (recently updated) 3dClustSim program with 10000 iterations, the cluster threshold was determined through Monte Carlo simulations that estimate the chance probability of spatially contiguous voxels exceeding the voxelwise p threshold, i.e., of false positive noise clusters. The analysis was restricted to a mask that excluded areas outside the brain, deep white matter areas, and the ventricles.

Fixation-Related fMRI Analysis. The eye-movement data were analyzed off-line to identify fixations and saccades using DataViewer (SR Research Ltd, version 1.11.1). All fixations meeting the following criteria were included in the analyses: A fixation could not have a blink immediately before or after, had to fall within a word region, had to have a duration between 50 and 1500 ms, and could not follow a saccade greater than 14°. This resulted in the inclusion of 22,178 fixations across subjects. The data were hand-corrected when needed to account for drift, but this was not frequently needed due to wide line spacing. As shown in Table 1, eye movement characteristics were similar to those typically observed in reading (Rayner, 2009).

Table 1. Eye-movement Measures. Means for All Fixation Duration (ms; mean of all fixations on a word), First Fixation Duration (ms), Gaze Duration (ms; sum of all first-pass fixations on a word), Inter-Word Regression Rate (proportion), and Saccade Amplitude (deg).

	All Fixation Duration	First Fixation Duration	Gaze Duration	Regression Rate	Saccade Amplitude
M (sd)	222 (86)	226 (83)	265 (131)	0.06 (0.23)	2.76 (2.96)

The fMRI and eyetracking data were synchronized so that fixation onset from the eyetracker could be aligned with the fMRI data. This was accomplished by aligning the onset of the trial run with the onset of the functional scan. Times of experiment onset, block onsets, and fixation onsets were saved in the eye-movement record by the Experiment Builder program controlling the experiment. Timing was obtained by recording a TTL pulse from the scanner to the eyetracker computer, making it possible to co-register eye movement and fMRI events.

Areas associated with general semantics, such as the angular gyrus (AG), posterior cingulate/precuneus (pCi/pCu), and medial superior frontal gyrus (mSFG) (Binder et al., 2009; Binder and Desai, 2011), are also associated with concreteness (Wang et al., 2010). In our data, there was a negative correlation between frequency and concreteness ($r = -0.203$, $p < 0.001$), and thus correlations with frequency can potentially be driven by concreteness instead. Specifically, this can weaken activation in semantic areas that show concrete > abstract effects (e.g., AG, pCi/pCu) and show stronger effects in abstract > concrete regions such as the anterior temporal lobe (ATL) and inferior frontal gyrus (IFG). To address this, we selected a subset of the stimuli with 250 words (160 unique words) such that frequency and concreteness were decorrelated ($r = 0.037$, $p > 0.6$). We repeated the analysis with this decorrelated set to examine effects of frequency. Thus, the main results of interest come from analysis of this subset. In the subset, there was also a negative correlation between number of letters and WF ($r = -0.432$, $p < 0.001$) and number of syllables and WF ($r = -0.364$, $p < 0.001$). Both number of letters (which is highly correlated with the number of syllables) and fixation duration were entered as covariates in this analysis.

Table 2. Correlations with frequency for the subset of words where frequency and concreteness were decorrelated. Volume (mm^3), peak z-score, Talairach coordinates, and approximate anatomical regions for the cluster are shown. L=left hemisphere, R=right hemisphere, STG=superior temporal gyrus, MTG=middle temporal gyrus, G=gyrus, S=sulcus. * indicates the cluster that was significant only in the left IFG ROI analysis.

Volume	Max	x	y	z	Anatomical regions
Positive correlations					
11772	5.7	-1	-58	38	L/R precuneus, posterior cingulate G
6318	5.4	55	7	-12	R anterior STG, anterior MTG
5751	4.4	40	-52	26	R angular G
5643	5.3	-49	-58	23	L angular G, supramarginal G
4455	4.9	-55	-1	-18	L anterior STG, anterior MTG
Negative correlations					
2295	-3.9	1	13	50	R/L medial superior frontal G
1971	-4.6	-52	-37	38	L intraparietal S, supramarginal G
1917	-4.2	43	46	14	R middle frontal G
243*	-4.1	-43	34	17	L inferior frontal G

In narratives, an additional factor that can drive activations related to individual words is predictability or surprisal associated with each word. For example, Kliegl et al. (2004) found that in a corpus of single sentence stimuli, both frequency and predictability affected the probability of multiple fixations and reading times. Here, we used surprisal measures developed by Roark et al. (2001; 2009). This method uses an incremental top-down parser that builds sets of partial derivations and weights them according to a probabilistic context-free grammar, to estimate lexical and syntactic surprisal. In this parser, total surprisal is decomposed into portions related to syntactic structure associated with building nonterminal syntactic nodes (syntactic surprisal), and to building lexical terminal items (i.e., words) in the parse tree (lexical surprisal). In our stimuli, syntactic surprisal had a small but significant positive correlation to frequency ($r = 0.15$, $p < 0.025$) and lexical surprisal had a stronger negative correlation to frequency ($r = -0.43$, $p < 0.001$). We added both surprisal measures simultaneously as covariates in the analysis with the subset matched for concreteness, to examine effects of frequency not explained by these surprisal measures.

Results

The main eyetracking measures are presented in Table 1. There was a small but significant correlation between fixation duration and WF ($r = - 0.07$, $p < 0.05$), and there was also a correlation between gaze duration and WF ($r = -0.2$, $p < 0.001$) for content words. The correlation between fixation duration and WF is lower than found in some eye-tracking studies. A potential reason may be that due the narrative style of stimuli (as opposed to single sentence corpora used in other studies) many words are repeated within and across passages. Fixation duration on the same word can be modulated due to context, reducing the correlation. For example, a low frequency word occurring many times in a narrative can effectively be processed as a high frequency word with reduced fixation duration.

The fixation-related fMRI analysis produced activation correlated with fixation onset (Figure 1) and with the frequency of the currently fixated word (Figure 2; Tables 2, 3). The onset results are not of particular theoretical interest, but do demonstrate general activation in the language and reading networks in temporal, frontal, and inferior parietal regions as expected. The onset results are similar to those from a block analysis of a subset of these data (Choi et al., 2014), indicating that the onset component of the fixation-related fMRI analysis accounts for general language processing associated with fixations. Specifically, there was extensive activation in the left superior temporal gyrus and sulcus (STG/STS), supramarginal gyrus (SMG), and angular gyrus (AG), as well as the left inferior frontal gyrus (IFG), precentral gyrus, and superior frontal gyrus (SFG). Lesser activation was observed in the right STG, STS, AG, SMG, IFG, and SFG. Extensive activation associated with visual analysis was seen in bilateral occipital lobes, including cuneus, lingual, and fusiform gyri. Consistent with the control of eye movements, activation was observed in left middle frontal gyrus (MFG) including lateral frontal eye field, left superior frontal gyrus including supplementary eye field, and subcortical bilateral regions of cerebellum, putamen, and thalamus.

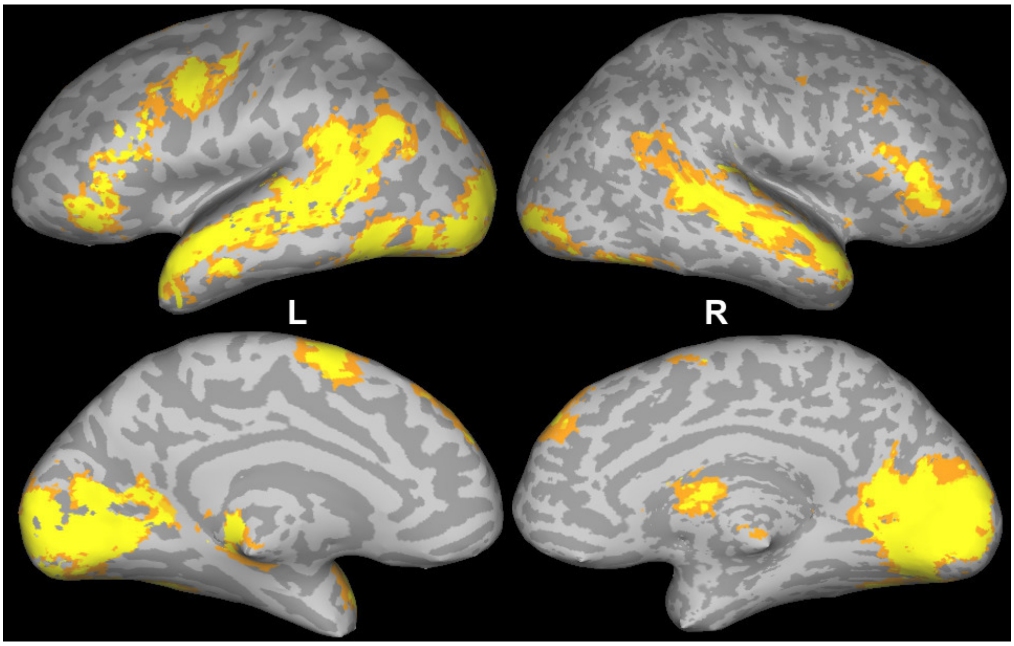

Figure 1. Fixation onset activation. Areas of activation positively related to fixation onset. Activation is displayed on an inflated cortical surface map of a representative subject using Caret (Van Essen et al., 2001), with gyri shown as light gray and sulci shown as dark gray.

Of primary interest was the activation correlated to the frequency of the currently fixated word for first fixations, for the subset where WF and concreteness were decorrelated. Positive correlation was observed in bilateral AG and pCi/pCu (Figure 2A), and in bilateral ATL, including anterior STG, STS, and MTG. Negative correlation with frequency was observed in the left IPS, SMG, bilateral medial SFG including pre/SMA, and the right MFG.

For comparison, considering WF correlated activity using all content words, positively correlated activity was observed in the left AG/SMG and pCu and in bilateral ATL, including anterior STG, STS, and MTG (Figure 2B). Negative correlation with frequency was observed in the left IPS, SMG, bilateral medial SFG, the right MFG and cuneus. Thus, with the decorrelated subset, much stronger activation was observed in the bilateral AG and pCi/pCu relative to the full set, while activation in the bilateral ATL was somewhat weaker.

Table 3. Correlations with frequency for all content words. For abbreviations see Table 2.

Volume	Max	x	y	z	Anatomical regions
Positive correlations					
7263	5.3	49	13	-15	R anterior STG, anterior MTG
6777	5.5	-49	7	-12	L anterior STG, anterior MTG
3348	4.3	-49	-61	29	L angular G, supramarginal G
1674	5.5	-22	-76	-27	L cerebellum
1620	4.1	-7	-55	35	L precuneus
1431	5.3	25	-73	-30	R cerebellum
Negative correlations					
3078	-4.8	-1	10	50	L/R medial superior frontal G
1755	-4.2	-40	-43	44	L supramarginal G

1593	-4.8	40	43	17	R middle frontal G
1512	-4.1	-52	-34	35	L intraparietal S
1485	-4.1	7	-70	11	R cuneus

Negative correlation with frequency is commonly observed in the left IFG, but here we obtained no clusters in the whole-brain analysis. Given that whole-brain analysis is conservative, an ROI analysis was conducted for the decorrelated subset with small-volume correction for the left IFG (defined using DKD_Desai_MPM maximum probability atlas included with AFNI, which is based on Desikan-Killiany parcellation). A cluster negatively correlated with WF was obtained in this ROI, in dorsal pars triangularis.

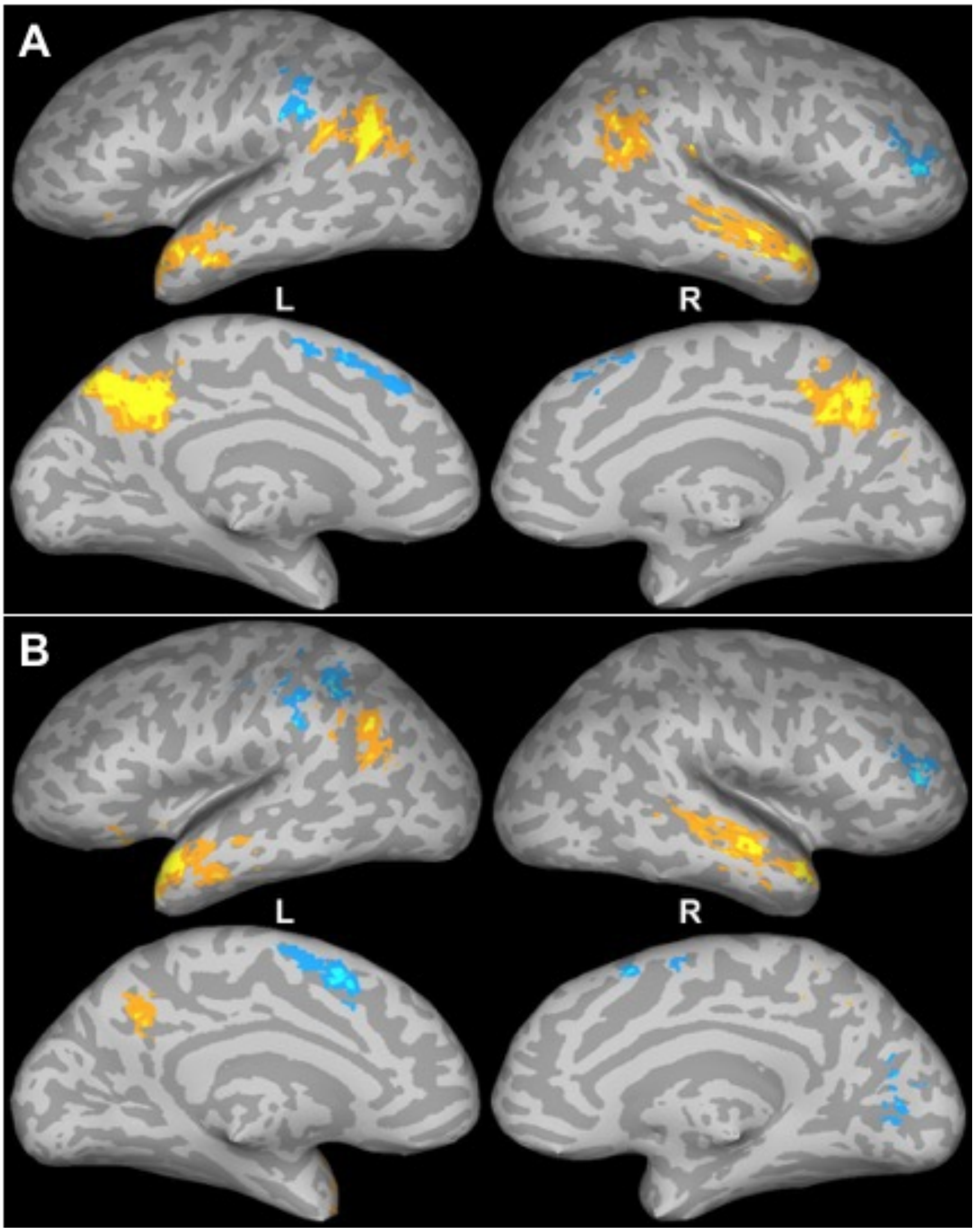

Figure 2. Fixation-related frequency activation. Areas of activation correlated with the frequency of the fixated word during natural reading in a whole-brain analysis. Hot regions show positive correlation and cool regions show negative correlation. Panel A shows results

using a subset of data controlling for concreteness. Panel B shows analysis including all content words.

To examine the extent of overlap of areas modulated by frequency and those associated with general semantics, we used activation likelihood maps from a large-scale meta-analysis of semantics (Binder et al., 2009). An overlap map of general semantic activations and those modulated by WF is shown in Figure 3. An overlap of positively correlated regions was found in the bilateral AG and pCi/pCu, and in the left ATL. No overlap was found between negatively correlated regions and semantic regions.

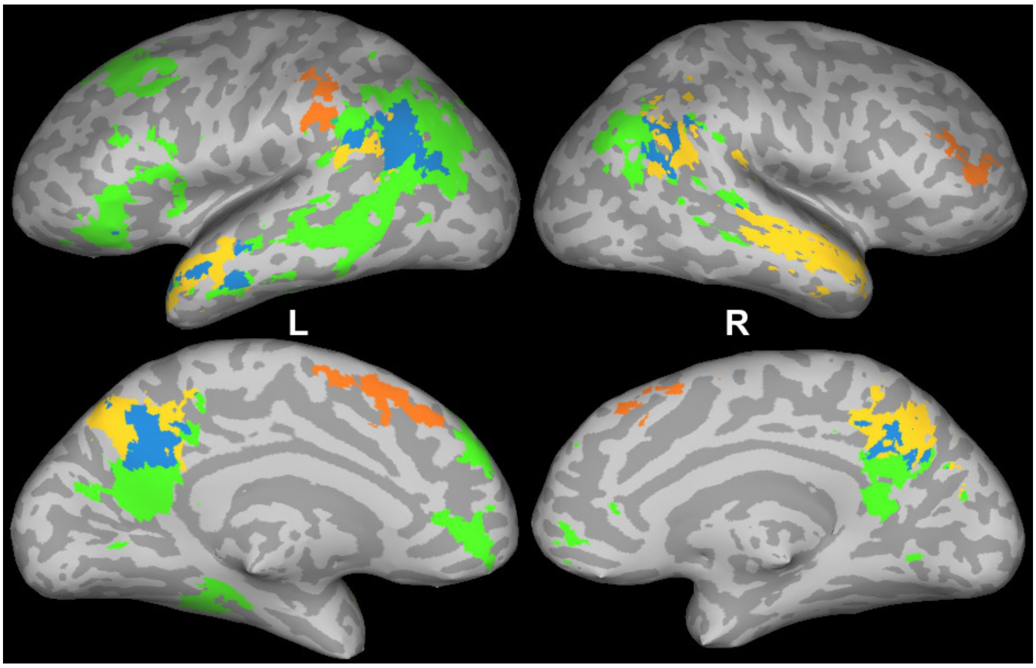

Figure 3. A comparison of areas associated with semantics from a large-scale meta-analysis and those showing correlation with frequency. Green – semantic activation from Binder et al. 2009. Yellow – areas positively correlated with frequency (when controlling for concreteness). Blue – overlap between the two. Orange – areas negatively correlated with frequency.

Finally, in the analysis that included syntactic and lexical surprisal measures, the results were similar to the analysis without these regressors, but the extent of activation was reduced overall (Figure 4, Table 4). Positive correlation with frequency was observed in bilateral AG/SMG, pCi/pCu, and ATL. Negative correlation with frequency was observed in the left IPS and SMG, and the right MFG. Lexical surprisal was significantly correlated with fixation duration ($r = 0.024$, $p < 0.001$), but syntactic surpisal was not ($r = -0.002$, $p > 0.77$).

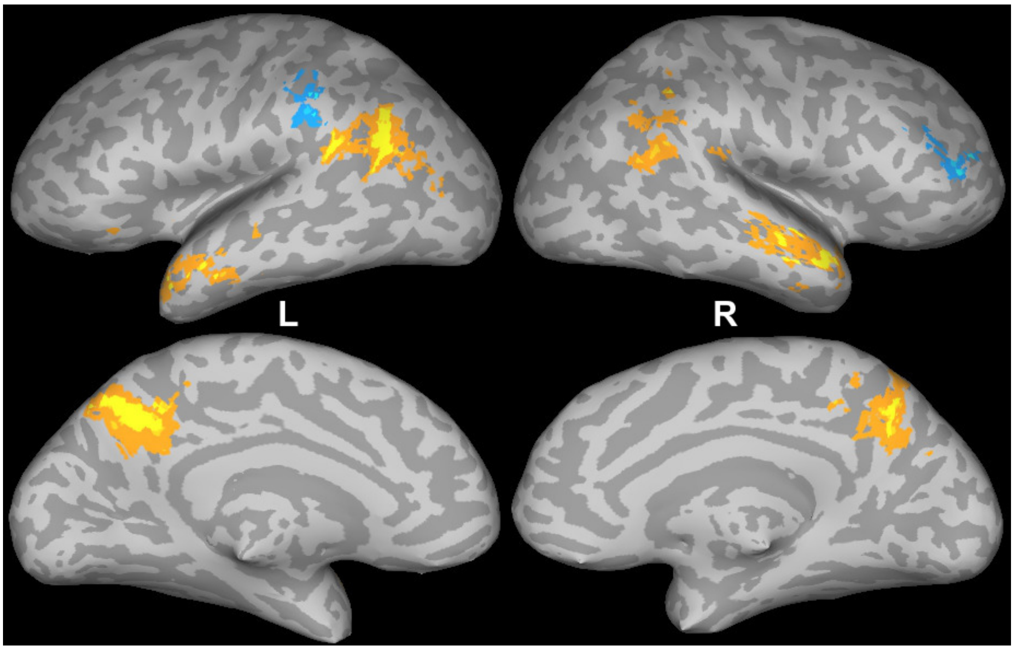

Figure 4. Fixation-related frequency activation in the analysis where lexical and syntactic surprisal measures were included as covariates. Other parameters were the same as for the analysis shown in Fig. 2(A).

Table 4. Correlations with frequency for the subset of words where frequency and concreteness were decorrelated, and syntactic and lexical surprisal were factored out. For abbreviations see Table 2.

Volume	Max	x	y	z	Anatomical regions
Positive Correlations					
10368	5.1	-7	-52	35	L/R precuneus, posterior cingulate G
6831	4.7	-49	-58	26	L angular G, supramarginal G, middle occipital G
4536	5.0	46	-46	32	R supramarginal G, angular G
4428	5.3	55	7	-12	R anterior STG, anterior MTG
3861	4.3	-55	-1	-15	L anterior STG, anterior MTG
1728	4.2	-22	-70	-30	L cerebellum
Negative correlations					
1809	-4.2	43	46	14	R middle frontal G
1674	-4.4	-52	-37	38	L intraparietal S, supramarginal G

Discussion

We investigated parametric variation in BOLD activity related to WF of the currently fixated word in a naturalistic reading task. The results demonstrate a modulation of brain activity in both semantic and executive regions due to WF.

WF is correlated with and reflects multiple levels of analysis in the language processing system. Increasing activation with higher frequency words was observed in bilateral temporal and inferior parietal areas. The extent of repeated exposure to a lexico-semantic concept is correlated with increasing WF, and hence more extensive and automatic activation of semantic systems is expected for higher frequency words. As mentioned in the Introduction, there is a positive correlation between semantic richness and WF, where 'richness' can be defined in a variety of ways, including number of features, number of similar and associated concepts, semantic neighborhood density, and number of senses. We observed strong positive correlation with WF in bilateral AG, pCu/pCi, and ATL. These regions have been seen in a large number of studies of semantics. The comparison with the results of a meta-analysis revealed an overlap between general semantics and positive correlation with frequency in bilateral AG and pCu/pCi, as well as the left ATL, corroborating the suggestion that the positive correlations indicate richer semantic access for high frequency words.

Some differences were also observed between the semantic map and the positive correlations, apart from the more widespread activation for semantics. In pCi/pCu, more ventral activation in the retrosplenial cortex was observed for semantics, more dorsal activation for frequency, with overlap in between. The retrosplenial cortex is associated with episodic memory in general, but is thought to be especially important for mental imagery and spatial memory (Epstein et al., 2007; Vann et al., 2009). Two functional subdivisions of pCu have been suggested, where the anterior/ventral section is involved in mental imagery, and the posterior/dorsal division in episodic memory retrieval (Cavanna and Trimble, 2006). The Binder et al. (2009) meta-analysis predominantly contained studies that used concrete linguistic stimuli, which may evoke spatial mental imagery to a greater extent compared to our stimuli, leading to more ventral/anterior activation in pCi/pCu. Our stimuli were more abstract, and may rely on episodic retrieval that is less spatial in nature, leading to more dorsal/posterior activation. Another difference was that frequency modulated activation strongly even in the right ATL, which was not seen in the meta-analysis. Integrative and combinatorial processes for words embedded in context may lead to activation in the ATL, which is associated with sentence processing and combinatorial semantics (e.g., Humphries et al., 2001; Humphries et al., 2005; Rogalsky and Hickok, 2009; Magnusdottir et al., 2013; Wilson et al., 2014). Majority of the studies in the meta-analysis used word stimuli, which would not be expected to evoke combinatorial and higher order integrative processing. Additionally, the more abstract nature of our stimuli may similarly play a role in ATL activation.

Increased activation especially in the AG and pCi/pCu has been observed in studies using single word stimuli (Carreiras, Riba, Vergara, Heldmann, & Münte, 2009; Graves et al., 2010; Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006). The results are largely similar to that of (Graves et al., 2010), who used a large set (465 words) where frequency was decorrelated from length, consistency, imageability, as well as bigram and biphone frequency. The main difference in positive correlations between those and our results is that we additionally observed activation in the bilateral ATL, which can again potentially be explained by differences in concreteness or imageability (mean imageability 4.89 in Graves et al.; mean concreteness 3.02 here), and by combinatorial processing evoked in the current study.

Among studies that did not find positive activation for high compared to low frequency words, three masked the analysis to regions that showed words > resting activation (Fiez et al., 1999; Fiebach et al., 2002; Joubert et al., 2004; Kronbichler et al., 2004; Carreiras et al., 2006; Hauk et al., 2008; Yarkoni et al., 2008; Graves et al., 2010), which can eliminate semantic regions such as AG and pCi/pCu that are active at rest (Binder et al., 2009). Hauk et al. (2008) presented stimuli briefly and rapidly (100 ms display with 2.5 s SOA), which can reduce spread of semantic associations. It is less clear why Schuster et al. (2016) did not find positive correlations with frequency in their large scale, rigorous study. Their stimuli were sentences as opposed to paragraphs, and as they pointed out, single sentences provide a limited amount of contextual information. The effects of predictability may also be easier to quantify in single sentence stimuli than in narratives, due to effects spanning multiple sentences or paragraphs. For example, in narratives, many words are repeated, and multiple occurrences can have different predictability but have identical frequency. That study also did not consider the effects of concreteness (or the highly correlated variable of imageability) of the stimuli, which modulates areas involved in general semantics, especially AG and pCi/pCu. These regions show lower activation for less concrete items, which can counteract increasing activation due to frequency.

Negative correlations with WF have been consistently found in previous studies (Fiez et al., 1999; Fiebach et al., 2002; Joubert et al., 2004; Kronbichler et al., 2004; Carreiras et al., 2006; Hauk et al., 2008; Yarkoni et al., 2008; Carreiras et al., 2009; Graves et al., 2010). The current results differ in the relatively low levels of negatively correlated activity. A commonly activated region of bilateral IFG/insula were not found here in the whole brain analysis, and a small cluster was found in the par triangularis in the ROI analysis. IFG activation is often interpreted as phonological processing or retrieval (Bookheimer, 2002). This account points to the role of IFG in grapheme-to-phoneme mapping. Consistent with the models of lexical decision, it also suggests that low frequency words require more phonological mediation, while high frequency words can be identified directly from orthography. Alternative views suggest more effortful semantic retrieval (Chee et al., 2002; Devlin et al., 2003), or general executive processing including attentional demands (Carreiras et al., 2009; Graves et al., 2010). Pars opercularis and ventral precentral gyrus are associated with phonological processing (e.g., Mechelli et al., 2005), while the current cluster was found in pars triengularis, suggesting a semantic or general executive role.

Negative correlation was also found in the left IPS and posterior SMG. The IPS is strongly associated with visual attention (Corbetta and Shulman, 2002; Dosenbach et al., 2008; Corbetta and Shulman, 2011). It also contains parietal eye fields, and its activation is consistent with greater fixation duration for lower frequency words, and supports a view of greater attentional demands for lower frequency words. A large body of literature associates posterior SMG with storage for phonological forms (for a review, see Binder, 2017). This supports the view of greater phonological demands for low frequency words, but with an anatomical locus in the left SMG rather than the IFG.

An alternative explanation for the positive correlations found here is that they reflect surprisal/predictability, rather than frequency *per se*. This was addressed by using both syntactic and lexical surprisal measures as covariates. The positive activations discussed above were still found, supporting the view that these activations are due to frequency rather than surprisal (at least as calculated by the particular algorithm used). The overall level of activation was reduced, which is expected given that frequency is used to calculate lexical surprisal, and was correlated with it. The negative correlation was also reduced, with the medial SFG activation eliminated, suggesting relatively lower costs for processing low frequency words during naturalistic reading.

These results provide a demonstration that neural systems supporting word-specific aspects of processing during natural reading can be successfully investigated using fixation-related fMRI. Specifically, we show that a parametric regressor coding a linguistic factor (frequency) that is tied to each fixated word can be used to study neurocognitive processes in natural reading. The method can be used to investigate the role of other lexical variables, as well as other levels of language representation such as syntax and compositional semantics (Desai et al., 2016; Henderson et al., 2016). The method is also valuable for investigating how the language and attention networks interact in an integrated manner to support fluent skilled reading (Henderson et al., 2015). During natural reading, eyetracking studies suggest that the majority of word encoding takes place incrementally as each word is fixated (Rayner, 2009; Clifton et al., 2016). The current results provide evidence for the hypothesized incremental nature of word encoding (Rayner et al., 2003; Rayner and Clifton, 2009), and are consistent with current computational models of reading (Reichle et al., 2003; Engbert et al., 2005).

In summary, we find clear associations during natural reading between WF and activation in language-related areas previously identified in single-word studies. We find that positive correlations are enhanced and activate the semantic system while, relative to single-word studies, negative correlations are reduced. This suggests that integration into context generates richer semantic representations for higher frequency words, while executive demands for processing low frequency words is minimized likely due to contextual aptness. As noted in the Introduction, a large number of variables are correlated with WF both at the lexical and sentential levels of representation (e.g., letter and phoneme length, bigram and biphone frequency, orthographic and phonological neighborhood size, spelling-sound consistency, syntactic and lexical predictability). At the lexical level, some of these factors are found to have independent effects on word processing (Graves et al., 2010). We accounted for imageability, letter length, and surprisal effects, but a limitation of the study is that we are not able to examine all of the additional factors simultaneously due to the less controlled nature of the stimuli. There are a variety of methods for quantifying predictability in text, including behavioral methods based on the CLOZE task (e.g., Lowder, Choi, Ferreira & Henderson, 2018) and computational methods based on the statistical properties of large language corpora. In the present study, we used computational surprisal measures developed by Roark et al., but it is likely that surprisal effects in narrative text are not fully accounted for by this (or any single) method. Some residual surprisal effects may possibly be reflected in the current results that could be better captured by combination with other approaches. The results suggest that the fixation-related fMRI approach may provide a fruitful new method for teasing apart sub-components of reading.

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