A functional magnetic resonance imaging study of the tradeoff between semantics and phonology in reading aloud

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Using functional magnetic resonance imaging, we explored the role of semantics in mediating orthographic-to-phonological processing in reading aloud, focusing on the interaction of imageability with spelling-to-sound consistency for low-frequency words. Behaviorally, high-imageable words attenuate the standard latency and accuracy disadvantage for low-frequency inconsistent words relative to their consistent counterparts. Neurobiologically, high-imageable words reduced consistency-related activation in the inferior frontal gyrus but increased posterior activation in the angular and middle temporal gyri, representing a possible neural signature of the tradeoff between semantics and phonology in reading aloud. We discuss implications for neurobiological models of reading in terms of understanding the interplay among areas associated with component processes and suggest that the results constitute an important step toward integrating neurobiological and computational models of reading. *NeuroReport* 16:621–624 © 2005 Lippincott Williams & Wilkins.

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INTRODUCTION

A principal aim of many neuroimaging studies of word recognition is to identify the functional neuroanatomy associated with component processes. Rather than isolating and comparing activation in brain regions associated with orthographic, phonological, and lexico-semantic processing as many previous studies have done, the current study focuses on the coordination among the processes that support reading, examining the relationship between semantics and phonology.

Recent behavioral studies by Strain *et al.* [1,2] have explored this issue, examining the effects of a semantic variable, imageability, on spelling-to-sound consistency effects in printed word naming. 'Consistency effects' refer to findings that responses are faster and more accurate for low-frequency words that have consistent (1:1) correspondences between the orthographic body and phonological rime (e.g. -ill only corresponds to /Il/ as in *pill, mill*) than for inconsistent words that have multiple body-rime correspondences (e.g. -int corresponds to /Int/ as in *mint* and /aInt/ as in *pint*). In their studies, Strain *et al.* observed two critical effects. First, consistency effects were observed primarily on words that are low in both frequency *and* imageability—consistency effects for high-imageable, low-frequency words were either attenuated or not reliable across experiments. Second, an imageability effect (faster and more accurate responses for high-imageable words than low-imageable words) was found for low-frequency inconsistent words but not for low-frequency consistent words. They interpreted this finding as support for a coordination of semantic and phonological information such that a word's semantic characteristics can influence the process of phonological assembly. A recent simulation of this interaction of consistency and imageability for low-frequency words supports the conclusions of Strain *et al.*, demonstrating that although reading is primarily governed by the computation of phonology directly from the orthographic input, a tradeoff between phonology and semantics occurs in conditions under which (1) the computation of phonological information is slowest and most error prone, and (2) the computation of semantic information is fastest [3].

In the current study, we examine the neurobiological signature of the interaction of consistency and imageability for low-frequency words. On the basis of the behavioral findings [1,2] and computational modeling [3], we predict that the activation of brain regions associated with phonological and semantic processing will trade off as a function of the difficulty of the spelling-to-sound mapping relative to the semantic richness of the words. We focus on three left hemisphere (LH) regions of interest—the inferior frontal gyrus (IFG), the middle temporal gyrus (MTG), and the angular gyrus (AG) in the inferior parietal cortex. The inferior aspect of IFG [Brodmann's area (BA) 44/45] is the primary site that has exhibited sensitivity to consistency in previous studies, showing increased activation for low-frequency inconsistent words as compared with

low-frequency consistent words [4–6]. MTG and AG have been implicated in lexico-semantic processing [7–10]. We predict that activation in IFG will be strongest for low-imageable, low-frequency inconsistent words, with attenuated activation for their high-imageable counterparts. In turn, the reduction in IFG activation should be accompanied by an increase in activation for high-imageable words as compared with low-imageable words in the posterior regions, given the richer semantic representations for high-imageable tokens.

In addition to providing information about the neurobiological signature of the interplay between phonological and semantic processes, the current experiment also contributes to the broader goal of providing a more fine-grained account of the neural organization of the reading system than would be attainable through examination of the main effects alone. Indeed, a demonstration of complex tradeoffs in activation among areas associated with different component processes would challenge existing accounts of the functional anatomy of reading [11,12]. To our knowledge, no current neurobiological models of reading incorporate mechanisms to account for interregional tradeoffs in the context of complex stimulus interactions. Computational models already provide potential mechanisms to account for such interactions, but to date have not been forced to incorporate how and where these mechanisms are instantiated in the brain. To motivate interest in linking these two levels of analysis in model development, we need to demonstrate that neuroimaging measures can reveal the expected modulation and tradeoffs that behavioral data suggest must be operating.

MATERIALS AND METHODS

Participants: Twenty-two native English speakers (11 men, 11 women) participated in exchange for payment. All reported normal or corrected-to-normal vision and no history of neurological impairment. The experiment was conducted with the understanding and the written consent of each participant and all procedures were approved by the Yale Institutional Review Board.

Stimuli: Word stimuli represented the crossing of frequency (low, high), imageability (low, high), and spelling-to-sound consistency (consistent, inconsistent) with 40 words per condition, yielding a total of 320 'go' trials. Eighty additional pseudowords, matched on factors including length, bigram frequency, and initial phoneme, served as 'no-go' trials.

Procedure: A naming paradigm in which participants respond only if the item presented is a word (go/no-go naming) was employed in a block design. During activation blocks, participants saw a letter string and were instructed to name it aloud only if it was a word. Word stimuli within each block corresponded to one of the eight conditions representing the factorial crossing of consistency, imageability, and frequency. During baseline blocks, participants passively viewed displays of intermixed hash marks and asterisks.

Functional magnetic resonance image acquisition and analysis: Imaging was performed on a 1.5 T GE Signa MR system. Prior to functional imaging, 20 axial-oblique anatomic images (TE, 11 ms; TR, 500 ms; FOV, 40 × 40 cm; 6 mm slice thickness, no gap; 256 × 192 × 2 NEX) were prescribed parallel to the intercommissural line (TE, 11; TR, 600 ms; FOV, 24 cm; 5 mm slice thickness, no gap; 256 × 192 × 1 NEX). Activation images were collected at these same slice locations using single shot, gradient echo, echo planar acquisitions (flip angle, 80°; TE, 50 ms; TR, 2000 ms; FOV, 20 × 20 cm; 6 mm slice thickness, no gap; 64 × 64 × 1 NEX).

Functional images were corrected for slice acquisition time, motion-corrected [13], and spatially smoothed with a 3.125 mm full-width at half-maximum Gaussian filter. For across-participants comparisons, participants' anatomic images were mapped into the standard brain space defined by the Montreal Neurological Institute (MNI) with an affine transformation [14].

Each functional run consisted of eight 20-s activation blocks (one for each stimulus condition) of four word trials and one pseudoword trial, with five 20-s baseline blocks. Ten functional scans were conducted, yielding 100 images for each activation condition and 500 images in the baseline condition. The order of activation block types was counterbalanced across runs.

Region of interest coordinates were defined by peak activation sites within an initial omnibus analysis that contrasted all the linguistic conditions versus the non-linguistic baseline condition, and full regions of interest encompassing a volume of 1699 mm^3 about that point. For each participant and region, activation values for subconditions were then computed using a linear regression model with predictors for experimental conditions, run effects, and low-frequency drift. These parameter estimates were compared across participants with a 2 × 2 × 2 (Frequency × Imageability × Consistency) repeated measure ANOVA.

RESULTS

Activation patterns in our three *a priori* regions of interest were examined. Figure 1 presents the pattern of brain activations across levels of consistency, imageability, and frequency for (1) LH IFG (BA 44/45), the primary region implicated across previous studies of consistency effects [4,5], (2) LH MTG (BA 21), and (3) LH AG (BA 39), two posterior regions implicated in lexico-semantic processing [7–10].

For the IFG region of interest, a significant effect of imageability was observed such that activation in IFG was greater for low-imageable than high-imageable words [F(1,21)=8.49, $p<0.01$]. Importantly, planned comparison on the frequency × imageability × consistency interaction revealed that the activation pattern in IFG mirrored the critical behavioral findings of Strain *et al.* [1,2]: consistency effects were limited to low-frequency, low-imageable words [t(1,21)=4.97, $p<0.05$] and semantics attenuated the deleterious effects of spelling-to-sound inconsistency for high-imageable, low-frequency words [t(1,21)=11.17, $p<0.005$]. With respect to the posterior regions, a main effect of imageability on activation in MTG was observed [F(1,21)=5.95, $p<0.05$], which was qualified such that imageability effects were limited to low-frequency words [F(1,21)=5.63, $p<0.05$]. The same effect was observed in the AG: an effect of imageability [F(1,21)=15.68, $p<0.001$] that
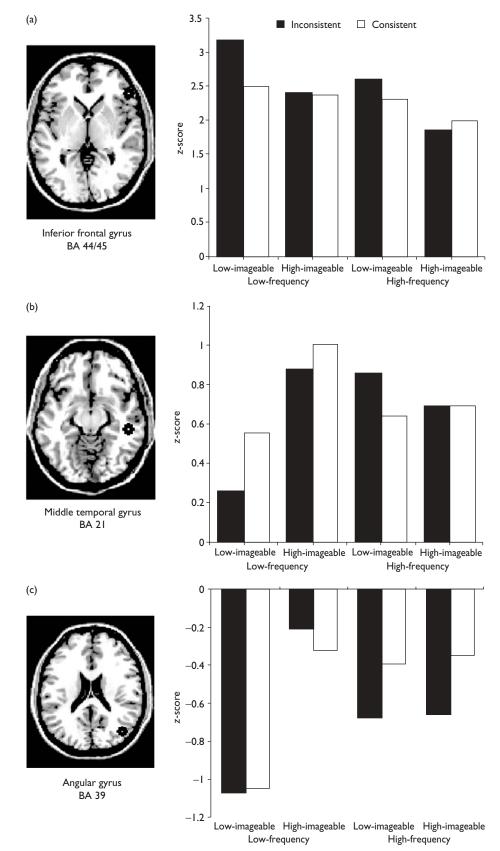
Fig. I. Standardized activation values for the eight conditions representing the crossing of frequency, imageability, and consistency in three left hemisphere (LH) regions of interest: (a) the inferior frontal gyrus, Talairach coordinates in mm, x: −31; y: +27; z: +5; (b) the middle temporal gyrus, Talairach coordinates in mm, x: −42; y: −27; z: −7; and (c) the angular gyrus, Talairach coordinates in mm, x: −42; y: −69; z: +25.

was limited to low-frequency words [F(1,21)=11.52, $p<0.001$].

Between-region planned comparisons on the imageability effect on low-frequency, inconsistent words revealed another aspect of the tradeoff between semantics and phonology observed behaviorally: as imageability alleviates consistency-related activation in IFG (Fig. 1a, columns 1–4), corresponding increases are observed in MTG [Fig. 1b, columns 1–4; F(1,21)=29.49, $p<0.0001$] and the AG [Fig. 1c, columns 1–4; F(1,21)=43.30, $p<0.0001$].

DISCUSSION

The purpose of the current study was to refine our understanding of the coordination among cortical regions engaged in phonological and semantic processing by examining the neurobiological signature of the interaction of consistency and imageability for low-frequency words. The findings demonstrate that, as predicted, activation in the LH IFG and LH MTG/AG exhibited the precise pattern as the interaction between phonology and semantics, respectively, that has been observed in behavioral studies [1,2].

In addition to providing new information about the manner in which cortical areas involved in reading aloud interact within the context of a complex interaction among stimulus dimensions, the effects of consistency and imageability on the activation of anterior and posterior regions, previously associated with main effects of phonological and semantic variables, interacted in a manner consonant with expectations based on findings from behavioral and computational studies. That is, the *modulation* of activation patterns at the anterior and posterior sites, which mirror the complex tradeoffs observed in behavior, increases our confidence that these regions are meaningfully linked to phonological and semantic component processes. The current results also reveal the sensitivity of neuroimaging techniques to detect theoretically relevant interactions among cognitive processes. It has been argued that inherent nonlinearities associated with complex interactions might render neuroimaging data uninterpretable when interactions are examined with these measures [15]. However, the behavior of the regions associated with phonological and semantic processing (LH IFG and LH MTG/AG, respectively) reveals a coherent response pattern; decreases in one are associated with corresponding increases in the others. At least under these conditions, the behavior of the reading-related, distributed circuitry in the context of a three-way interaction was quite predictable.

As noted earlier, extant computational models have the means to account for these patterns in behavioral performance (e.g. [3]), but they have not yet incorporated information about the functional architecture of the cortical reading system. That is, although it has been argued that even abstract parallel distributed processing models tend to develop spatial localization and subspecialization [16], the absence of any constraining data on cortical patterning has limited the development of more biologically realistic models. On the other hand, current models of the functional neuroanatomy of reading incorporate no mechanism(s) to account for the interregional relational processing associated with the complex tradeoffs revealed in the current study. Thus, given the limits on explanation associated with both functional neuroanatomical and abstract computational models proposed to date, the need for integration is clear. The current findings suggest that these levels of analysis can be made to speak to one another more directly, given that patterning in the brain and in behavioral performance appear to be coherently related to one another. We suggest that the next phase of neuroimaging research needs to focus on understanding how cortical regions operate as interdependent components that work to form the functional architecture of cognitive systems.

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