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Multi-voxel pattern analysis of noun and verb differences in ventral temporal cortex

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ABSTRACT

Recent evidence suggests a probabilistic relationship exists between the phonological/orthographic form of a word and its lexical-syntactic category (specifically nouns vs. verbs) such that syntactic prediction may elicit form-based estimates in sensory cortex. We tested this hypothesis by conducting multi-voxel pattern analysis (MVPA) of fMRI data from early visual cortex (EVC), left ventral temporal (VT) cortex, and a subregion of the latter – the left mid fusiform gyrus (mid FG), sometimes called the "visual word form area." Crucially, we examined only those volumes sampled when subjects were predicting, *but not viewing*, nouns and verbs. This allowed us to investigate prediction effects in visual areas without any bottom-up orthographic input. We found that voxels in VT and mid FG, but not in EVC, were able to classify noun-predictive trials vs. verb-predictive trials in sentence contexts, suggesting that sentence-level predictions are sufficient to generate word form-based estimates in visual areas.

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1. Introduction

Language, like any other temporally ordered behavior, makes use of top-down predictions in order to reduce uncertainty about upcoming events. The fact that language processing is so remarkably fast is likely due to our ability to predict the types of structures found in natural language, whether these be phonological, morpho-syntactic, lexical-semantic, or pragmatic. Given the immense generative power of language, it is unlikely that linguistic prediction operates only over the surface statistics of a language; rather, efficiency would dictate that predictions be based on the language's "category statistics," or the likelihood that one set of elements is followed by another (Hunt & Aslin, 2010). The existence of linguistic categories such as, say, nouns and verbs, is relatively easy to determine, but the predictive power of these categories is limited, if not entirely obfuscated, by the apparently arbitrary relationship between a word's syntactic category and the phonological features of that category's members. The venerable principle of the "arbitrariness of the sign" has provided not only a descriptive account of why the phonological similarity of words, such as *cat*, *sat*, and *fat*, determines neither their semantic meaning nor syntactic category (de Saussure, 1916; Tanenhaus & Hare, 2007) but also a functional account: if a word's form is uncoupled from its meaning, this allows a finite set of forms to combine to denote an infinite set of meanings (Chomsky, 1965). Thus it would seem that language's infinite generativity is at odds with optimal conditions for word form prediction.

However, a study by Farmer, Christiansen, and Monaghan (2006) provided evidence that a probabilistic relationship may indeed exist between the phonological/orthographic form of a word and its lexical category, which could in principle be used by a reader/listener to predict word form features during sentence processing. The study was prompted by a renewed interest in research demonstrating that systematic, probabilistic, form-based regularities exist among the words of a given lexical category (Arciuli & Monaghan, 2009; Cassidy & Kelly, 1991; Kelly, 1992; Monaghan, Christiansen, & Chater, 2007; but cf. Staub, Grant, Clifton, & Rayner, 2009). In a corpus analysis of the phonological properties of nouns and verbs, Farmer et al. found these two lexical categories formed distinct clusters when plotted in a multidimensional form feature space. They calculated the form feature distance between each possible two-word comparison based on the number of overlapping and non-overlapping phonetic features. They then obtained a "form typicality score" for each word by subtracting its distance to all verbs from its distance to all nouns. While many words were "neutral" – not strongly typical of either nouns or verbs – the centers of noun-typicality and verb-typicality were separated in this feature space such that clusters of typical nouns and typical verbs could be distinguished. Furthermore, the noun- or verb-typicality of a word was found to predict lexical naming latencies and reading times. This typicality measure also

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influenced syntactic processing: whether a noun–verb homonym was more typical of a noun or a verb predicted whether participants expected a noun or verb continuation of a given ambiguous sentence. The effect of this typicality measure was significant even after accounting for effects of onset phoneme, frequency, length, neighborhood size, familiarity, and imageability.

The present work uses fMRI multi-voxel pattern classification to test whether readers predict word forms corresponding to noun and verb syntactic categories and to examine the neural instantiation of these putative predictions. There are several candidates for the neural read-out of such a predictive system. In this study, we will explore areas where this prediction may engage the brain's extended visual system. Although Farmer et al. (2006) quantified form typicality using a phonological feature metric and not a visual orthographic metric per se, they found evidence that this form typicality metric predicted reading times. English's use of a phonemic orthography (in which graphemes have a correspondence to phonemes) leads one to expect that a syntactic–phonological–orthographic correspondence could play a role in using lexical category expectations to predict visual word form features. If so, we would expect such prediction to recruit areas of the brain sensitive to features of words and letter strings. One such candidate region is the left mid fusiform gyrus, referred to by some as the "visual word form area" due to its putative specialization in identifying visual word forms (Dehaene & Cohen, 2011). Although the functional specificity of this area is not uncontroversial, and there may be other areas of the brain subserving written word recognition, the left mid fusiform gyrus is robustly sensitive to visual word stimuli, and thus could be involved in generating word form predictions. We also looked at a larger swathe of ventral temporal cortex surrounding mid FG, since the mid FG may be part of a more diffuse posterior-to-anterior tuning gradient extending along the left ventral temporal cortex and sensitive to (non-)orthographic line junctions, alphabetic letters, bigrams, morphemes, and whole words (Haushofer, Livingstone, & Kanwisher, 2008; Vinckier et al., 2007).

Rather more controversial, however, is evidence that syntactic predictions during reading may generate form-based estimates as early as occipital cortex (Dikker, Rabagliati, Farmer, & Pylkkanen, 2010). In an event-related magnetoencephalographic (MEG) study, Dikker et al. compared brain responses across two syntactic violation conditions. In both conditions, the syntax of the sentence selected for a verb, but in one case the next word was a form-typical noun and in the other it was a form-neutral noun, which had form features consistent with both nouns and verbs. It was found that the amplitude of the MEG component called the M100 (i.e., 100 ms post-stimulus onset) was significantly greater when a typical noun violated the sentence continuation than when a neutral noun did. Although the type of syntactic violation was equivalent in both cases, only the typicality scores predicted this M100 modulation. In other work, the M100 has been localized to early visual cortex (EVC) – specifically the cuneus, lingual gyrus, and BA 17 (Itier, Herdman, George, Cheyne, & Taylor, 2006). Thus, these data compelled us to look at EVC in addition to more anterior regions in VT.

In the present work, we were concerned not only with the question of *where* in the brain lexical-syntactic categories might map onto form features, but also the questions of *how* and *when*. Could the early visual form typicality effect in MEG have marked an *in situ* violation detection, or might a lexical class violation generate an error signal elsewhere in the brain that is then relayed to visual areas via re-entrant pathways? Is the expectation violation detected first in higher-level areas, *after* the word has been fully analyzed for lexical syntactic properties, or do visual areas have enough information about the predicted word form features to "raise the first alarm"? One hypothesis entails top-down prediction, while the other requires no such prediction, but rather a fast bottom-up analysis of a word before the lexical class violation can be detected. While the M100 has been shown to be sensitive to orthographic frequency and transition probability of letter strings, there is no evidence that the M100 is sensitive to lexical factors of words in isolation (Solomyak & Marantz, 2009; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). For this reason, the MEG findings led to the hypothesis that top-down prediction must be involved (Dikker et al., 2010); however, this hypothesis has not been directly tested until now.

One way to distinguish top-down prediction effects of word form estimation from bottom-up perceptual effects of word recognition is simply to remove the word stimulus. We did just this in the following experiment: we presented subjects with syntactically predictive sentence fragment cues followed by a series of random dot patterns in which the subject was to search for either a noun or a verb. Subjects viewed sentence fragments that highly constrained the category of word that could continue the sentence (e.g., a noun was expected but not a verb, or vice versa) but did not constrain expectation for a specific word within that category (see Appendix for list of stimuli). Instead of seeing the sentence-final word immediately, subjects searched for an appropriate sentence completion in a series of noisy images and indicated when an appropriate word was discernible (see Fig. 1).

There is precedent in the MVPA literature for successful decoding of imagined shapes (Stokes, Thompson, Cusack, & Duncan, 2009; Stokes, Thompson, Nobre, & Duncan, 2009), objects (Lee, Kravitz, & Baker, 2012), and object categories (e.g., people vs. cars; Peelen & Kastner, 2011) from distributed BOLD activity. Extending this method to highly abstract grammatical word categories, we were able to successfully classify nouns vs. verbs in VT and mid FG when a syntactic context was provided. In contrast, EVC did not support classification in this study. These results suggest that syntactic, or at least sentence-level, prediction prompts form-based estimates in early visual word form areas, and that a probabilistic relationship between word form and word category is indeed exploited by the neural circuitry.

2. Material and methods

2.1. Participants

Twelve subjects participated in this study. Two subjects' data were excluded due to excessive motion artifact, leaving ten subjects analyzed here. Subjects ranged in age from 18 to 38 years, and all were right-handed native speakers of English with normal or corrected-to-normal vision and no reported history of neurologic problems. Subjects gave written informed consent and were provided monetary compensation for their time. The human subjects review board at the University of Pennsylvania approved all experimental procedures.

2.2. Task and stimuli

2.2.1. Sentence norming

The sentences used in this study were constructed such that the final word in the sentence could be predicted with near certainty to be either a noun or a verb, depending on the condition. Four sentence conditions were included: two noun-terminal ("Noun1" and "Noun2" conditions) and two verb-terminal ("Verb1" and "Verb2" conditions), each corresponding to a different structural template as in (1)–(4) below. "*Wh*" indicates a *wh*-word, "V_{aux}" indicates an auxiliary verb (either *did* or *was*), "NP" indicates a noun phrase, "VP" indicates a verb phrase, and "PP" indicates a prepositional phrase.

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