Without morpheme-level automatizability, the skill of reading might never have transformed modern cultures so profoundly (or at least those few with near-optimal writing systems).

Towards a universal neurobiological architecture for learning to read

doi:10.1017/S0140525X12000283

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Abstract: Letter-position tolerance varies across languages. This observation suggests that the neural code for letter strings may also be subtly different. Although language-specific models remain useful, we should endeavor to develop a universal model of reading acquisition which incorporates crucial neurobiological constraints. Such a model, through a progressive internalization of phonological and lexical regularities, could perhaps converge onto the language-specific properties outlined by Frost.

"Cmabirdge" reads almost as well as "Cambridge," but only in some languages. Ram Frost is right in pointing out that tolerance to letter-position swaps is not a universal feature of reading. His hypothesis that writing systems "optimally represent the languages' phonological spaces" (sect. 3, para. 1) is appealing and is indeed a crucial consideration when discussing the possibility of spelling reform – some variations in writing systems may be more "rational" than they first appear (Dehaene 2009, pp. 32–37). Does it follow, however, that current open-bigram models of orthographic processing are, in Ram Frost's words, "ill-advised"? And what is the best strategy to achieve a "universal model of reading"?

From a neuroscientific perspective, much insight can be gained from limited models that consider in detail not only the problems raised by a specific script and language, but also the neurobiological constraints on how the brain might solve them. Our *bigram neuron* hypothesis, which postulates that the left occipitotemporal visual word form area (VWFA) may contain neurons tuned to ordered letter pairs, was presented in this context as a useful solution to position-invariant recognition of written words in English, French, and related Roman scripts (Dehaene et al. 2005). A functional magnetic resonance imaging (fMRI) experiment aimed at testing the predictions of this model demonstrated that reading indeed relies on a hierarchy of brain areas sensitive to increasingly complex properties, from individual letters to bigrams and to higher-order combinations of abstract letter representations (Vinckier et al. 2007). These regions form a gradient of selectivity through the occipitotemporal cortex, with activation becoming more selective for higher-level stimuli towards the anterior fusiform region (Fig. 1) (see also Binder 2006). Interestingly, a similar gradient may also exist in Chinese script (Chan et al. 2009). It would be important to probe it in Hebrew readers.

We agree with Frost that developing a more general, language-universal model of reading acquisition is a major goal for future research. However, crucially, we would add that such a universal model should incorporate strong constraints from brain architecture and not just linguistics. Existing connectionist models typically incorporate few neurobiological constraints and, as a result, provide information-processing solutions that need not be realistic at the brain level. Reading is a ventral visual stream process that "recycles" existing visual mechanisms used for object recognition (Dehaene 2009; Szwed et al. 2009; 2011; however, see Reich et al. 2011) As such, it is heavily constrained by the limitations of the visual brain, for example, the necessity to process information

Components of stimulus strings

	Types of stimuli					
	Words	Frequent Quadrigrams	Frequent Bigrams	Frequent Letters	Infrequent Letters	False Font
Strings	high	0	0	0	0	0
Quadrigrams	high	high	low	low	low	0
Bigrams	high	high	high	low	low	0
Letters	high	high	high	high	low	0
Features	high	high	high	high	high	high
Example	MOUTON	AVONIL	OUMBSS	OOADTO	JZWYWK	[illegible]

← Structural similarity to real words

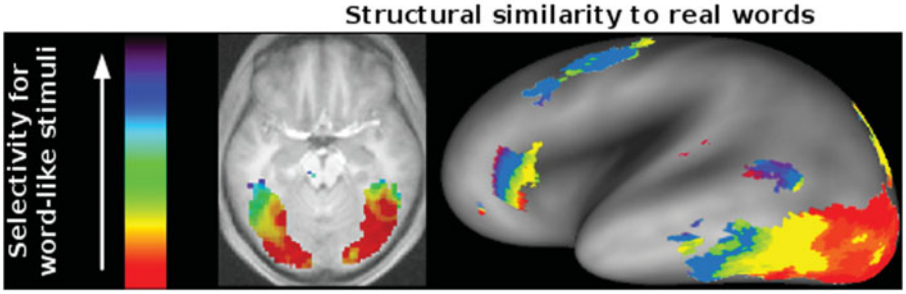

Figure 1 (Szwed et al.). Hierarchical Coding of Letter Strings in the Ventral Visual Stream. **Up:** Design and examples of stimuli used, with an increasing structural similarity to real words. **Down:** fMRI results The image illustrates the spatial layout of sensitivity of the occipitotemporal cortex to letter strings of different similarity to real words. Activations become more selective for higher-level stimuli (i.e., stimuli more similar to real words) toward the anterior fusiform regions. This is taken as evidence for a hierarchy of brain areas sensitive to increasingly complex properties, from individual letters to bigrams and to higher-order combinations of letters. (Adapted from Vinckier et al. 2007).

step by step through distinct visual areas with increasing receptive fields (V1, V2, V3, V4, V5, LO, MT …). Implementing these constraints into general models has proven very challenging so far (although see Mozer 1987). Indeed, important advances in the field have been predominantly guided by narrow, language-specific theories that hardwire these constraints into their architectures. Nevertheless, the vast neurobiological knowledge about these regions should ultimately be tapped by a more general model. Starting from a generic, biologically realistic neuronal architecture, and using realistic synaptic plasticity rules, the future model would converge on a specific architecture for the VWFA in any language. It could include a Bayesian implementation of the informative fragments model, which falls close to predicting the real-life responses of ventral visual stream neurons involved in object recognition (Ullman 2007).

Would such a model, once developed, substantiate Frost's claim that the internal code for letter strings varies strongly across languages, depending on their phonology and word structure? Here, we should clear up a frequent confusion. During *online* processing, when an actual word is read by a fluent reader, magnetoencephalography (MEG) experiments, with their high temporal resolution, have shown that the first major response of the visual system, peaking roughly 130 msec after seeing a word, is determined overwhelmingly by the frequency of letter combinations that make up a word, whereas lexical and phonological effects come into play much later (Simos et al. 2002; Solomyak & Marantz 2010). Thus, in adults, the VWFA may reflect a relatively isolated stage of orthographic processing that is essentially immune to phonological and semantic influences (Dehaene & Cohen 2011; but see Price & Devlin 2011). However, this is not to say that, in the course of *learning*, the acquired orthographical code cannot be influenced by the needs of the phonological and semantic systems to which the VWFA ultimately projects. The anatomical localization of the VWFA is strongly influenced, not only by bottom visual constraints (Hasson et al. 2002), but also by the lateralization of the target spoken language (Pinel & Dehaene 2009). MEG shows that, in English readers, the visual word form system decomposes the words' morphology into prefixes, roots, and affixes about 170 msec after stimulus onset (Solomyak & Marantz 2010). Such decomposition is automatic and operates even with pseudo-affixed words like "brother" that can be falsely decomposed into "broth" and "er" (Lewis et al. 2011). Thus, the visual system has internalized orthographic units that are relevant to morphological and lexical knowledge. Although not yet demonstrated, we consider it likely that the VWFA also codes for frequent substrings that facilitate the mapping onto phonemes, such as "th" or "ain" in English. Indeed, this hypothesis may explain why English reading, with its complex grapheme–phoneme mappings, causes greater activation in the VWFA than does Italian reading (Paulesu et al. 2000).

In this context, we have no difficulty in accepting Frost's argument that the optimal neural code for letter strings might have to be much less tolerant to letter swaps in Hebrew than in English. This view predicts root detectors in the more anterior part of VWFA of Hebrew readers and sharper tuning curves for letters and bigrams detectors. Testing such predictions for scripts other than Latin is an important goal for future neuroimaging experiments. A readily available tool is fMRI repetition suppression, which has proven sensitive to subtle properties of object, number, and letter tuning (Dehaene et al. 2004; Grill-Spector et al. 1999). Alternatively, multivariate pattern analysis may provide more direct access to the fine-tuning characteristic of the VWFA (Braet et al. 2012).

ACKNOWLEDGMENT

MS was funded by an Iuventus Plus grant from the Polish Ministry of Science and Higher Education and an ERC (European Research Council) advanced Grant 230313.

The study of orthographic processing has broadened research in visual word recognition

doi:10.1017/S0140525X12000131

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Abstract: Interest in orthographic processing reflects an expansion, not constriction, of the scope of research in visual word recognition (VWR). Transposition effects are merely one aspect of investigations into orthographic encoding, while open bigrams can accommodate differences across languages. The target article's inaccurate characterization of the study of orthographic processing is not conducive to the advancement of VWR research.

The target article accuses researchers in orthographic processing of inadvisedly narrowing the scope of investigation in visual word recognition (VWR). However, the article actually reflects the narrowness of the author's own outlook, rather than the existence of any constrictions on VWR research.

The article makes the obvious point that VWR is not limited to orthographic processing, but must include phonological, morphological, and semantic analysis. None of us who investigate orthographic processing would disagree. The current attention being paid to the topic of letter-position encoding simply reflects the fact that this aspect of VWR has been neglected in the past; we have now successfully pointed out the interesting and important questions associated with this topic.

Frost characterizes research in orthographic processing as focusing on transposed-letter effects, and points to the lack of transposed-letter priming for Hebrew roots as evidence that our research does not address universal questions in VWR. However, his article is inaccurate on both these counts. Research on orthographic processing attempts to answer the question of how a feature-based retinotopic representation is converted into abstract representations of letter identity and order that support morphological, lexical, and phonological analysis. It employs behavioral and brain-imaging experiments evaluating the effects of retinotopic position, within-string letter position, word length, and letter insertions, deletions, and transpositions within and across phonological and morphological boundaries.

Such investigations have led some researchers to propose an open-bigram encoding for lexicosemantic access, as noted in the target article. Although the proposal of open bigrams was based on research in European languages, this type of representation happens to be particularly suited for Hebrew roots, because it encodes the order of non-contiguous letters. Under a universal open-bigram encoding, the degree of sensitivity to transposed-letter priming may simply be a function of the relative strength of inhibitory and excitatory connections between open bigrams and morphological units. For example, a strong inhibitory connection from open-bigram BA to root ABC would prevent facilitation by the prime BAC. In fact, evidence for such inhibition comes from an English study that compared the effect on the target ABCD of the reversed prime DCBA versus a control prime containing none of the target's letters (Still & Morris 2010). The reversed prime yielded inhibition with respect to the control, suggesting the existence of inhibitory input from bigrams that are reversals of the word's bigrams. The relative influence of such inhibition may vary with morpheme length, language, and reading experience. Research, not ranting, is required to resolve the issue of whether differences in transposition effects across languages reflect *quanti*tative differences in orthographic processing (as suggested here) or *quali*tative differences (as claimed in the target article).

However, the study of orthographic processing encompasses much more than the question of what type of representation contacts the lexical/morphological level. It addresses lower levels of processing, asking how a retinotopic representation is converted into a location-invariant encoding, including the issue of how information