Where Visual Word Form Areas Come From

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As you are reading this, your brain is analyzing incoming visual information in order to identify each grapheme (Tan, Laird, Li, & Fox, 2005). These graphemes are then grouped together to form morphemes with a specific orthography, which are bound to the corresponding phonemes (Schlaggar & McCandliss, 2007), allowing you to extract the semantic meaning of each word (Blomert, 2011). This complex process is done so rapidly and seamlessly that once reading expertise has been acquired, it is almost effortless. While it is tempting to say that we are just “wired” for reading, this is extremely unlikely, as written language has only emerged within the past 6000 years (Ansari, 2013; Dehaene, Cohen, Sigman, & Vinckier, 2005; Price & Devlin, 2003), which is simply not enough time to evolve neural mechanisms specific to reading. Therefore any neural substrates found to respond preferentially to written language must have been recycled from already-existing neural systems.

One region in particular which has garnered significant of attention is the visual word form area (VWFA; Cohen, Lehéricy, Chochon, Lemer, Rivaud, & Dehaene, 2002) within the left fusiform gyrus, which has consistently been found to respond preferentially to visually-presented words and pseudowords (Dehaene, Pegado, Braga, Ventura, Filho, Jobert, & Dehaene-Lambertz, 2010; Glexer, Jiang, & Riesenhuber, 2009; Szwed, Dehaene, Kleinschmidt, Eger, Valabrègue, Amadon, & Cohen, 2011), and has been shown to respond weakly in poor readers (Dehaene et al., 2010). While the special role of written language in the VWFA has been contested (Price & Devlin, 2003), it is still generally regarded as an important region for orthographic processing (Ball, 2012; Schlaggar & McCandlissm 2007; Szwed et al., 2011; Price & Devlin, 2003; Yeatman, Rauschecker, & Wandell, 2012). This begs the question, however: What makes this region so well-suited for processing written language, and how does it change over the course of development? This paper will attempt to explore this question by examining unique properties in its cortical location and function.

A proposal by Dehaene and colleagues (2005) argued the case for a hierarchical model of visual reading, wherein a series of "local combination detectors" (LCDs; Dehaene et al., 2005, p. 337), beginning bilaterally in the lateral geniculate nucleus and gradually extending and lateralizing toward the left occipito-temporal sulcus (OTS), processes visual word forms of written language. These neural signals are likely carried by the inferior longitudinal fasciculus (ILF), a white matter tract extending from the occipital lobe to the medial and anterior temporal cortex (Yeatman et al., 2012a; Yeatman et al., 2012b) (The role of white matter tracts in the development of reading will be discussed in further detail later in this paper). While at the lower levels these LCDs have a very limited receptive field, allowing for minor shape discrimination, within the OTS, each LCD has a much wider receptive field and processes significantly more complex visual stimuli such as whole words (Dehaene et al., 2005; Köhler, 2011a). Adjacent to the left OTS is the VWFA, which they propose houses the "neural code" for seeing written words (Dehaene et al., 2005). While the precise mechanics of this code are beyond the scope of this paper, there are numerous objections which may be raised at the notion of the VWFA being specialized to process patterns of visual orthographic print.

A commentary by Price and Devlin (2003) observed that while the VWFA was the only left-lateralized region which demonstrated greater cortical response to printed words versus false fonts, indicating that it was indeed involved in processing visual language, it also showed preferential activation for processes which involved no reading whatsoever. These processes included identifying visually-presented objects (Price & Devlin, 2003), as well as facial recognition (Deheane et al., 2010).

One possibility which Price and Devlin (2003) proposed to account for such varied responses in the VWFA is that a single unknown cognitive function underlies these cortical responses. An interesting proposition for this underlying cognitive process comes from a study by Szwed et al. (2011), who noted that the presence of vertices, occurring at the point where two or more lines intersect, was a common feature in every written language. The presence of vertices has also been demonstrated to be important in object recognition (Biederman et al., 1987, as cited in Szwed et al., 2011, p. 331). Wishing to test if the VWFA responded to the presence of vertices, and that it was merely adapted through learning to process orthography, Szwed et al. (2011) presented participants with a series of words and line drawings which were degraded in one of two ways: either the vertices were preserved and the midsegments of the lines were deleted, or the midsegments were preserved and the vertices were deleted. To control for differences in the number of segments in each stimulus, the degraded words or drawings were also presented as scrambled words or drawings (see Figure 1 in Szwed et al., 2011, p. 332).

As expected, they found that participants were able to respond faster and more accurately when presented with vertex-preserved stimuli than when presented with midsegment-preserved stimuli (Szwed et al., 2011). Interestingly, when examining cortical activation patterns, they found that early visual areas in the left-lateralized V1/V2 and V3V/V4 demonstrated preferential activation to words compared to scrambled words, but not objects relative to scrambled objects. Identified V1/V2 regions were heavily focused on the VWFA within the identified reading area - located by contrasting words and control stimuli - supporting their hypothesis that the VWFA is sensitive to the presence of line junctions of written language. Furthermore, the early left-lateralization of these visual regions is supportive of the previously-discussed model proposed by Dehaene et al. (2005 Dehaene et al., 2005), which proposes a bilateral-to-left shift of lateralization as we move from posterior to anterior visual cortical regions. The models therefore are very complimentary to one another, suggesting that the VWFA does play a part in the neural coding of written words, and it does so by selectively attending to the statistical regularities of vertices within print (Dehaene et al., 2005; Szwed et al., 2011).

However, as skilled reading requires input from multiple cortical regions, it stands to reason that the VWFA must be able to communicate wiith relevant cortical regions through the use of long-range connections. This paper will focus on two main fiber fascicles: the ventral occipital fasciculus (VOF) and previously-mentioned ILF. Damage to these surrounding white matter tracts has been found to produce severe reading deficits (Yeatman et al., 2012a).

The VOF begins near the occipito-temporal sulcus, travelling near the VWFA (some white matter fibers likely terminate on the VWFA, though this is not always detectable by the scanner), and finally terminating on the lateral-occipital and inferior parietal cortex (Yeatman et al., 2012b). The inferior parietal cortex was found to be associated with receptive language processing, allowing individuals to extract meaning not only from the words of others, but also in their own (Köhler, 2011a). Lesions to this area have been shown to result in a receptive aphasia (Bureau , 2011; Köhler, 2011b) causing difficulty in afflicted individuals when difficulties interpreting the speech of others, as well as conveying meaningful thoughts orally, while leaving their vocabulary relatively intact (Bureau , 2011; Köhler, 2011b). Due to the above, we can see that the VWFA is in an excellent location for extracting meaning from written language through the integration of visual information within the occipito-temporal sulcus and language meaning within the inferior parietal cortex.

The ILF runs throughout the ventral occipito-temporal cortex, connecting with the VWFA (Yeatman et al., 2012a; Yeatman et al., 2012b), and extending towards the anterior temporal cortex (Yeatman et al., 2012b), carrying with it information that is crucial for seeing written words (Yeatman et al., 2012a). The anterior temporal cortex has been proposed to function as a cortical repository of our vocabulary and semantic knowledge (Köhler, 2011b; Nakamura, Kuo, Pegado, Cohen, Tzeng, & Deheane, 2012; Rapp & Lipka, 2011). Atrophy of this region has been associated with semantic dementia, wherein the progression of this degeneration of the anterior temporal cortex causes individuals to gradually lose knowledge of word meanings, while preserving working and episodic memory (Köhler, 2011b). Therefore, the close proximity of the VWFA to the ILF places it in a unique position where it may integrate visual information of written language with semantic knowledge.

Thus, it is clear that the VWFA may communicate with both visual and language centers in order to bind phonological and orthographic data, and enable humans to possess written language (Yeatman et al., 2012b). However, the function of the VWFA is not fixed, but is rather fine-tuned through extensive years of extensive literacy training.

A recent 3-year longitudinal study by Yeatman et al. (2012a) examined differences in the progression of white matter fractional anisotropy (FA) within the ILF between children and adolescents who are above-average and below-average readers. While all children did improve in reading ability over time, they generally remained in the same ranking relative to each other (i.e., above-average readers stayed above average, below-average readers stayed below average). They found that children with higher reading scores initially had lower ILF FA than those with low reading scores. However, over time this relationship reversed, and those with better reading scores showed greater ILF FA than those with low reading scores. These changes in ILF were also more closely correlated with reading skills than IQ for nearly all participants (Yeatman et al., 2012a). The authors attributed this reversal in ILF FA and reading skills to an asynchronous pattern of myelination and pruning in white matter development. While above-average readers show a more steady progression of FA, below-average readers are characterized by a rapid increase in myelination and ILF FA in early development, while later development is largely influenced by pruning and a decrease of ILF FA. This ultimately results in a loss of cortical plasticity, decreasing the capacity of the below-average readers to recycle cortical structures such as the left fusiform gyrus for visual word forms (Yeatman et al., 2012a).

Wishing to examine how precisely literacy training may recycle cortical brain regions, Dehaene and colleagues (2010) studied samples of literate, illiterate, and ex-illiterate individuals and examined their cortical activation patterns in response to a battery of visual stimuli. Unsurprisingly, they found that in the VWFA, literate participants showed the greatest activation in response to being presented with letter strings, followed by ex-illiterates, and finally illiterates. However, they also discovered that for other categories of stimuli, such as checkers, objects, houses and faces, there was an inverse relationship between the cortical response in the VWFA and literacy. Literate individuals were found to show the least activation, followed by ex-illiterates, and finally illiterates had the greatest cortical response (Deheane et al., 2010). This inverse relationship was most significant in faces. The authors proposed that this may be due to competition for cortical representation with other near-by cortical structures- specifically, with the fusiform face area (FFA), which has been proposed as a facial recognition region (McCarthy, Puce, Gore & Allison, 1997). While the FFA is right-lateralized, there is left-hemispheric activation very close to the VWFA. Curiously, the FFA is a region with a very similar controversy to the VWFA McCarthy et al., 1997); is it truly a region specific for face-processing? Or is it merely involved in object-recognition and become specialized for recognizing faces? The authors argue that cortical competition for representation between these two regions causes the lateralization; the VWFA forces the FFA to the right, and vice-versa (Deheane et al., 2010).

The VWFA may generally take the left hemisphere due to its greater affinity for part-based processing, which is more suitable to letter-processing, while the FFA may take the right hemisphere due to its greater affinity for holistic processing, which is more suitable for facial recognition (Köhler, 2011a). This hypothesis seems supported by their finding that illiterate individuals with less VWFA activation show greater activation in the right fusiform gyrus when presented with facial stimuli.

To sum up, the literature does seem to support the VWFA as a “hub” of orthographic language, though not innately so. It seems to accomplish this feat by using a neural code to detect and read letters (Dehaene et al., 2005), which is does so by taking advantage of its natural preference for line junctions in order to detect statistical regularities in orthography (Szwed et al., 2011), as well as use its convenient location relative to white matter tracts such as the VOT and the ILF, allowing the VFWA to integrate both meaning and semantic knowledge with incoming visual information form the occipital regions (Dehaene et al., 2005; Yeatman et al., 2012a; Yeatman et al., 2012b). The role of education is clearly key, as reading is not something humans just “do”. Effortful literacy education seems to recycle object recognition centers in the left fusiform gyrus in order to become better attuned to print, possibly taking away from cortex that would originally have gone to processing facial stimuli (Dehaene et al., 2010).

While these ideas are currently very hypothetical, future research may wish to more closely examine the relationship between the bilateral fusiform gyri in association with both literacy education and facial processing. Should these ideas hold, examining these two together may reveal more about their function than when examining them apart.

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