The unique role of the visual word form area in reading

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Reading systematically activates the left lateral occipitotemporal sulcus, at a site known as the visual word form area (VWFA). This site is reproducible across individuals/scripts, attuned to reading-specific processes, and partially selective for written strings relative to other categories such as line drawings. Lesions affecting the VWFA cause pure alexia, a selective deficit in word recognition. These findings must be reconciled with the fact that human genome evolution cannot have been influenced by such a recent and culturally variable activity as reading. Capitalizing on recent functional magnetic resonance imaging experiments, we provide strong corroborating evidence for the hypothesis that reading acquisition partially recycles a cortical territory evolved for object and face recognition, the prior properties of which influenced the form of writing systems.

The visual word form area hypothesis revisited

Nineteenth century neuropsychology [1], as well as 20th century intracranial recordings [2] and brain imaging [3], have long associated written word recognition with the left fusiform gyrus. In 2000, using functional magnetic resonance imaging (fMRI) and event-related potentials in normal subjects and in two patients with callosal lesions, we found that reading was associated with the activation of a precise and reproducible site in the left lateral occipitotemporal sulcus [4]. Its response was strictly visual and prelexical [5], yet invariant for location [4] and the case [6] of the stimulus words. This pattern fitted with the previous neuropsychological inference of an abstract representation of the 'visual word form'; that is, the abstract sequence of letters that composes a written string [7]. We tentatively termed this region the visual word form area (VWFA). Both the name and the concept, however, were challenged on the grounds that the empirical evidence suggested a mixture of reading and non-reading functions for this region, and that the whole pattern could be explained by top-down signals arising from higher level language areas [8,9]. A flurry of empirical work ensued. In the present article, we review how the VWFA hypothesis holds up a decade later.

The neuronal recycling hypothesis

Our starting point for thinking about the VWFA is the fact that the human brain cannot have evolved a dedicated mechanism for reading. The invention of writing is too recent and, until the last century, concerned too small a fraction of humanity to have influenced the human genome. Thus, learning to read must involve a 'neuronal recycling' process [10,11] whereby pre-existing cortical systems are harnessed for the novel task of recognizing written words. The concept is similar to the notions of evolutionary 'exaptation' [12] or 'tinkering' (bricolage) [13], but we use the term 'neuronal recycling' specifically to refer to educational changes that occur in developmental time and without any change in the human genetic make-up.

The recycling hypothesis does not postulate any novel form of learning or plasticity, but it emphasizes that plastic neuronal changes occur in the context of strong constraints imposed by the prior evolution of the cortex. Far from being a *tabula rasa* or a malleable system capable of learning almost any regularity [14], the pre-school child's brain is tightly organized as a consequence of both genetic constraints on cell types, receptor densities or connectivity patterns, and early internalization of dominant environmental statistics (e.g. those governing object contours). Education-induced changes must fit within the fringe of plasticity left open, within some of these cortical systems, by learning algorithms which are themselves under strong genetic and connectional constraints. Thus, the recycling view predicts bidirectional constraints between brain and culture. On the one hand, reading acquisition should 'encroach' on particular areas of the cortex – those that possess the appropriate receptive fields to recognize the small contrasted shapes that are used as characters, and the appropriate connections to send this information to temporal lobe language areas. On the other hand, the cultural form of writing systems must have evolved in accordance with the brain's learnability constraints, converging progressively on a small set of symbol shapes that can be optimally learned by these particular visual areas.

We have proposed that writing evolved as a recycling of the ventral visual cortex's competence for extracting configurations of object contours [10,11]. When projected on the retina, the contours of objects form typical patterns

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(e.g. T, L, Y) that have been termed 'non-accidental properties' because they tend to be highly invariant across viewpoints and to provide essential information about object shapes and spatial relations [15,16]. A T junction, for example, often signals occlusion of a surface by another. The visual system relies strongly on such line junctions to recognize objects, particularly line drawings [15].

In support of this hypothesis, we recently showed that reading, like object recognition, is specifically impaired when line configurations are deleted [17,18]. Furthermore, as predicted, the VWFA overlaps with a subpart of the ventral visual cortex that exhibits a special sensitivity to the presence of such line junctions [18]. Also, cross-cultural analysis shows that all of the world's writing and symbol systems make use of the same set of line junctions, with a frequency pattern that matches the frequency profile of natural scenes [19]. These findings suggest that cerebral constraints have indeed influenced the form of writing systems, and strengthen the hypothesis that visual word recognition is recycled from a prior cortical competence for invariant object recognition.

Is the VWFA 'specialized' for reading?

The recycling view clarifies the vexing issue of 'specialization' in the VWFA. Price and Devlin state that 'neither neuropsychological nor neuroimaging data are consistent

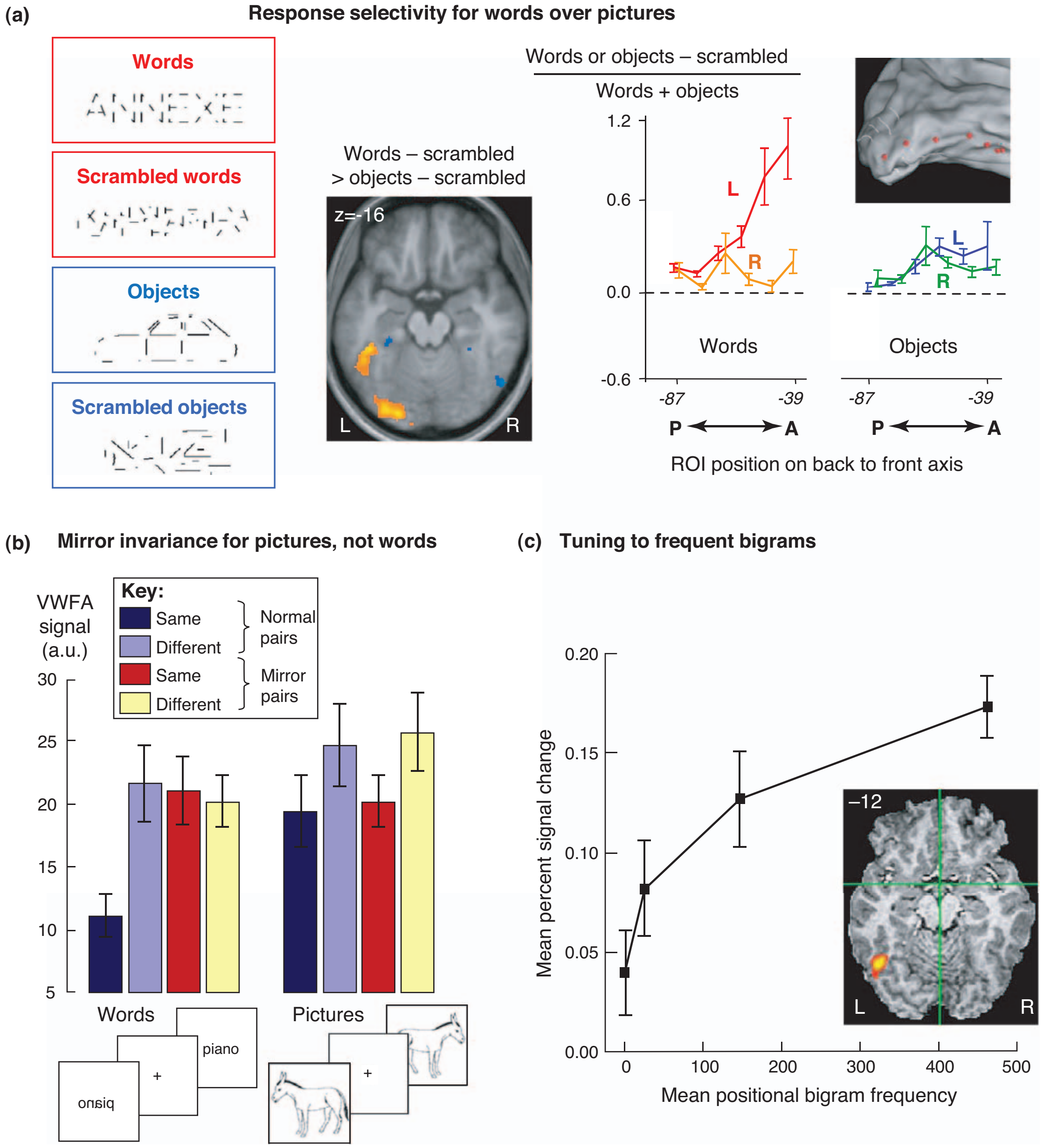

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Figure 1. Evidence of functional selectivity for letter strings in the visual word form area (VWFA). **(a)** When words are matched to pictures in terms of number of strokes, using scrambled stimuli as a control, a clear superiority for words over pictures is found in the left occipitotemporal sulcus (VWFA) as well as in a more posterior left occipital area (after [18]). **(b)** Even when they are not matched in complexity, words and pictures are distinguished in the VWFA by their different pattern of mirror invariance; there is repetition suppression for mirror pictures, but not for mirror words, presumably reflecting 'unlearning' of mirror invariance during reading acquisition (after [37]). **(c)** The VWFA also encodes language-specific orthographic knowledge, as indicated by a monotonic increase of its response to meaningless letter strings as a function of their average bigram frequency (after [32]). ROI, region of interest.

with a cortical region specialized for visual word form representations' [8] and that 'vOT [ventral occipitotemporal] neuronal populations are not specifically tuned to orthographic inputs' [9]. We disagree, but we note that the debate rests largely on the ill-defined terms 'specialization' and 'specific' [20] The recycling view predicts that reading acquisition should always occur at a reproducible localization in the visual cortex and with a functional specialization for reading-specific processes, although not necessarily with full regional specificity because both word and object recognition may still be intermixed at the same cortical site. Recent results have largely supported these conclusions.

Reproducible localization

Meta-analyses have confirmed that the same region of the left lateral occipitotemporal sulcus always is activated, to within a few millimeters, whenever literate humans read [4,5,21,22]. This localization is surprisingly reproducible across cultures that vary greatly in reading direction or type of script (alphabetic, syllabic as in Japanese Kana or morphosyllabic as in Chinese) [21]. It can be explained by a combination of early biases that conspire to make this cortical site nearly optimal for written word recognition, including: (1) a preference for high-resolution foveal shapes [23]; (2) sensitivity to line configurations [18]; and (3) a tight proximity and, presumably, strong reciprocal interconnection to spoken language representations in the lateral temporal lobe. The latter constraint is probably essential. Temporal lobe language representations antedate reading; they are already present in 3-month-old babies [24], and there is now evidence that the hemispheric lateralization of the VWFA is strongly correlated with the lateralization of spoken language processing [25–27]. Nevertheless, these constraints act only as biases that can be overridden. For example, the region exactly symmetrical to the VWFA, in the right hemisphere, can take over when the original VWFA site suffers a lesion in childhood [28].

Functional specialization

Growing evidence confirms that the VWFA performs computations that are unique to reading in the learned script [29] and cannot be reduced to generic visual recognition processes (Figure 1). For example, fMRI adaptation shows that the VWFA is the first cortical site to recognize letters invariantly in upper and lower case [6,30]. Using letters that have different shapes in upper and lower case (e.g. RAGE versus rage), we showed that this property does not result solely from generic size invariance (e.g. o versus O), but implies an internalization of arbitrary cultural rules unique to the Western alphabet [30]. Recently, the VWFA was also found to be invariant for printed versus handwritten words [31].

Other evidence for functional specialization includes the following.

- The VWFA is the only region sensitive to bigram frequency; that is, it has internalized the statistics of letter pairings in the participant's language [32,33].
- The VWFA shows a word-specific pattern of orthographic priming [34], suggesting that it may contain neural populations sensitive to morphemes or short words in the reader's language [35].
- The VWFA distinguishes between words and their mirror images [36,37] – an indispensable feature given the presence of mirror letters such as b and d in Latin-based alphabets – but remains mirror-invariant for pictures and faces.
- A similar specialization is seen for Chinese characters in Chinese readers [38,39].

Most recent results appear compatible with the local combination detector (LCD) model of the VWFA [35], according to which a fraction of occipitotemporal neurons become attuned to fragments of writing (some discrepant findings are discussed in Box 1). The LCD model postulates a highly parallel process whereby written words are encoded by a hierarchy of neurons with increasingly larger

Box 1. Methodological concerns

Our proposal that the visual word form area (VWFA) contains populations of neurons tuned to orthographic features has been challenged empirically on the grounds that activation in this region can be modulated by the lexical, semantic or even pictorial content of stimuli [8,48,60–63]. In our opinion, some controversies might arise from inappropriate consideration of the limits of functional magnetic resonance imaging (fMRI).

First, fMRI has a coarse spatial resolution, especially when averaging across subjects, and the finding of overlapping activation in two conditions need not imply that the same circuit has been activated twice. Averaging across subjects might obscure the distinction between the VWFA and neighboring areas [64]. Thus, overlapping activation for written words and for faces [48] or line drawings [8] does not imply lack of specialization for written words, but merely tight proximity or even intermingling of the neural circuits processing these visual categories.

Second, fMRI signals in the ventral visual cortex can be affected by low-level visual features. Unless very simple images are used, the number of line junctions is usually much greater in line drawings than in words, which may explain the strong response to pictures in the VWFA. This confound can be eliminated by starting with words and pictures matched for total line length, deleting some segments to equalize the number of line endings, and scrambling the remaining segments to create low-level retinotopic controls (Figure 1). Using this procedure, Szwed et al. [18] have consistently observed a stronger response to written words than to pictures in the VWFA and even in the occipital cortex.

Third, because fMRI integrates over a long period of time, increased fMRI activation may reflect stronger neural coding, but also increased top-down activation or greater processing time (Box 3). To test models of neural coding in the VWFA, it is essential to use short presentation times and minimal tasks that emphasize bottom-up processing (e.g. passive viewing or simple target detection). In this situation, the VWFA typically responds equally to words and to matched pseudowords [5,33], and more strongly to frequent than to infrequent letters, bigrams or quadrigrams [32,33]. These effects can be reversed, however, when using slower and more complex tasks (e.g. one-back, phonological judgment or even naming) [60,65]. This is presumably because pseudowords and low-frequency items are typically processed slowly and therefore induce an elevated level of activation throughout the reading circuit [61]. At the very least, response times should be collected in the scanner and regressed out of the fMRI activations before inferences are made about the local neural code [32]. A recent and surprising finding of subliminal picture-word fMRI adaptation in the VWFA [62], which used naming and unfortunately failed to record response times, can be tentatively explained by assuming shorter processing in repeated than in non-repeated trials, as expected from behavioral studies [66].

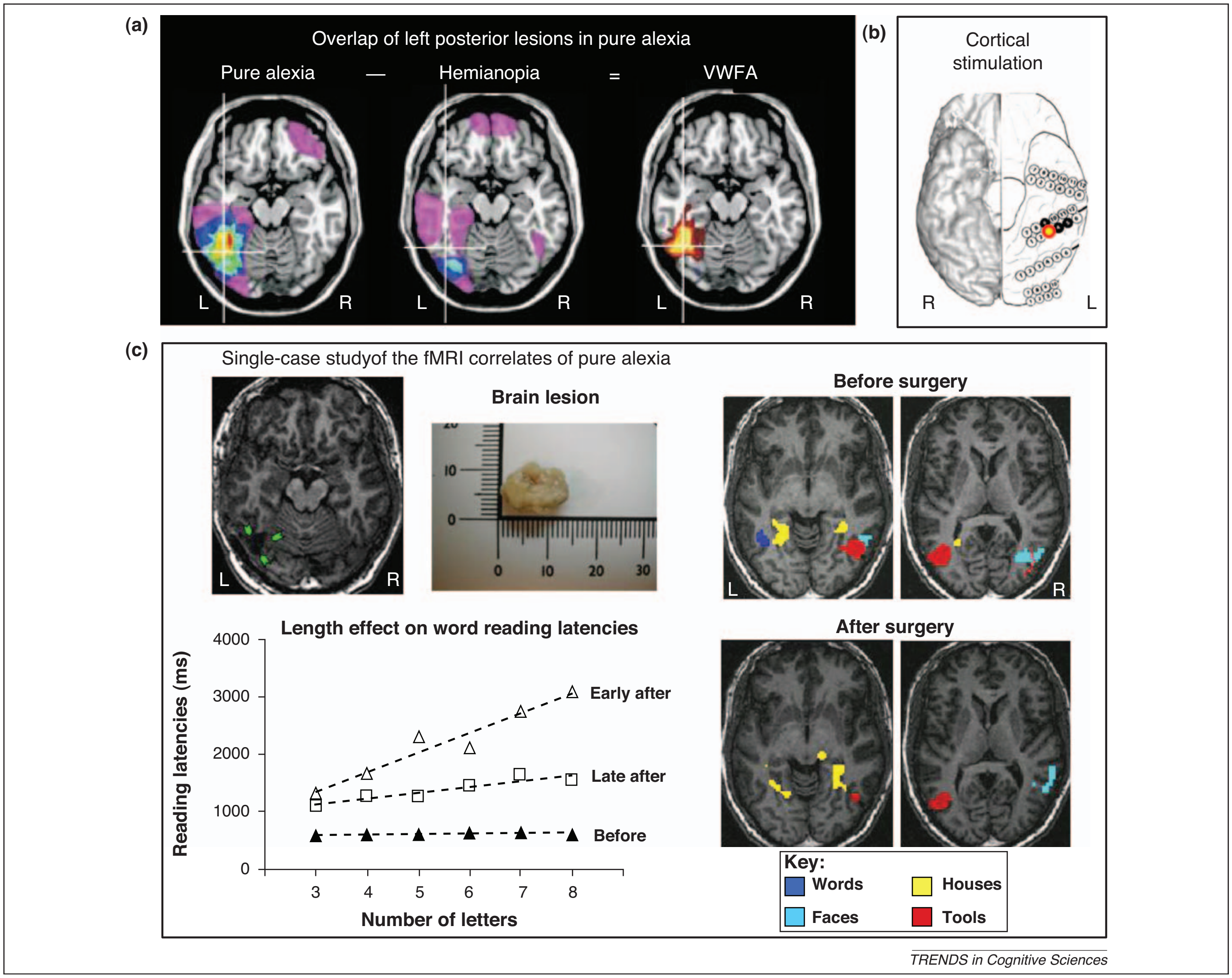

Figure 2. Evidence that the visual word form area (VWFA) plays a causal role in the orthographic stage of reading. **(a)** Overlap of lesions in six patients with pure alexia (left) and six patients with right visual field hemianopia but without pure alexia (middle) (after [70]). Subtraction (right) reveals that the location most predictive of pure alexia coincides with the VWFA (white crosshair, peak of the meta-analysis from [22]). **(b)** In implanted epileptic patients, focal cortical stimulation at sites close to the VWFA yields transient alexia. The figure shows a ventral view of the brain of a single patient in whom stimulation at the yellow spot yielded alexia without any associated object naming impairment (after [76]; note that on this three-dimensional view of the ventral side of the brain, the left hemisphere appears on the right). **(c)** Functional magnetic resonance imaging (fMRI) correlates of pure alexia in a single-case study. A minute surgical resection in the left occipitotemporal region (top left) caused letter-by-letter reading, as indexed by a positive correlation between reading latencies and word length (lower left), together with selective disappearance of word-related fMRI activations (right) (after [75]).

receptive fields, successively tuned to abstract letter identities, bigrams (ordered pairs of letters), morphemes and small words [35]. fMRI has confirmed the existence of a tuning gradient [33], with successive responses to letter identity [30], bigrams [32] and small words [34]. The hypothesis that all of a word's letters are processed in parallel has been confirmed behaviorally [40] and by brain imaging [41].

Following a lesion of the VWFA or its connections, efficient parallel processing of letter strings vanishes and a severe visual reading impairment known as pure alexia ensues (Figure 2 and Box 2). Pure alexia can be global or with letter-by-letter reading. Functionally, letter-by-letter reading, which also occurs in normal subjects when reading rotated or degraded words, arises not from the VWFA itself, but from the deployment of additional top-down processes of serial orientation of spatial attention, associated with activation of the posterior parietal cortex [31,42].

Partial regional specificity

We fully agree with Price and Devlin [8,9] that the VWFA does not respond solely to written words. Even in fluent readers, it continues to respond to other visual categories that strongly activate the surrounding cortices, including objects and faces [8,29,37,43–45]. Precisely as expected from the recycling hypothesis, line drawings, which typically contain an uncontrolled number of line junctions, are particularly good at activating the VWFA [8,37,43,45]. Nevertheless, when drawings are matched in visual complexity to written words, a significantly stronger response to written words emerges in the left VWFA [18,44]. Furthermore, when using high resolution fMRI and single-subject analyses, some VWFA voxels exhibit a greater response to the known script than to line drawings, strings of digits or unknown characters [18,29,44]. As expected from our theory, such regional specificity increases with reading speed and expertise [45]. Reading acquisition also

Box 2. The causal role of the visual word form area in efficient reading

Lesion and interference studies have demonstrated the causal role of the visual word form area (VWFA) in reading. According to our model, a lesion in the VWFA should result in the loss of the ability efficiently to identify strings of letters, irrespective of their lexical status, whereas speech production and comprehension as well as writing abilities should be spared. This pattern corresponds precisely to the syndrome of pure alexia as described more than a century ago [1]. Perception of the equivalence of upper and lower case letters may be lost [67], but features irrelevant to the invariant recognition of letter identities, such as handwriting style [68], are processed normally. Studies of lesion overlap in patients with left occipitotemporal stroke confirm that injury to the VWFA accurately predicts the occurrence of pure alexia (PA) [69–71] (Figure 2a), although it may also result from VWFA deffarentation [72–74]. Gaillard et al. [75] compared reading performance and fMRI activations before and after a minute left occipitotemporal resection, which showed that PA is related to the selective disappearance of occipitotemporal word-related activations (Figure 3c). Similarly, focal cortical inactivation of the VWFA by intracranial electrical stimulation can yield alexia in the absence of any object naming deficit [76] (Figure 3b).

In many cases of PA, the reading deficit vastly exceeds any other visual impairment. The most striking illustration of such functional specialization is provided by global alexic patients who are incapable of naming single letters but can fluently identify faces, objects or even Arabic numerals [1]. Some case reports of PA have described concomitant visual deficits affecting stimuli other than alphabetic strings and proposed that this observation supports a 'general visual' as opposed to a 'domain-specific' theory of PA. However, the existence of associated deficits is by itself of limited interest, because brain lesions should not be expected to respect the exact boundaries of the VWFA. Demonstrating a necessary association between PA and another deficit would shed more light on the computations performed by the VWFA, but even this would not necessarily contradict the neuronal recycling view of the VWFA, because the recycled cortex is expected to still contribute to the encoding of other non-alphabetic visual objects. It is even possible that the fine tuning of the visual cortex that accompanies reading acquisition [45] benefits other perceptual abilities. This might explain the reduced performance with line drawings observed in some PA patients with a lesion in the VWFA [71], and the decreased activation of the VWFA by words and drawings seen in dyslexic subjects [63].

leads to increased activation in occipital areas, including the primary visual cortex, in response to print and to other categories of visual stimuli such as checkerboards [18,45,46].

How learning to read transforms the VWFA

We directly tested the VWFA's role in literacy by comparing functional brain organization in illiterate versus literate adults [45]. Activation at the precise coordinates of the

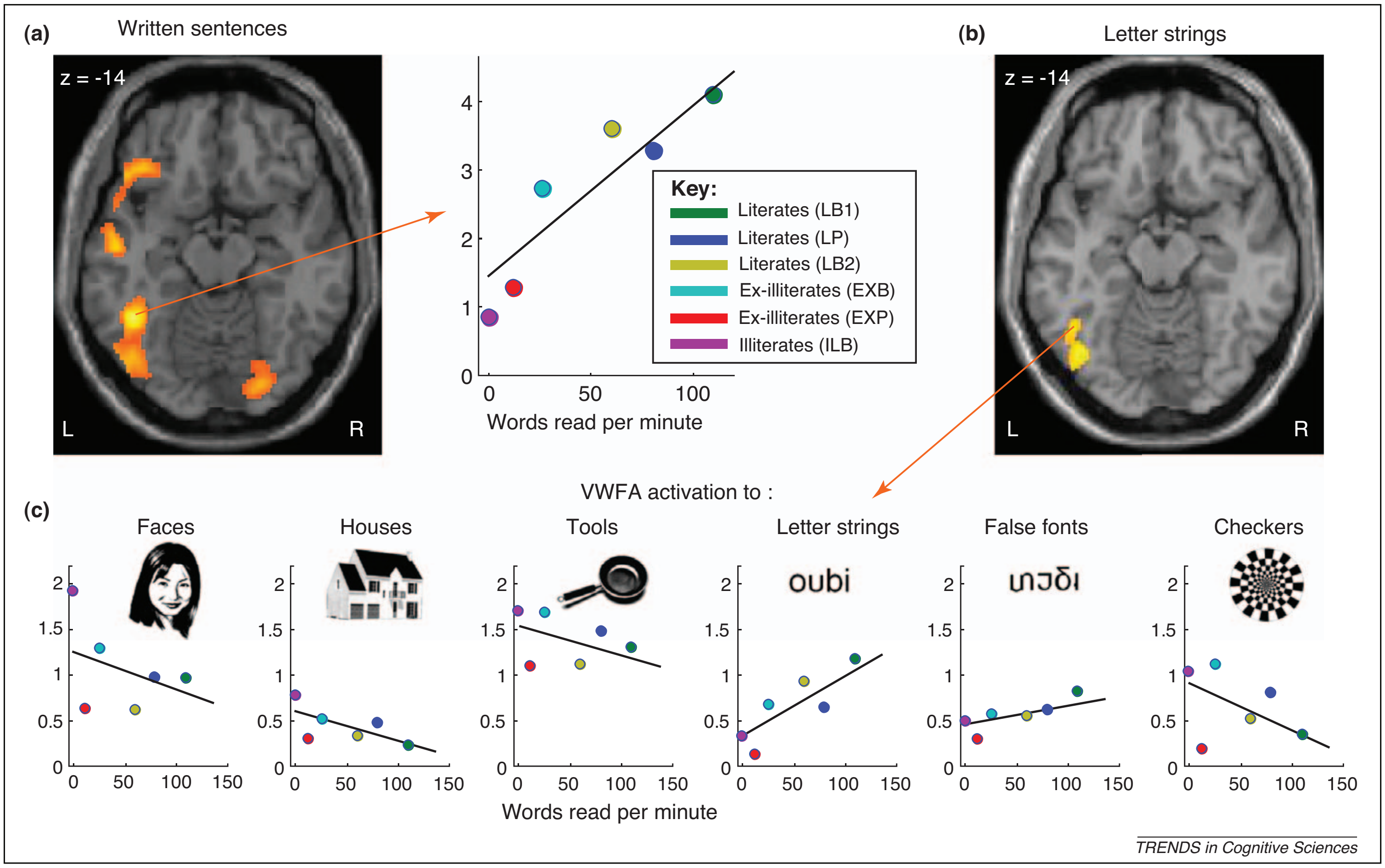

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Figure 3. Evidence that the visual word form area (VWFA) is a major site of literacy acquisition. In this functional magnetic resonance imaging experiment [45], schooled and unschooled adult participants of varying degrees of literacy were scanned. **(a)** When participants were presented with written sentences, the activation in the VWFA increased in proportion to reading performance (words read per minute). The VWFA, in particular, showed little activation in illiterates, but its activation increased sharply with literacy, even in unschooled participants who learned to read as adults (ex-illiterates). **(b)** The VWFA activation increase with literacy was replicated in a distinct block with passive presentation of letter strings. In this case, no other brain region was modulated by literacy, making it difficult to explain the VWFA activation as a top-down effect from higher-level regions. **(c)** The VWFA was also activated by passive presentation of faces, tools and checkers, particularly in illiterates. In agreement with the neuronal recycling hypothesis, this activation decreased with reading performance, suggesting a competition between the nascent orthographic code and prior visual responses (replotted from data in [45]).

VWFA, in response to either written sentences or individual pseudowords, was the main correlate of reading ability (Figure 3). Even after searching for the most active peak in each subject, enhancement of the response to letter strings was seen in this region, predictive of about one-half of the variance in reading speed across participants. Remarkably, with increasing literacy we also observed a small but significant decrease in responses to faces at the VWFA. Activation to faces was displaced to the right hemispheric fusiform gyrus, where it increased with literacy. Similarly, Cantlon et al. [47], in an fMRI study of four-year-olds, found that performance in identifying digits or letters was correlated with a decrease in responses to faces in the left lateral fusiform gyrus. Both observations support the existence of competition for cortical space between the nascent VWFA and the pre-existing neural coding of other categories, particularly faces. Faces and written words activate very close or even overlapping sectors of the ventral visual cortex [48], probably because of the demands they both place on high-resolution foveal processing [23].

Scanning of ‘ex-illiterate’ adults who learned to read during adulthood has demonstrated that the VWFA is highly plastic, even in adults, and quickly enhances its response to letter strings as soon as the rudiments of reading are in place [45] (Figure 3). A longitudinal study of kindergarten children supports this conclusion [46]; eight weeks of training with the GraphoGame – a computerized grapheme-phoneme training program – for a total of approximately 3.6 hours sufficed to enhance the response to letter strings relative to false fonts in the VWFA. Interestingly, VWFA specialization fails in dyslexic children [49,50], although whether this is a cause or a consequence of the reading deficit remains uncertain, because dyslexia seems to be primarily imputable to a phonological deficit in a majority of cases [51].

Reading acquisition can be simulated by training educated adults to recognize a new script [52–54]. These studies confirm the VWFA as a major neural correlate of literacy acquisition, capable of quickly increasing its response after just a few reading sessions. Interestingly, purely visual exposure by itself is insufficient; left VWFA changes occur only with systematic attention to the correspondences between print and speech sounds [52–54]. Thus, the emphasis that the LCD model places on the visual determinants of VWFA organization has to be qualified [55]. There is increasing evidence that the VWFA is selected, at least in part, because of its ‘projective field’ to language areas, and that its response is shaped not only by bottom-up statistics such as bigram frequency [32,33], but also by factors such as phonological neighborhood size and

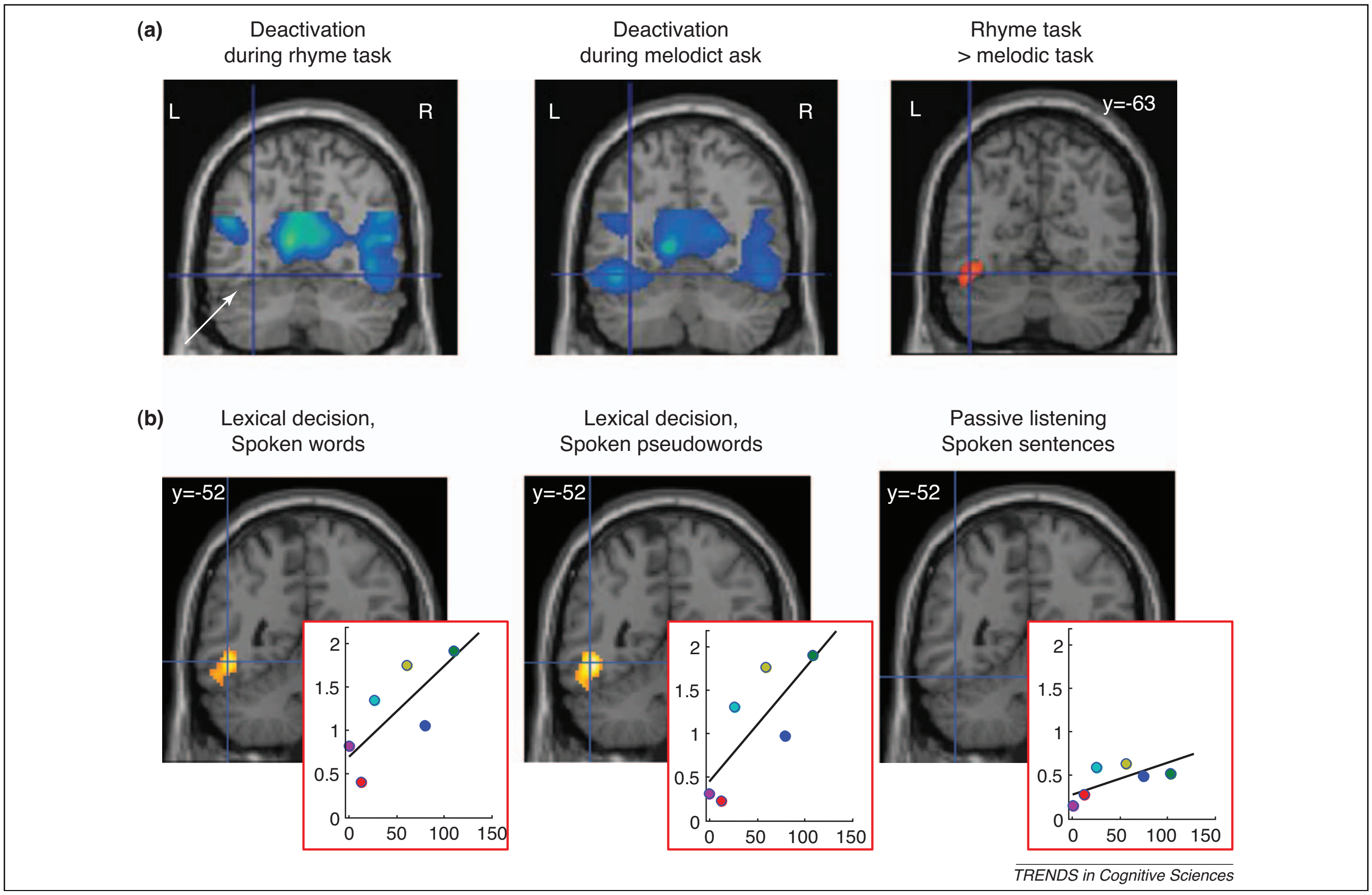

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Figure 4. Evidence that the visual word form area (VWFA) can be optionally recruited in a top-down manner during speech processing. **(a)** Visual areas are systematically deactivated during auditory tasks, but in a differential manner: lesser deactivation is seen in the VWFA when the subject attends to word rhymes than to superimposed melodic patterns (after [77]). **(b)** Top-down VWFA activation to speech is optional; it is evoked by a single spoken item during a lexical decision task, but not by a full sentence comprising multiple words during a passive listening task. Insets show VWFA activation as a function of reading performance in six groups varying in literacy (same format as Figure 3). The absence of top-down VWFA activation in illiterates, and its direct relation to reading performance, suggests the activation of an orthographic code (redrawn from data in [45]).

Box 3. Top-down activation of the visual word form area during spoken language processing

The visual word form area (VWFA) belongs to the ventral visual pathway and is thus typically inactive during auditory stimulation; for example, when listening passively to spoken words [5,64]. However, recent functional magnetic resonance imaging observations indicate that it can, under some circumstances, be activated in a top-down manner during spoken language tasks. These observations are not inconsistent with the VWFA hypothesis. Rather, they indicate that literacy provides an optional orthographic code for language in the VWFA [45] that can be mobilized when needed to facilitate speech processing. They do not support the broad claim that the VWFA is not 'specialized' for orthographic processing [8].

In Yoncheva et al.'s elegant study [77], participants listened to composite stimuli comprising an auditory word and a tone triplet. In distinct blocks, they compared the same stimuli for their speech content or for their tonal content. Although both auditory tasks led to a broad deactivation of bilateral visual areas relative to rest, only selective attention to speech led to a deactivation everywhere but in the VWFA (Figure 4a).

The possibility of activating the VWFA in a top-down manner from spoken inputs was confirmed by our recent study of the functional impact of literacy [45]; during a spoken lexical decision task, the VWFA was activated only in literate subjects, in direct relation to the subject's reading performance (Figure 4b). The direct relation with reading scores, focal activation restricted to the left lateral occipito-temporal cortex, and the absence of activation in illiterates help to refute an alternative interpretation in terms of visual imagery for imageable words. It is probable that the observed activation corresponds to top-down recruitment of an orthographic code for the sequence of letters spelling the word, and not the activation of amodal lexical or semantic representations. There is, however, continuing debate about whether top-down effects activate the VWFA selectively or also activate the more lateral sectors of the inferior temporal cortex (the lateral inferotemporal multimodal area) [64].

In our study of literacy [45], the VWFA failed to activate in the same adult literate participants during passive listening to simple sentences. This important observation suggests that top-down recruitment of the VWFA is optional and deployed only during difficult tasks such as lexical decision [45], rhyming [78] or spelling [64]. Interestingly, top-down VWFA activation is absent in children with dyslexia [78], suggesting that an inability to form bidirectional links between phonology and orthography is also an important component of impaired reading acquisition.

Box 4. Questions for further research

- What is the neural code for words in the visual word form area (VWFA)? Do some neurons become tuned to individual letters and letter groups [35]? Is this tuning demonstrably influenced by the grapheme-to-phoneme correspondences of the target language?
- What is the role of top-down projections in creating the VWFA in literate brains? Are top-down inputs from phonological coding regions of the superior temporal gyrus essential for reading acquisition? Do they affect merely the late interactive dynamics of VWFA activity, as proposed by Price and Devlin [9], or also the local feed-forward tuning curves of VWFA neurons, as we propose [35]?
- What are the precise connections of the VWFA? Does this site project preferentially to language areas, even before we learn to read, and can its connectivity pattern explain its specific role in written word recognition [59]?
- Are there systematic parallels between face and word recognition in the fusiform gyrus? Can a system of specialized cortical patches be identified for word recognition, as in the monkey face recognition system [79]? Does reading specifically recycle the face recognition system, and if so, why? It is simply because face and word recognition place similar demands on high resolution foveal processing? Or is it because this region connects to areas encoding facial movements, which might be essential for phoneme perception [80]?

syllable count [56]. Indeed, the VWFA can be activated in a purely top-down manner during some speech processing tasks (Box 3).

A remarkable observation also supports this conclusion: in blind subjects, Braille reading specifically activates the VWFA relative to a tactile control task [57]. This area is therefore 'meta-modal'; it may possess a general capacity for identifying shapes, whether visual or tactile, and mapping them onto language areas. The fact that the mosaic of ventral occipitotemporal preferences for written words and for category-specific knowledge of animals versus objects [58] remains present in people who are blind suggests that purely bottom-up visual factors are not the sole determinants of its organization. Rather, both receptive and projective connectivity, including top-down projections, must constrain the emergence of specialization in this region [59].

Challenges for future research

In conclusion, recent research confirms the VWFA as a major, reproducible site of visual orthographic knowledge. However, much remains to be discovered regarding how the neural code in this area changes with literacy, plausibly under the influence of top-down constraints arising from spoken language and motor areas (Box 4). An important challenge for future research is the development of techniques to characterize the tuning curves and projective fields of neurons in the VWFA. Characterizing them before and after reading would help to explain how we acquire the evolutionarily unexpected feat of reading.

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