

THE MASSIVE IMPACT OF LITERACY ON THE BRAIN AND ITS CONSEQUENCES FOR EDUCATION

■ STANISLAS DEHAENE

Introduction

It was once claimed that the bridge from brain research to education was ‘a bridge too far’ (Bruer, 1997). In the past decade, however, important progress has been made in bridging this gap, taking advantage of the improved ability to image the human brain in adults and children, in experimental paradigms relevant to learning and education. I would like to argue that, in fact, considerable cognitive neuroscience knowledge is already highly relevant to education. Our understanding of learning algorithms, including the known importance of active prediction, prediction error, or sleep consolidation, is directly relevant to the design of efficient learning environments, at school or through educational games. Our comprehension of the role of attention and reward (and their flip sides, the negative effects of distraction and punishment), or of the switch from explicit to implicit learning, are equally important generic findings that already affect much thinking in education.

Above all, human cognitive neuroscience has made enormous strides in understanding the specific cerebral circuits underlying particular domains of education, such as mathematics, reading and second-language acquisition. The human brain can be seen as a collection of evolved devices, inherited from our evolutionary history, and that address specific problems such as navigating in space and remembering locations, representing time, acquiring a sense of number for concrete sets, recognizing objects and faces, representing sounds and particularly the speech sounds typical of our species, and so on. I have argued that, through education, we take advantage of these pre-existing representations and *recycle* them towards novel uses, particularly because we are the only species capable of attaching arbitrary *symbols* to these representations and tying them together into elaborate symbol systems (Dehaene, 1977/2011, 2005, 2009; Dehaene & Cohen, 2007). Deficient operation of these specialized subsystems, or of the ability to attach symbols to them, can explain some developmental deficits such as dyscalculia, dyslexia, or dyspraxia.

In the present chapter, I briefly recapitulate how the recycling theory plays out in the domain of reading acquisition. I focus on recent discoveries

that demonstrate how the brain is changed by learning to read, and how these results illuminate the specific hurdles that children face as they learn to read. I am convinced that empowering teachers with the appropriate knowledge of the principles of human neuroplasticity and learning will lead to better classroom practices. Indeed, it is a shame that teachers still have a better idea of how their car works than of the inner functioning of their pupils' brains! Thus, my goal here is to summarize neuroimaging results on reading in an accessible manner, and to use these results to think about their consequences for education. I am also convinced that neuro-education research should not be performed solely in brain imaging labs. Experimentation in schools is indispensable to validate and expand the hypotheses that we form about optimal education practices. Thus, another goal of this chapter is to stir communication between cognitive neuroscientists and educators, in the hope that they actively collaborate towards the development of innovative teaching devices.

The cerebral mechanisms of adult reading

What is reading? It is a wonderful cultural invention that allows us to hold 'a conversation with the deceased', a way to 'listen to the dead with my eyes' (Francisco de Quevedo). By learning to read, we learn to access our knowledge of spoken language through a novel modality, one that was never anticipated by evolution: vision. Writing is a remarkably clever encryption device by which we turn spoken language into a rich visual texture of marks on stone, clay or paper. Reading corresponds to the decryption of this texture. During reading acquisition, we transform some of the visual structures of our brain in order to turn them into a specialized interface between vision and language. Because reading is an extremely recent invention in evolutionary terms, and until recently concerned a small minority of humans, the human genome cannot contain any instructions for reading-specific brain circuits. Instead, we have to recycle existing brain systems for this novel use.

Cognitive neuroimaging in literate adults has clarified how reading operates at the cortical level. A large set of regions of the left hemisphere is identically activated when we read a sentence and when we listen to it (Devauchelle, Oppenheim, Rizzi, Dehaene, & Pallier, 2009). This a-modal language network comprises temporal-lobe regions, most prominently the entire length of the superior temporal sulcus, from the temporal pole to the posterior temporal-parietal junction, as well as distinct regions of the left inferior frontal lobe. All of these regions are thus not unique to reading. Rather, these are spoken-language areas, and reading provides access to them

through vision. Indeed, their activation is already present, with a left-hemispheric lateralization, when two-month-old babies listen to sentences in their mother tongue (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; Dehaene-Lambertz, *et al.*, 2006; Dehaene-Lambertz, *et al.*, 2009). They obviously reflect an ancient and probably evolved system responsible for spoken language acquisition. When a child first enters primary school, this spoken language system, with its subcomponents of lexical, morphological, prosodic, syntactic and semantic processing, is already in place. What this child has to acquire is the visual interface into the language system.

Neuro-imaging studies of single-word reading have begun to clarify the localization and organization of this visual interface system. Visual words, when presented to adult readers, systematically activate a specific region of the left-hemispheric ventral visual cortex, which my colleagues and I have termed the *visual word form area* (VWFA in short) (Cohen, *et al.*, 2000). Its response is strictly visual and pre-lexical: it responds to all sorts of strings of letters, whether they form words or pseudowords devoid of any meaning such as ‘flinter’ (Dehaene, Le Clec’H, Poline, Le Bihan, & Cohen, 2002). Its localization is remarkably reproducible across individuals and even across cultures (Bolger, Perfetti, & Schneider, 2005; Cohen, *et al.*, 2000; Dehaene, *et al.*, 2002; Jobard, Crivello, & Tzourio-Mazoyer, 2003). It is always located at the same coordinates in the left lateral occipito-temporal sulcus, within a few millimeters. Furthermore, in a literate adult, its lesion systematically causes pure alexia, a selective inability to read (Déjerine, 1891; Gaillard, *et al.*, 2006). Thus, it clearly plays an indispensable role in reading.

We now know that, with literacy, this region becomes functionally specialized for reading in a specific script. Not only does it activate more to written words than to other categories of visual knowledge, such as faces (Puce, Allison, Asgari, Gore, & McCarthy, 1996) or line drawings of objects (Szwed, *et al.*, 2011), but it also activates more to a known script (e.g. Hebrew in Hebrew readers) than to other unknown scripts (Baker, *et al.*, 2007). Indeed, it has become attuned to quite specific cultural properties of the learned script, such as the relation between upper and lower-case letters of the Western alphabet: only this region recognizes the identity between, say, the words ‘rage’ and ‘RAGE’, which requires an internalization of arbitrary reading conventions (Dehaene, *et al.*, 2004; Dehaene, *et al.*, 2001). Recently, the VWFA has even been found to be invariant for printed versus hand-written words (Qiao, *et al.*, 2010). Thus, the VWFA is the main region that allows us to recognize a word like radio, RADIO, or *radio*, regardless of its exact font, size, and location. Remarkably, these invariant processes are so automated that they are deployed non-consciously.

My colleagues and I have proposed that, in the course of reading acquisition, the VWFA region gets selected as the primary area of learning because it possesses prior properties, inherited from primate evolution, that make it especially appropriate for reading. The first property is a preference for high-resolution shapes presented in the fovea, the high-resolution center of the retina (Hasson, Levy, Behrmann, Hendler, & Malach, 2002). Such high resolution is probably indispensable in order to read small print. The second property is a sensitivity to line configurations (Szwed, *et al.*, 2011): this region is part of a chunk of bilateral cortex called the fusiform gyrus that reacts strongly whenever the image contains line junctions forming shapes like T, L, Y, F, etc. These shapes may have been selected initially for their usefulness in *object* recognition – for instance a ‘T’ contour robustly signals that one object edge lies in front of another, and piecing this information together provides view-point invariant information about 3-D shapes (Biederman, 1987). My colleagues and I hypothesize that, in our literate culture, we recycled this ancient capacity by specifically selecting letter shapes that fit with this pre-existing cortical architecture (Dehaene, 2009). There is, indeed, evidence that all writing systems of the world make use of the same elementary ‘alphabet’ of line configurations (Changizi, Zhang, Ye, & Shimojo, 2006).

Third, finally, the precise location of the visual word form area is probably determined by its proximity and tight connections to cortical areas for spoken language processing in the lateral temporal lobe. Indeed, the hemispheric lateralization of the VWFA relates to the prior lateralization of spoken language processing, which is usually but not always in the left hemisphere (Cai, Lavidor, Brysbaert, Paulignan, & Nazir, 2007; Cai, Paulignan, Brysbaert, Ibarrola, & Nazir, 2010; Pinel & Dehaene, 2009). Interestingly, in children, the region exactly symmetrical to the VWFA, in the right hemisphere, can take over when the original VWFA site is damaged in early childhood (Cohen, Lehericy, *et al.*, 2004).

Most results to date appear compatible with a model of the neural architecture of visual word recognition called the ‘local combination detector’ (LCD) model (Dehaene, Cohen, Sigman, & Vinckier, 2005). This model assumes that a hierarchy of occipito-temporal neurons become attuned to fragments of writing, from line junctions to single letters, pairs of letters (bigrams), morphemes, and small words (Dehaene, *et al.*, 2005). Indeed, fMRI has now confirmed the existence of a tuning gradient with the VWFA (Vinckier, *et al.*, 2007), with successive responses to letters (Dehaene, *et al.*, 2004), bigrams (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006), and small words (Glezer, Jiang, & Riesenhuber, 2009).

The current thinking is that, during reading of a single word, millions of hierarchically organized neurons, each tuned to a specific local property (a letter, a bigram, or a morpheme), collectively contribute to visual recognition. This massively parallel architecture explains the speed and robustness of visual word recognition. Most importantly, for educators and teachers, it creates an *illusion* of whole-word reading. Because reading is so fast and takes about the same time for short and long words, some have assumed that the overall whole-word shape is being used for recognition, and that we should therefore teach whole-word reading rather than by letter-to-sound decoding. This inference is wrong, however. All the evidence to date suggests that visual words are being analyzed into their elementary components (strokes, letters, bigrams, morphemes) before the whole word can be put back together and recognized. However, this decomposition is so fast, parallel, and efficient as to seem almost instantaneous (it actually takes about one fifth of a second). Educational evidence concurs in showing that teaching of grapheme-phoneme correspondences is the fastest, most efficient way of making children efficient readers, both for pronunciation and for comprehension purposes (Ehri, Nunes, Stahl, & Willows, 2001).

How literacy changes the brain

We directly tested the VWFA's role in literacy by comparing brain organization in illiterate versus literate adults (Dehaene, Pegado, *et al.*, 2010). There were several purposes to this study. First, we wanted to make a whole-brain image of the changes induced by reading acquisition – not only in the visual word form area, but also within the temporal-lobe language system and also early in the occipital visual cortex. Second, this was a unique opportunity to test the recycling hypothesis by examining what stimuli activate the VWFA site in people who have not learned to read, and whether we gain but also lose some functionality at this site as we learn to read. Third, we wondered whether these brain changes needed to occur at an early age, in the school years, or whether the adult brain was plastic enough for them to occur later on in life, during adulthood. To this aim, we tested pure illiterates (10 Brazilian adults who did not have the possibility to attend school in childhood and could barely recognize individual letters), ex-illiterates (21 unschooled Brazilian and Portuguese adults who attended adult literacy courses and reached variable levels of reading ability), and literates (32 Brazilian and Portuguese adults of various socio-economic communities, some tightly matched to the other groups).

Our results first confirmed that the VWFA is a major correlate of literacy. Activation at the precise coordinates of the VWFA, in response either to

written sentences or to individual pseudowords, was the main correlate of reading performance (see Figures 1 and 2, pp. 237–238). A massive enhancement of the response to letter strings was seen in this region, predictive of about half of the variance in reading speed across participants. We could now ask, what activates this region prior to reading, in illiterate participants? We saw a strong response to faces, objects and checkerboard patterns, indicating that this area specializes for visual object and face recognition before committing to visual word recognition. In excellent agreement with the recycling hypothesis, we observed a small but significant decrease in responses to these non-reading categories, particularly faces, with increasing literacy. As reading performance increased, activation to faces was increasingly displaced to the right-hemispheric fusiform gyrus. Similarly, Cantlon *et al.* (Cantlon, Pinel, Dehaene, & Pelphrey, 2011), in an fMRI study of four-year-olds, found that performance in identifying digits or letters was correlated with a decrease in the responses to faces in the left lateral fusiform gyrus. Both observations suggest that there is a competition for cortical space, and that reading acquisition must compete with pre-existing categories in the visual cortex. We literally ‘make room’ for reading on the surface of the cortex, by shifting the boundaries of other nearby regions.

In fact, we found that the visual changes due to literacy extended much more broadly than expected in the visual cortex, way beyond the VWFA. The posterior occipital cortex showed a globally increased response to all contrasted black-and-white pictures in our study, suggesting that literacy refines visual coding at an early level. Indeed, even the primary visual cortex (area V1) increased its activation only in response to horizontal checkerboards, not vertical ones. We interpret this finding as showing that expertise in reading refines the precision of visual coding, precisely for those regions of the retina that are useful for reading, i.e. the horizontal part of the visual field where alphabetic words always appear in Western culture.

A third type of change was seen in the superior temporal lobe, at a site called the planum temporale. There, activation to *spoken* language changed with literacy: it nearly doubled in good readers compared to illiterates. Because that region has been associated with a phonological code (e.g. Jacquemot, Pallier, LeBihan, Dehaene, & Dupoux, 2003), we believe that it relates to the acquisition of phonemic awareness, a major correlate of literacy. Illiterate adults have long been known to be unable to consciously detect or manipulate phonemes in tasks such as dropping the first phoneme of a word (e.g. Vatican → atican) (Morais, Cary, Alegria, & Bertelson, 1979). The ability to consciously represent the phoneme as the smallest relevant unit of speech is the result of alphabetization. The left planum temporale may be a

crucial target of reading acquisition, the point where graphemic knowledge extracted from ventral visual areas first contacts phonemic representations of spoken language, thus permitting grapheme-to-phoneme conversion. Indeed, this cortical site is sensitive to the congruity between a speech sound and a simultaneously presented visual letter (van Atteveldt, Formisano, Goebel, & Blomert, 2004), an effect which is reduced or absent in dyslexic subjects (Blau, *et al.*, 2010).

Overall, then, the comparison of literate and illiterate brains emphasizes the degree to which reading acquisition changes the brain, not just within the visual word form area, but also earlier in the visual system and later on in the phonological system. By studying the data from the ex-illiterate adults, we were able to demonstrate that these systems are highly plastic: virtually all of the above changes were visible, in partial form, in the ex-illiterate adults who learned to read during adulthood (Dehaene, Pegado, *et al.*, 2010) (see Figure 2). Thus, even a small amount of literacy training changes the brain. A longitudinal study of kindergarten children supports this conclusion (Brem, *et al.*, 2010): eight weeks of training with the GraphoGame, a computerized grapheme-phoneme training program, suffice to cause an enhanced response to letter strings relative to false fonts in the VWFA. Similarly, training adults to recognize a new script leads to massive changes in the VWFA after a few training sessions (Hashimoto & Sakai, 2004; Song, Hu, Li, Li, & Liu, 2010; Yoncheva, Blau, Maurer, & McCandliss, 2010). Interestingly, these reading-induced changes only occur with a systematic attention to the correspondences between print and speech sounds. Thus, the VWFA response is shaped not only by bottom-up statistics of the visual input, but also by top-down factors coming from the target phonological code (Goswami & Ziegler, 2006). Learning to read requires a bidirectional dialogue in the brain, between the visual areas coding for letter strings and the auditory areas coding for the phonological segments of speech. This bidirectional dialogue, with a strong top-down component, can now be directly visualized by neuroimaging techniques: even in the absence of any visual input, good readers can optionally activate their VWFA from a purely spoken language input, whenever it is useful for them to activate an orthographic code (Cohen, Jobert, Le Bihan, & Dehaene, 2004; Dehaene, Pegado, *et al.*, 2010; Desroches, *et al.*, 2010; Yoncheva, Zevin, Maurer, & McCandliss, 2010).

Consequences for education

We should be careful about transposing these brain results directly to the education domain. Observing how the brain is changed does not lead to a direct prescription of the best education method. Nevertheless, I

strongly believe that educators will strongly benefit from a better understanding of what is going on in their pupils' brains as they learn to read. Just like a mechanic can diagnose an engine problem by visualizing the engine's operation, educators who can visualize how the child's brain works will, spontaneously, conceive better ways of teaching. With this idea in mind, instead of designing a specific brain-based 'method' for teaching reading, my colleagues and I are attempting to draft a series of cognitive principles that are at work in reading acquisition and that should be taken into consideration by any teaching method.

Brain-imaging experiments lead to a clearer view of the amount of cortical transformation which is required for reading acquisition. Reading is not a natural task, and children are not biologically prepared to it by evolution (unlike spoken language acquisition). Thus, teachers must be aware that many of the reading steps that they take for granted, because they are expert readers and have a fully automated and non-conscious reading system, are not at all obvious for young children. Massive changes are needed, at the phonological and at the visual level, before children master the skill of reading. The very notion that phonemes exist, that there is the same sound at the beginning of 'rat', in the middle of 'brat', and at the end of 'car', is not available to illiterates, and is the result of alphabetization. Likewise, the notion that written words are composed of elementary objects, letters, and that each of these letters or groups of letters (graphemes) correspond to a speech sound or phoneme, is a non-trivial idea. Grapheme-phoneme correspondences must be systematically taught, one by one: the amount of such teaching is the best predictor of reading performance, including reading comprehension, in young children (Ehri, *et al.*, 2001). In brief, all aspects of the alphabetic code must be patiently explained to children: that words are made of letters or graphemes; that graphemes map onto to phonemes; that letters should be decoded from left to right; that the spatial left-to-right organization corresponds to the temporal order in which they are uttered; and that by changing their spatial order, one can compose new syllables and words.

It should be clear that I am advocating here a strong 'phonics' approach to teaching, and against a whole-word or whole-language approach. Several converging elements support this conclusion (for a longer development, see Dehaene, 2009). First, analysis of how reading operates at the brain level provides no support for the notion that words are recognized globally by their overall shape or contour. Rather, letters and groups of letters such as bigrams and morphemes are the units of recognition. Second, experiments with adults taught to read the same novel script with a whole-word versus

grapheme–phoneme approach show dramatic differences (Yoncheva, Blau, *et al.*, 2010): only the grapheme–phoneme group generalizes to novel word and trains the left-hemispheric VWFA. Adults whose attention was drawn to the global shape of words, by whole–word training, showed brain changes in the homolog region of the right hemisphere, clearly not the normal circuit for expert reading. Third, finally, these theoretical and laboratory–based arguments converge with school–based studies that prove the inferiority of the whole–word approach in bringing about fast improvements in reading acquisition. The whole–word approach will certainly not create dyslexia, which is a biological and partially genetic anomaly, but it does lead to avoidable delays in reading acquisition.

Another important observation for education is that the speed of reading acquisition varies dramatically with the regularity of grapheme–phoneme relations, which changes across languages (Paulesu, *et al.*, 2000; Seymour, Aro, & Erskine, 2003; Ziegler & Goswami, 2006). In Italy and Germany, children acquire reading in a few months, simply because the writing is highly regular, such that knowledge of the grapheme–phoneme correspondences suffices to read essentially all words. English and French lie on the other end of the scale of alphabetic transparency: they are highly irregular systems in which exceptions abound (e.g. ‘though’ versus ‘tough’) and are disambiguated only by lexical context. Behavioral research shows that English learners have to dedicate at least two more years of training before they read at the same level as Italian children (Seymour, *et al.*, 2003). Neuroimaging experiments show that, to do so, they expand their brain activation in the VWFA and the precentral cortex relative to Italian readers (Paulesu, *et al.*, 2000). Thus, teachers should be aware of the spelling irregularities in the language that they are teaching. They should prepare a rational progression, starting with the more regular and more frequent grapheme–phoneme correspondence, and ending with the exceptions. They should also pay attention to the complexity of syllables and start with the simpler consonant–vowel structures before moving on to more complex multi-consonant clusters. Mute letters, irregular spellings, and spellings inherited from Greek and Roman etymologies (e.g. ‘ph’) should all be addressed across the years, with frequent repetition. A good reading course should not stop at the simplest grapheme–phoneme correspondences: morphology, the understanding of prefixes, suffixes, roots, and grammatical endings is equally important in the brain of expert readers (Devlin, Jamison, Matthews, & Gonnerman, 2004).

Recently, our growing understanding of how the brain is recycled for reading has led to a clarification of another mysterious phenomenon that occurs during childhood: mirror reading and mirror writing. Many young readers confuse mirror letters such as p and q or b and d. Furthermore, they

occasionally write in mirror form, from right to left, quite competently and without seemingly noticing their error. This peculiar behavior can be explained by considering that the function of the ventral visual cortex, prior to reading, is the invariant recognition of objects, faces and scenes. In the natural world, very few objects have a distinct identity for left and right views. In most cases, the left and right views of a natural object are mirror images of each other, and it is useful to generalize across them and treat them as the same object. Single-cell recordings in monkeys show that this principle is deeply embedded in the visual system: many neurons in the occipito-temporal visual cortex fire identically to the left and right views of the same object or face (Freiwald & Tsao, 2010; Logothetis, Pauls, & Poggio, 1995; Rollenhagen & Olson, 2000). Using neuroimaging, my colleagues and I have shown that, in the human brain, it is precisely the VWFA which is the dominant site for this mirror-image invariance (Dehaene, Nakamura, *et al.*, 2010; Pegado, Nakamura, Cohen, & Dehaene, 2011). No wonder, then, that young children confuse b and d: they are trying to learn to read with precisely the brain area that confuses left and right of images! Mirror confusion is a normal property of the visual system, which is seen in all children and illiterate subjects, and which disappears for letters and geometric symbols when literacy sets in (Cornell, 1985; Kolinsky, *et al.*, 2010). Only its prolongation in late childhood is a sign of dyslexia (Lachmann & van Leeuwen, 2007; Schneps, Rose, & Fischer, 2007). Teachers should therefore be aware of the specific difficulty posed by mirror letters, and should take the time to explain why b and d are distinct letters corresponding to distinct phonemes (it is particularly unfortunate that these phonemes are quite similar and easily confused). Interestingly, teaching the gestures of writing can improve reading, perhaps because it helps store view-specific memories of the letters and their corresponding phonemes (Fredembach, de Boisferon, & Gentaz, 2009; Gentaz, Colé, & Bara, 2003).

All of the above ideas are already applied in many schools, and did not await the advent of cognitive neuroscience. I merely hope that, by bringing to light their cerebral foundations, cognitive neuroscience studies of reading can help spread the word and eventually lead to a more systematic and rational approach to reading education. A true science of reading is emerging. In the future, new experiments, involving a tight collaboration between scientists and educators, should lead to an even clearer picture of the learning algorithms used by the brain, and how they can be harnessed to facilitate learning in the classroom.

References

- Baker, C.I., Liu, J., Wald, L.L., Kwong, K.K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proc Natl Acad Sci U S A*, *104*(21), 9087-9092.
- Biederman, I. (1987). Recognition-by-components: a theory of human image understanding. *Psychol Rev*, *94*(2), 115-147.
- Binder, J.R., Medler, D.A., Westbury, C.F., Liebenthal, E., & Buchanan, L. (2006). Tuning of the human left fusiform gyrus to sublexical orthographic structure. *Neuroimage*, *33*(2), 739-748.
- Blau, V., Reithler, J., van Atteveldt, N., Seitz, J., Gerretsen, P., Goebel, R., et al. (2010). Deviant processing of letters and speech sounds as proximate cause of reading failure: a functional magnetic resonance imaging study of dyslexic children. *Brain*.
- Bolger, D.J., Perfetti, C.A., & Schneider, W. (2005). Cross-cultural effect on the brain revisited: universal structures plus writing system variation. *Hum Brain Mapp*, *25*(1), 92-104.
- Brem, S., Bach, S., Kucian, K., Guttorm, T.K., Martin, E., Lyytinen, H., et al. (2010). Brain sensitivity to print emerges when children learn letter-speech sound correspondences. *Proc Natl Acad Sci U S A*, *107*(17), 7939-7944.
- Bruer, J.T. (1997). Education and the brain: A bridge too far. *Educational Researcher*, *26*(8), 4-16.
- Cai, Q., Lavidor, M., Brysbaert, M., Paulignan, Y., & Nazir, T. (2008). Cerebral lateralization of frontal lobe language processes and lateralization of the posterior visual word processing system. *J Cog Neurosci*, *20*, 672-681.
- Cai, Q., Paulignan, Y., Brysbaert, M., Ibarrola, D., & Nazir, T.A. (2010). The left ventral occipito-temporal response to words depends on language lateralization but not on visual familiarity. *Cereb Cortex*, *20*(5), 1153-1163.
- Cantlon, J.F., Pinel, P., Dehaene, S., & Pelphey, K.A. (2011). Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cereb Cortex*, *21*(1), 191-199.
- Changizi, M.A., Zhang, Q., Ye, H., & Shimojo, S. (2006). The Structures of Letters and Symbols throughout Human History Are Selected to Match Those Found in Objects in Natural Scenes. *Am Nat*, *167*(5), E117-139.
- Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain*, *123*, 291-307.
- Cohen, L., Jobert, A., Le Bihan, D., & Dehaene, S. (2004). Distinct unimodal and multimodal regions for word processing in the left temporal cortex. *Neuroimage*, *23*(4), 1256-1270.
- Cohen, L., Lehericy, S., Henry, C., Bourgeois, M., Larroque, C., Sainte-Rose, C., et al. (2004). Learning to read without a left occipital lobe: right-hemispheric shift of visual word form area. *Ann Neurol*, *56*(6), 890-894.
- Cornell (1985). Spontaneous mirror-writing in children. *Can J Exp Psychol*, *39*, 174-179.
- Dehaene-Lambertz, G., Dehaene, S., & Hertz-Pannier, L. (2002). Functional neuroimaging of speech perception in infants. *Science*, *298*(5600), 2013-2015.
- Dehaene-Lambertz, G., Hertz-Pannier, L., Dubois, J., Meriaux, S., Roche, A., Sigman, M., et al. (2006). Functional organization of perisylvian activation during presentation of sentences in preverbal infants. *Proc Natl Acad Sci U S A*, *103*(38), 14240-14245.
- Dehaene-Lambertz, G., Montavont, A., Jobert, A., Allriol, L., Dubois, J., Hertz-Pannier, L., et al. (2009). Language or

- music, mother or Mozart? Structural and environmental influences on infants' language networks. *Brain Lang.*
- Dehaene, S. (1977/2011). *The number sense (2nd edition)*. New York: Oxford University Press.
- Dehaene, S. (2005). Evolution of human cortical circuits for reading and arithmetic: The 'neuronal recycling' hypothesis. In S. Dehaene, J.R. Duhamel, M. Hauser & G. Rizzolatti (eds.), *From monkey brain to human brain* (pp. 133-157). Cambridge, Massachusetts: MIT Press.
- Dehaene, S. (2009). *Reading in the brain*. New York: Penguin Viking.
- Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, 56(2), 384-398.
- Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: a proposal. *Trends Cogn Sci*, 9(7), 335-341.
- Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J.B., Le Bihan, D., et al. (2004). Letter binding and invariant recognition of masked words: behavioral and neuroimaging evidence. *Psychol Sci*, 15(5), 307-313.
- Dehaene, S., Le Clec'H, G., Poline, J.B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: a prelexical representation of visual words in the fusiform gyrus. *Neuroreport*, 13(3), 321-325.
- Dehaene, S., Naccache, L., Cohen, L., Bihan, D.L., Mangin, J.F., Poline, J.B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nat Neurosci*, 4(7), 752-758.
- Dehaene, S., Nakamura, K., Jobert, A., Kuroki, C., Ogawa, S., & Cohen, L. (2010). Why do children make mirror errors in reading? Neural correlates of mirror invariance in the visual word form area. *Neuroimage*, 49(2), 1837-1848.
- Dehaene, S., Pegado, F., Braga, L.W., Ventura, P., Nunes Filho, G., Jobert, A., et al. (2010). How learning to read changes the cortical networks for vision and language. *Science*, 330(6009), 1359-1364.
- Déjerine, J. (1891). Sur un cas de cécité verbale avec agraphie suivi d'autopsie. *Mémoires de la Société de Biologie*, 3, 197-201.
- Desroches, A.S., Cone, N.E., Bolger, D.J., Bitan, T., Burman, D.D., & Booth, J.R. (2010). Children with reading difficulties show differences in brain regions associated with orthographic processing during spoken language processing. *Brain Res.*
- Devauchelle, A.D., Oppenheim, C., Rizzi, L., Dehaene, S., & Pallier, C. (2009). Sentence syntax and content in the human temporal lobe: an fMRI adaptation study in auditory and visual modalities. *J Cogn Neurosci*, 21(5), 1000-1012.
- Devlin, J.T., Jamison, H.L., Matthews, P.M., & Gonnerman, L.M. (2004). Morphology and the internal structure of words. *Proc Natl Acad Sci U S A*, 101(41), 14984-14988.
- Ehri, L.C., Nunes, S.R., Stahl, S.A., & Willows, D.M.M. (2001). Systematic phonics instruction helps students learn to read: Evidence from the National Reading Panel's meta-analysis. *Review of Educational Research*, 71, 393-447.
- Fredembach, B., de Boisferon, A.H., & Genotaz, E. (2009). Learning of arbitrary association between visual and auditory novel stimuli in adults: the 'bond effect' of haptic exploration. *PLoS One*, 4(3), e4844.
- Freiwald, W.A., & Tsao, D.Y. (2010). Functional compartmentalization and viewpoint generalization within the macaque face-processing system. *Science*, 330(6005), 845-851.
- Gaillard, R., Naccache, L., Pinel, P., Clemenceau, S., Volle, E., Hasboun, D., et al. (2006). Direct intracranial, fMRI, and lesion evidence for the causal role of left inferotemporal cortex in reading. *Neuron*, 50(2), 191-204.

- Gentaz, E., Colé, P., & Bara, F. (2003). Evaluation d'entraînements multisensoriels de préparation à la lecture pour les enfants en grande section de maternelle : une étude sur la contribution du système haptique manuel. *L'Année Psychologique*, *104*, 561-584.
- Glezer, L.S., Jiang, X., & Riesenhuber, M. (2009). Evidence for highly selective neuronal tuning to whole words in the 'visual word form area'. *Neuron*, *62*(2), 199-204.
- Goswami, U., & Ziegler, J.C. (2006). A developmental perspective on the neural code for written words. *Trends Cogn Sci*, *10*(4), 142-143.
- Hashimoto, R., & Sakai, K.L. (2004). Learning letters in adulthood: direct visualization of cortical plasticity for forming a new link between orthography and phonology. *Neuron*, *42*(2), 311-322.
- Hasson, U., Levy, I., Behrmann, M., Hendler, T., & Malach, R. (2002). Eccentricity bias as an organizing principle for human high-order object areas. *Neuron*, *34*(3), 479-490.
- Jacquemot, C., Pallier, C., LeBihan, D., Dehaene, S., & Dupoux, E. (2003). Phonological grammar shapes the auditory cortex: a functional magnetic resonance imaging study. *J Neurosci*, *23*(29), 9541-9546.
- Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: a meta-analysis of 35 neuroimaging studies. *Neuroimage*, *20*(2), 693-712.
- Kolinsky, R., Verhaeghe, A., Fernandes, T., Mengarda, E.J., Grimm-Cabral, L., & Morais, J. (2010). Enantiomorphy through the Looking-Glass: Literacy effects on mirror-image discrimination. *JEP: General*, in 2nd revision.
- Lachmann, T., & van Leeuwen, C. (2007). Paradoxical enhancement of letter recognition in developmental dyslexia. *Dev Neuropsychol*, *31*(1), 61-77.
- Logothetis, N.K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Curr Biol*, *5*(5), 552-563.
- Morais, J., Cary, L., Alegria, J., & Bertelson, P. (1979). Does awareness of speech as a sequence of phones arise spontaneously? *Cognition*, *7*, 323-331.
- Paulesu, E., McCrory, E., Fazio, F., Menoncello, L., Brunswick, N., Cappa, S.F., et al. (2000). A cultural effect on brain function. *Nat Neurosci*, *3*(1), 91-96.
- Pegado, F., Nakamura, K., Cohen, L., & Dehaene, S. (2011). Breaking the symmetry: Mirror discrimination for single letters but not for pictures in the Visual Word Form Area. *Neuroimage*, *55*, 742-749.
- Pinel, P., & Dehaene, S. (2009). Beyond hemispheric dominance: brain regions underlying the joint lateralization of language and arithmetic to the left hemisphere. *J Cogn Neurosci*, *22*(1), 48-66.
- Puce, A., Allison, T., Asgari, M., Gore, J.C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *Journal of Neuroscience*, *16*, 5205-5215.
- Qiao, E., Vinckier, F., Szwed, M., Naccache, L., Valabregue, R., Dehaene, S., et al. (2010). Unconsciously deciphering handwriting: subliminal invariance for handwritten words in the visual word form area. *Neuroimage*, *49*(2), 1786-1799.
- Rollenhagen, J.E., & Olson, C.R. (2000). Mirror-image confusion in single neurons of the macaque inferotemporal cortex. *Science*, *287*(5457), 1506-1508.
- Schneps, M.H., Rose, L.T., & Fischer, K.W. (2007). Visual learning and the brain: Implications for dyslexia. *Mind, Brain and Education*, *1*(3), 128-139.
- Seymour, P.H., Aro, M., & Erskine, J.M. (2003). Foundation literacy acquisition in European orthographies. *Br J Psychol*, *94*(Pt 2), 143-174.
- Song, Y., Hu, S., Li, X., Li, W., & Liu, J. (2010). The role of top-down task context in learning to perceive objects. *J Neurosci*, *30*(29), 9869-9876.

- Szwed, M., Dehaene, S., Kleinschmidt, A., Eger, E., Valabregue, R., Amadon, A., *et al.* (2011). Specialization for written words over objects in the visual cortex. *Neuroimage*.
- van Atteveldt, N., Formisano, E., Goebel, R., & Blomert, L. (2004). Integration of letters and speech sounds in the human brain. *Neuron*, *43*(2), 271-282.
- Vinckier, F., Dehaene, S., Jobert, A., Dubus, J.P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: dissecting the inner organization of the visual word-form system. *Neuron*, *55*(1), 143-156.
- Yoncheva, Y.N., Blau, V.C., Maurer, U., & McCandliss, B.D. (2010). Attentional focus during learning impacts N170 ERP responses to an artificial script. *Dev Neuropsychol*, *35*(4), 423-445.
- Yoncheva, Y.N., Zevin, J.D., Maurer, U., & McCandliss, B.D. (2010). Auditory selective attention to speech modulates activity in the visual word form area. *Cereb Cortex*, *20*(3), 622-632.
- Ziegler, J.C., & Goswami, U. (2006). Becoming literate in different languages: similar problems, different solutions. *Dev Sci*, *9*(5), 429-436.

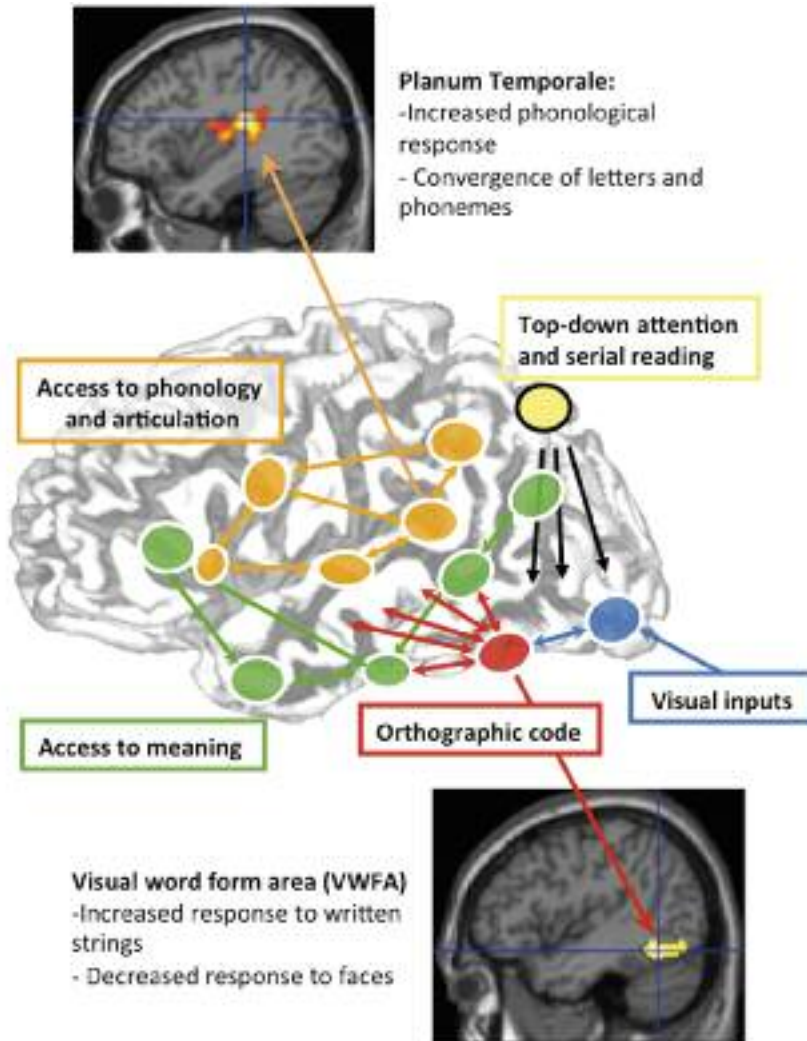


Figure 1. Overview of the brain systems for reading, showing two major sites of change induced by literacy. The central diagram, taken from (Dehaene, 2009), illustrates the major left-hemisphere regions involved in expert reading. During reading, the written word projected onto the retina first reaches the occipital visual cortex. From there, it is channeled to the left-hemisphere visual word form area (VWFA), which encodes the visual orthography of the string: the sequence of letters and their relations. Most words are identified quickly and effortlessly, in parallel, but for long or hard-to-read words, a left-to-right serial orientation of attention to the sequence, arising from dorsal parietal cortex, may be needed. The identified visual string is then transmitted to distinct areas involved in meaning and in pronunciation (auditory phonology and articulatory). The insets show two brain regions where activation is dramatically increased in literate relative to illiterate adults (redrawn from data in Dehaene, Pegado, *et al.*, 2010): the visual word form area (bottom) and the planum temporale (top). These regions contribute to a grapheme-to-phoneme conversion route. Developing this pathway is an essential goal of reading acquisition.

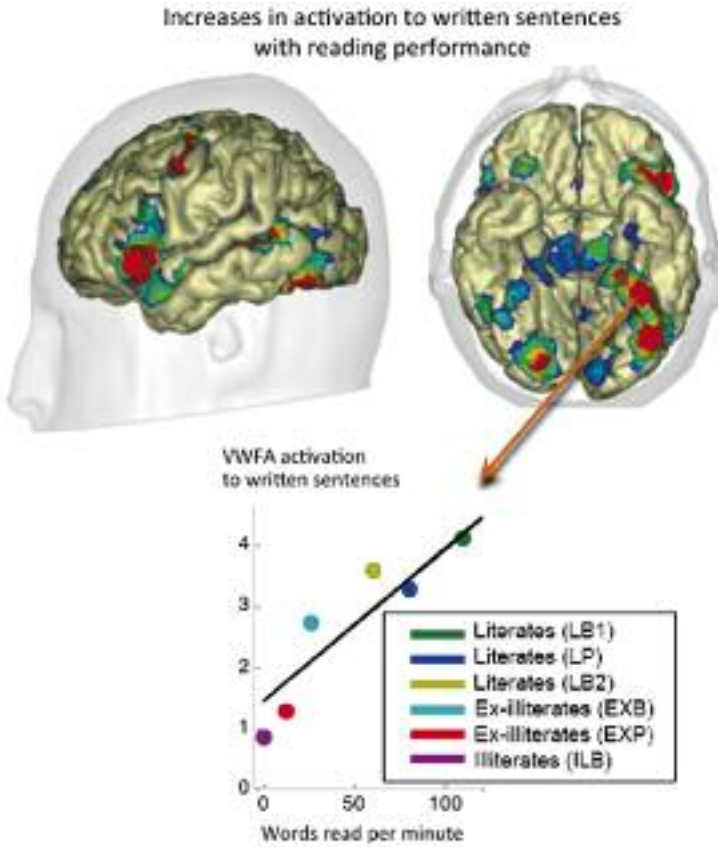


Figure 2. Overview of changes induced by learning to read in adults. The image shows all the regions where activation increased with reading performance, in response to the visual presentation of written sentences (redrawn from data in Dehaene, Pegado, *et al.*, 2010). Literacy increases activation in the visual word form area (VWFA, inset graph), even in unschooled ex-illiterate adults who learned to read during adulthood. Literacy also allows the entire left-hemisphere network of language areas to be activated through the visual modality.