OPINION

Illiterate to literate: behavioural and cerebral changes induced by reading acquisition

Stanislas Dehaene, Laurent Cohen, José Morais and Régine Kolinsky

Abstract | The acquisition of literacy transforms the human brain. By reviewing studies of illiterate subjects, we propose specific hypotheses on how the functions of core brain systems are partially reoriented or 'recycled' when learning to read. Literacy acquisition improves early visual processing and reorganizes the ventral occipito-temporal pathway: responses to written characters are increased in the left occipito-temporal sulcus, whereas responses to faces shift towards the right hemisphere. Literacy also modifies phonological coding and strengthens the functional and anatomical link between phonemic and graphemic representations. Literacy acquisition therefore provides a remarkable example of how the brain reorganizes to accommodate a novel cultural skill.

Abraham Lincoln called writing "the great invention of the world" (REF. 1). Indeed, scholars consider that the invention of writing has profoundly transformed human culture, economy, science and the law[2]. It is only recently, however, that psychology and cognitive neuroscience have begun to gather objective evidence of the major positive effects of literacy on the brain.

Here, we review the existing knowledge of the impact of literacy on the brain. Our goal is not to review how reading circuits operate; indeed, this is far from being fully known[3,4]. Rather, we focus on research on the illiterate brain and how it changes with literacy acquisition. We primarily emphasize three major brain systems in which changes are observed: the early visual system, the ventral visual pathway and the phonological coding system. We also discuss the other anatomical, connectional and behavioural changes reported in the literature as being associated with learning to read. We end by briefly discussing the impact of literacy on higher-level cognitive abilities, such as working memory, semantic organization, reasoning and executive functions, although these effects remain understudied.

Literacy is a multidimensional concept, the visual, phonological, motor and cultural dimensions of which have only begun to be separated experimentally[5,6] (BOX 1). Literacy implies knowledge of both reading and writing at a series of nested levels, ranging from individual letters and sound units, to words and texts. This knowledge may vary in part with the script that is learned (BOX 2). Literacy is a graded variable; there are large variations in reading performance between beginners, who hesitantly decipher words letter by letter, and experts, who read more than 100 words per minute and exhibit constant identification times for words ranging from three to eight letters[7]. Finally, literacy is often confounded by other social variables, such as schooling. In this Opinion article, we put a stronger emphasis on the brain-imaging studies that have attempted to isolate the impact of literacy itself[8–13], even though this has rarely been achieved. From an analysis of these studies, we hypothesize that the core brain systems whose function is partially reoriented or 'recycled' (REF. 14) when learning to read are involved in early vision, letter analysis, phonological analysis and their reciprocal interconnections.

Early visual processing

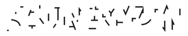
Reading, especially in fine print, places a strong emphasis on visual skills and may therefore improve them. Indeed, when compared with illiterate individuals, literate adults who have learnt the alphabet as adults or children show increased bilateral occipital functional MRI (fMRI) activation in response to various visual stimuli (including letters, faces and pictures)[8]. Literacy also enhances the early occipital event-related potentials (ERPs) that are evoked 140–180 ms after the presentation of the same stimuli[9]. Moreover, repetition suppression (that is, the reduction of ERP amplitude in response to the second of two repeated stimuli, relative to two distinct stimuli) in an earlier time window (100–150 ms) is augmented in literate compared with illiterate individuals[9]. As repetition suppression reflects the brain's capacity to discriminate two items, these results suggest that literacy facilitates the fast discrimination of similar-looking visual stimuli.

All of these effects occur in response to various visual stimuli, not just to letter strings. In alphabetic readers (readers of alphabetic script), literacy even enhances the retinotopic fMRI responses to checker-boards in the bilateral calcarine cortex, at the location of primary visual area V1 (REF. 8). This effect is selective for horizontal over vertical checker-boards, thus indicating that visual cortex has become specifically responsive to the location at which alphabetic words appear on the retina.

These effects on vision may arise, at least in part, because readers become attuned to frequent occurrences of letters and letter combinations at different locations within words, thus resulting in perceptual learning[15]; that is, a target- and location-specific improvement in the identification of well-learnt stimuli[16,17]. Indeed, extensive training to detect a specific shape (such as an inverted T) leads to an increased response in human V1 on seeing that shape[18], mimicking the effect of reading acquisition[8]. The Roman alphabet provides an excellent stimulus for perceptual learning because it comprises only 26 letters, all of which are seen millions of times at roughly fixed locations on the retina. Furthermore, words can be read in very small print (corresponding to a visual angle as small as 0.2° per letter)[19] — a fine visual resolution that may only be available at early stages of the visual processing pathway. In agreement with this notion, word stimuli such as


(1)

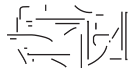
evoke more fMRI-detected activation than do well-matched scrambled controls such as


(2)

in areas V1 and V2 of expert alphabetic readers[20,21]. Interestingly, in equally expert Chinese readers contrasting, for instance,

股票 (3)

versus


(4)

this effect is not observed in V1 and V2, but in V3 and V4 (REF. 21). This is probably because Chinese writing systems, unlike alphabets, do not comprise a restricted set of shape primitives (letters). BOX 2 further discusses how different writing systems may lead to slightly different brain changes.

These changes to early visual processing benefit several behavioural tasks, even outside the reading domain. Literate adults and ex-illiterate adults (that is, people who learned to read as adults) are better than illiterate adults at deciding whether the bottom halves of faces or houses are the same or different, without being distracted by the top part of the images[22], suggesting that literacy improves an analytical strategy of attending to pictures. Literate individuals also surpass illiterate individuals in their ability to detect a transposition among a string of letters or non-letter symbols[23], suggesting a refined sense of relative letter position. Literate individuals may also be at an advantage when visually integrating stimuli; for instance, they show superior capacity in connecting line segments into an overall shape[12]; an ability that animal studies have linked to the function of area V1 (REF. 17).

The ventral visual pathway

In all primates, further processing within the ventral visual pathway, beyond the early visual cortex, is needed to achieve visual recognition invariantly over changes in retinal illumination, image size and orientation. Because written words form a special visual category with its own invariances for changes in case or font, it should not be surprising that literacy acquisition results in important changes in the ventral visual pathway.

The visual word form area. Whenever children or adult readers are presented with a readable word or pseudoword in a script that they have learned, there is a consistent and selective functional response[5,6] in a specific region of the left ventral occipito-temporal cortex (left VOT) that is located at a very similar location in English, French, Hebrew and Chinese readers[21,24,25]. This region has been called the 'visual word form area' (VWFA) to reflect the localized and reproducible response to written words and pseudowords at this site[26,27], although it should be noted that even after reading acquisition, this region continues to respond, to a lesser extent, to visual stimuli besides script.

The responsivity of the VWFA to script is clearly an outcome of literacy acquisition: the VWFA responds more to a given script than to faces, objects or places only in people who have learned to read that script[21,28]. Indeed, in illiterate individuals, letter strings elicit a VWFA response that is much smaller than in literate individuals[8] and that does not typically exceed the activation in response to pictures of faces, tools or checker-boards (FIG. 1). In a group of participants whose reading ability ranged from purely illiterate to highly literate, reading speed was monotonically related to VWFA activation: approximately half of the variability in reading fluency could be predicted by the fMRI response to written words[8]. ERP data revealed the timing of this effect: the left-lateralized negative N170 component of the ERP that arises from the left VOT 170 ms after the presentation of a visual letter string is strongly enhanced in literate and ex-illiterate individuals compared with illiterate individuals[9]. A similar effect exists in children who are learning a new script[29,30]. As such, the VWFA and its associated N170 component seem to be major correlates of literacy.

Script-specific activity in the VWFA emerges rapidly during reading acquisition: a strong selectivity for words is already observed in 9-year-old children who have been learning to read for 2–3 years[31]. Even 6-year-old readers already show a greater VWFA activation to words than to other visual stimuli, whereas 6-year-old non-readers do not[32]. A study of 6-year-old kindergarten children indicated that just a few weeks of computerized training in letter–sound correspondences can establish a greater VWFA response to words than to false fonts (symbols with the same level of graphic complexity as letters)[33]. In adults, even a few days of training in associating speech sounds with a novel script or alphabet is sufficient to increase activation in response to such symbols at or very near the VWFA[34–37]. Adult plasticity is thus sufficient to permit the emergence of a functional response even when literacy is acquired in adulthood[8]; however, there are possible limits to such plasticity in adults (BOX 3).

Box 1 | Methodological considerations in literacy research

Understanding how the acquisition of literacy transforms the brain is conceptually simple: it involves using brain-imaging methods such as functional MRI (fMRI), magnetoencephalography (MEG) or electroencephalography (EEG) to scan adults or children who have or have not learned to read, everything else being equal. However, in practice, such research faces important methodological challenges. Comparing unschooled illiterate adults with schooled literate adults[93] mixes the effects of literacy and schooling. Following children longitudinally, thereby scanning them at various stages of literacy acquisition, confounds literacy with both schooling and age[57,59]. Cross-sectional designs can be used to compare age-matched groups of literate and pre-literate children[95] — for instance, by taking advantage of societal variability in the age at which children enter school — but this comparison is confounded by schooling and possibly other social variables, such as socioeconomic status.

In adults, a better design involves examining the pure effect of literacy by identifying two matched populations, both equally deprived of early schooling but with one population consisting of individuals who eventually learnt to read (ex-illiterates) while the other population remained illiterate[8–10]. Such a design, however, focuses exclusively on late learners, who may be unable to achieve the same level of reading fluency and brain changes as do early learners[155]. Also, in all published studies so far, individuals were not randomly assigned to these groups, leaving open the possibility that there were confounding motivational or socioeconomic variables. Following reading acquisition, ex-illiterate adults may also differ from illiterate adults in that they practice more demanding professions, develop better processing strategies, gain familiarity with testing-like situations, acquire self-confidence and higher socioeconomic status, and so on.

Another source of difficulty is that pre- and post-literate populations are inhomogeneous in many ways. Some illiterate adults or pre-literate children know many letters, whereas others know almost none[104,156]. Some illiterate adults attended school for a few years as children yet still failed to acquire reading, raising a suspicion of dyslexia.

One way to address such confounds is to carry out multiple regression with participants' scores in various reading tests together with their age, socioeconomic status and other confounding variables[6,8]. To de-correlate the variables, a large number of participants is necessary. Ultimately, the field needs large, longitudinal studies that systematically track behavioural improvements and brain changes in adults or children as they learn to read[57,59]. Ideally, participants should be randomly assigned to a literacy training group or to a control group, and both groups should be exposed to equally demanding training for the same amount of time. By imposing a delay in literacy acquisition, however, such a design raises important ethical issues. It has therefore been applied only for very short periods of time: a study in 6-year-old kindergarten children demonstrated that 8 weeks of training was sufficient for the visual word form area (VWFA) selectivity for written words to emerge[33].

Box 2 | **Literacy in different cultures**

The world's writing systems vary considerably in terms of shape, number of characters and size of the denoted unit[157]: abjads comprise only consonants; abugidas consist primarily of consonants, with vowels being depicted by diacritical marks; alphabets contain consonants and vowels; syllabaries, such as Japanese kana, depict syllables; and Chinese or Japanese logographic systems, which are sometimes described as 'morphosyllabic' (REF. 157), depict whole words or morphemes. Does this variability affect reading acquisition and its impact on brain circuitry and behaviour?

The bulk of the evidence suggests that, at the coarse scale provided by functional MRI (fMRI), reading relies on similar brain circuits in all cultures[24,158]. In particular, the visual word form area (VWFA) plays a central role in all writing systems[24], including Hebrew[25,28] (which is read right to left), Japanese kana[159], Japanese kanji[158,159] and Chinese writing systems[21,160,161]. However, when adapting to a specific script, this universal biological circuit converges onto slightly different strategies[71,162]. Alphabetic learning, with its small inventory of letter shapes, promotes perceptual learning in the early visual areas V1 and V2, whereas Chinese characters may promote shape learning in areas V3 and V4 (REF. 21). Whole-character learning (for instance, in Chinese) may induce a greater right lateralization[37,163] or greater mesial localization[159] of the VWFA than does alphabetic learning.

Variability is even evident within alphabets. A greater sensitivity to letter order and morphology exists in Hebrew than in English[164,165] — an effect imputed to the presence of compact three-letter roots in Hebrew. Most importantly, orthographic transparency — the regularity of the correspondence between written symbols and the corresponding phonemes — affects the speed of reading acquisition: roughly two more years are required to learn non-transparent alphabetic codes such as English than to learn transparent ones such as Italian[166]. As a result, English readers exhibit greater activations in the VWFA in response to written words than do Italian readers[167], presumably because many irregular combinations of letters (such as 'ough' or 'tion') must be stored in English but not in Italian. Conversely, learning to read in Italian promotes a stronger activation of the planum temporale than does learning to read in English, presumably reflecting a more efficient access to phonology in Italian readers[167].

Phonological awareness varies most strongly between readers of alphabetic systems versus those of logographic or morphosyllabic systems. Learning an alphabet improves performance on phonological awareness tasks, such as phoneme deletion or phoneme reversal[103]. Chinese readers rely on an implicit sublexical conversion procedure that statistically maps certain parts of Chinese characters (called phonetic radicals) to their probable pronunciation[160], but at an explicit level, Chinese readers who have not been exposed to any alphabet have illiterate-like behavioural responses in auditory phonological awareness tasks[168–170]. A recent developmental fMRI study[112] showed that learning an alphabet (English) increases activation of the left superior temporal gyrus (close to the planum temporale) and left inferior frontal and inferior parietal cortices in response to spoken words — an effect that is absent in Chinese readers.

Finally, a left lateral and dorsal prefrontal region within Brodmann's area 9 was proposed to be selectively[171] or more strongly[24,161] activated in Chinese readers than in alphabetic readers. However, when comparable handwritten stimuli were used in both languages, no fMRI difference was found[158]. Brodmann's area 9 comprises a left superior prefrontal region called 'Exner's area', lesions of which cause reading and writing deficits (such as alexia with agraphia). This region is thought to encode handwriting gestures and to help decipher handwriting by mentally reconstructing the intended gesture used to generate the written symbol[158]. In all cultures, reading acquisition is facilitated by handwriting training[172–175]. This effect may be stronger for Chinese systems because Chinese printed characters resemble handwriting and because a gesture-based mnemonic strategy may facilitate the learning of thousands of Chinese characters[171].

The VWFA is generally agreed to intervene in the efficient identification of orthographic stimuli[38] and to enable quick association of such stimuli with phonological and lexical information[34]. However, at a more detailed level, theories differ on how specialized the VWFA is for reading and on the respective roles of bottom-up and top-down factors in its activation[3,4,39]. One view[3] proposes that the VWFA contains specialized neuronal circuitry for orthographic coding: with alphabetic expertise, the VWFA, much like the face recognition system[40], develops an efficient bottom-up hierarchy of tuned cells for letters, bigrams (also known as letter pairs: for example, 'th', 're' and 'in'), morphemes (which include roots and suffixes such as '-tion' and '-ing') and short words[41]. Indeed, in expert alphabetic readers, the VWFA is organized in a posterior-to-anterior hierarchy[42–44]: posterior parts respond to individual letters[43] (irrespective of case[44]), whereas anterior parts respond to letter combinations such as bigrams[42,45]. An fMRI study using repetition suppression even suggests that some neurons in the VWFA may sharply tune to known words: the VWFA reduces its activation the second time a written word is presented (repetition suppression to 'boat–boat'), but a change in a single letter (such as 'coat–boat') has the same effect as changing the entire word ('fish–boat') and suffices to eradicate the repetition suppression effect[46].

Alternative 'interactive' theories of the function of the VWFA[39] propose that such tuning is only apparent in that it arises solely from top-down prediction effects in a generic circuit that bidirectionally links visual areas with language areas. Indeed, some studies report that during a picture- and word-naming task, activation is just as strong for pictures as for words at the VWFA site[47]. One study reported bidirectional priming between pictures and words, whereby the presentation of a picture before a written word caused the same amount of repetition suppression as the repetition of the written word, suggesting that an abstract, non-orthographic code was involved[48]. Furthermore, the specificity for words over other stimuli in the VWFA in passive viewing is stronger during a phonological naming task than during a visual discrimination task, suggesting that specialization for written words may be a task-dependent effect rather than a purely stimulus-driven effect[49].

Proponents of the orthographic coding view stress that these observations do not refute the existence of a specialized orthographic representation at this location, possibly intermixed with other non-reading-specific visual responses. Indeed, the theoretical disagreement does not revolve around the existence of top-down influences on the VWFA — which, as further discussed below, is clearly attested[8,50]. The issue, rather, is whether such top-down inputs contact a specialized orthographic code (the orthographic tuning hypothesis) or, instead, a generic code that is "not tuned selectively to orthographic inputs" (REF. 39) but is efficiently predicted by top-down phonological information in expert readers only. In this respect, several arguments support the tuning hypothesis, although the issue remains open. First, in expert readers, the similarity of VWFA activation patterns in response to letters specifically correlates with the orthographic similarity between the tested letters[51]. Second, in literate participants only, VWFA selectivity for the learned script is observed even in simple visual detection tasks that do not involve naming or activation of naming circuitry[8,9]. Third, a recent study in which participants learned to read a new script while electrocorticographic signals were recorded from over the VWFA has dissociated the dynamics of orthographic training: in the first few days of training, learning results in a late

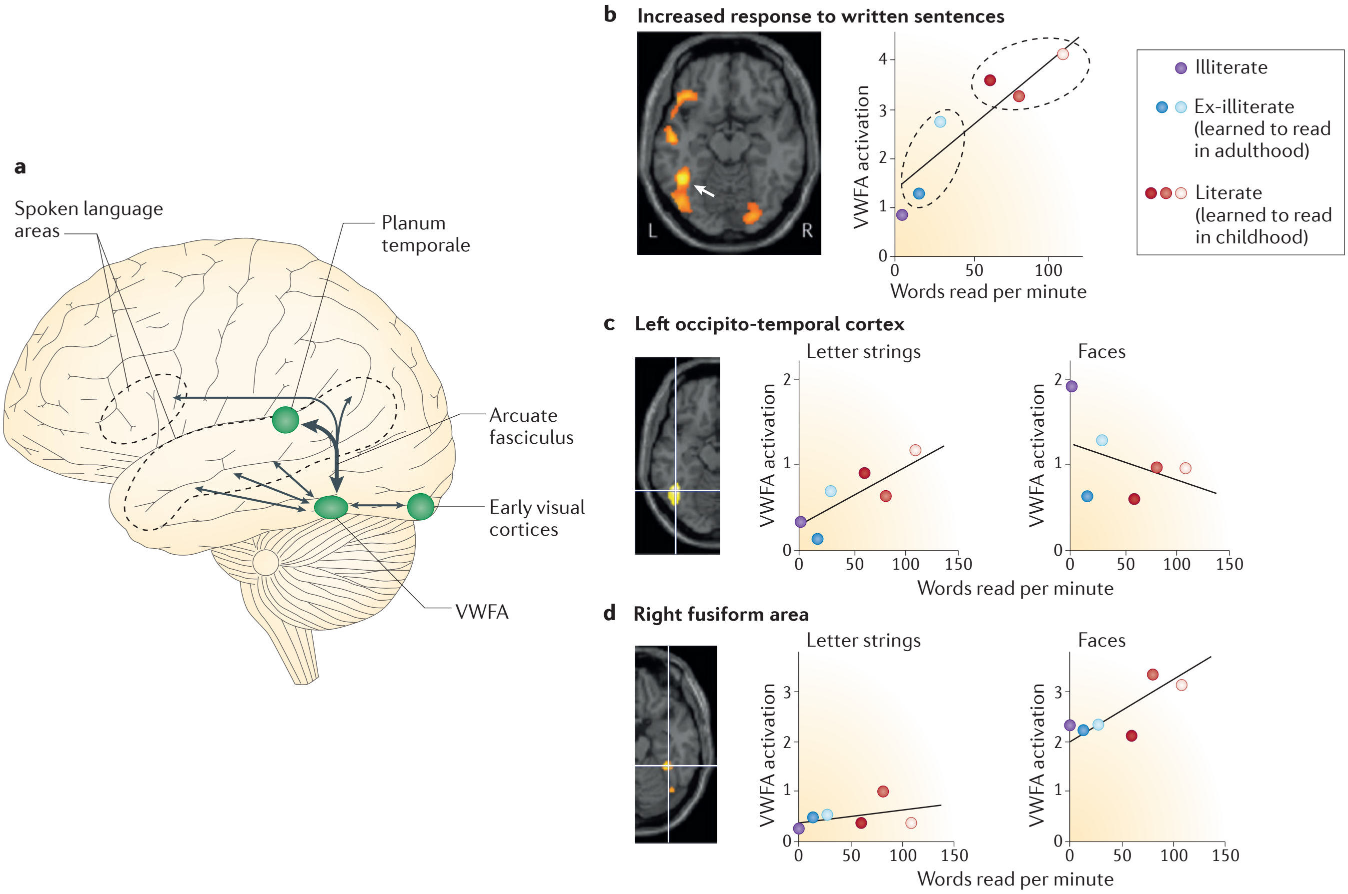


Figure 1 | **A pivotal role of the ventral occipito-temporal cortex in reading acquisition.** **a** | Learning to read involves developing an efficient interface between vision and spoken language. The regions outlined by the dashed lines are all involved in processing spoken language prior to reading acquisition[95,178]. The visual word form area (VWFA), which is located in the ventral left occipito-temporal sulcus, and its afferents and efferents are thought to play a pivotal role in reading acquisition by enabling the rapid recognition of strings of letters and their translation into sequences of sounds. The regions in green — the VWFA, early visual cortices (V1 and V2) and planum temporale are all demonstrably enhanced by reading acquisition. The connections between them (shown by arrows) may also be enhanced — this has been directly demonstrated in the case of the posterior part of the arcuate fasciculus (thick arrow). **b**–**d** | The acquisition of literacy is reflected by important changes in ventral visual responses. Brain maps indicate the cortical locations at which the activation evoked by short written sentences (**b**) or written pseudowords (**c**) is positively correlated with literacy level (measured by the number of words read per minute)[8]. A particularly strong correlation is observed at the VWFA site (indicated by an arrow in the image in part **b**; additional areas are activated by visual or sentence content). Data points represent the average activation of the VWFA (blood-oxygen-level-dependent (BOLD) signal, expressed as a percentage of the whole-brain mean) in each of six groups of subjects of different levels of literacy (purple, blue and red coloured circles depict groups of illiterate, ex-illiterate and literate individuals, respectively, with lighter shades indicating higher reading ability). Remarkably, the increase in VWFA response to letter strings is accompanied by a decrease in responses to other categories, particularly faces, at the VWFA location in the left hemisphere (**c**)[8]. Correspondingly, the activation of the right hemisphere in response to faces increases at the site of the fusiform face area (FFA) (**d**). In this right-hemispheric region, letter strings evoke very little or no response. Parts **b**–**d** are adapted from Dehaene, S. *et al.* How learning to read changes the cortical networks for vision and language. *Science* **330**, 1359–1364 (2010). Reprinted with permission from AAAS.

top-down effect at the VWFA site, whereas faster and presumably bottom-up tuning arises only a few days later[35].

Although such data strongly suggest orthographic tuning, the term 'visual word form area' has been challenged by recent observations that the VWFA site also emerges at an identical cortical location when congenitally blind adults learn to read in Braille[52,53] or learn to recognize letter shapes using an auditory sensory substitution device[54]. Thus, the VWFA is not exclusively linked to the visual modality and supports literacy acquisition in any modality. This and other observations of specialization in congenitally blind individuals[55,56], although not fully understood, suggest two important refinements to current theories. First, the entire ventral 'visual' cortex may actually be 'meta-modal' (REF. 52); that is, tuned to abstract shape information that can be conveyed by various modalities. It merely becomes 'visual' because, in sighted individuals, it is the visual modality that conveys the highest-quality evidence about shape. Second, within the vast expanse of the ventral visual pathway, the VWFA site may owe its specificity for reading to a special pattern of connectivity that enables shapes to be linked to the spoken language system. This view is supported by the finding of a specific connectivity of the VWFA to language areas[57–59], as well as by the fact that the VWFA systematically lateralizes to the same hemisphere that supports spoken language[60,61].

The face recognition system. In literate people, the VWFA is always located next to a cortical region that is selective for faces: the left fusiform face area (left FFA)[62–64]. Remarkably, the boundary between these two regions seems to shift during reading acquisition[8]. In illiterate individuals, the VWFA is not inactive but can be strongly activated by stimuli such as pictures of faces, tools or checkerboards. As literacy increases, face responses undergo an inter-hemispheric displacement: face-induced fMRI responses in the left hemisphere become slightly smaller but increase substantially in the right fusiform gyrus, at or near the classical right-hemispheric site of the FFA[8] (FIG. 1).

This face-response displacement effect was initially observed in an fMRI study on adults[8] and was later replicated in an fMRI study on children[31] and ERP studies on children and adults[9,65]. It is consistent with observations that the sizes of responses to written words and faces are inversely correlated in adults[60,66], and that reading competence correlates with the extent of the left visual field advantage during a face-discrimination task, a behavioural measure of right-hemispheric superiority for face processing[67]. There is evidence that the competition between symbols and faces in the ventral visual cortex may start as early as the age of four[68]. The gradual emergence of detectable face-specific fMRI patches during child development extends through adolescence[69,70], and thus may be particularly susceptible to influences from education.

The reason for the competition between reading and face recognition during development is unknown. It is possible that both functions call upon a shared operation, namely the invariant visual recognition of shapes with high foveal resolution[14,71]. A recently identified cytoarchitectonic area, the human fusiform gyrus region known as 'FG2', seems to afford fMRI responses both to words and to faces[72,73] and therefore may be the shared neuroanatomical resource for which both categories of stimuli compete.

Literacy studies suggest that the right-hemispheric lateralization of the FFA may be caused in large part by the acquisition of words and symbols in the left hemisphere. Importantly, however, a slight right-hemispheric dominance of face responses exists even in illiterate adults[8]. More studies are needed to understand whether this effect reflects an innate right-hemisphere bias for faces[68,69] or a partial acculturation of most illiterate individuals to signs and written symbols such as numbers and a few isolated letters.

Box 3 | **Can the brain changes associated with literacy acquisition occur in adults?**

Can literacy be acquired equally easily at any age, or is there a limit on adult plasticity for reading? A few studies have addressed this question by comparing illiterate adults with ex-illiterate adults. These studies are important not only in practice but also in theory because they dissociate literacy from early schooling, which is absent in both groups (BOX 1).

Generally, the findings indicate that reading relies on the same brain circuit when literacy is acquired in adulthood or in childhood, and that the majority of behavioural and brain changes induced by literacy can therefore occur in adulthood. Anatomically, adult literacy acquisition yields detectable changes in grey- and white-matter anatomy, particularly in the left arcuate fasciculus and posterior corpus callosum[10,13]. Functionally, ex-illiterate adults show most of the effects reported in this article, including increased visual word form area (VWFA) responses to letter strings; activation of the left-hemispheric spoken language network by written sentences; increased responses of the occipital and calcarine cortex to non-reading-related stimuli; and enhanced planum temporale and top-down VWFA activation in response to spoken words and pseudowords[8,9]. Behaviourally, adult literacy acquisition affects both visual processing[11,12,22,83,86] and phonological awareness[103,108].

These effects are generally smaller in ex-illiterate adults than in literate adults who learnt to read and were schooled at an early age, but it is currently not possible to determine whether this arises simply from reduced reading experience or is due to reduced brain plasticity in adulthood or other sociocultural factors (BOX 1). A few ex-illiterate adults do become fluent readers and spellers, reading in excess of 50 words per minute[8]. However, a common observation is that reading in late-learned scripts often remains dysfluent[176]. Furthermore, literacy does not have the same impact on the face recognition system when it is acquired in adulthood compared with when it is acquired in childhood, suggesting that the adult ventral visual system cannot be as flexibly reorganized: literate individuals who learnt to read at a young age showed reduced activation to faces compared with illiterate adults, whereas there was no statistically significant difference between illiterate and ex-illiterate adults[8]. Furthermore, even after adjusting for variations in reading score, ex-illiterate adults still showed a significantly smaller reduction in face-evoked responses than did schooled literate individuals of matched social origin[8]. These findings suggest that face responses, which stabilize in late childhood[69,70], may become entrenched in adulthood to such an extent that they may no longer be shifted by literacy acquisition, perhaps placing constraints on the ease and speed with which fluent sight-reading can be acquired in adults[176].

Interestingly, direct evidence for reduced visual plasticity in adulthood has been obtained in non-human primates: following identical and extensive symbol training, specialized inferotemporal cortical patches, functionally similar to the human VWFA, emerged in juvenile monkeys but not in adults[155]. We know of no such study in humans and, as a result, although the plasticity of children's brains is impressive[177], it remains unknown whether there is an optimal age for reading acquisition. Comparing learning speeds and plasticity at different ages should be a high priority for educational neuroscience.

Mirror invariance. Another example of competition in the ventral visual cortex is provided by the effect of literacy on mirror invariance. Mirror invariance is the capacity to recognize a visual image as identical after a left–right inversion. Mirror invariance is useful in the natural world because a lateral reversal usually does not affect the identity of natural objects: "a tiger is equally threatening when seen in right or left profile" (REF. 74). However, mirror invariance is undesirable for reading, when it is necessary to discriminate mirror letters such as 'p' and 'q', or 'b' and 'd'. It has therefore been suggested that learning to read requires the 'unlearning' of mirror invariance[14,71].

In humans and primates, left–right mirror invariance is achieved at a specific level in the cortical hierarchy[40,75,76]. A patch of inferotemporal cortex contains neurons that generalize over mirror images, treating them as two views of the same object[40,74,77]. In humans, a left occipito-temporal site overlapping with the VWFA exhibits mirror invariance for objects and faces[78–82], but fMRI studies based on repetition suppression (which can indicate which stimuli are discriminated by a given brain area) indicate that, in expert adult readers, this site fails to show mirror invariance specifically for words or letters[78,81]. This finding, which indicates that letters escape the mirror-invariance mechanism, was recently replicated using ERPs in response to mirror images[9]. Furthermore, the acquisition of literacy interferes demonstrably with behavioural judgements of mirror invariance: literate adults are slower in judging whether two images represent the same object if they are mirror images than if they are physically identical, whereas illiterate adults do not present any such cost for mirrored pairs[78,83,84].

Thus, literacy acquisition does interfere with mirror invariance. This impact, however, should not be exaggerated. It is small and occurs in the context of a general improvement of visual 'same–different' judgements[9,83]. Furthermore, it may only occur in readers of scripts that include mirrored characters[85]. Finally, the original mirror invariance of the occipito-temporal region is not entirely erased: even fluent readers find mirror-image discrimination of non-linguistic materials harder than non-mirror-image orientation discrimination[11,86]. Non-reversible letters such as 'R' remain susceptible to mirror generalization[87], and the suppression of mirror generalization for reversible letters is an active process that is vulnerable to interference from mirrored letters[88].

The small cost of literacy on mirror invariance does come with an advantage: literate individuals, unlike illiterate people, acquire an ability to discriminate mirror pictures and symbols[11,86,89,90]. Although mirror-image contrasts are registered pre-attentively, independent of literacy[91], their explicit discrimination is vastly improved by literacy: illiterate adults find it extremely hard to intentionally discriminate mirrored nonsense shapes[11,89] such as ├ and ┤ or mirrored images of familiar objects[86], whereas these differences become obvious both to ex-illiterate and literate adults[11,86,89]. At the neural level, ERP recordings also indicate that an early (100–150 ms) marker of mirror-image discrimination is enhanced by literacy acquisition[9]. This adds to the evidence that literacy enhances visual discrimination abilities, as described above.

Speech-processing changes

The main purpose of reading is to recover spoken language from vision. It is therefore not surprising that almost the whole left perisylvian language network (except the primary auditory cortex and its vicinity) responds just as robustly to written sentences as to spoken language in literate[92] but not in illiterate adults[8].

Perhaps more surprisingly, literacy enhances the activations evoked by spoken language. This was first shown by a positron emission tomography study that compared illiterate and literate adults in a spoken repetition task[93]. This study revealed that literate participants, compared with illiterate participants, had an increased activation of distributed cortical and subcortical areas in response to pseudowords relative to words; this difference between groups was probably due to poorer phonological coding of pseudowords in illiterate individuals[94].

More recently, fMRI comparisons of illiterate versus ex-illiterate and literate adults[8], and of pre-literate versus literate age-matched children[95], have demonstrated that literacy modifies spoken-language processing by enhancing spoken-language activation in two brain regions: the planum temporale (PT) and the VWFA.

The planum temporale. The bilateral superior temporal regions that are just posterior to Heschl's gyrus constitute the PT. Together with surrounding superior temporal and supramarginal cortices, the PT houses a neuronal representation of the consonants and vowels of spoken language[96,97]. It is attuned to the phonological rules that are specific to the person's native language[98], and it also responds during silent lip-reading[99].

We discovered that when listening to speech, the amplitude of PT activation is approximately twofold higher in literate than in illiterate adults[8]. This effect was observed both when listening passively to spoken sentences and in an auditory lexical decision task, in which participants have to decide whether a spoken item is a word (FIG. 2). A similar enhancement of PT responses to speech was later observed in a cross-sectional study of children comparing 6-year-old readers with age-matched non-readers[95].

In expert readers, activity in the PT in response to spoken speech sounds (phonemes) is also enhanced when a congruent letter or grapheme is simultaneously presented[100] (FIG. 2b). Interestingly, this effect is absent in children with dyslexia[101], who also display reduced responses to speech alone in subparts of the PT[31,101]. It is, however, unknown whether this is a consequence or a cause of their abnormal reading acquisition.

The literacy-associated increase in PT activation may indicate a refinement of one or more types of phonological representation. Indeed, phonological representations vary in size (from phonetic features or phonemes to syllables and larger units) and are ascribed with different levels of 'awareness' (the degree to which a phonological unit can be explicitly segregated and manipulated). Behaviourally, phoneme awareness is known to develop when children or adults learn to read in an alphabetic code[102,103]. For instance, pre-literate children[102] and illiterate adults[103,104] typically cannot tell that there are three sound 'segments' in the spoken word /kab/, and are unable to delete phonemes from a spoken word (for example, from /kab/ to give /ab/), unless they have begun to acquire the phonological correspondences of some letters and to use them in decoding attempts.

Several findings show that literacy affects explicit phoneme manipulations much more than the implicit phonological representations used during perception. For instance, illiterate adults discriminate between syllables such as /pa/ and /ba/ almost perfectly[105] and display the same form of categorical perception for speech as literate individuals do; that is, they neglect irrelevant (intra-category) acoustical variations in the stimuli when discriminating between syllables such as /ba/ and /da/[106]. In a similar way to literate individuals, illiterate people exhibit a phonologically restructured auditory lexicon; that is, their internal codes for spoken words are finely tuned to the frequency and proximity of words in their mother tongue[107]. They also use implicit phonemic codes in spoken-word recognition[108] and production[109]. However, in one study, illiterate individuals presented a less pronounced categorical boundary between phonemes, suggesting that compared with literate individuals they may be less sensitive to changes in phoneme identity when the auditory properties of the stimulus are varied continuously[106].

In children, PT activation correlates not only with reading level but also with vocabulary, verbal memory and phonological awareness performance[31]. Increases in activation during aural rhyming judgement (especially for words with conflicting orthography, such as 'pint–mint') between 8- to 12-year-old children and adults have also been reported in the inferior frontal areas that are typically involved in phonological awareness tasks[110,111] and in phonology-associated areas of the left superior temporal gyrus, near the PT[112]. We speculate that these changes may also reflect the development of explicit phonological representations during the acquisition of the alphabet.

Top-down VWFA activation. Reading requires the activation of phonological representations from written words but, conversely, after literacy is acquired, does spoken-word processing lead to an automatic activation of orthographic representations? An activation of the VWFA to spoken words is indeed observed in tasks that involve an explicit conversion from phonology to orthography[113,114]. Most crucially, orthography intervenes even in purely auditory tasks: literate individuals show a strong activation in the left fusiform gyrus (including the VWFA) during rhyme judgements compared with other auditory judgements on the same stimuli[50], and this effect is enhanced when spelling conflicts with the rhyming judgement (such as in 'pint–mint')[115–117]. Activation of the VWFA is also seen in difficult spoken-language judgements: for instance, when deciding whether a spoken utterance is a word or not[8] or whether two spoken utterances are the 'same' or 'different' when stimuli require phoneme segmentation[110,118]. Such findings suggest that literate people can activate the orthographic representations in their VWFA from spoken words in a top-down manner. There is direct evidence that this top-down effect is due to literacy, as it is proportional to reading score and absent in illiterate adults[8].

Many behavioural studies confirm that, in literate individuals, orthography affects spoken-word recognition processes. For instance, literate people are faster to decide whether two spoken words rhyme when spellings are similar (for example, 'toast–roast') than when they are not (for instance, 'toast–ghost')[119]. Furthermore, performance on tasks of lexical decision, semantic judgement and gender categorization (in languages in which words can be feminine or masculine) is enhanced in words for which the rhyming part can be spelled just one way (for example, 'sit') compared with words for which the rhyming segment can be spelled in multiple ways (for example, 'deep' and 'heap')[120–122]. ERP recordings indicate that this orthographic-consistency effect occurs early enough following stimulus presentation that it could modulate the core processes of lexical access[120,123,124].

Psycholinguists have long debated whether such behavioural effects of orthography on spoken-language processing indicate that orthographic representations are activated in a top-down manner whenever we process a spoken word[122] or whether reading acquisition refines the phonological representations themselves[124,125]. The brain-imaging studies discussed above suggest that both phenomena exist: the VWFA can be activated in a top-down manner only in literate individuals, and phonological representations of spoken language are enhanced by literacy acquisition.

The bidirectional links that literacy establishes between speech sounds and orthographic codes may also help to develop verbal memory for spoken materials. In serial recall of lists of words or digits, literate adults exhibit a much larger verbal memory than do illiterate individuals[126,127] (non-verbal memory is less affected). This effect may partly reflect a benefit from spelling knowledge, which provides an additional code that supports memorization. One indication to support this is that, for literate adults, lists of words with different spellings of the same rhyme (for example, 'right–kite–height') are easier to remember than are lists of rhyming words with the same spelling[128].

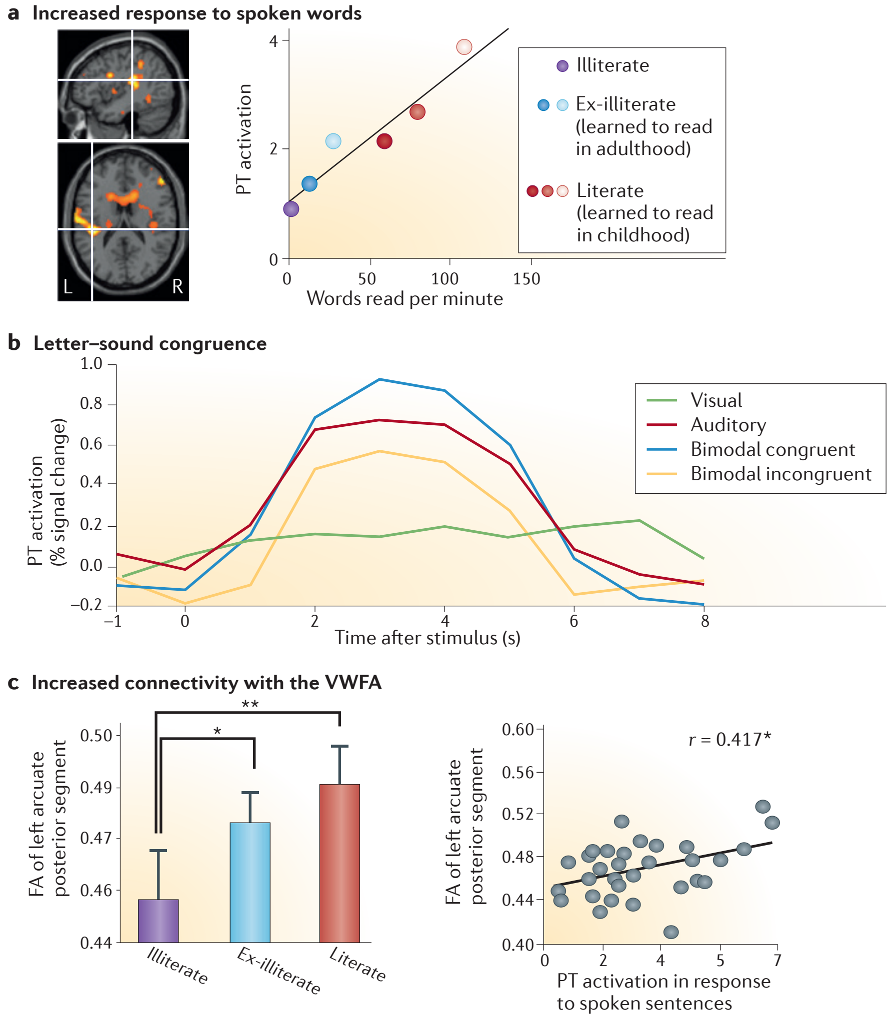


Figure 2 | **Impact of reading acquisition on the planum temporale.** Reading acquisition transforms the left planum temporale (PT) and the surrounding superior temporal cortex (a region involved in the auditory processing of speech). **a** | Enhanced brain responses to speech. Coloured voxels indicate the brain locations where the functional MRI blood-oxygen-level-dependent (BOLD) response evoked by spoken words increases with reading ability. A strong correlation is found within the left PT, across participants ranging from completely illiterate to expert[8]. This may reflect a refinement in phonological awareness that is induced by alphabetic literacy. Data points represent the activation of the PT averaged across subjects in each of six groups of subjects of different levels of literacy, expressed as a percentage of the whole-brain BOLD signal (purple, blue and red coloured circles depict groups of illiterate, ex-illiterate and literate individuals, respectively, with lighter shades indicating higher reading ability). Axial and sagittal slices indicate the loci of peak correlation of BOLD activity with reading score. **b** | Letter–sound integration. Literate adults passively listened to and/or viewed unimodally or bimodally presented speech sounds and letters; bimodal stimuli were either congruent or incongruent. The PT does not respond to visual letters alone (green), but it becomes activated in response to spoken letters (red). Moreover, PT activation is greater in response to congruent (blue) than to incongruent (yellow) letter–sound pairs, suggesting it has a role in linking letters to sounds. **c** | Enhanced connectivity. The structural link between the visual orthographic (visual word form area; VWFA) and the auditory phonological (PT) systems becomes enhanced with literacy: there is an increase in fractional anisotropy (FA) in the posterior branch of the left arcuate fasciculus in literate and ex-illiterate relative to illiterate participants (left histogram). This increase in FA with literacy correlates with the activation of the PT in response to spoken sentences (right histogram). Error bars represent one standard error. *$p < 0.05$; **$p < 0.001$; r, Pearson's correlation coefficient. Part **a** is adapted from Dehaene, S. *et al.* How learning to read changes the cortical networks for vision and language. *Science* **330**, 1359–1364 (2010). Reprinted with permission from AAAS. Part **b** is adapted with permission from REF. 100, Elsevier. Part **c** is adapted from Thiebaut de Schotten, M., Cohen, L., Amemiya, E., Braga, L. W. & Dehaene, S. Learning to read improves the structure of the arcuate fasciculus. *Cereb. Cortex* (2012) **24** (4), 989–995, by permission of Oxford University Press.

Language-circuit anatomy

As literacy establishes a functional link between phonological and orthographic representations, one might expect that it should also lead to structural changes in the connections linking the corresponding areas. Indeed, recent studies have revealed changes in anatomical connectivity in literate compared with illiterate individuals.

First, literacy modifies the posterior temporoparietal portion of the left arcuate fasciculus (FIG. 2c) — a bundle of axons that putatively link the ventral temporal lobe (including the VWFA) with inferior parietal and posterior superior temporal regions (including the PT)[13]. In literate compared with illiterate individuals, the posterior arcuate shows an increase in fractional anisotropy[13], which is an MRI index of white-matter organization that may reflect improved fibre alignment and myelination. This anatomical change correlates with the degree of functional activation of the VWFA in response to letter strings and of the PT in response to speech[13]. This bundle may therefore participate in the development of the grapheme-to-phoneme conversion route, which is one of the key functions of literacy[129]. Indeed, the fractional anisotropy of the arcuate fasciculus changes during reading acquisition in children, in direct correlation with reading ability[59,130]. It is strongly correlated with phonological awareness in children[130], including 4- to 6-year-old pre-reading and early-reading kindergarten children[131]. Thus, the arcuate fasciculus may plausibly be considered as a central pathway for the fast transmission of letter and sound information during literacy acquisition.

Another change that is reliably induced by literacy is the thickening of the splenium and/or the isthmus of the corpus callosum[10,132,133]. This physical change is consistent with an enhanced inter-hemispheric transfer of phonological and/or visual information. Indeed, lesion studies have shown that these sectors of the corpus callosum are involved in the rapid integration of written information that appears in the left and right hemifields[26,134].

Literacy acquisition has also been reported to lead to increases in grey-matter density in several regions of the angular, supramarginal and temporal gyri, which are also activated during reading[10,132,133]. In one important study comparing two carefully matched groups of illiterate and ex-illiterate individuals[10], literacy was found to enhance the density of grey matter in the bilateral dorsal occipito-parietal region, bilateral middle temporal gyri and left supramarginal and superior temporal gyri. Connectivity data acquired from expert literate individuals suggest that these regions are anatomically interconnected via the splenium of the corpus callosum and are functionally correlated during reading. These areas are all thought to contribute to the conversion of letters into sound patterns[135,136], particularly during the early stages of reading acquisition[115,116,136]. Dorsal occipito-parietal regions are strongly activated during word naming compared with object naming[47], particularly when unschooled adults begin to acquire reading (that is, in ex-illiterate adults)[8]. In expert literate adults, posterior parietal regions exhibit higher activity when reading is made more difficult and requires a serial process of letter-by-letter processing (owing to unusual word orientation or letter spacing)[137]. These regions also activate when subjects attend to the fine-grained differences between two letter strings in which letters are transposed (for example, when deciding whether 'SJTD' and 'STJD' are different strings)[138]. Thus, these regions participate in an extended network for effortful letter-position coding and/or grapheme-to-phoneme conversion and may be among the first brain systems to change during literacy acquisition[136].

Beyond the language system

Literacy provides a unique means of acquiring and structuring new knowledge and is therefore likely to affect many aspects of higher-level cognition. However, such effects remain understudied. Only a few behavioural experiments have been carried out, and in many the effects of literacy are confounded by schooling. The absence of early schooling may indeed be the major factor explaining the often-reported reduced cognitive abilities of illiterate people. Owing to such caveats, here we touch only briefly on this area (for reviews, see REFS 139,140).

Within the semantic domain, literacy has a major impact on semantic fluency tasks: when cued to generate, for instance, animal names, illiterate individuals list a much smaller number of words than do early-literate individuals[141–143], and a similar difference exists between pre-literate children and age-matched 6- to 13-year-old reading beginners[144]. This effect, however, may not reflect a distinct semantic organization, but merely the absence of graphotactic cues and strategies or knowledge learned at school[143].

Regarding the executive attention system, preliminary data[143,145] suggest that there is a general effect of schooling — but not of literacy — on the ability to plan and organize behaviour, inhibit irrelevant information, selectively attend to one stimulus dimension (such as size or colour) or shift between alternative dimensions[143]. Literacy may have a more specific impact on complex working-memory tasks such as listening span (in which listeners have to retain the final word of each of several sentences), but not in simpler tasks, such as backward digit span, in which a memorized list of digits must be recited backwards[127,143].

In the 1970s, Goody and Luria proposed that literacy is a prerequisite for syllogism resolution[146,147]. However, illiterate adults are relatively good at solving syllogisms that are based on familiar information[148] and, when given the instruction to think of unfamiliar syllogistic premises as pertaining to a distant planet, can set aside empirical considerations and reason appropriately[149]. It is also formal education, rather than literacy *per se*, that influences performance on 'intelligence' tests[150]. After a 1-year alphabetization course[151], adults who were initially almost illiterate showed an improvement in 'crystallized' intelligence (the ability to use skills, knowledge and experience) but not in 'fluid' intelligence (the capacity to think logically and solve problems in new situations independently of acquired knowledge).

Conclusion

Given the evidence discussed above, we reach a conclusion that literacy affects brain organization primarily by creating and automating an efficient interface between vision and language. This broad change is mediated by a reorganization of the left VOT (the VWFA). Its putative afferents (the bilateral occipital visual cortices) and its putative efferents (the left superior temporal regions, such as the PT for phonological analysis) are also enhanced. Finally, an extended network of surrounding temporal and occipito-parietal areas is also improved, particularly when effortful grapheme-to-phoneme conversion is called for. Anatomically, the physical connections among these areas — notably, the posterior corpus callosum and left arcuate — are changed in a detectable manner. Functionally, these changes result in fluid, bidirectional interactions between the internal representations of written symbols and spoken language.

Although we suspect that future studies may discover additional changes associated with the acquisition of literacy — particularly in anterior temporal circuits for lexical meaning and syntax — at present, the main observed change concerns the grapheme-to-phoneme conversion pathway. This finding corresponds with educational research that indicates that focused training in phonics is the most efficient strategy for reading education, particularly for children with poor phonological abilities and even in non-transparent orthographies such as English[33,152]. In the future, carefully monitoring the brain changes induced by literacy (including the left-lateralized N170 component[29], the VWFA response[31], the anisotropy of the arcuate fasciculus[153] and perhaps other biological measures of visual-cortex organization[154]) may lead to the development of efficient biomarkers to assess the progress of reading acquisition in normal and impaired children.

Stanislas Dehaene is at the Collège de France, 11 Place Marcelin Berthelot, 75005 Paris, France; INSERM, Cognitive Neuroimaging Unit, NeuroSpin Center, Gif sur Yvette 91191, France; Commissariat à l'Energie Atomique, Direction des Sciences du Vivant, I2BM, Neurospin Center, Gif sur Yvette 91191, France; and Université Paris-Sud 11, 91405 Orsay, France.

Laurent Cohen is at the Institut du Cerveau et de la Moelle épinière, ICM, F-75013 Paris, France; INSERM, U 1127, F-75013 Paris, France; Sorbonne Universités, UPMC Université Paris 06, UMR S 1127, F-75013 Paris, France; CNRS, UMR 7225, F-75013 Paris, France; and the Assistance Publique Hôpitaux de Paris (AP-HP) Hôpital de la Pitié Salpêtrière, Department of Neurology, F-75013 Paris, France.

José Morais is at the Unité de Recherche en Neurosciences Cognitives (UNESCOG), Center for Research in Cognition and Neurosciences (CRCN), Université Libre de Bruxelles (ULB), CP 191, Avenue F. Roosevelt, 50, B-1050 Brussels, Belgium.

Régine Kolinsky is at the Unité de Recherche en Neurosciences Cognitives (UNESCOG), Center for Research in Cognition and Neurosciences (CRCN), Université Libre de Bruxelles (ULB), CP 191, Avenue F. Roosevelt, 50, B-1050 Brussels, Belgium; and the Fonds de la Recherche Scientifique-FNRS, Rue d'Egmont, 5, B-1000 Brussels, Belgium.

Correspondence to S.D.
e-mail: stanislas.dehaene@cea.fr

doi:10.1038/nrn3924

1. Lincoln, A. *Discoveries and Inventions: A Lecture by Abraham Lincoln Delivered in 1860* (Kessinger Publishing, 2004).
2. Ong, W. *Orality and Literacy: 30th Anniversary Edition* (Routledge, 2012).
3. Dehaene, S. & Cohen, L. The unique role of the visual word form area in reading. *Trends Cogn. Sci.* **15**, 254–262 (2011).
4. Carreiras, M., Armstrong, B. C., Perea, M. & Frost, R. The what, when, where and how of visual word recognition. *Trends Cogn. Sci.* **18**, 90–98 (2014).
5. Pugh, K. R. *et al.* The relationship between phonological and auditory processing and brain organization in beginning readers. *Brain Lang.* **125**, 173–183 (2013).
6. Turkeltaub, P. E., Gareau, L., Flowers, D. L., Zeffiro, T. A. & Eden, G. F. Development of neural mechanisms for reading. *Nature Neurosci.* **6**, 767–773 (2003).
7. New, B., Ferrand, L., Pallier, C. & Brysbaert, M. Reexamining the word length effect in visual word recognition: new evidence from the English Lexicon Project. *Psychon Bull. Rev.* **13**, 45–52 (2006).
8. Dehaene, S. *et al.* How learning to read changes the cortical networks for vision and language. *Science* **330**, 1359–1364 (2010).
9. Pegado, F. *et al.* Timing the impact of literacy on visual processing. *Proc. Natl Acad. Sci. USA* **111**, E5233–E5242 (2014).
10. Carreiras, M. *et al.* An anatomical signature for literacy. *Nature* **461**, 983–986 (2009).
11. Kolinsky, R. *et al.* Enantiomorphy through the looking-glass: literacy effects on mirror-image discrimination. *J. Exp. Psychol. Gen.* **140**, 210–238 (2011).
12. Szwed, M., Ventura, P., Querido, L., Cohen, L. & Dehaene, S. Reading acquisition enhances an early visual process of contour integration. *Dev. Sci.* **15**, 139–149 (2012).
13. Thiebaut de Schotten, M., Cohen, L., Amemiya, E., Braga, L. W. & Dehaene, S. Learning to read improves the structure of the arcuate fasciculus. *Cereb. Cortex* **24**, 989–995 (2012).
14. Dehaene, S. & Cohen, L. Cultural recycling of cortical maps. *Neuron* **56**, 384–398 (2007).
15. Nazir, T. A., Ben-Boutayab, N., Decoppet, N., Deutsch, A. & Frost, R. Reading habits, perceptual learning, and recognition of printed words. *Brain Lang.* **88**, 294–311 (2004).
16. Li, W., Piech, V. & Gilbert, C. D. Perceptual learning and top-down influences in primary visual cortex. *Nature Neurosci.* **7**, 651–657 (2004).
17. Li, W., Piech, V. & Gilbert, C. D. Learning to link visual contours. *Neuron* **57**, 442–451 (2008).
18. Sigman, M. *et al.* Top-down reorganization of activity in the visual pathway after learning a shape identification task. *Neuron* **46**, 823–835 (2005).
19. Legge, G. E. & Bigelow, C. A. Does print size matter for reading? A review of findings from vision science and typography. *J. Vis.* **11**, 8 (2011).
20. Szwed, M. *et al.* Specialization for written words over objects in the visual cortex. *NeuroImage* **56**, 330–344 (2011).
21. Szwed, M., Qiao, E., Jobert, A., Dehaene, S. & Cohen, L. Effects of literacy in early visual and occipitotemporal areas of Chinese and French readers. *J. Cogn. Neurosci.* **26**, 459–475 (2014).
22. Ventura, P. *et al.* Literacy acquisition reduces the influence of automatic holistic processing of faces and houses. *Neurosci. Lett.* **554**, 105–109 (2013).
23. Duñabeitia, J. A., Orihuela, K. & Carreiras, M. Orthographic coding in illiterates and literates. *Psychol. Sci.* **25**, 1275–1280 (2014).
24. Bolger, D. J., Perfetti, C. A. & Schneider, W. Cross-cultural effect on the brain revisited: universal structures plus writing system variation. *Hum. Brain Mapp.* **25**, 92–104 (2005).
25. Hasson, U., Levy, I., Behrmann, M., Hendler, T. & Malach, R. Eccentricity bias as an organizing principle for human high-order object areas. *Neuron* **34**, 479–490 (2002).
26. Cohen, L. *et al.* 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 (2000).
27. Dehaene, S. *et al.* The visual word form area: a prelexical representation of visual words in the fusiform gyrus. *Neuroreport* **13**, 321–325 (2002).
28. Baker, C. I. *et al.* Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proc. Natl Acad. Sci. USA* **104**, 9087–9092 (2007).
29. Brem, S. *et al.* An electrophysiological study of print processing in kindergarten: the contribution of the visual n1 as a predictor of reading outcome. *Dev. Neuropsychol.* **38**, 567–594 (2013).
30. Maurer, U., Brem, S., Bucher, K. & Brandeis, D. Emerging neurophysiological specialization for letter strings. *J. Cogn Neurosci.* **17**, 1532–1552 (2005).
31. Monzalvo, K., Fluss, J., Billard, C., Dehaene, S. & Dehaene-Lambertz, G. Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status. *NeuroImage* **61**, 258–274 (2012).
32. Monzalvo, K. *Etude chez l'enfant normal et dyslexique de l'impact sur les réseaux corticaux et linguistiques d'une activité culturelle: la lecture.* Thesis, Univ. Paris, (2011).
33. Brem, S. *et al.* Brain sensitivity to print emerges when children learn letter-speech sound correspondences. *Proc. Natl Acad. Sci. USA* **107**, 7939–7944 (2010).
34. Hashimoto, R. & Sakai, K. L. Learning letters in adulthood: direct visualization of cortical plasticity for forming a new link between orthography and phonology. *Neuron* **42**, 311–322 (2004).
35. Perrone-Bertolotti, M. *et al.* Turning visual shapes into sounds: early stages of reading acquisition revealed in the ventral occipitotemporal cortex. *NeuroImage* **90**, 298–307 (2014).
36. Xue, G., Chen, C., Jin, Z. & Dong, Q. Language experience shapes fusiform activation when processing a logographic artificial language: an fMRI training study. *NeuroImage* **31**, 1315–1326 (2006).
37. Mei, L. *et al.* Orthographic transparency modulates the functional asymmetry in the fusiform cortex: an artificial language training study. *Brain Lang.* **125**, 165–172 (2013).
38. Dehaene, S. *et al.* Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neurosci.* **4**, 752–758 (2001).
39. Price, C. J. & Devlin, J. T. The interactive account of ventral occipitotemporal contributions to reading. *Trends Cogn. Sci.* **15**, 246–253 (2011).
40. Freiwald, W. A. & Tsao, D. Y. Functional compartmentalization and viewpoint generalization within the macaque face-processing system. *Science* **330**, 845–851 (2010).
41. Dehaene, S., Cohen, L., Sigman, M. & Vinckier, F. The neural code for written words: a proposal. *Trends Cogn. Sci.* **9**, 335–341 (2005).
42. Vinckier, F. *et al.* Hierarchical coding of letter strings in the ventral stream: dissecting the inner organization of the visual word-form system. *Neuron* **55**, 143–156 (2007).
43. Thesen, T. *et al.* Sequential then interactive processing of letters and words in the left fusiform gyrus. *Nature Commun.* **3**, 1284 (2012).
44. Dehaene, S. *et al.* Letter binding and invariant recognition of masked words: behavioral and neuroimaging evidence. *Psychol. Sci.* **15**, 307–313 (2004).
45. Binder, J. R., Medler, D. A., Westbury, C. F., Liebenthal, E. & Buchanan, L. Tuning of the human left fusiform gyrus to sublexical orthographic structure. *NeuroImage* **33**, 739–748 (2006).
46. Glezer, L. S., Jiang, X. & Riesenhuber, M. Evidence for highly selective neuronal tuning to whole words in the 'visual word form area'. *Neuron* **62**, 199–204 (2009).
47. Taylor, J. S. H., Rastle, K. & Davis, M. H. Distinct neural specializations for learning to read words and name objects. *J. Cogn. Neurosci.* **26**, 2128–2154 (2014).
48. Kherif, F., Josse, G. & Price, C. J. Automatic top-down processing explains common left occipito-temporal responses to visual words and objects. *Cereb. Cortex* **21**, 103–114 (2010).
49. Mano, Q. R. *et al.* The role of left occipitotemporal cortex in reading: reconciling stimulus, task, and lexicality effects. *Cereb. Cortex* **23**, 988–1001 (2013).
50. Yoncheva, Y. N., Zevin, J. D., Maurer, U. & McCandliss, B. D. Auditory selective attention to speech modulates activity in the visual word form area. *Cereb. Cortex* **20**, 622–632 (2010).
51. Rothlein, D. & Rapp, B. The similarity structure of distributed neural responses reveals the multiple representations of letters. *NeuroImage* **89**, 331–344 (2014).
52. Reich, L., Szwed, M., Cohen, L. & Amedi, A. A ventral visual stream reading center independent of visual experience. *Curr. Biol.* **21**, 363–368 (2011).
53. Buchel, C., Price, C. & Friston, K. A multimodal language region in the ventral visual pathway. *Nature* **394**, 274–277 (1998).
54. Striem-Amit, E., Cohen, L., Dehaene, S. & Amedi, A. Reading with sounds: sensory substitution selectively activates the visual word form area in the blind. *Neuron* **76**, 640–652 (2012).
55. Striem-Amit, E. & Amedi, A. Visual cortex extrastriate body-selective area activation in congenitally blind people 'seeing' by using sounds. *Curr. Biol.* **24**, 687–692 (2014).
56. Striem-Amit, E., Dakwar, O., Reich, L. & Amedi, A. The large-scale organization of 'visual' streams emerges without visual experience. *Cereb. Cortex* **22**, 1698–1709 (2012).
57. Wandell, B. A. & Yeatman, J. D. Biological development of reading circuits. *Curr. Opin. Neurobiol.* **23**, 261–268 (2013).
58. Bouhali, F. *et al.* Anatomical connections of the visual word form area. *J. Neurosci.* **34**, 15402–15414 (2014).
59. Yeatman, J. D., Dougherty, R. F., Ben-Shachar, M. & Wandell, B. A. Development of white matter and reading skills. *Proc. Natl Acad. Sci. USA* **109**, E3045–E3053 (2012).
60. Pinel, P. & Dehaene, S. Beyond hemispheric dominance: brain regions underlying the joint lateralization of language and arithmetic to the left hemisphere. *J. Cogn. Neurosci.* **22**, 48–66 (2009).

61. Cai, Q., Paulignan, Y., Brysbaert, M., Ibarrola, D. & Nazir, T. A. The left ventral occipito-temporal response to words depends on language lateralization but not on visual familiarity. *Cereb. Cortex* **20**, 1153–1163 (2010).
62. Allison, T., McCarthy, G., Nobre, A. C., Puce, A. & Belger, A. Human extrastriate visual cortex and the perception of faces, words, numbers and colors. *Cereb. Cortex* **5**, 544–554 (1994).
63. Nestor, A., Plaut, D. C. & Behrmann, M. Unraveling the distributed neural code of facial identity through spatiotemporal pattern analysis. *Proc. Natl Acad. Sci. USA* **108**, 9998–10003 (2011).
64. Puce, A., Allison, T., Asgari, M., Gore, J. C. & McCarthy, G. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *J. Neurosci.* **16**, 5205–5215 (1996).
65. Li, S. *et al.* Neural competition as a developmental process: early hemispheric specialization for word processing delays specialization for face processing. *Neuropsychologia* **5**, 950–959 (2013).
66. Pinel, P. *et al.* Genetic and environmental influences on the visual word form and fusiform face areas. *Cereb. Cortex* http://dx.doi.org/10.1093/cercor/bhu048 (2014).
67. Dundas, E. M., Plaut, D. C. & Behrmann, M. The joint development of hemispheric lateralization for words and faces. *J. Exp. Psychol. Gen.* **142**, 348–358 (2013).
68. Cantlon, J. F., Pinel, P., Dehaene, S. & Pelphrey, K. A. Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cereb. Cortex* **21**, 191–199 (2011).
69. Golarai, G. *et al.* Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neurosci.* **10**, 512–522 (2007).
70. Scherf, K. S., Luna, B., Avidan, G. & Behrmann, M. 'What' precedes 'which': developmental neural tuning in face- and place-related cortex. *Cereb. Cortex* **21**, 1963–1980 (2011).
71. Dehaene, S. *Reading in the Brain* (Penguin Viking, 2009).
72. Weiner, K. S. *et al.* The mid-fusiform sulcus: a landmark identifying both cytoarchitectonic and functional divisions of human ventral temporal cortex. *NeuroImage* **84**, 453–465 (2014).
73. Grill-Spector, K. & Weiner, K. S. The functional architecture of the ventral temporal cortex and its role in categorization. *Nature Rev. Neurosci.* **15**, 536–548 (2014).
74. Rollenhagen, J. E. & Olson, C. R. Mirror-image confusion in single neurons of the macaque inferotemporal cortex. *Science* **287**, 1506–1508 (2000).
75. Axelrod, V. & Yovel, G. Hierarchical processing of face viewpoint in human visual cortex. *J. Neurosci.* **32**, 2442–2452 (2012).
76. Kietzmann, T. C., Swisher, J. D., Konig, P. & Tong, F. Prevalence of selectivity for mirror-symmetric views of faces in the ventral and dorsal visual pathways. *J. Neurosci.* **32**, 11763–11772 (2012).
77. Logothetis, N. K., Pauls, J. & Poggio, T. Shape representation in the inferior temporal cortex of monkeys. *Curr. Biol.* **5**, 552–563 (1995).
78. Dehaene, S. *et al.* Why do children make mirror errors in reading? Neural correlates of mirror invariance in the visual word form area. *NeuroImage* **49**, 1837–1848 (2010).
79. Dilks, D. D., Julian, J. B., Kubilius, J., Spelke, E. S. & Kanwisher, N. Mirror-image sensitivity and invariance in object and scene processing pathways. *J. Neurosci.* **31**, 11305–11312 (2011).
80. Eger, E., Henson, R. N., Driver, J. & Dolan, R. J. BOLD repetition decreases in object-responsive ventral visual areas depend on spatial attention. *J. Neurophysiol.* **92**, 1241–1247 (2004).
81. Pegado, F., Nakamura, K., Cohen, L. & Dehaene, S. Breaking the symmetry: mirror discrimination for single letters but not for pictures in the visual word form area. *NeuroImage* **55**, 742–749 (2011).
82. Vuilleumier, P., Schwartz, S., Duhoux, S., Dolan, R. J. & Driver, J. Selective attention modulates neural substrates of repetition priming and 'implicit' visual memory: suppressions and enhancements revealed by fMRI. *J. Cogn. Neurosci.* **17**, 1245–1260 (2005).
83. Pegado, F. *et al.* Literacy breaks mirror invariance for visual stimuli: a behavioral study with adult illiterates. *J. Exp. Psychol. Gen.* **143**, 887–894 (2014).
84. Kolinsky, R. & Fernandes, T. A cultural side effect: learning to read interferes with identity processing of familiar objects. *Front. Psychol.* **5**, 1224 (2014).
85. Danziger, E. & Pederson, E. Through the looking glass: literacy, writing systems and mirror-image discrimination. *Writ. Lang. Lit.* **1**, 153–167 (1998).
86. Fernandes, T. & Kolinsky, R. From hand to eye: the role of literacy, familiarity, graspability, and vision-for-action on enantiomorphy. *Acta Psychol. (Amst.)* **142**, 51–61 (2013).
87. Duñabeitia, J. A., Molinaro, N. & Carreiras, M. Through the looking-glass: mirror reading. *NeuroImage* **54**, 3004–3009 (2011).
88. Perea, M., Moret-Tatay, C. & Panadero, V. Suppression of mirror generalization for reversible letters: evidence from masked priming. *J. Mem. Lang.* **65**, 237–246 (2011).
89. Dehaene, S., Izard, V., Pica, P. & Spelke, E. Core knowledge of geometry in an Amazonian indigene group. *Science* **311**, 381–384 (2006).
90. Duñabeitia, J. A., Dimitropoulou, M., Estévez, A. & Carreiras, M. The influence of reading expertise in mirror-letter perception: evidence from beginning and expert readers. *Mind Brain Educ.* **7**, 124–135 (2013).
91. Kolinsky, R., Morais, J. & Verhaeghe, A. Visual separability: a study on unschooled adults. *Perception* **23**, 471–486 (1994).
92. Vagharchakian, L., Dehaene-Lambertz, G., Pallier, C. & Dehaene, S. A temporal bottleneck in the language comprehension network. *J. Neurosci.* **32**, 9089–9102 (2012).
93. Castro-Caldas, A., Petersson, K. M., Reis, A., Stone-Elander, S. & Ingvar, M. The illiterate brain. Learning to read and write during childhood influences the functional organization of the adult brain. *Brain* **121**, 1053–1063 (1998).
94. Nation, K. & Hulme, C. Learning to read changes children's phonological skills: evidence from a latent variable longitudinal study of reading and nonword repetition. *Dev. Sci.* **14**, 649–659 (2011).
95. Monzalvo, K. & Dehaene-Lambertz, G. How reading acquisition changes children's spoken language network. *Brain Lang.* **127**, 356–365 (2013).
96. Chang, E. F. *et al.* Categorical speech representation in human superior temporal gyrus. *Nature Neurosci.* **13**, 1428–1432 (2010).
97. Mesgarani, N., Cheung, C., Johnson, K. & Chang, E. F. Phonetic feature encoding in human superior temporal gyrus. *Science* **343**, 1006–1010 (2014).
98. Jacquemot, C., Pallier, C., LeBihan, D., Dehaene, S. & Dupoux, E. Phonological grammar shapes the auditory cortex: a functional magnetic resonance imaging study. *J. Neurosci.* **23**, 9541–9546 (2003).
99. Calvert, G. A. *et al.* Activation of auditory cortex during silent lipreading. *Science* **276**, 593–596 (1997).
100. Van Atteveldt, N., Formisano, E., Goebel, R. & Blomert, L. Integration of letters and speech sounds in the human brain. *Neuron* **43**, 271–282 (2004).
101. Blau, V., van Atteveldt, N., Ekkebus, M., Goebel, R. & Blomert, L. Reduced neural integration of letters and speech sounds links phonological and reading deficits in adult dyslexia. *Curr. Biol.* **19**, 503–508 (2009).
102. Liberman, I. Y., Shankweiler, D., Fischer, F. W. & Carter, B. Explicit syllable and phoneme segmentation in the young child. *J. Exp. Child Psychol.* **18**, 201–212 (1974).
103. Morais, J., Cary, L., Alegria, J. & Bertelson, P. Does awareness of speech as a sequence of phones arise spontaneously? *Cognition* **7**, 323–331 (1979).
104. Lukatela, K., Carello, C., Shankweiler, D. & Liberman, I. Y. Phonological awareness in illiterates: observations from Serbo-Croatian. *Appl. Psycholinguist.* **16**, 463–488 (1995).
105. Adrian, A., Alegria, J. & Morais, J. Metaphonological abilities of Spanish illiterate adults. *Int. J. Psychol.* **30**, 329–351 (1995).
106. Serniclaes, W., Ventura, P., Morais, J. & Kolinsky, R. Categorical perception of speech sounds in illiterate adults. *Cognition* **98**, B35–B44 (2005).
107. Ventura, P., Kolinsky, R., Fernandes, S., Querido, L. & Morais, J. Lexical restructuring in the absence of literacy. *Cognition* **105**, 334–361 (2007).
108. Morais, J. & Kolinsky, R. Perception and awareness in phonological processing: the case of the phoneme. *Cognition* **50**, 287–297 (1994).
109. Ventura, P., Kolinsky, R., Querido, J.-L., Fernandes, S. & Morais, J. Is phonological encoding in naming influenced by literacy? *J. Psycholinguist. Res.* **36**, 341–360 (2007).
110. Burton, M. W., Small, S. L. & Blumstein, S. E. The role of segmentation in phonological processing: an fMRI investigation. *J. Cogn. Neurosci.* **12**, 679–690 (2000).
111. Zatorre, R. J., Meyer, E., Gjedde, A. & Evans, A. C. PET studies of phonetic processing of speech: review, replication, and reanalysis. *Cereb. Cortex* **6**, 21–30 (1996).
112. Brennan, C., Cao, F., Pedroarena-Leal, N., McNorgan, C. & Booth, J. R. Reading acquisition reorganizes the phonological awareness network only in alphabetic writing systems. *Hum. Brain Mapp.* **34**, 3354–3368 (2013).
113. Booth, J. R. *et al.* Functional anatomy of intra- and cross-modal lexical tasks. *NeuroImage* **16**, 7–22 (2002).
114. Cohen, L., Jobert, A., Le Bihan, D. & Dehaene, S. Distinct unimodal and multimodal regions for word processing in the left temporal cortex. *NeuroImage* **23**, 1256–1270 (2004).
115. Booth, J. R. *et al.* Development of brain mechanisms for processing orthographic and phonologic representations. *J. Cogn. Neurosci.* **16**, 1234–1249 (2004).
116. Cone, N. E., Burman, D. D., Bitan, T., Bolger, D. J. & Booth, J. R. Developmental changes in brain regions involved in phonological and orthographic processing during spoken language processing. *NeuroImage* **41**, 623–635 (2008).
117. Desroches, A. S. *et al.* Children with reading difficulties show differences in brain regions associated with orthographic processing during spoken language processing. *Brain Res.* **1356**, 73–84 (2010).
118. Burton, M. W., Locasto, P. C., Krebs-Noble, D. & Gullapalli, R. P. A systematic investigation of the functional neuroanatomy of auditory and visual phonological processing. *NeuroImage* **26**, 647–661 (2005).
119. Seidenberg, M. S. & Tanenhaus, M. K. Orthographic effects on rhyme monitoring. *Q. J. Exp. Psychol. (Hove)* **5**, 546–554 (1979).
120. Pattamadilok, C., Perre, L., Dufau, S. & Ziegler, J. C. On-line orthographic influences on spoken language in a semantic task. *J. Cogn. Neurosci.* **21**, 169–179 (2009).
121. Peereman, R., Dufour, S. & Burt, J. S. Orthographic influences in spoken word recognition: the consistency effect in semantic and gender categorization tasks. *Psychon. Bull. Rev.* **16**, 363–368 (2009).
122. Ziegler, J. C. & Ferrand, L. Orthography shapes the perception of speech: the consistency effect in auditory word recognition. *Psychon. Bull. Rev.* **5**, 683–689 (1998).
123. Perre, L. & Ziegler, J. C. On-line activation of orthography in spoken word recognition. *Brain Res.* **1188**, 132–138 (2008).
124. Perre, L., Pattamadilok, C., Montant, M. & Ziegler, J. C. Orthographic effects in spoken language: on-line activation or phonological restructuring? *Brain Res.* **1275**, 73–80 (2009).
125. Pattamadilok, C., Knierim, I. N., Kawabata Duncan, K. J. & Devlin, J. T. How does learning to read affect speech perception? *J. Neurosci.* **30**, 8435–8444 (2010).
126. Morais, J., Bertelson, P., Cary, L. & Alegria, J. Literacy training and speech segmentation. *Cognition* **24**, 45–64 (1986).
127. Kosmidis, M. H., Zafiri, M. & Politimou, N. Literacy versus formal schooling: influence on working memory. *Arch. Clin. Neuropsychol.* **26**, 575–582 (2011).
128. Pattamadilok, C., Lafontaine, H., Morais, J. & Kolinsky, R. Auditory word serial recall benefits from orthographic dissimilarity. *Lang. Speech* **53**, 321–341 (2010).
129. Share, D. L. Phonological recoding and self-teaching: *sine qua non* of reading acquisition. *Cognition* **55**, 151–218; discussion 219–226 (1995).
130. Yeatman, J. D. *et al.* Anatomical properties of the arcuate fasciculus predict phonological and reading skills in children. *J. Cogn. Neurosci.* **23**, 3304–3317 (2011).
131. Saygin, Z. M. *et al.* Tracking the roots of reading ability: white matter volume and integrity correlate with phonological awareness in prereading and early-reading kindergarten children. *J. Neurosci.* **33**, 13251–13258 (2013).
132. Castro-Caldas, A. *et al.* Influence of learning to read and write on the morphology of the corpus callosum. *Eur. J. Neurol.* **6**, 23–28 (1999).

133. Petersson, K. M., Silva, C., Castro-Caldas, A., Ingvar, M. & Reis, A. Literacy: a cultural influence on functional left–right differences in the inferior parietal cortex. *Eur. J. Neurosci.* **26**, 791–799 (2007).
134. Molko, N. *et al.* Visualizing the neural bases of a disconnection syndrome with diffusion tensor imaging. *J. Cogn. Neurosci.* **14**, 629–636 (2002).
135. Taylor, J. S. H., Rastle, K. & Davis, M. H. Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. *Psychol. Bull.* **139**, 766–791 (2013).
136. Pugh, K. R. *et al.* Neurobiological studies of reading and reading disability. *J. Commun. Disord.* **34**, 479–492 (2001).
137. Cohen, L., Dehaene, S., Vinckier, F., Jobert, A. & Montavont, A. Reading normal and degraded words: contribution of the dorsal and ventral visual pathways. *NeuroImage* **40**, 353–366 (2008).
138. Carreiras, M., Quiñones, I., Hernández-Cabrera, J. A. & Duñabeitia, J. A. Orthographic coding: brain activation for letters, symbols, and digits. *Cereb. Cortex* http://dx.doi.org/10.1093/cercor/bhu163 (2014).
139. Huettig, F. & Mishra, R. K. How literacy acquisition affects the illiterate mind – a critical examination of theories and evidence. *Lang. Linguist. Compass* **8**, 401–427 (2014).
140. Kolinsky, R. in *The Oxford Handbook of Reading* (eds Pollatsek, A. & Treiman, R.) (Oxford Univ. Press, 2014).
141. Ratcliff, G. *et al.* Effects of literacy and education on measures of word fluency. *Brain Lang.* **61**, 115–122 (1998).
142. Reis, A. & Castro-Caldas, A. Illiteracy: a cause for biased cognitive development. *J. Int. Neuropsychol. Soc.* **3**, 444–450 (1997).
143. Kolinsky, R. *et al.* How formal education and literacy impact on the content and structure of semantic categories. *Trends Neurosci. Educ.* **3**, 106–121 (2014).
144. Matute, E. *et al.* Comparing cognitive performance in illiterate and literate children. *Int. Rev. Educ.* **58**, 109–127 (2012).
145. Morais, J. & Kolinsky, R. in *Psychology at the Turn of the Millennium* (eds Bäckman, L. & von Hofsten, C.) 507–530 (Psychology Press, 2002).
146. Goody, J. *Literacy in Traditional Societies* (Cambridge Univ. Press, 1968).
147. Luria, A. R. *Cognitive Development. Its Cultural and Social Foundations* (Harvard Univ. Press, 1976).
148. Scribner, S. & Cole, M. *The Psychology of Literacy* (Harvard Univ. Press, 1981).
149. Dias, M., Roazzi, A. & Harris, P. L. Reasoning from unfamiliar premises: a study with unschooled adults. *Psychol. Sci.* **16**, 550–554 (2005).
150. Verhaeghe, A. & Kolinsky, R. *What Illiterate People Teach us about Intelligence Tests* (Fund Gulbenkian-FCT, 2006) (in Portuguese).
151. Landgraf, S. Dissociating improvement of attention and intelligence during written language acquisition in adults. *Int. J. Intell. Sci.* **1**, 17–24 (2011).
152. National Institute of Child Health and Human Development. *Report of the National Reading Panel. Teaching Children to Read: An Evidence-Based Assessment of the Scientific Research Literature on Reading and Its Implications for Reading Instruction*. NIH Publication No. 00–4769 (US Government Printing Office, 2000).
153. Hoeft, F. *et al.* Neural systems predicting long-term outcome in dyslexia. *Proc. Natl Acad. Sci. USA* **108**, 361–366 (2011).
154. Pugh, K. R. *et al.* Glutamate and choline levels predict individual differences in reading ability in emergent readers. *J. Neurosci.* **34**, 4082–4089 (2014).
155. Srihasam, K., Mandeville, J. B., Morocz, I. A., Sullivan, K. J. & Livingstone, M. S. Behavioral and anatomical consequences of early versus late symbol training in macaques. *Neuron* **73**, 608–619 (2012).
156. Fernandes, T., Vale, A. P., Martins, B., Morais, J. & Kolinsky, R. The deficit of letter processing in developmental dyslexia: combining evidence from dyslexics, typical readers and illiterate adults. *Dev. Sci.* **17**, 125–141 (2014).
157. DeFrancis, J. *Visible Speech: The Diverse Oneness of Writing Systems* (Univ. of Hawaii, 1989).
158. Nakamura, K. *et al.* Universal brain systems for recognizing word shapes and handwriting gestures during reading. *Proc. Natl Acad. Sci. USA* **109**, 20762–20767 (2012).
159. Nakamura, K., Dehaene, S., Jobert, A., Le Bihan, D. & Kouider, S. Subliminal convergence of Kanji and Kana words: further evidence for functional parcellation of the posterior temporal cortex in visual word perception. *J. Cogn. Neurosci.* **17**, 954–968 (2005).
160. Lee, C. Y. *et al.* Neuronal correlates of consistency and frequency effects on Chinese character naming: an event-related fMRI study. *NeuroImage* **23**, 1235–1245 (2004).
161. Wu, C. Y., Ho, M. H. & Chen, S. H. A meta-analysis of fMRI studies on Chinese orthographic, phonological, and semantic processing. *NeuroImage* **63**, 381–391 (2012).
162. Frost, R. Towards a universal model of reading. *Behav. Brain Sci.* **35**, 263–279 (2012).
163. Yoncheva, Y. N., Blau, V. C., Maurer, U. & McCandliss, B. D. Attentional focus during learning impacts N170 ERP responses to an artificial script. *Dev. Neuropsychol.* **35**, 423–445 (2010).
164. Velan, H. & Frost, R. Letter-transposition effects are not universal: the impact of transposing letters in Hebrew. *J. Mem. Lang.* **61**, 285–302 (2009).
165. Bick, A. S., Goelman, G. & Frost, R. Hebrew brain versus English brain: language modulates the way it is processed. *J. Cogn. Neurosci.* **23**, 2280–2290 (2011).
166. Seymour, P. H., Aro, M. & Erskine, J. M. Foundation literacy acquisition in European orthographies. *Br. J. Psychol.* **94**, 143–174 (2003).
167. Paulesu, E. *et al.* A cultural effect on brain function. *Nature Neurosci.* **3**, 91–96 (2000).
168. Cheung, H., Chen, H. C., Lai, C. Y., Wong, O. C. & Hills, M. The development of phonological awareness: effects of spoken language experience and orthography. *Cognition* **81**, 227–241 (2001).
169. Cheung, H. & Chen, H. C. Early orthographic experience modifies both phonological awareness and on-line speech processing. *Lang. Cogn. Process.* **19**, 1–28 (2004).
170. Read, C., Zhang, Y. F., Nie, H. Y. & Ding, B. Q. The ability to manipulate speech sounds depends on knowing alphabetic writing. *Cognition* **24**, 31–44 (1986).
171. Tan, L. H., Laird, A. R., Li, K. & Fox, P. T. Neuroanatomical correlates of phonological processing of Chinese characters and alphabetic words: a meta-analysis. *Hum. Brain Mapp.* **25**, 83–91 (2005).
172. Bara, F., Gentaz, E., Colé, P. & Sprenger-Charolles, L. The visuo-haptic and haptic exploration of letters increases the kindergarten-children's understanding of the alphabetic principle. *Cogn. Dev.* **19**, 433–449 (2004).
173. James, K. H. Sensori-motor experience leads to changes in visual processing in the developing brain. *Dev. Sci.* **13**, 279–288 (2010).
174. Longcamp, M. *et al.* Learning through hand- or typewriting influences visual recognition of new graphic shapes: behavioral and functional imaging evidence. *J. Cogn. Neurosci.* **20**, 802–815 (2008).
175. Tan, L. H., Spinks, J. A., Eden, G. F., Perfetti, C. A. & Siok, W. T. Reading depends on writing, in Chinese. *Proc. Natl Acad. Sci. USA* **102**, 8781–8785 (2005).
176. Abadzi, H. Can adults become fluent readers in newly learned scripts? *Educ. Res. Int.* **2012**, 1–8 (2012).
177. Wilhelm, I. *et al.* The sleeping child outplays the adult's capacity to convert implicit into explicit knowledge. *Nature Neurosci.* **16**, 391–393 (2013).
178. Dehaene-Lambertz, G., Dehaene, S. & Hertz-Pannier, L. Functional neuroimaging of speech perception in infants. *Science* **298**, 2013–2015 (2002).

Acknowledgements

This work was supported by the French Institut National de la Santé et de la Recherche Médicale (INSERM), the French Commissariat à l'Energie Atomique (CEA), the Collège de France, an Agence Nationale de la Recherche grant to S.D. and L.C. (project CoreLex), the Fonds de la Recherche Scientifique-FNRS (FRS-FNRS, grant FRFC 2.4515.12) and an Interuniversity Attraction Poles (IAP) grant 7/33, Belspo to R.K.

Competing interests statement

The authors declare no competing interests.