The neural basis of reading acquisition

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Unlike language, reading is not one of those “natural” human skills that may have evolved under the pressure of natural selection. Rather, like tennis or chess, it is a recent cultural invention (about 5000 years), and one that puts considerable demands to our cognitive system. Nevertheless, in societies where reading is taught systematically, it is acquired early on by most children, who go on to mastering it to a high degree of skill. Those who fail to do so (“dyslexics”) pose major issues of social integration.

As the study of adult reading shows, this high degree of skill is achieved by a whole network of brain areas, some of which seem exquisitely specific and dedicated to the sole task of reading (see Hillis and Rapp, this volume). Understanding reading acquisition therefore requires answers to the following questions: What cognitive resources does the child bring to the task? What is the nature of the input necessary for learning to occur? And how, starting with these cognitive resources, and under the influence of this input, does the brain partly reshape itself into a proficient reading machine?

Cognitive modeling of reading acquisition

Formally, the bare essentials of reading are a set of external symbols that represent words of the language, which, in order to be understood and verbalized, need to be mentally represented, and connected to the corresponding items of the mental lexicon. Every school child starts with two mental lexicons: one storing the meanings of words (the semantic lexicon) and one storing the forms of words: the phonological lexicon, where phonology is an abstract representation of speech (except in deaf signers). Figure 1 shows a minimal information-processing model of this ‘initial state’ with respect to the task of reading acquisition. In this and other models, the components are usually justified by psycholinguistic and neuropsychological data which is reported in Hillis and Rapp (see also Caramazza, 1997b; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Levelt, Roelofs, & Meyer, 1999; Morton, 1969, 1980; Ramus, 2001). One important aspect of this model is the distinction between the phonological lexicon and sublexical phonological representations, the latter being a temporary store for anything that can be represented in a phonological format and articulated, including words, phrases and nonsense sequences of phonological units (e.g., nonwords).

Internally representing the set of written symbols means creating an orthographic lexicon, and those new representations need to be connected with the corresponding items in the semantic and phonological lexicons. Moreover, phonological representations are combinatorial: they are made of smaller units that include phonemes. Alphabetic writing systems exploit this natural combinatoriality: in those systems, written symbols are themselves combinations of smaller units (letters), which correspond (more or less well) to phonemes. Then, any string of letters can be mentally represented, which again justifies the existence of a sub-lexical (alphabetic) representation for letter strings. And there are obvious connections between representations of letter strings and the corresponding sublexical phonological representations. The mature reading system therefore has to resemble the one presented in Figure 2 (see papers in Caramazza, 1997a).

Proficient readers typically access written words’ meanings automatically and almost instantly; such high proficiency is commonly illustrated by the Stroop effect in most adult readers: people are slower to name the ink color (e.g., red) of a printed word if the word is a conflicting color name (“green”) (Stroop, 1935), demonstrating how difficult it is to inhibit reading whenever a word is being looked at. For the child, getting there is a long and arduous way which will involve specific teaching and massive exposure to print. Several models describe this process. There is little hope that one single specific model will be able to account for all cases of reading acquisition, if only because each developmental path will depend on the child’s own experience with print, his/her own cognitive style or capacities, and the instruction received (or the absence thereof). Nevertheless, keeping in mind this caveat, it seems possible to make general observations on how reading acquisition unfolds, at least within one particular writing system.

The standard model of reading acquisition in alphabetic systems has been proposed by Frith (1985; 1986; see Morton, 1989 for an information-processing account). It postulates that the child goes through three main stages, called logographic, alphabetic and orthographic respectively. Between two stages, new representations are set up and new connections are established between representations.

In the *logographic* stage (Figure 1), the child processes words just like any other visual object or symbol. Word meanings are associated with global visual shapes and features, which means that word recognition is highly inaccurate, overly reliant on fonts, patterns, colors, etc., and partly insensitive to precise letter order.

From there, it is assumed that alphabetic and phonics teaching are necessary to progress, i.e., to acquire an explicit knowledge of phonemes, their correspondences with letters, and how to merge those sounds into words. In this *alphabetic* stage, the child needs to visually represent words in a different format from other objects or symbols: he/she needs to represent ordered sequences of letters (in fact, abstract representations of letters, independent of font, size and color). Furthermore, these representations of letters must connect with their corresponding sounds in the child's sub-lexical phonological representation. This has a cognitive pre-requisite, that is, the ability to pay attention to units of this sub-lexical phonological level, and in particular to phonemes: this is called phoneme awareness, and is assumed to arise naturally in children at age 5 or 6. With this architecture in place (Fig. 3), the child can read by sounding out a sequence of letters and merging those sounds into a word. Word recognition occurs through the phonological lexicon. Of course, this way of reading is tedious and relatively inefficient, as it requires letter-by-letter processing, and in certain spelling systems like that of English, the letter-sound correspondence is not reliable enough to ensure total accuracy. A further refinement of the alphabetic stage is to associate phonemes not just to single letters, but to *graphemes*, i. e., letters or sequences of letters that have a more reliable correspondence with phonemes[1] (for instance, in English, one had better associate the grapheme "oa" with the phoneme [o] than try to sound out "o" and "a" separately).

Finally, repeated exposure to the same words leads the child to store whole-word grapheme sequences, i.e., to constitute an orthographic lexicon. With this new component in the system (Fig. 2), word recognition may occur through direct connections from the orthographic to the semantic lexicon. And reading aloud can proceed directly through the phonological lexicon (lexicalized phonological recoding, Share, 1995), without going through grapheme-phoneme conversion. There is good evidence that morphological units play an important role in the orthographic lexicon, as they may provide reliable, conveniently-sized units that can be quickly assembled to recognize complex words. Through the accumulation of orthographic lexical items, and their connections with phonological lexical items, new sublexical letter-sound regularities may implicitly be acquired (induced sublexical relations, Thompson, Cottrell, & Fletcher-Flinn, 1996). For instance, the child may implicitly learn that the pronunciation of the sequence "eal" can be deduced systematically from the surrounding context (e.g., depending on whether it is followed by s, t, e, i etc.), something that is usually not explicitly taught. Therefore, in the mature reading system (Fig. 2), the connections between sublexical alphabetic and phonological representations are in part explicitly learnt grapheme-phoneme rules, and in part implicitly acquired more complex sublexical relations.

Many people are suspicious of models requiring discrete developmental stages. But this only happens if one takes the model too literally. Of course, it is not assumed that those developmental stages are disjoint periods demarcated by abrupt cognitive changes. Rather, they reflect three types of reading strategies that progressively take precedence over each other. The beginnings of the alphabetic stage may well see remnants of logographic reading. Furthermore, alphabetic reading is never entirely abandoned, since it is often necessary to read unknown words; rather, the more the orthographic lexicon grows, the less alphabetic reading is employed.

Perhaps the most valid criticism of Frith's (1985) model is that it assumes a particular class of teaching methods, based on explicit phonics instruction. Although there is a huge controversy as to whether phonics is an essential component of good teaching, it is a fact that other teaching methods exist, and that some children manage to become fluent readers without ever receiving explicit phonics instruction. For those children, the scenario certainly needs to be revised to a certain extent. Beyond the logographic stage, it seems that instead of going through an alphabetic stage, they start building directly an orthographic lexicon connected to the other two lexicons (albeit painstakingly, perhaps like Chinese children learn their language's characters) (Figure 4). From there, they acquire implicit sublexical relations (including standard grapheme-phoneme correspondences), so that their mature reading system closely resembles that of phonics-taught children (Fig. 2), except that the sublexical letter-sound connections are all implicit. This revised scenario seems to apply not only to students taught with

[1] This definition of the word grapheme is the one used in the reading literature and is different from the one used in neuropsychology, where it usually refers to abstract letter representations (e.g., Hillis & Rapp, this volume).

‘global’ methods, but also to precocious readers who learn to read by themselves without any reading instruction (Fletcher-Flinn & Thompson, 2000, in press).

The present scenario of reading acquisition presupposes certain answers to the first two questions that we have raised: the necessary cognitive resources brought by the child to the task of learning to read would seem to include fully functional phonological (and therefore auditory), lexical and visual systems. The input necessary for learning to occur includes massive exposure to written words, presented together with their phonological forms (at least at the beginning). Explicit instruction of letter sounds and grapheme-phoneme correspondences would seem to be a facilitating factor for most children, in that it does allow to bootstrap the formation of the orthographic lexicon: without it, the child has to rely for a very long time on the simultaneous presentation of written and verbal forms to acquire new words; with it, it is possible to read aloud, understand and therefore learn new words by applying grapheme-phoneme correspondences. Nevertheless, this facilitating factor is not entirely necessary, and many children can do without it.

As we will see below, these answers will be refined by taking into consideration possible disorders of these systems and their impact on reading acquisition.

Insights from developmental disorders

Fifty ways to fail reading acquisition

Just as in a car the failure of many different parts can prevent the car from functioning, there are many different ways in which reading acquisition can go wrong.

The most obvious ones are cases of major sensory deprivation. Blindness, severe ophthalmologic impairments or simply uncorrected hyperopia (farsightedness), preventing the formation of alphabetic representations, are of course major obstacles to the acquisition of reading. Similarly, deafness prevents the formation of phonological representations related to speech, and the units of sign-language phonological representations have little to do with phonemes or letters, which makes the alphabetic principle meaningless to profoundly deaf people and only leaves them the possibility of logographic reading.

Another obvious cause of reading disability is mental retardation. More generally it is well-known that reading ability is correlated with intelligence quotient (IQ) (Snowling, 2000), so difficulties in learning to read are straightforwardly predicted at the bottom end of the IQ scale.

Language itself is of course a prerequisite of reading; at the very least the child’s vocabulary (i.e., semantic and phonological lexicons) sets an upper limit on the development of the orthographic lexicon, and reading comprehension can never be better than language comprehension. It is therefore not surprising that children with language impairments generally have problems acquiring reading.

Finally, there can also be more extrinsic factors: one can imagine a variety of emotional, social or educational contexts in which the acquisition of reading can be difficult.

Developmental dyslexia

It is quite remarkable that, even after excluding the obvious causes of failure mentioned above, about 5% of schoolchildren still have great difficulties learning to read. Such a specific reading disability without apparent endogenous or exogenous cause is generally called developmental dyslexia. Even within this more limited diagnostic category, it seems that heterogeneous causes are to be found. Traditionally, two distinct causes have been envisioned: visual and phonological.

Since major ophthalmologic problems are already excluded from the definition of dyslexia, any remaining visual cause must be relatively subtle, i.e., have little impact on everyday life outside reading. This is reflected in the term “congenital word blindness” which was used to describe one of the very first cases of dyslexia ever reported (Morgan, 1896). Again, there are several possibilities: poor vergence that would affect the capacity to focus at short distance, instability of binocular fixations leading to unstable visual images, and poor saccade planning that would affect fluent text reading have been argued to be major causes of reading disability (Stein & Walsh, 1997). Another relevant disorder is visual stress, which is manifested in migraines, visual distortions and apparent movements, when the viewer is confronted to a high-contrast black-and-white page of text (Wilkins, 1995). Research into visual causes of dyslexia has remained controversial and subject to intense debate (Skottun, 1997; Stein, Talcott, & Walsh, 2000). It is fair to say that there is evidence that both binocular control dysfunction and visual stress can be factors of reading disability and that visually-based treatments can help in those cases (Bouldoukian, Wilkins, & Evans, 2002; Stein, Richardson, & Fowler, 2000), but most practitioners and scientists find that these visual disorders concern only a small fraction of dyslexics.

The other major, and now most widely accepted explanation of developmental dyslexia has to do with the phonological system. The hypothesis is quite simply that a deficit in phonological representations and processing would impair the ability to access representations of phonemes, and associate them with graphemes (Shankweiler & Liberman, 1972; Snowling, 2000; Stanovich, 1988; Vellutino, 1979). This hypothesis is supported by widespread evidence that most dyslexics have difficulties with at least three types of tasks involving phonological representations and processing (Morris et al., 1998): these include phoneme awareness tasks (like swapping phonemes between two words to perform spoonerisms), verbal short-term memory, and speeded naming of objects (or digits, letters or colors)… Among the different manifestations of the phonological deficit, it appears that poor phoneme awareness is the most proximal cause of reading difficulties. Phoneme awareness is the awareness that speech is combinatorial, made up of a limited number of sounds that are combined to make words. This is obviously crucial to master the alphabetic principle; the hypothesis is that dyslexic children have insufficient phoneme awareness, and therefore have difficulties reaching the alphabetic stage of reading. The importance of the alphabetic stage in bootstrapping reading acquisition implies that the phonological deficit will have further developmental consequences, disrupting the whole acquisition of the reading system, notably the acquisition of the orthographic lexicon.

It is not entirely clear what the three different manifestations of the phonological deficit have in common so that they could be reduced to some common substrate. It can be argued that phoneme awareness requires a good verbal short-term memory to simultaneously pay attention to phonemes and to their combinations, so that a deficit in the latter would entail one in the former (Baddeley, 1979). And it has also been argued that the rapid naming deficit is in fact independent from poor phoneme awareness, although often associated (Wolf & Bowers, 1999). However, discussions of the phonological deficit have seldom been framed within an information-processing model such as Figure 2. Within such a framework, the exact locus of the phonological deficit remains uncertain. Some theorists would situate it at the lexical level, and rather in output processes (Elbro, 1996; Snowling, 2000), while others argue for a sublexical locus, either abstract (Ramus, 2001) or specific to input processes (Mody, Studdert-Kennedy, & Brady, 1997; Serniclaes, Sprenger-Charolles, Carré, & Démonet, 2001). Unfortunately, it seems that investigations into the phonological deficit have not yet reached the degree of sophistication necessary to really tease apart these hypotheses (Ramus, 2001).

Although most researchers agree that a phonological deficit is the most likely proximal cause of dyslexia, there is another debate regarding whether the deficit is specific to the phonological system or whether it is secondary to a more basic auditory impairment. There is indeed evidence that dyslexics have, on average, poorer performance than controls on a range of auditory tasks (Farmer & Klein, 1995; McAnally & Stein, 1996; Tallal, 1980; Witton, Stein, Stoodley, Rosner, & Talcott, 2002). It is of course perfectly plausible that a mild auditory disorder would have an impact on the development of the phonological system, deafness being only an extreme case in point. The question is whether the auditory disorders observed in dyslexics are of the nature and severity to cause the type of phonological disruption that leads to dyslexia. In fact it seems that they are mostly unrelated to speech perception and phonological processing (Mody et al., 1997; Ramus et al., 2003; Rosen & Manganari, 2001). It also appears that auditory disorders are restricted to a subset of dyslexics (Amitay, Ahissar, & Nelken, 2002; McArthur & Bishop, 2001) and that they are not necessary for a phonological deficit to arise (Ramus et al., 2003; White et al., submitted). Overall, there is overwhelming evidence that for the vast majority of children with dyslexia, a specific deficit of the phonological system is the main culprit (see reviews in Ramus, 2003; Rosen, in press).

Cognitive pre-requisites of reading acquisition

Returning to the question of cognitive pre-requisites, of course every component of the reading system is important, be it visual, auditory or more specifically linguistic: the total disruption of any of them can prevent normal reading acquisition. Nevertheless, it is quite remarkable that even in the case of blindness the visual medium can easily be replaced with a tactile one (Braille). This shows that the brain does not expect orthographic representations to come in a particular modality (indeed, it does not expect orthographic representations at all, as this is a cultural invention). Rather, it has the potential to create an orthographic lexicon in the relevant modality, be it visual or tactile. And when the new representations are combinatorial and their units are in a reliable correspondence to phonological units, then appropriate sublexical representations are also created and connected to sublexical phonology (Braille is also an alphabet).

The case of profound deafness is more complicated, as letters cannot connect to relevant phonological units. But even in this extreme case, partial information about relevant phonological units can be obtained by representing the speaker's articulatory gestures (lip-reading), which provides certain phonetic features (e.g., rounding of the lips, labial articulation place) but not others (voicing). The missing phonetic features can even be complemented by a specific system of manual cues that the speaker can produce as he speaks (cued speech, Cornett, 1967). In this case, both speech comprehension and reading acquisition become accessible to deaf people. Furthermore, any residual hearing can also provide disambiguating cues and complement the representation of phonological units. So it seems that when standard sublexical phonological representations are absent or insufficient, the brain can make appropriate ones with any combination of auditory and visual cues so as to properly connect them to alphabetic representations.

Different reading systems can provide more insights: when the units that make up the written symbols do not correspond to phonological units but to whole words or morphemes (like in Chinese characters), then no sublexical relations can be formed, and reading acquisition has to proceed through rote learning of all the arbitrary pairs of orthographic and phonological lexical items[2]. Nevertheless most Chinese children are able to learn the few thousand characters that are most useful for everyday life. Other writing systems can also be based on different phonological units than phonemes: this is the case of the Japanese *hiragana*, where each character represents a syllable[3]. Because there are few different syllables in Japanese (unlike in English), this system is as easy to learn as an alphabet. Sublexical relations are then established between *hiragana* representations, and the corresponding sublexical phonological units, i.e., syllables.

The diversity of writing systems and the alternative reading strategies that are set up when one modality is not available show that there is little fixed or necessary in the architecture of the reading system; rather, when presented with a new set of lexical symbols, the brain has the capacity to create a new lexicon to represent them, and when their combinatorial structure bears any relationship with phonological or other related representations, it establishes the corresponding sublexical connections which significantly increase the efficiency of the acquisition process.

With such flexibility of reading acquisition, it can be expected to be relatively resistant to more moderate disruptions of any single component. Developmental dyslexia itself is seldom a total incapacity to learn to read: it makes the process significantly harder to the extent that the trouble can only partially be overcome, generally through alternative reading strategies requiring inordinate intellectual effort or prowess. Most ophthalmologic disorders do not prevent reading, but rather disrupt its fluency to various degrees (Legge, Rubin, Pelli, & Schleske, 1985). And mild to moderate hearing loss, whilst disrupting the formation of accurate phonological representations and often disturbing speech perception and production, does not necessary lead to difficulties to learn to read (Briscoe, Bishop, & Norbury, 2001).

This leads us to a paradox: on the one hand, hearing loss that significantly disturbs phonological representations can still allow for normal reading acquisition; on the other, a rather mild phonological deficit (mild in the sense that it leaves speech production and comprehension intact), can impair reading acquisition very consistently in a large proportion of the population. This suggests that there is something special to normally developed phonology that dramatically facilitates reading acquisition, that is disrupted in dyslexia, but not necessarily by moderate hearing loss. Phoneme awareness seems the most likely candidate, which justifiably makes it the single most important cognitive pre-requisite to reading acquisition.

Reading acquisition in the brain

Putting together the rough sketch of reading acquisition outlined here, and what we know of the correspondence between functional modules and brain areas (see Hillis and Rapp, and Cutler and Indefrey, this volume), it becomes possible to make specific predictions concerning the specialization of the child's brain for reading. In particular, brain imaging studies performed on children at different stages of reading acquisition would be expected to reflect the emergence of new representations for alphabetic strings and orthographic lexical items. The results of such imaging studies could therefore be used to confirm or infirm theories of reading acquisition.

[2] In fact, even in Chinese characters there are implicit sublexical relations which make it possible to guess the pronunciation of a new character slightly better than chance.
[3] Actually each character represents a mora, where the mora is a phonological unit slightly smaller than the syllable. In Japanese, with a few exceptions, moras are almost always syllables, so it is a reasonable approximation to talk about a syllabic writing.

Unfortunately, the current state of the art can only give us a very preliminary picture: functional brain imaging studies of children are scarce, and the tasks used and subtractions reported, together with the limited anatomical resolution, do not allow for a clear identification of the components of the lexical system. Nevertheless it is possible to provide a rough overview.

The clearest brain/function mapping demonstrated in the reading system lies in alphabetic/orthographic processing: this has been reliably associated with the occipito-temporal region of the left hemisphere (see reviews in McCandliss, Cohen, & Dehaene, 2003; Pugh et al., 2001 and Hillis and Rapp). According to the analysis by Cohen et al. (2002), there seems to be a whole hierarchy of representations in this region (more than sketched in Fig. 2), with the more posterior areas (in the occipital lobe) being specifically visual and perhaps related to processing of low-level visual features and letter-shapes, while they seem to get progressively more abstract as they get more anterior in the ventral temporal lobe: the mid-portion of the left fusiform gyrus would support representations of abstract letter strings of both words and non-words, while the more anterior portion might be more specific to words (however in many studies this distinction is not explicitly made). Furthermore these reading-related areas are embedded within a larger ventral object-recognition system with similar perceptual gradients (Lerner, Hendler, Ben-Bashat, Harel, & Malach, 2001), so that one can see the development of this orthographic system as reflecting the specialization, under the pressure of the input, of object recognition areas that happen to be tuned to certain visual properties that are particularly suitable for representing letter strings (Cohen et al., 2002). From the fusiform gyrus, the hierarchy of more and more abstract orthographic representations seems to progress over the posterior portions of the inferior and medial temporal gyri, the latter being a possible locus for the orthographic lexicon (Simos, Breier et al., 2002).

Developmentally, across a large group of children aged from 7 to 17, Shaywitz and colleagues have shown that activation in those occipital-temporal areas when reading increases with reading skill[4] (B. A. Shaywitz et al., 2002) (see also Booth et al., 2001; Schlaggar et al., 2002; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003), which is consistent with the idea of the progressive formation of alphabetic and orthographic representations. Moving to studies of developmental dyslexia, there is reliable evidence that these same areas are hypo-activated in both child and adult dyslexics during reading tasks (e.g., Brunswick, McCrory, Price, Frith, & Frith, 1999; B. A. Shaywitz et al., 2002; S. E. Shaywitz et al., 1998). This does not entail that a dysfunction in these areas is the cause of dyslexia; rather, it is compatible with the prediction that orthographic representations develop abnormally as a result of the phonological deficit.

The other major component in the reading system is the temporo-parietal junction, including the posterior superior temporal gyrus (STGp), the angular gyrus and the supra-marginal gyrus, predominantly in the left hemisphere. A clear decomposition of this large region into functional areas has not been achieved yet, but it is assumed to be generally involved in the lexicon (with the angular gyrus another contender for the seat of the orthographic lexicon; see Hillis & Rapp, this volume), in sub-lexical phonology (STGp and anterior supra-marginal gyrus, Jacquemot, Pallier, Le Bihan, Dehaene, & Dupoux, submitted) as well as in computing grapheme-phoneme correspondences (particularly the STGp, Simos, Breier et al., 2002). The activation of the temporo-parietal junction in reading occurs after that of the occipito-temporal areas (Simos, Breier, Fletcher, Bergman, & Papanicolaou, 2000; Simos, Breier et al., 2002), consistently with the view that visual/alphabetic processing precedes phonological processing and lexical access. Interestingly, children seem to activate the left STGp more than adults in tasks requiring word reading (Booth et al., 2001). This is again consistent with the idea that they rely more on alphabetic and less on orthographic strategies. Furthermore activation in the neighboring left posterior superior temporal sulcus was found to be correlated with a measure of phonological awareness in children (Turkeltaub et al., 2003). In contrast, dyslexic children and adults have consistently been found to activate less this area (indeed, the whole temporo-parietal junction) than controls (Paulesu et al., 2001; Simos, Fletcher, Bergman et al., 2002; Simos, Fletcher, Foorman et al., 2002; Temple et al., 2001; see review by Temple, 2002), consistently with the idea that they have a phonological deficit and difficulties with grapheme-phoneme processing. Interestingly, dyslexics seem to compensate by hyper-activating the symmetric right-hemisphere areas as compared to controls (S. E. Shaywitz et al., 1998; Simos, Fletcher, Bergman et al., 2002; Simos, Fletcher, Foorman et al., 2002). A remediation study further showed that, following a phonological awareness training program, dyslexic children not only improved behaviorally but also were able to involve their

[4] Actually these authors found a correlation between activation in the occipito-temporal areas (as well as other areas) and *non-word reading*. However, non-word reading was the only reading measure reported and it is usually highly correlated with reading skill of all types of words, so that the correlation should be expected to hold with reading skill more generally. In fact, considering the function attributed to those areas, one would predict the highest correlation with performance in a more specifically orthographic task.

left STGp in nonword reading tasks significantly more than before the treatment (Simos, Fletcher, Bergman et al., 2002).

Another way in which dyslexics may compensate for their orthographic-phonological processing difficulties in tasks like nonword reading is through the increased involvement of the inferior frontal gyrus (Broca's area) bilaterally, another area which, in the left hemisphere, is often involved in reading (Pugh et al., 2000; S. E. Shaywitz et al., 1998; Temple et al., 2001). One possible explanation is that slow and effortful grapheme-phoneme processing may increase the load on verbal working memory, as the subject needs to keep in store the beginning of the word while processing the end, perhaps engaging in covert articulation or rehearsal. Moreover this hyperactivation seems to increase with age in dyslexics (B. A. Shaywitz et al., 2002).

It is quite tempting to ascribe dyslexics' difficulties to a congenital dysfunction of the left temporo-parietal junction (Temple, 2002), resulting in disrupted sub-lexical phonological representations and difficulties to learn alphabetic reading, with further consequences for the acquisition of the orthographic lexicon. This hypothesis is compatible with some anatomical data indicating structural and metabolic anomalies in these areas of dyslexics' brains (Brown et al., 2001; Galaburda, Sherman, Rosen, Aboitiz, & Geschwind, 1985; Rae et al., 1998). However it should be emphasized that many areas of the brain have been found to be 'different' in dyslexics on average (Habib, 2000), but the functional significance of none of these differences has been established.

Perhaps the currently most promising hypothesis is that of a partial disconnection of left temporo-parietal areas from the temporo-occipital language areas (but see Paulesu et al., 1996 for another disconnection hypothesis): this is supported by diffusion tensor imaging showing disruption in the underlying white matter (Klingberg et al., 2000), and becomes interesting in the light of evidence that, unlike in controls, functional activations in dyslexics' angular gyrus fail to be correlated with activations in the ventral orthographic system (Horwitz, Rumsey, & Donohue, 1998; Pugh et al., 2000; Simos et al., 2000).

Other hypotheses exist concerning the neurological origin of dyslexia, in particular related to alternative cognitive theories (auditory, visual). The most notable of those, the "magnocellular theory" (Stein, 2001), hypothesizes that magno-cells in all sensory pathways are deficient, leading both to visual disorders causing reading difficulties, and to auditory disorders causing the phonological deficit. Beyond the criticism already mentioned concerning the prevalence and the causal role of those sensory deficits, the magnocellular theory also faces more specific challenges. In particular, it predicts that dyslexics' sensory deficits will be observed for stimuli in a certain range of spatial and temporal frequencies characteristic of the response domain of magno-cells. In the auditory domain, this translates into the hypothesis of a "rapid auditory processing" deficit proposed by Tallal (1980). The empirical evidence is highly contradictory, split between findings consistent and inconsistent with the theory (see reviews in Ramus, 2003; Rosen, in press; Skottun, 2000). Overall the magnocellular theory in its present state does not seem to be able to adequately characterize the sensory deficits of even the fraction of dyslexics that are so impaired.

Conclusion

The human brain has not evolved to learn to read, but it has the potential to acquire an additional lexicon in a new modality (usually visual). Representations for visual forms of words progressively settle in the occipito-temporal cortex, recruiting for their own purpose a subset of a functionally appropriate object recognition region. These new functional areas have to connect with the existing lexicon in the temporo-parietal junction. In alphabetic writing systems, the acquisition of orthographic lexical items and their connection with phonological and semantic ones is greatly facilitated by the acquisition of sublexical relations between graphemes and phonemes: such orthographic-phonological conversion is likely performed by the posterior superior temporal gyrus. In developmental dyslexia, reading acquisition difficulties seem to stem from a specific phonological deficit comprising an impaired phonological awareness, leading to a poor ability to learn grapheme-phoneme correspondences. At the neural level, this may result from a dysfunction of the temporo-parietal brain areas, or of their underlying connections with orthographic representations.

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Figure 1. The initial state: logographic reading stage

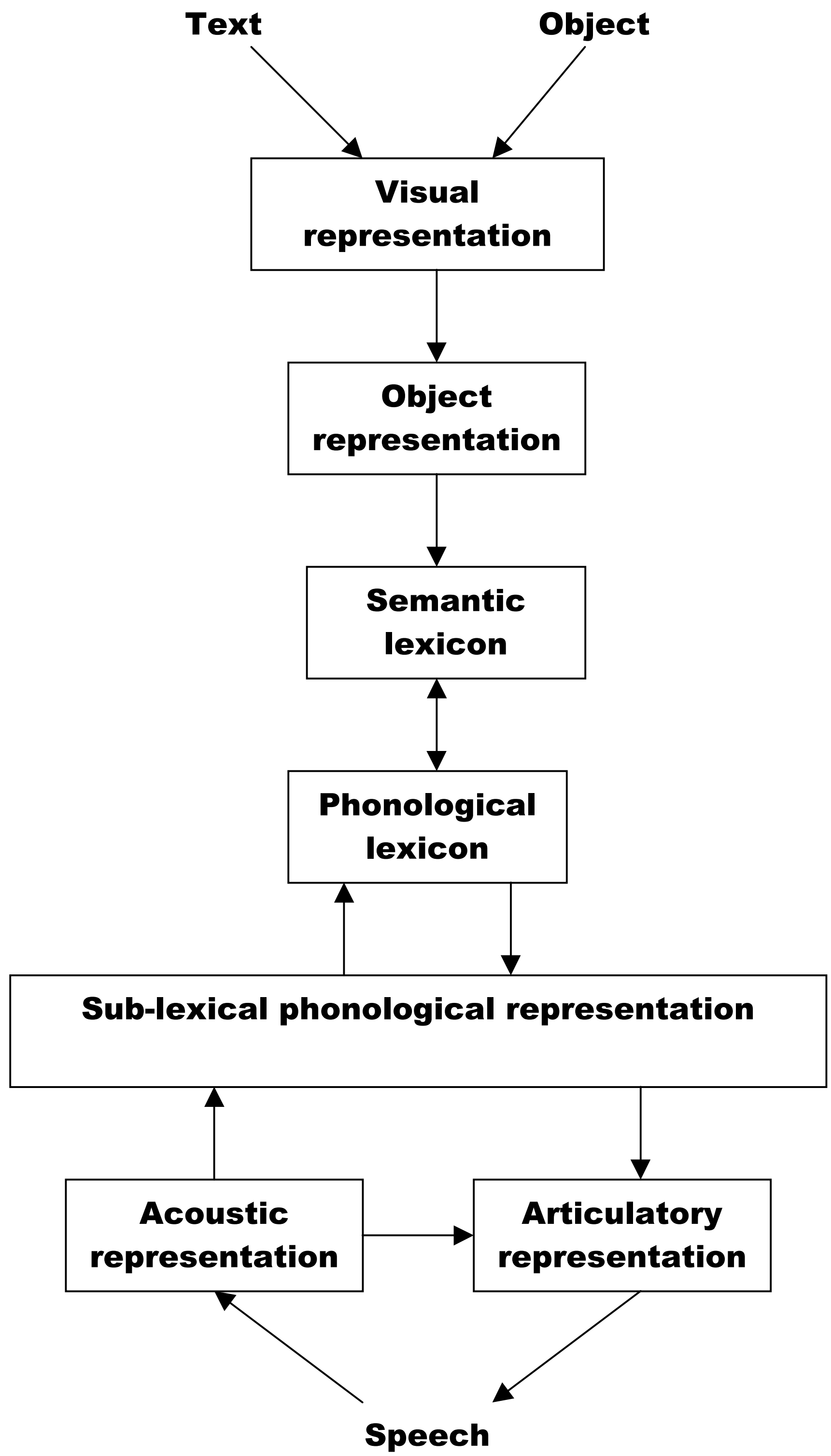

Figure 2. The final state: orthographic reading stage

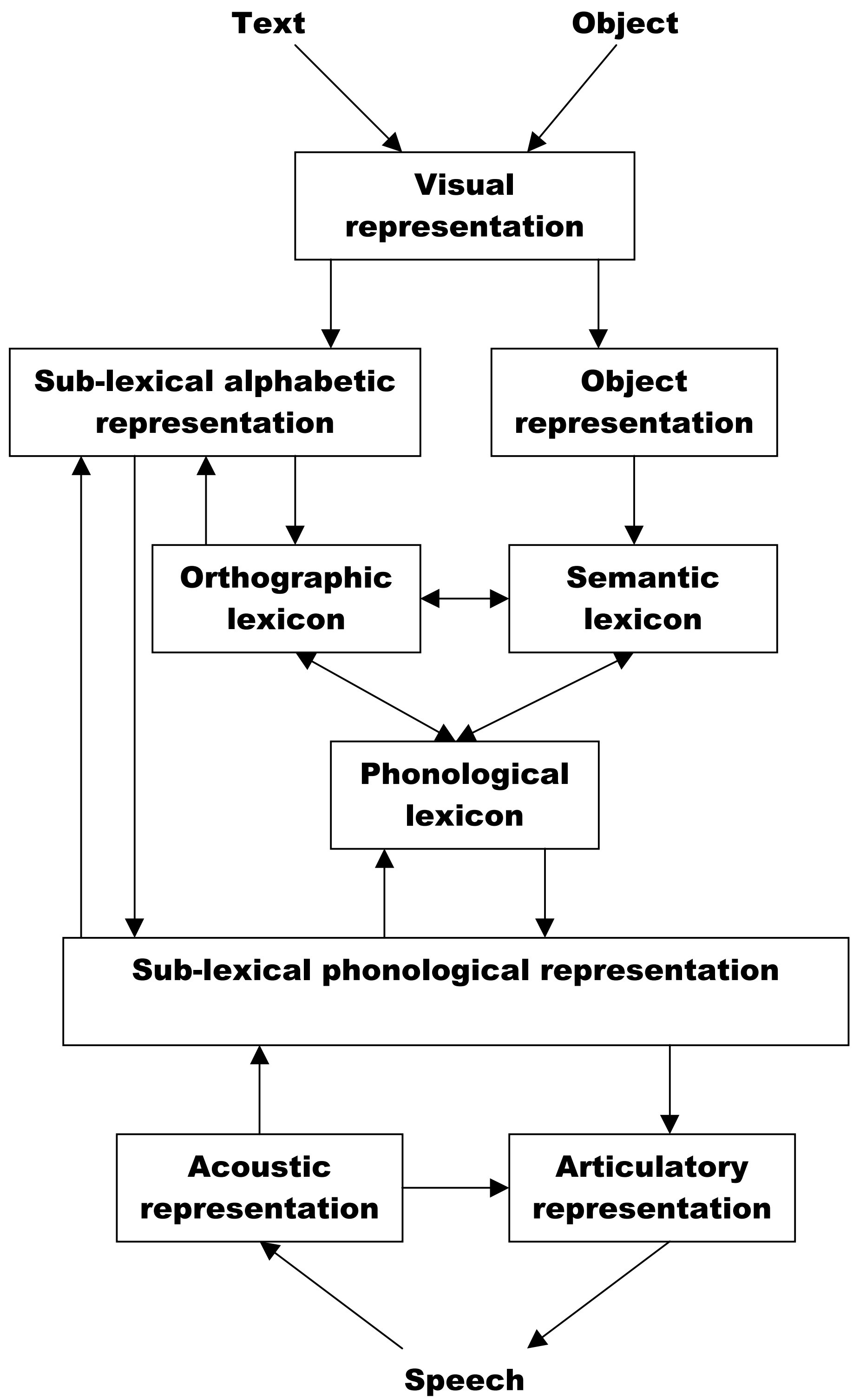

Figure 3. An intermediate state: alphabetic reading stage

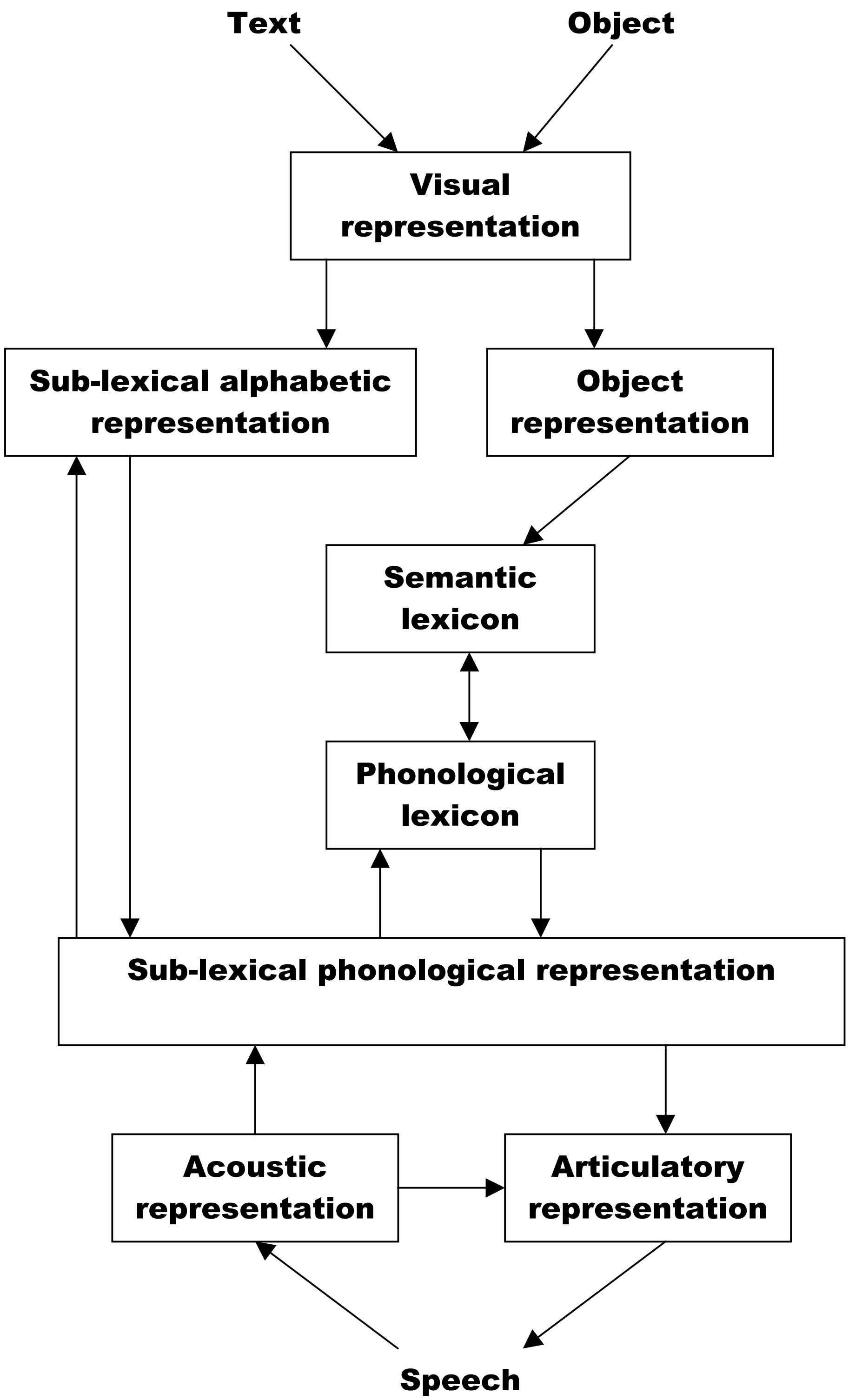

Figure 4. An alternative intermediate stage without explicit phonics teaching