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Reading, dyslexia and the brain

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Background: Neuroimaging offers unique opportunities for understanding the acquisition of reading by children and for unravelling the mystery of developmental dyslexia. Here, I provide a selective overview of recent neuroimaging studies, drawing out implications for education and the teaching of reading.

Purpose: The different neuroimaging technologies available offer complementary techniques for revealing the biological basis of reading and dyslexia. Functional magnetic resonance imaging (fMRI) is most suited to localisation of function, and hence to investigating the neural networks that underpin efficient (or inefficient) reading. Electroencephalography (EEG) is sensitive to millisecond differences in timing, hence it is suited to studying the time course of processing; for example, it can reveal when networks relevant to phonology versus semantics are activated. Magnetic source imaging (MSI) gives information about both location in the brain and the time course of activation. I illustrate how each technology is most suited to answering particular questions about the core neural systems for reading, and how these systems interact, and what might go wrong in the dyslexic brain.

Design and methods: Following a brief overview of behavioural studies of reading acquisition in different languages, selected neuroimaging studies of typical development are discussed and analysed. Those studies including the widest age ranges of children have been selected. Neuroimaging studies of developmental dyslexia are then reviewed, focusing on (a) the neural networks recruited for reading, (b) the time course of neural activation and (c) the neural effects of remediation. Representative studies using the different methodologies are selected. It is shown that studies converge in showing that the dyslexic brain is characterised by *under-activation* of the key neural networks for reading.

Conclusions: Different neuroimaging methods can contribute different kinds of data relevant to key questions in education. The most informative studies with respect to causation will be longitudinal prospective studies, which are currently rare.

Keywords: reading; phonology; dyslexia; brain imaging

How universal are the neural demands made by learning to read in different languages? What are the core neural systems involved, and what goes wrong in the dyslexic brain? Current neuroimaging technologies are able to throw light on research questions such as these, as will be illustrated below. In some instances, neuroimaging technologies can contribute unique information that behavioural methodologies are simply unable to provide. This includes information about the time processes in reading, and information about the parts of the brain that are affected by remedial packages for developmental

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dyslexia. Some neuroimaging methodologies can gather data without requiring overt attention on the part of the child. These methodologies are particularly powerful for contributing to our understanding of the biological basis of developmental dyslexia.

The history of research on developmental dyslexia has been dominated by visual theories of the disorder, ever since Hinshelwood (1896) described it as 'congenital word blindness'. Historically, theories of reading development also assumed that visual processing was core to individual differences in the acquisition of reading. In the 1970s, for example, there was much discussion of 'Phonecian' versus 'Chinese' reading acquisition strategies. It was assumed that children who were learning to read character-based orthographies like Chinese required excellent visual memory skills in order to distinguish between the visually complex characters that represented spoken words. Hence visual memory or 'logographic' strategies were assumed core to reading acquisition of languages like Chinese and Japanese. Children who were learning to read languages like Greek or Italian, which were alphabetic and transparent (each letter corresponding to one, and only one, sound) appeared to require code-breaking skills. It was assumed that once the brain had learned the symbol–sound code, reading should be largely a process of phonological assembly. Many experiments were conducted with children learning to read in English, to compare the contribution of 'Chinese' versus 'Phonecian' acquisition strategies (e.g., Baron 1979). Dual-route models of reading, originally developed using data from adults, were applied to children who were learning to read (Stuart and Coltheart 1988). It was assumed that, developmentally, children could choose to learn to read by either Chinese or Phonecian strategies.

These ideas about individual differences have not gone away (e.g., Stein and Walsh 1997; Stuart 2006), but they are looking increasingly dated with the advent of brain imaging. Neuroimaging has also shed light on the processes underpinning the development of reading in deaf children, whom it was once assumed had no choice but to rely on visual memorisation strategies (e.g., Conrad 1979). Essentially, neuroscience is showing that despite the apparently different demands on the brain made by learning to read English, Greek or Chinese, and the apparently different processing strategies used by children who are deaf or who are dyslexic, reading across orthographies depends on the adequate functioning of the phonological system. Even for languages like Chinese, which would appear reliant on visual processing, it is oral language skills that underpin the acquisition of reading.

As I show in this review, brain imaging studies demonstrate that reading begins primarily as a phonological process. In the early phases of learning to read, it is the neural structures for spoken language that are particularly active. As reading expertise develops, an area in the visual cortex originally named the 'visual word form area' (VWFA) becomes increasingly active (Cohen and Dehaene 2004). This area is not a logographic system, even though it is very close to the visual areas that are active during picture naming. The VWFA is also active during nonsense word reading, and as nonsense words do not have word forms in the mental lexicon, the VWFA is thought to store orthography–phonology connections at different grain sizes (Goswami and Ziegler 2006a). Deaf readers rely on the same phonological system for reading as everyone else (MacSweeney et al. 2005). Children with developmental dyslexia show selective under-activation of key phonological areas of the brain, but targeted phonology-based interventions improve levels of activation in these areas, 'normalising' neural activity (Simos et al. 2002).

Learning to read: behavioural data

Many behavioural studies in developmental psychology show the critical role of 'phonological awareness' in learning to read (for a recent review see Ziegler and Goswami 2005). Phonological awareness is thought to develop via language acquisition. Between the ages of 1 and 6 years, children acquire words at an exponential rate. For example, the average 1-year-old might have a productive vocabulary of around 50–100 words, but by the age of 6 the average child's receptive vocabulary will contain around 14,000 words (Dollaghan 1994). In order for the brain to represent each word as a distinct and unique sequence of sounds, each entry in the 'mental lexicon' must incorporate phonological information along with information about meaning. For example, there must be implicit knowledge of the sounds that comprise a particular word, and the order in which they occur. Phonological awareness is essentially the child's ability to reflect on this implicit knowledge, and to make judgements based on it. Hence phonological awareness is typically measured by a child's ability to detect and manipulate component sounds in words, for example, by deciding whether words rhyme, or by removing the initial sound from a spoken word.

The syllable is the primary processing unit across the world's languages (Port 2006). In fact, there is an apparently language-universal sequence in the development of phonological awareness, from syllable awareness, through 'onset-rime' awareness to 'phoneme' awareness. Syllables ('university' has five syllables, 'coffee' has two syllables) can be segmented into sub-parts called onsets and rimes. The onset is the sound or sounds before the vowel, such as the 'spr' sound in 'spring' and the 'st' sound in 'sting'. The rime is the vowel and any subsequent sounds in the syllable, such as the 'ing' sound in 'spring' and 'string'. The phoneme is the smallest unit of sound that changes meaning. 'Spring' and 'string' differ in meaning because the second sound is different in each word ('p' versus 't' respectively). In many of the world's languages, onsets and rimes are the same as phonemes. This is because the dominant syllable structure across the world's languages is consonant–vowel (CV). Relatively few words in English are CV syllables (5% of English monosyllables follow a CV structure: see De Cara and Goswami 2002). Examples of English words comprised of CV syllables are 'go', 'do' and 'yoyo'.

Behavioural studies across languages have shown that phonological sensitivity at all three linguistic levels (syllable, onset-rime, phoneme) predicts the acquisition of reading (for a review see Ziegler and Goswami 2005). Furthermore, it has been demonstrated that training phonological awareness has positive effects on reading acquisition across languages, particularly when it is combined with training about how letters or letter sequences correspond to sounds in that language (e.g., Bradley and Bryant 1983; Schneider, Roth, and Ennemoser 2000). Children with developmental dyslexia across languages appear to have specific problems in detecting and manipulating component sounds in words (called a 'phonological deficit': see, e.g., Snowling 2000). For example, they find it difficult to count the number of syllables in different words, to recognise rhymes, to distinguish shared phonemes and to delete phonemes or substitute one phoneme for another (Korean: Kim and Davis 2004; German: Wimmer 1996; Greek: Porpodas 1999; Hebrew: Share and Levin 1999; for a comprehensive review see Ziegler and Goswami 2005). Dyslexic children are developing some awareness of phonology, but this is a slow and effortful process. Deaf children also develop phonological codes, for example, via lip reading ('speech reading') and vibrational cues. This is the case even if signing is their native language. Phonology is essentially the smallest contrastive

units of a language that create new meanings. In signed languages, phonology depends on visual/manual elements, with handshapes, movements and locations combined to form signs (Sandler and Lillo-Martin 2006). For deaf children too, individual differences in phonological awareness are related to reading acquisition (e.g., Harris and Beech 1998).

Reading and learning to read: neuroimaging data

To date, most neuroimaging studies of reading have been conducted with adults (see Price and McCrory 2005 for a recent synthesis). This was partly due to the methodologies available. The most popular methods for studying the brain during the act of reading depended on imaging techniques like functional magnetic resonance imaging (fMRI) and positron emission tomography (PET). The fMRI technique measures changes in blood flow in the brain, which take approximately 6–8 seconds to reach a maximum value (i.e. maximum activity will be measurable 6–8 seconds after reading a particular word). fMRI works by measuring the magnetic resonance signal generated by the protons of water molecules in brain cells, generating a BOLD (blood oxygenation level dependent) response. The fMRI method is excellent for the localisation of function, but because changes in brain activity are summated over time, it cannot provide information about the sequence in which different neural networks become engaged during the act of reading. In PET, radioactive tracers are injected into the bloodstream and provide an index of brain metabolism. Because of the use of radioactive tracers, PET is not suitable for studying children.

More recently, the value of the electroencephalogram (EEG) methodology for studying reading is being recognised. Neurons communicate on a millisecond scale, with the earliest stages of cognitive information processing beginning between 100 ms and 200 ms after stimulus presentation. EEG methods can measure the low-voltage changes caused by the electro-chemical activity of brain cells, thereby reflecting the direct electrical activity of neurons at the time of stimulation (e.g., at the time of seeing a word). Initially, EEG methods were less widely used in the neuroscience of reading, because it is difficult to localise function using EEG. However, developmentally, information about the time course of processing is very important. Data from EEG studies suggest that the brain has decided whether it is reading a real word or a nonsense word within 160–180 ms of presentation, for children and adults across languages (Csepe and Szucs 2003; Suaseng, Bergmann, and Wimmer 2004).

Adult studies of reading based on PET and fMRI have focused on a relatively small range of reading and reading-related tasks, and studies of children using fMRI have followed suit. Typical tasks include asking participants to read single words and then comparing brain activation to a resting condition with the eyes closed; asking participants to pick out target visual features while reading print or 'false font' (false font is made up of meaningless symbols matched to letters for visual features like the 'ascenders' in the letters b, d, k); making phonological judgements while reading words or nonsense words (e.g., 'do these items rhyme?': leat, jete) and making lexical decisions (e.g., pressing a button when a word is presented, and a different button when a nonsense word is presented). Adult experiments show a very consistent picture concerning the neural networks that underpin skilled reading (e.g., Price et al. 2003; Rumsey et al. 1997; see for comments on divergence Price and McCrory 2005). Word recognition in skilled readers appears to depend on a left-lateralised network of frontal, temporoparietal and occipitotemporal regions, whatever language they are reading (see Figure 1). However,
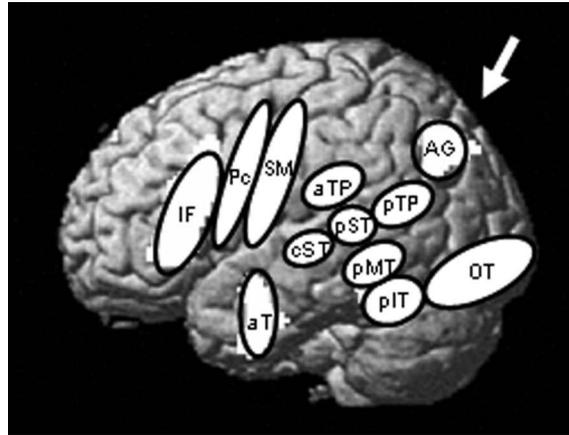
AG = Angular Gyrus
OT = Occipito-Temporal
pTP = posterior Temporo-Parietal
pST = posterior Superior Temporal
pIT = posterior Inferior Temporal
pMT = posterior Middle Temporal
aTP = anterior Temporo-Parietal
aT = anterior Temporal
cST = central Superior Temporal
IF = Inferior Frontal
Pc = Precentral gyrus
SM = Sensori-motor cortex

Figure 1.   A schematic depiction of some of the neural areas involved in reading (left hemisphere depiction) (from Price and McCrory 2005).

there is some additional recruitment of visuo-spatial areas for languages with non-alphabetic orthographies (e.g., left middle frontal gyrus for Chinese: see meta-analysis by Tan et al. 2005). The frontal, temporoparietal and occipitotemporal regions essentially comprise the language, auditory, cross-modal and visual areas of the brain. At a very simple level, semantic and memory processing is thought to occur in temporal and frontal areas, auditory and phonological processing in temporal areas, articulation in frontal areas, visual processing in occipital areas and cross-modal processing in parietal areas.

Although there are still relatively few neuroimaging studies of children reading, the studies that have been done show a high degree of consistency in the neural networks recruited by novice and expert readers. For example, work by Turkeltaub and colleagues has used fMRI and the false font task to compare neural activation in English-speaking participants aged from 7 to 22 years (Turkeltaub et al. 2003). Importantly, 7-year-olds can perform the 'false font' task as well as adults, hence changes in reading-related neural activity are likely to reflect developmental differences rather than differences in reading expertise. Turkeltaub et al. (2003) reported that adults performing their task activated the usual left hemisphere sites, including left

posterior temporal and left inferior frontal cortex. They then restricted the analyses to children below 9 years of age. Now the main area engaged was left posterior superior temporal cortex. This region is traditionally considered the focus of phonological activity, and is thus thought to be active during grapheme–phoneme translation. As reading developed, activity in left temporal and frontal areas increased, while activity previously observed in right posterior areas declined. This pattern was interpreted as showing that reading-related activity in the brain becomes more left-lateralised with development.

In further analyses focusing just on the younger children, the researchers investigated the relationships between three core phonological skills and word processing. The three core phonological skills are usually taken to be phonological awareness, phonological memory and rapid automatised naming (RAN). I will focus on the phonological awareness findings here. Turkeltaub et al. (2003) calculated partial correlations between activated brain regions and each of these three measures while controlling for the effects of the other two measures. They reported that the three different measures correlated with three distinct patterns of brain activity. Brain activity during phonological awareness tasks appeared to depend on a network of areas in left posterior superior temporal cortex (phonology and grapheme–phoneme translation) and inferior frontal gyrus (articulation). The level of the children's phonological skills modulated the amount of activity in this network. As noted earlier, the left posterior temporal sulcus was the primary area recruited by young children at the beginning of reading development. Therefore, neuroimaging data suggest that phonological recoding to sound rather than logographic recognition is the key early reading strategy. Activity in the inferior frontal gyrus increased with reading ability. This area is also a key phonological area (Broca's area), important for the motor production of speech. Left inferior frontal gyrus is also activated when deaf children perform phonological awareness tasks silently in fMRI studies (MacSweeney et al. 2005).

An fMRI study of 119 typically developing readers aged from 7 years to 17 years by Shaywitz and colleagues found a similar developmental pattern (Shaywitz et al. 2007). Instead of the false font task, this study used a rhyme decision task (e.g., 'do these items rhyme?': leat, kete), and a visual line orientation task (e.g., 'Do [\\V] and [\\V] match?'). Shaywitz and his colleagues reported that networks in both left and right superior and middle frontal regions were more active in younger readers, with activity declining as reading developed. In contrast, activity in the left anterior lateral occipitotemporal region increased. This region includes the putative visual word form area (VWFA). Hence both Turkeltaub et al. (2003) and Shaywitz et al. (2007) found decreased right hemisphere involvement as reading developed, but found this for somewhat different neural networks. The difference in the behavioural tasks used (e.g., false font versus rhyme judgement) may explain some of these differences.

Overall, therefore, current neuroimaging data support a 'single route' model of reading development, based on a process of developing orthographic–phonological connections at different grain sizes (Ziegler and Goswami 2006). Reading is founded in phonology from the beginning (Goswami and Ziegler 2006b). The VWFA becomes more active as reading develops, reflecting the development of an orthographic lexicon containing both whole words and fragments of familiar words such as orthographic rimes (Pugh 2006). The VWFA is not a logographic or visual lexicon, able to support 'Chinese' processing or the 'direct route' from printed word to meaning postulated by 'dual-route' theory. Neuroimaging studies of typically developing readers show that the

neural networks for spoken language play an important developmental role in reading from the outset.

Neuroimaging studies of dyslexia
The networks recruited for reading

Neuroimaging studies of adult readers with developmental dyslexia suggest that there is atypical activation in the three important neural sites for reading, namely the left posterior temporal regions, the left inferior frontal regions and the left occipitotemporal regions (such as the VWFA). These data suggest both problems with the phonological aspects of reading and with the efficient development of an orthographic lexicon (e.g., Brunswick et al. 1999). These fMRI and PET studies typically rely on tasks such as word and nonsense word reading (e.g., 'valley', 'carrot', 'vassey', 'cassot'), and the 'false font' task. Again, the experimental picture is largely one of convergence across orthographies. For example, adult dyslexics in Italian, French and English all showed activation of a left-lateralised neural network based around posterior inferior temporal areas and middle occipital gyrus (Paulesu et al. 2001). This was a cross-language comparison within one study. However, issues of experimental design become critical when comparing individual imaging studies across languages. When studying any kind of disability, it is crucial to equate participant groups for their overall ability in the actual tasks being used to acquire the neuroimaging data. For example, it is impossible to interpret group differences in brain activity if the dyslexics are worse at reading the nonsense words being used than the control adults. In this case, differences in neural activation could simply reflect different skill levels (i.e., behavioural differences in reading performance). Similarly, it is critical to use the same criteria for acquiring images of the brain in different studies if interpretations about cross-language differences are being drawn (e.g., Ziegler 2005). Otherwise, apparent language-based differences could simply reflect differences in the significance thresholds or other experimental criteria used to acquire the images by different research groups.

Neuroimaging studies of children with developmental dyslexia report a very similar pattern to adult data (e.g., Shaywitz et al. 2002, 2007; Simos et al. 2000). For example, Shaywitz et al. (2002) studied 70 children with dyslexia aged on average 13 years, and compared them to 74 11-year-old typically developing controls (although the controls were not matched for reading level). Using fMRI, the children were scanned while performing a variety of reading-related tasks. These were letter identification (e.g., are t and V the same letter?); single letter rhyme (e.g., do V and C rhyme?); non-word rhyming (e.g., do leat and jete rhyme?); and reading for meaning (e.g., are corn and rice in the same semantic category?). Brain activity in each condition was contrasted with activity in a baseline condition, the line orientation task (e.g., do [\\V] and [\\V] match?). Shaywitz et al. (2002) reported that the children with developmental dyslexia showed under-activation in the core left temporoparietal networks, with older dyslexics showing over-activation in right inferior frontal gyrus. The children with developmental dyslexia also showed increased activation in right temporoparietal networks. One drawback of the study, however, was that there were group differences in behavioural performance in some of the component tasks. In the non-word rhyming measure, for example, the controls [79%] were significantly better than the children with dyslexia [59%]). This means that some of the differences found in brain activation could reflect differing levels of expertise rather than differences core to having developmental dyslexia. In a subsequent study of an expanded sample, Shaywitz et al. (2007) used in-magnet non-word reading ability as a covariate to control for this problem. Shaywitz et al. compared 113 dyslexic children aged 7–18 years to

the 119 typically developing readers discussed above in the non-word rhyme and visual line orientation tasks. Compared to the typically developing children, the dyslexic children showed no age-related increase in the activity of the VWFA. Instead, activity in the left inferior frontal gyrus (speech articulation) and the left posterior medial occipitotemporal system both increased, and reading did not become left-lateralized, with continued right hemisphere involvement.

There are also a few studies in the literature exploring the neural networks recruited for reading by dyslexic children in other languages. A study of 13 German dyslexic children aged 14–16 years was reported by Kronbichler et al. (2006). They used a sentence verification task (e.g., 'A flower needs water' – TRUE), in an fMRI design, to try and replicate natural reading. A false font task provided the control task. Consistent with studies of English dyslexics, they found reduced activation of left occipitotemporal networks and increased activation of left inferior frontal areas. A study of eight Chinese children with developmental dyslexia reported by Siok et al. (2004) claimed biological disunity, however. Their fMRI study used a homophone judgement task, in which the children had to decide whether two different Chinese characters made the same sound (an English homophone is <u>week</u> – <u>weak</u>), and a character decision task, in which the children saw one Chinese character and had to decide whether it was a real word or not. The first task was intended to measure orthography–phonology connections, and the second orthography–semantic relations. Siok et al. (2004) reported that the Chinese dyslexics did not demonstrate the reduced activation in left temporoparietal regions that would typically be found in developmental dyslexia in English during the homophone judgement task. Instead, an area involved in visuo-spatial analysis showed reduced activity, the left middle frontal gyrus. Siok et al. (2004) used this latter finding to argue that the biological marker for developmental dyslexia in Chinese was reduced activation of left middle frontal gyrus. However, the design of this study does not yet permit this conclusion. A control group matched for reading level is also required. Reduced activation in left middle frontal gyrus when making homophone judgements in Chinese might be expected for the level of reading achieved by the children with dyslexia. If this were to be the case, then increased involvement of networks for visuo-spatial analysis as reading develops would be part of typical reading development in Chinese, rather than a unique biological marker for developmental dyslexia.

Developmental differences in the time course of neural activation

While fMRI studies can provide important information about the neural networks supporting reading in typically developing versus dyslexic readers, they do not provide information about the time course of neural processing. This is important, as in typically developing readers words are distinguished from non-words within around 180 ms, suggesting early contact with the VWFA and semantic sites. It seems likely that this process would be delayed in developmental dyslexia. Similarly, it seems possible that cognitive processes such as grapheme–phoneme conversion might take longer in developmental dyslexia.

A longitudinal study of 33 English-speaking children using magnetic source imaging (MSI) compared brain activation in a letter–sound task (the child sees a letter and has to provide its sound) and a simple non-word reading task (e.g., 'lan') at the end of kindergarten and again at the end of grade 1 (Simos et al. 2005). Magnetic source imaging depends on a combination of magneto-encephalography (MEG) and MRI. The MEG measures the magnetic fields generated by the electrical activity in the brain rather than the

electrical activity itself (the latter is measured by EEG). These magnetic fields are tiny, they are one billion times smaller than the magnetic field generated by the electricity in a lightbulb. By combining this information with MRI scans, both the time course and spatial localisation of brain activity is possible. Of the 33 children studied, 16 were thought to be at high risk of developing dyslexia.

Simos et al. (2005) reported that the high-risk group were significantly slower to show neural activity in response to both letters and non-words in kindergarten in the occipitotemporal region (320 ms compared to 210 ms for those not at risk). The high-risk group also showed atypical activation in the left inferior frontal gyrus when performing the letter–sound task, with the onset of activity *increasing* from 603 ms in kindergarten to 786 ms in grade 1. The typically developing readers did not show this processing time increase. Comparing the onset of activity of the three core neural networks for reading, Simos et al. (2005) reported that low-risk children showed early activity in the left occipitotemporal regions, followed by activity in temporoparietal regions, predominantly in the left hemisphere, and then bilateral activity in inferior frontal regions. In contrast, high-risk children showed little differentiation in terms of the time course of activation between the occipitotemporal and temporoparietal regions. High-risk children who were non-responsive to a phonological remediation package also being administered ($n = 3$) were distinct in showing earlier onset of activity in inferior frontal gyrus compared to the temporoparietal regions. Given the current dearth of time-course studies by other research groups in either English or in other languages, it is difficult to interpret these differences in terms of the cognitive components of reading. Nevertheless, Simos et al. (2005) comment that the increased inferior frontal activation probably reflects the role of compensatory articulatory processes. As noted earlier, deaf children also show increased inferior frontal activation during phonological processing tasks. This may indicate that children with phonological difficulties rely more heavily on networks for articulation when phonological processing is required.

The neural effects of remediation

Although there are a variety of remediation packages for dyslexic children based on different theories of developmental dyslexia, the most effective packages across languages appear to be those offering intensive phonological intervention (e.g., Bradley and Bryant 1983; Schneider, Roth, and Ennemoser 2000). Simos and his research group (2002) used magnetic source imaging to explore neural activation in eight children with developmental dyslexia who had received 80 hours of intensive training with such a package and who had shown significant benefits from the remediation (Simos et al. 2002). MSI scans were taken during a non-word rhyme matching task (e.g., 'yoat', 'wote') both before the intervention and following remediation. Simos et al. (2002) reported that prior to the intervention, the dyslexic children showed the expected hypoactivation of left temporoparietal regions. Following the intervention, all eight children showed a dramatic increase in the activation of left temporoparietal regions, predominantly in the left posterior superior temporal gyrus (the networks supporting grapheme–phoneme recoding in typically developing readers: see Turkeltaub et al. 2003). These activation profiles were very similar to those of eight controls who also participated in the MSI study, but who did not require remediation. Nevertheless, even after remediation neural activity was delayed in the children with dyslexia relative to the controls. The peak in left superior temporal gyrus activity occurred at 837 ms on average for the dyslexic children, and at 600 ms for the controls. The data were taken to show a normalisation

of brain function with remediation. Nevertheless, Simos et al. (2002) commented that even with intensive remediation, children with dyslexia are slow to achieve the reading fluency shown by non-dyslexic children.

Shaywitz and Shaywitz (2005) used retrospective examination of the large sample of children with developmental dyslexia reported in Shaywitz et al. (2002) to compare the different developmental trajectories for children at risk for reading difficulties. Shaywitz and Shaywitz (2005) distinguished three groups within this sample when they were young adults. The first was a group of persistently poor readers (PPR), who had met criteria for poor reading in both the 2nd/3rd and the 9th/10th grades. The second was a group of accuracy-improved poor readers (AIR), who had met criteria for poor reading in the 2nd/3rd grades but who did not meet criteria in the 9th/10th grades. The third was a control group of non-impaired readers (C), who had never met criteria for poor reading (the participants had been studied since the age of 5 years). Shaywitz and Shaywitz (2005) reported that both the PPR and the AIR groups showed hypoactivation of the core left hemisphere sites when required to manipulate phonology. For example, in a nonsense word rhyming task, both groups of young adults still showed relative hypoactivity in neural networks in left superior temporal and occipitotemporal regions. However, the groups were distinguished by their neural activity when reading real words. The AIR group still demonstrated under-activation in the usual left posterior areas for real word reading, whereas the PPR group activated the left posterior regions to the same extent as controls (this was an unexpected finding).

Shaywitz and Shaywitz (2005) then carried out further analyses based on connectivity. Connectivity analyses examine the neural areas that are functionally connected to each other during reading. The connectivity analyses suggested that reading achievement depended on memory for the PPR group, and not on the normalised functioning of the left posterior regions. The unimpaired controls demonstrated functional connectivity between left hemisphere posterior and anterior reading systems, but the PPR group demonstrated functional connectivity between left hemisphere posterior regions and right prefrontal areas associated with working memory and memory retrieval. Shaywitz and Shaywitz (2005) speculated that the PPR group were reading primarily by memory. As the words used in the scanner were high-frequency, simple words, this is quite possible. However, this design choice complicates the interpretation of the neural differences found, as the PPR group may not be able to use memory strategies to read less frequent or less simple words. For such stimuli, the PPR and AIR groups may show similar neural profiles. It may also be important that the PPR group had, in general, lower IQ scores than the AIR group. Prospective longitudinal studies comparing patterns of neural activation and connectivity in dyslexic children as high-frequency words become over-learned would clearly be very valuable.

Different technologies, different research questions: the promise of brain imaging for understanding reading and developmental dyslexia

As will be clear from the foregoing review, most studies of reading development and of developmental dyslexia have relied on fMRI. These studies have provided excellent data regarding the neural networks underpinning reading in typically developing and dyslexic readers. They have also shown that the functional organisation of the networks for reading is similar in typical development and in dyslexia. Children with developmental dyslexia do not recruit radically different neural networks when they are reading. Rather, they show hypoactivation of crucial parts of the network of areas involved in word

recognition, and an atypical pattern of continuing right hemisphere involvement. Although highly informative, these studies are essentially correlational studies. They can answer research questions about the neural demands made by learning to read in different languages, and they can answer research questions about the core neural systems involved for dyslexic and typically developing readers. They can also answer research questions about the patterns of connectivity between different neural networks. However, they cannot answer research questions about what 'goes wrong' in the dyslexic brain, although they can help to rule out hypotheses (e.g., about the visual basis of developmental dyslexia; see Eden and Zeffiro 1998).

Neuroimaging methods that provide data on the time course of neural processing, such as MEG (MSI) and EEG, can begin to answer causal questions. As might be expected, it has been shown using MSI that neural activation is delayed in core components of the network of areas recruited for reading by children at risk for dyslexia. However, behavioural studies showing that children with developmental dyslexia are slower to read words aloud make the same point. When EEG or MSI techniques show that core components of the reading network are activated in a different order in dyslexia compared to typical reading, this is more informative with respect to causality. For example, Simos and his colleagues have shown atypically earlier onset of activity in inferior frontal gyrus (articulation) compared to the temporoparietal regions in three children at high risk for dyslexia who appear to be non-respondent to a phonological remediation package. If robust with larger samples and diagnosed dyslexics, such findings could suggest that there are different neuro-developmental routes to word recognition for dyslexic children compared to controls. Nevertheless, these different neuro-developmental routes are not the cause of dyslexia. Rather, they illustrate the response of a dyslexic brain to being trained to learn to read.

In my view, the most informative studies with respect to causation in developmental dyslexia are longitudinal prospective studies that use brain imaging to study basic sensory processing in at-risk children, with a view to understanding the causes of the phonological deficit. Here, the most promising studies to date are those investigating basic auditory processing using methodologies sensitive to the time course of auditory processing at the millisecond level. For example, a large-scale Finnish study (the Jyväskylä Longitudinal Study of Dyslexia (JLD): see Lyytinen et al. 2004a) has followed babies at familial risk for dyslexia since birth. A large variety of behavioural and EEG measures has been taken as the children have developed. EEG measures of auditory sensory processing (evoked response potentials to speech and non-speech cues) have been found to distinguish the at-risk babies from controls even during infancy (e.g., Lyytinen et al. 2005). For example, infants at risk for developmental dyslexia were less sensitive to the auditory cue of duration at six months of age (Richardson et al. 2003). The infant participants had to discriminate between two bisyllabic speech-like stimuli with a varying silent interval (e.g. 'ata' versus 'atta'). Duration discrimination was still impaired when the same children were 6.5 years of age (Lyytinen et al. 2004b).

English children with developmental dyslexia are also impaired in this duration discrimination task (Richardson et al. 2004). In addition, English children are impaired in discriminating the rise time of amplitude envelopes at onset, which is an important auditory cue to the onset of syllables in the speech stream (Goswami et al. 2002; Richardson et al. 2004). Finnish adults with developmental dyslexia also show rise time processing impairments, and individual differences in rise time sensitivity predicted up to 35% of unique variance in phonological tasks like rhyme recognition (Hämäläinen et al. 2005). In the English studies, individual differences in rise time sensitivity predict unique

variance in both phonological awareness measures (around 20%: Richardson et al. 2004) and in reading and spelling measures (around 25%: Goswami et al. 2002). We are currently collecting EEG data comparing rise time discrimination in English children with and without dyslexia. Data so far suggest that children with developmental dyslexia indeed show atypical auditory processing of rise time stimuli, with N1 amplitude (an EEG measure of sound registration) failing to reduce as amplitude envelope rise times become extended (Thomson, Baldeweg, and Goswami 2005). This suggests that neural responses in the dyslexic brain do not distinguish between different rise times, at least for the auditory processing comparisons used in our study (15 ms versus 90 ms rise times).

Conclusion

Different neuroimaging methodologies contribute complementary data regarding the neural networks underpinning reading acquisition and developmental dyslexia. While fMRI studies can identify the core neural systems involved in reading, EEG and MEG methodologies are required to investigate the time course of activation of the different networks that contribute to word recognition, and to investigate potential sensory precursors of the phonological deficit. With respect to key questions in education, each neuroimaging method can contribute different kinds of data. For example, when evaluating the claims made for different kinds of remediation package for developmental dyslexia, fMRI will be useful in assessing whether interventions affect the core neural networks for reading, or affect a different kind of network (e.g., motivational systems). When evaluating claims that the core cognitive difficulty in developmental dyslexia lies in forming a high-quality phonological representation, methodologies that can explore the time course of sensory processing such as EEG will be most useful. Neuroimaging methods are of optimal use when they can provide experimental data that is not available from behavioural investigations. For example, it is possible in principle to identify neural markers of risk for developmental dyslexia that can be measured in pre-verbal infants and in older children without requiring their explicit attention (Szücs and Goswami 2007). It is these areas of neuroscience that are likely to be of most potential benefit to educators.

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