The neural signature of orthographic–phonological binding in successful and failing reading development

Leo Blomert *

Dept. Cognitive Neuroscience, Faculty of Psychology & Neuroscience, Maastricht University, The Netherlands
Maastricht Brain Imaging Center, Maastricht University, The Netherlands

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ABSTRACT

Learning to read in alphabetic orthographies starts with learning a script code consisting of letter–speech sound pairs. Although children know which letters belong to which speech sounds within months, it takes much longer to automatically integrate them into newly constructed audiovisual objects. This extended learning process corresponds with observations that reliable letter and word specific activations in the fusiform cortex also occur relatively late in reading development. The present review discusses electrophysiological and neuroimaging studies of the nature and mechanisms involved in letter–speech sound integration in normal and dyslexic readers. It is demonstrated that letter–speech sound associations do not develop in parallel with visual letter recognition but immediately work in concert to form orthographic–phonological bonds which remain active even in experienced reading. Effective letter–speech sound integration may be necessary for reliable letter recognition to develop. In contrast, it is this basic integration of letters and speech sounds which poses an immediate problem for beginning dyslexic readers, and remains problematic in adult dyslexic readers. It is hypothesized that a specific orthographic–phonological binding deficit may not only act as a proximal cause for reading deficits in dyslexia, but may also explain the notorious lack of reading fluency. Finally, it is suggested that similar integrated audiovisual representations may also exist for larger grain-sizes in the same posterior occipitotemporal/inferoparietal network as identified for orthographic–phonological integration of letters and speech sounds.

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Introduction

In contrast to oral communication, reading is such a recent cognitive skill that evolution very probably did not have a chance to prepare our brains for it. Around ninety percent of people, nevertheless, learn to read without problems, if properly instructed. It is by now generally accepted that reading acquisition profits from an already developed evolutionary anchored spoken language system (e.g., Liberman et al., 1974). It is therefore of interest that there is a small group of developmentally dyslexic children who exhibit specific problems learning to read, consequent upon a genetic predisposition (e.g., Pennington and Olson, 2005; Schumacher et al., 2007). These children generally do not show salient spoken language impairments before reading acquisition starts (Byrne et al., 2008). The fact that learning to read and spoken language development show strong interactive influences (e.g., Morais et al., 1979; Perfetti et al., 1987) further suggests that cross-modal processing of spoken and written letter and word forms might be rather influential in successful and failing reading development.

Since complex cognitive functions like e.g. reading are built on connectivity within large scale neuronal networks, rather than on strictly localised processes (Engel et al., 2001), it is not unlikely that reading acquisition processes give rise to new functions and/or new configurations in the neural network for processing speech: Literate adults used rather different neural networks for processing auditory pseudowords than illiterates did (Castro-Caldas et al., 1998). Learning to read initiates massive cognitive adaptations of evolutionary ingrained brain systems for speech and visual object recognition and one may ask which functions we lose by such an acculturation of evolutionary precursor functions for reading (Dehaene and Cohen, 2007). So, do children who fail to learn to read still exhibit functions which have been modified or even been lost in more successful readers? For example: dyslexic children identified symmetrical dot patterns and letters equally fast, whereas their normal reading peers were slower for letters (Lachmann and Van Leeuwen, 2007). Successful readers have learned to suppress symmetry generalization, a function advantageous for visual object recognition, but obviously not for letter recognition (i.e., b vs. d) and reading. Furthermore, dyslexic readers exhibit better within speech sound category discrimination then normal readers (Serniclaes et al., 2001) and show less well separated and broader phonemic categories than normal readers (e.g., Godfrey et al., 1981). The detection of speech

* Dept. Cognitive Neuroscience, Faculty of Psychology & Neuroscience, Maastricht University, P.O. Box 616, 6200 MD Maastricht, The Netherlands.
E-mail address: l.blomert@maastrichtuniversity.nl.

sound details in originally redundant overlapping spoken speech representations may thus constitute an ability lost to normal readers, who have developed more distinct phonological representations under the influence of successful reading development. Such an interpretation questions the independence of speech sound categories used in speech perception and the ones involved in grapheme–phoneme associations (e.g., Grainger and Holcomb, 2009).

In sum; the absence of the modifying effects of successful reading in severely disabled readers may deeply compromise theoretical approaches that specify reported cognitive and perceptual deficits as the causative agents in reading deficits. However, the finding that forty percent of children at familial risk for dyslexia develop reading deficits (Byrne et al., 2008), which are already evident in a relatively transparent orthography within months after the start of reading instruction (Blomert and Willems, 2010), points to potential causes of reading deficits which were almost immediately present and (negatively) effective. It is therefore interesting to have a closer look at the learning milestones which characterize initial reading acqui-sition in normal and dyslexic readers.

Acquiring a basic alphabetic script code

Learning letters is one of the first steps in initial reading instruction and an elegant series of electrophysiological studies has provided insights in the developmental time course of letter recognition processes. Maurer et al. (2005) showed that children who did not read yet, but who exhibited considerable letter knowledge, did not show any neural tuning for print in kindergarten; i.e., no difference in activation between letter strings and symbol strings. Half of these children did show print-specific neural responses in first grade, but it took till second grade before all normal reading children showed reliable coarse tuning for the difference between printed words and symbol strings (Maurer et al., 2006). This finding closely corresponds with reports showing that the development of a specialisation for visual word recognition in the fusiform cortex also occurs comparably late in reading development (Booth et al., 2003; for review see Sandak et al., 2004). This late letter recognition development therefore does not seem a prime candidate to account for the finding of reading deficits within months in children at risk for dyslexia (Blomert and Willems, 2010).

Early interactions of print and speech

One of the first requirements for learning to read is the acquisition of a script code in which elements of the spoken language system, speech sounds, are linked with the letters or clusters of letters which are used to represent speech sounds (Ehri, 2005 for review). Reading acquisition thus starts by setting up *new* audiovisual grapheme–phoneme associations, which assumedly require extensive adapta-tions in the network connecting speech and visual object recognition and which may precede and/or work in concert with the development of reliable visual recognition of print in the fusiform cortex. This was recently illustrated in a combined ERP/fMRI study with pre-reading kindergarten children receiving a training aimed at learning letter–sound associations. The results revealed that successful learning of letter–speech sound associations resulted in an initial sensitization for print in occipitotemporal cortex (Brem et al., 2010). It may be remembered that familiarity with letters as such did not induce left lateralized print sensitivity in kindergarten children (see above, Maurer et al., 2005) and the emphasis on the connections between letters and speech sounds may have been critical in the Brem et al. study. An early study using magnetic source imaging asked children at the end of kindergarten to pronounce the sounds associated with visually presented letters (Simos et al., 2002). Children performing in the normal range of pre-reading behavioural tasks displayed a bilateral progressive increase in activation in the posterior superior

temporal gyrus up to approximately 400 ms and after this point in time only a further increase in left temporal cortex. This pattern thus already revealed a left lateralized response to letter–speech sound associations in pre-reading kindergarten children resembling similar results in adult normal readers for a similar task (Breier et al., 1999). In contrast, poor performers considered at-risk for developing reading deficits only revealed significant right superior temporal activation. This activation was also briefer, thus probably preventing, according to the authors, access to letter–speech sound representations. A recent study (Blomert and Willems, 2010) with pre-reading chil-dren at familial risk for dyslexia revealed that a substantial portion of these children showed severe problems in learning letter–sound associations during a training that was specifically designed to teach letter–sound associations (and identical to the one used in the neuroimaging study by Brem et al. described above). It is noteworthy that none of the at-risk children showing these letter–sound learning problems exhibited phonological deficits before or after the training. Early reading failure thus may relate to an early problem in setting up effective connections between brain areas involved in letter and speech sound processing. So, what do we know about the neural processes and mechanisms involved in letter–speech sound associa-tion in normal and abnormal reading development.

Letter–speech sound association in skilled readers

The network for orthographic–phonological integration

An early magneto-encephalographic (MEG) study found strong interactions between letters and speech sounds only in the superior temporal sulci (STS), occurring earlier in the left than in the right STS (Raij et al., 2000). A neuroimaging (fMRI) study complemented these findings by showing differences between existing and newly learned letter–speech sound associations (Hashimoto and Sakai, 2004). Japanese subjects were presented either with a string of three well-known Kana letters and Japanese speech sounds or with Korean Hangul letters combined with the same Japanese speech sounds or with letters combined with non-speech sounds. In the case of the well-known associations between Japanese speech sounds and letters, activation mainly occurred in occipitotemporal cortex, where-as the new associations between the Korean letters and Japanese speech sounds also recruited occipitoparietal areas.

A basic insight into the neural network for processing letters and speech sounds was reported in an fMRI study manipulating the congruency of letter–sound pairs (Van Atteveldt et al., 2004). Skilled readers were asked to watch letters and listen to speech sounds presented simultaneously without having to execute a task. The results revealed that areas in STS not only responded to isolated letters as well as to speech sounds, but also showed an enhanced response to bimodal stimulation whether congruent or incongruent. This finding confirmed the role of STS as an heteromodal audiovisual integration site for in-principle arbitrary associations (Calvert, 2001). Interestingly, the 'sensory specific' response from auditory cortex showed an enhancement to congruent and a suppression to in-congruent letter–sound pairs in comparison to the processing of speech sounds alone (see Fig. 1). Letters may thus systematically modulate speech sound activity in auditory cortex, in agreement with findings from animal studies showing that early auditory cortex is susceptible to cross-modal influences (Kayser and Logothetis, 2007). Evidence for feedback from heteromodal STS was confirmed in a Granger causality mapping analysis showing that the congruency effect in the planum temporale was very likely caused by feedback from STS (VanAtteveldt et al., 2009).

In sum; the network for the integration of letters and speech sounds encompassed the heteromodal superior temporal sulcus (STS) and the superior temporal gyrus (STG) extending posteriorly from the area around Heschl's gyrus into the superior temporal plane, but also