NeuroImage 128 (2016) 316–327

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Orthographic processing deficits in developmental dyslexia: Beyond the ventral visual stream

Marianna Boros [a], Jean-Luc Anton [b], Catherine Pech-Georgel [c], Jonathan Grainger [d], Marcin Szwed [a,*], Johannes C. Ziegler [d,*]

[a] Institute Of Psychology, Jagiellonian University, Kraków, Poland
[b] Centre D'IRM Fonctionnelle Cérébrale — Institut De Neurosciences De La Timone, Aix Marseille University, CNRS, Marseille, France
[c] Centre De Références Des Troubles D'Apprentissages, Institut du Développement de l'Enfant et de sa Communication (IDEC), Hôpital Salvator, Marseille, France
[d] Laboratoire De Psychologie Cognitive, Brain And Language Research Institute, Aix-Marseille University and CNRS, Marseille, France

ARTICLE INFO

Article history:
Received 14 April 2015
Accepted 6 January 2016
Available online 13 January 2016

Keywords:
Dyslexia
Visual Word Form Area
Dorsal stream
Ventral stream
Phonological deficit
Visuo-spatial processing
fMRI

ABSTRACT

Fast effortless reading has been associated with the Visual Word Form Area (VWFA), a region in the ventral visual stream that specializes in the recognition of letter strings. Several neuroimaging studies of dyslexia revealed an underactivation of this region. However, most of these studies used reading tasks and/or were carried out on adults. Given that fluent reading is severely impaired in dyslexics, any underactivation might simply reflect a well-established reading deficit in impaired readers and could be the consequence rather than the cause of dyslexia. Here, we designed a task that does not rely on reading per se but that tapped early visual orthographic processing that forms the basis of reading. Dyslexic children aged 8–12 years and age-matched controls were asked to search for letters, digits, and symbols in 5-element strings (Experiment 1). This novel task was complemented by a classic task known to activate the VWFA, namely the passive viewing of pseudowords and falsefonts (Experiment 2). We found that in addition to significant group differences in the VWFA, dyslexic children showed a significant underactivation of the middle occipital gyrus (MOG) relative to the control group. Several areas in the MOG are known for their engagement in visuospatial processing, and it has been proposed that the MOG is necessary for ordering the symbols in unfamiliar strings. Our results suggest that the VWFA deficit might be secondary to an impairment of visuospatial processing in the MOG. We argue that efficient processing in MOG in the course of reading acquisition is critical for the development of effortless fast visual word recognition in the VWFA.

1. Introduction

Learning to read is one of the most important educational milestones in a child's development. Normally developing children typically achieve fluent reading between 2nd and 4th grades depending on the orthography of the language (Vaessen et al., 2010; Ziegler and Goswami, 2005). During this important period, children's reading ability undergoes a transition from rather serial letter-by-letter decoding to parallel processing of words as a whole. Critically, children with developmental dyslexia (~5–15% of children in primary school) fail to make this transition. As a consequence, many of them will never develop fast automatic word recognition and fluent reading despite normal intelligence, adequate educational opportunities and in the absence of any obvious neurological or sensory deficiencies (Shaywitz and Shaywitz, 2005; Snowling, 2001).

1.1. Orthographic processing deficits in dyslexia

There is a tremendous amount of research on the neural basis of phonological processing deficits and how such deficits affect phonological decoding and therefore reading development (for review, see Paulesu et al., 2014). However, much less is known about basic orthographic processing deficits in dyslexia. Yet, children with dyslexia exhibit deficits in processing letter strings in tasks with minimal phonological or lexical involvement, such as when being asked to search for a target letter in an unpronounceable string of consonants (Bosse et al., 2007; Collis et al., 2013; Hawelka et al., 2006; Ziegler et al., 2010). The first explanation that comes to mind is that these deficits are simply the consequences of the weaker reading experience of children with dyslexia. However, the same deficits can be found with digit strings (Collis et al., 2013; Hawelka et al., 2006; Ziegler et al., 2010), which

Abbreviations: PPC, posterior parietal cortex; vOT, ventral occipitotemporal; VWFA, Visual Word Form Area; fMRI, functional magnetic resonance imaging; SPL, superior parietal lobule; RAN, rapid automatic naming; EPI, echo-planar imaging; MNI, Montreal Neurological Institute; DARTEL, Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra; FWE, familywise error; ROI, region of interest; BOLD, blood oxygenation level dependent; MOG, middle occipital gyrus; SVM, support vector machine; IPS, intraparietal sulcus; IPL, inferior parietal lobule; DMN, default mode network.

* Corresponding authors.
E-mail addresses: mfszwed@gmail.com (M. Szwed), Johannes.Ziegler@univ-amu.fr (J.C. Ziegler).

http://dx.doi.org/10.1016/j.neuroimage.2016.01.014
1053-8119/

undermines this explanation. Some authors have explained these deficits in terms of poor visual attentional processing (Dubois et al., 2010; Valdois et al., 2003; Vidyasagar and Pammer, 2010). Indeed, it has been shown that dyslexics who had the weakest performance in letter-in-string perception benefited the most from increased letter spacing, which has the effect of reducing the lateral masking of letters called crowding (Gori and Facoetti, 2015; Zorzi et al., 2012). Others have attributed poor letter-in-string perception to deficient letter position coding. Indeed, Collis et al. (2013) used a partial report task with letter, digit, and symbol strings. The response alternatives included other characters in the string, which made it possible to investigate position as well as intrusion errors. As in Ziegler et al. (2010), dyslexics performed significantly worse than age-matched controls with letter and digit strings but not with symbol strings. However, the dyslexics' deficits with letter string stimuli were limited to position errors, specifically at the string-interior positions 2 and 4. These results were taken to suggest that dyslexics have a deficit in processing a string of letters in parallel, probably due to difficulty in the coding of letter position.

The literature on letter-in-string processing can be placed in the more general context of deficits in visual search in dyslexia. Indeed, in classic visual search tasks using symbols, it has been shown that dyslexic children exhibited longer search times with an increasing number of distractors than age-matched controls (Casco et al., 1998; Vidyasagar and Pammer, 1999). Similarly, dyslexic children performed below their control peers in tasks where they had to report the number of elements belonging to a certain category in a string of symbols (Lobier et al., 2012b; Valdois et al., 2012). Moreover, serial visual search abilities in kindergarten were found to be predictive of future reading skills at first and second grades of primary school (Franceschini et al., 2012; Gori et al., 2015).

1.2. The link between focused attention and reading

What is the link between visual search and reading? Clearly, during beginning reading, letters are recognized sequentially, with only a few letters being processed at a time. In current computational models of reading aloud (Perry et al., 2013, 2010, 2007,), this process has been implemented as an attentional window that moves across a letter string and provides the input to the phonological decoding network, which is necessary for orthographic learning (Ziegler et al., 2014). Focused spatial attention is needed for this operation. The visual guidance of attention is achieved through the dorsal stream, which receives its major input from the magnocellular system (see Vidyasagar and Pammer, 2010). The magnocellular dorsal pathway consists of large heavily myelinated neurons with fast conduction velocity, it passes dorsally to the visual motion-sensitive areas (MT/V5) situated at the occipitotemporal junction and from there onto the posterior parietal cortical (PPC) angular and supramarginal gyrus. Although it has been known for a long time that these areas are important for reading, it has recently been suggested that the angular and supramarginal gyri are involved in focusing visual attention very rapidly on the letters and their order in words rather than associating the visual form of a word with its sound and meaning (Stein, 2014). The visual part of this association is achieved by the ventral occipitotemporal cortex (vOT), which hosts the Visual Word Form Area (VWFA).

The VWFA is located in the fusiform gyrus. It receives its main input from the parvocellular system, and its main function is to detect the texture, form and colour of objects. The ventral route, which hosts the VWFA, can recognize letter strings but it cannot code their precise location, which of course is vital for reading development. Hypothetically, the rapid dorsal route provides feedback to V1 and the VWFA about where to attend in order to identify letters and specify their order in a word (Vidyasagar and Pammer, 2010). Thus, during reading development, the dorsal stream might allocate attention to appropriate areas of text, thus providing feedback to the ventral stream to allow fined-grained analyses of letters (Jones et al., 2008).

1.3. fMRI studies on dyslexia

There are an increasing number of neuroimaging studies on dyslexia (for reviews and meta-analyses, see Martin et al., 2015; Norton et al., 2015; Paulesu et al., 2014; Richlan et al., 2011, 2009). Almost all of them showed an underactivation of the vOT area in dyslexics (Blau et al., 2010; Brunswick et al., 1999; Horwitz et al., 1998; Kronbichler et al., 2004; Paulesu et al., 2001; Shaywitz et al., 2002, 1998; van der Mark et al., 2009). This is not really surprising because the vOT contains the Visual Word Form Area (VWFA), a region specifically tuned to process letter strings (Cohen et al., 2002; Dehaene and Cohen, 2011; Dehaene et al., 2002). Because activation in this region increases with reading skill, Shaywitz et al. (2002) referred to the left vOT as a "reading skill zone". Because reading skills are impaired in dyslexia, it seems obvious to find an underactivation of the vOT in dyslexia (Sandak et al., 2004; Shaywitz and Shaywitz, 2005).

Some authors have suggested that the dysfunctional activation of the VWFA is secondary to a primary dysfunction of the temporoparietal reading system involved in controlled attention-demanding grapheme–phoneme processing and phonological decoding (McCandliss and Noble, 2003; Pugh et al., 2000). Several neuroimaging studies demonstrated underactivation of this left temporoparietal reading system, which includes the posterior superior temporal, supramarginal and angular gyri (Backes et al., 2002; Hoeft et al., 2006; Shaywitz et al., 2002; Temple et al., 2001). As suggested above, these regions might be involved in phonological decoding precisely because they make it possible to select graphemes, which are the input to the phonological decoding network.

In a recent meta-analysis of all neuroimaging studies on dyslexia published until September 2013, only three studies investigated letter-string processing with minimal lexical or phonological involvement (Peyrin et al., 2012; Reilhac et al., 2013; Temple et al., 2001). Studies from the Valdois group, including a recent fMRI study using adult dyslexics (Lobier et al., 2014), showed an underactivation of the bilateral superior parietal lobule (SPL) in processing letter or symbol strings. The activation of the posterior parietal cortex was found to be stronger for multiple-element than for single-element processing in skilled adult readers (Lobier et al., 2012a), which is supportive of its role in focusing attention. The study by Temple et al. (2001) showed reduced activation in extrastriate regions in letter matching, which included bilateral (left greater than right) middle/superior occipital gyrus and superior parietal lobe.

1.4. The present study

The goal of the present study was to investigate the interplay between the dorsal and ventral streams in basic orthographic processing, which involves processing of letter identities and letter position. Previous studies found a general underactivation of the VWFA in dyslexic readers. However, these studies are not very informative with respect to a causal deficit in orthographic processing because subjects were either asked to read out loud (Brunswick et al., 1999; Kronbichler et al., 2004; Paulesu et al., 2001), perform a rhyming task (Backes et al., 2002; Hoeft et al., 2006; Shaywitz et al., 1998) or make lexical or semantic decisions (Shaywitz et al., 2002, 1998; van der Mark et al., 2011, 2009) on words, pseudowords, irregular words or even sentences. Thus, underactivation can be expected because of the lack of reading experience. In particular, many of the studies scanned adult dyslexics, which leaves open possibility that the underactivations found in either the ventral stream (Brunswick et al., 1999; Paulesu et al., 2001; Shaywitz et al., 1998) or the parietal lobe (Lobier et al., 2014) are a consequence of long lasting deficits in reading fluency that occur earlier in development. In support of this interpretation, Richlan et al.'s (2009) meta-analysis showed that the underactivation in VWFA was mainly found in studies testing adult dyslexics (see also Martin et al., 2015).