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Phonological impairment in developmental dyslexia during reading: when, insights from event-related potentials

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Phonological impairment in developmental dyslexia during reading: When? Insights from event-related potentials

A thesis by

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Abstract

Research addressing cognitive deficits in developmental dyslexia is divided between phonological and visual processing camps, with little crosstalk between the two. However, reading – the activity impaired in dyslexia – is the faculty to access spoken language information in written form, i.e., visual input. Therefore, understanding of how reading operates, and may be disrupted, requires the study of phonological and semantic processing from orthographic information. Based on the theoretical literature on dyslexia as a reading deficit (Chapter One), and what we have learnt about normal reading from event-related potentials (ERPs; Chapter Two), the present thesis describes a programme of research investigating orthographic and phonological processing during reading with ERPs to characterise their interplay in dyslexia over time. The aim is to examine the extent to which these processes interact in dyslexia and if group differences are attributable to perceptual processes, attentional processes or both.

Throughout the studies reported, phonological content of written words appears to be processed similarly in dyslexic and control adults until post-perceptual processing stages. In Study 1, which tested orthographic and phonological priming effects during phonological decisions on pseudoword-word pairs, phonological priming did not differ between dyslexic and control readers until a late stage associated with stimulus reprocessing, indexed by the P600 wave. The earliest orthographic similarity responses (N1 amplitude) were reduced, however, and interacted with phonological processing at a later stage (N2-P3 ERP range). Study 2 showed that, even in a highly-constraining sentence context, phonological priming can override orthographic mismatches in skilled readers since homophones and pseudohomophones of highly expected words are

integrated similarly to best completion words during early phonological analysis (attenuated N2) and later semantic processing (attenuated N400). Following the rationale of Study 2, Study 3 compared the performance of dyslexic and control readers in a similar paradigm. Early phonological integration, indexed by N2, and conflicts between orthographic and phonological information, indexed by P2, were similar in the two groups but ERP modulations specific to phonologically acceptable misspellings failed to capture dyslexic participants attention to the same extent as it did in control participants in the P3a range. Thus, phonological processing differences seem to emerge at a late stage of orientation of attention towards phonological information after a 'normal' stage of perceptual decoding. Study 4 tested the reliability and generality of differences in attentional orienting responses using an adapted oddball design prone to elicit P3a effects. Replicating Study 3, responses to pseudohomophones were significantly attenuated in dyslexic readers, while P3a amplitudes elicited by deviants in a nonverbal control task were similar between the two groups of participants.

Overall, a consistent pattern has emerged from these studies: Detection and integration of phonological information from written words is early and automatic in both normal and dyslexic readers. In dyslexics, the deficit in reading appears to emerge at the stage of attentional orientation to phonological information, particularly when it conflicts with orthographic information. It remains unclear however, whether this effect is accompanied by an overall reduced sensitivity to orthographic form. In sum, deficient interactions between phonological, orthographic, and attentional processes appear to be at the core of the reading deficit in dyslexia, and these cannot really be considered separately.

Chapter One

General Introduction: Theoretical Background

Right now, your brain is adeptly translating an arbitrary visual code of letter strings (orthographic representation) into their pronunciations (phonological representation), and their meaning (semantic representation). For dyslexic readers, converting some or all of these codes will take a more concerted effort, with a possibly erroneous outcome. The present research focuses on the stage(s) of processing in which problems occur, the timing of occurrence of these problems, and how they can be understood in terms of broader, concurrent cognitive processes.

Here, after describing typical behavioural expressions of developmental dyslexia and how it is diagnosed, an overview will be given of the theoretical literature in dyslexia organised according to its relative phonological, visual or attentional focus. Since the overall focus of this PhD research is directed at the definitional impairment at the core of developmental dyslexia– the disruption of visual word recognition– the introduction will present the major cognitive perspectives in relation to their explanations of reading impairment, before justifying the rationale for this PhD research.

Overview of Developmental Dyslexia and its characteristics

Developmental dyslexia (henceforth dyslexia) is a specific difficulty in reading and spelling. It is the most common neurodevelopmental disorder, with an estimated prevalence of between 5% and 10% of the population (Shaywitz, 1996). It occurs in all known languages (Paulesu et al., 2001; Ziegler & Goswami, 2005). Despite reading being a recent human activity, which natural evolution has had little time to shape or regulate, there are clear albeit complex and unresolved genetic factors implicated in the manifestation of dyslexia, which appear to influence neuronal migration and axon growth (see Galaburda, LoTurco, Ramus, Fitch & Rosen, 2006; Schumacher, Hoffman, Schmäl, Schulte-Körne & Nöthen, 2007 for reviews). Presumably, the genetic bases of dyslexia, and, by extension, of successful reading, affect neurobiological and cognitive systems that are functionally adaptable to supporting reading. Honing in on the nature of these cognitive and neurobiological factors at the core of a fairly consistent pattern of behavioural deficits, and across subsets of dyslexic individuals, remains a primary ongoing research endeavour. The overall objective is to understand normal and dysfunctional reading processes and their interplay with other cognitive functions, to ensure accurate diagnosis, to optimise teaching methods, and to remediate reading difficulties in an optimal fashion.

The behavioural expression of dyslexia tends to vary with the orthographic characteristics of languages. In the case of orthographically opaque languages, such as English or French, reading (in)accuracy alone is usually an indicator of dyslexia, whereas in the case of orthographically consistent languages with reliable mappings between letters and sounds, like Italian or Welsh, a diagnosis of dyslexia is formed more on the observation of slow and effortful phonological recoding and poor spelling (Ziegler & Goswami, 2005). These differential manifestations in reading, dependent upon the relative consistency between orthographic form and pronunciation, highlights how the process of accessing phonological information in reading is important to reading outcome in dyslexia.

Phonological recoding has been described as the *sine qua non* condition of successful reading (Share, 1995; Ziegler & Goswami, 2005). Processing impairments in dyslexia are consistently observed in phonological awareness tasks, which require explicit manipulation of phonological information (e.g., phonemes). Phonological awareness (PA) tasks include tasks such as nonword repetition (Elbro, Borstom, & Petersen, 1998; Snowling, 1981), phonemic fluency (Frith, Landerl, & Frith, 1995), picture naming (Snowling, Watgendonk, & Stafford, 1988), spoonerisms (Perin, 1983; Landerl, Wimmer & Frith, 1997), phonemic substitution and deletion (Content, Kolinsky, Morais & Bertelson, 1986), and verbal short-term memory (e.g., Griffiths & Snowling, 2002). PA has strong established links with measures of reading ability (see Goswami & Bryant, 1990; Hansen & Bowey, 1994 Huang & Hanley, 1995), and is a good predictor of reading proficiency (e.g., Bradley & Bryant, 1983; Elbro et al., 1998; De Jong & Van der Leij, 1999). One of the skills most reliably revealed as impaired in dyslexia, across ages, ability, and level of compensation for reading difficulty, is pseudoword reading, which requires the decoding of pronounceable but lexically inexistent visual words (Bruck, 1992; Rack, Snowling, & Olson, 1992; Van Ijzendoorn & Bus, 1994).[1]

Phonological problems and reading difficulty alone, however, are insufficient indicators of dyslexia. Phonological problems are commonly associated with broader developmental disorders, such as apraxia of speech, specific language impairment, or more generalised learning disorders, such as Down's syndrome (see Snowling & Hulme, 2005). Most

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[1] The persistence of pseudoword reading deficits is a useful index of residual phonological deficits in high-functioning dyslexic adults. This dyslexic population is useful for research given the opportunity to recruit homogenous control samples with similar levels of reading experience. Group differences are then more easily attributable to cognitive differences than confounding experiential factors.

descriptions of dyslexia refer to a discrepancy between intelligence (i.e., IQ) and reading level (such that reading ability is below expectation based on intelligence), and have exclusion criteria such as symptoms of basic sensory or language impairments, or inadequate motivation or learning opportunity (International Dyslexia Association, 2002; World Health Organization, 1992). However, discrepancy-based definitions remain somewhat controversial because of the arbitrary cut-off values used when comparing IQ and reading ability (e.g., Siegel, 1992). This being said, strong longitudinal links between IQ and reading levels that dissociate in dyslexic individuals (Ferrer, Shaywitz, Holahan, Marchione & Shaywitz, 2010) support the use of IQ-reading discrepancy as a diagnostic heuristic. Discrepancy-based criteria are important in the diagnosis of dyslexia in adults, particularly within higher education, for whom an average reading level may have been attained but a relative disadvantage remains and has potential academic consequences (Rack, 1997). Beyond these descriptions, difficulties in processing phonological information have been integrated into working definitions of developmental dyslexia (e.g., International Dyslexia Association, 2002; Lyon, Shaywitz & Shaywitz, 2003), reflecting their status as an established symptom.

A diagnosis of developmental dyslexia currently requires a broad approach that expands beyond working definitions. An Educational Psychologist-led assessment consists of several hours of literacy and psychometric testing, selected to map relative strengths and weakness. In addition to measures of speeded and untimed word reading (usually of irregular words requiring whole string recognition), and measures of spelling and phonological skill, impairment may be expected on IQ subtests for which performance is less obviously related to reading. For example, the ACID profile (Arithmetic, Coding, Information and Digit Span subtests of the WAIS; Thomson & Grant, 1979) has long been considered a reliable indicator of dyslexia; while common observations of children having difficulty telling left from right and recalling sequences, such as reciting the months of the year, are reflected in the checks included in the Bangor Dyslexia Test (Miles, 1982) and Dyslexia Screening Test (Nicolson & Fawcett, 1996). These difficulties point to a global syndrome giving dyslexia the traits of a neurobiological disorder. Underperformance on the above measures is generally compared to comprehension and nonverbal IQ, which are usually relatively preserved (Nation & Snowling, 1997). There are, however, no commonly agreed criteria or test scores for a diagnosis of dyslexia. Profiles of difficulty and severity vary between dyslexic readers. Some poor readers and spellers, for example, may have poor exception word reading, but show no clear signs of phonological impairments; a profile often referred to as 'surface dyslexia' (see Bosse, Tainturier & Valdois, 2007, for one of the few theories that specifically attempts to account for this clinical profile). Since 'surface' and 'phonological' dyslexia may have significantly differing origins, most studies have focused on one or the other to prevent spurious effects arising from heterogenous aetiology of the participants. In the research reported here, for instance, participants were selected on the basis of phonological difficulties since our key objective was to investigate phonological deficits in reading.

Theoretical Perspectives: Phonological impairment

Impaired phonological representations

Possibly the most influential hypothesis regarding cognitive deficits in dyslexia is the phonological representations hypothesis ('PRH'; see Swan & Goswami, 1997; Snowling, 2000; Griffiths & Snowling, 2002; Vellutino et al., 2004). Indeed, there is general agreement across the dyslexia research field that some form of phonological processing impairment contributes to reading difficulty, and most theoretical perspectives on dyslexia attempt to account for, or relate their interpretation, to deficient phonological processes in some way (see Ramus et al., 2003). However, the phonological representations hypothesis takes a hard, fundamental view of the deficit. According to the PRH, phonological impairment is driven by poorly specified phonological representations and is at the core of developmental dyslexia (Stanovich & Siegel, 1994; Snowling, 2000). In other words, it is the coding of sounds itself that is coarse or poorly defined, making the individual less sensitive to phonemic information (the smallest units of sound in a language). Thus, the deficit is primarily thought to impact the decoding phase of reading, via the acquisition, and subsequent use, of grapheme to phoneme correspondence (GPC) rules; but is also thought to impact subsequent blending, retrieval, and maintenance of the phonological code (Snowling, 1989; Castles & Coltheart, 2004). Therefore, under the PRH, overall reading is expected to be impaired, with particular difficulties for words requiring GPC decoding. Evidence cited in support for this hypothesis comes from observations in dyslexic children of deficits in verbal short term memory (i.e., the maintenance of phonological information in working memory; Hulme, 1981), confrontation and rapid naming (involving the rapid generation of a lexico-phonological code; Snowling, van Wagtendonk & Stafford, 1988; Snowling & Hulme, 1994), verbal repetition of polysyllabic nonwords (involving articulation of phonological trace in verbal working memory; Snowling, 1981), verbal paired associate learning (i.e., the learning of unfamiliar phonological labels for items; Wimmer, Mayringer & Landerl, 1998), phonological awareness (cf., PA tasks above) and, albeit inconsistently, speech perception (McBride-Chang, 1996; Brady, 1997). Therefore, the PRH has gathered substantial behavioural evidence of deficient use of phonological information in dyslexia, and demonstrated its relevance to reading. However, its weakness is the questionable validity of a deficit circumscribed at the level of perceptual discrimination of phonemes given that the behavioural, meta-linguistic tasks used in most assessments have clear attentional and working memory components.

Impaired phonological representation due to an auditory processing deficit

Deficient phonological representations are also predicted by theories proposing that dyslexia stems from basic auditory deficits. This is the claim behind the rapid auditory temporal processing theory (Tallal, 1980; Tallal, Miller & Fitch, 1993). Based on research first carried out with children with specific language impairment (Tallal & Piercy, 1973), Tallal and colleagues found that individuals with dyslexia show deficits in temporal order judgement on sequences of complex tones when stimuli are brief and presented at short inter-stimulus intervals (ISIs; Tallal & Piercy, 1980; Reed, 1989; Martino, Espesser, Rey & Habib, 2001). They proposed that the phonological deficit has its roots in the perception of short or rapidly changing sounds (Tallal, 1980; Tallal et al., 1993). Specifically, slow auditory temporal processing would affect access to phonetic structure during the perception of speech, which would particularly impair sensitivity to components of speech that are only tens of millisecond long (e.g., formant transitions; necessary for detection of stop consonants; Tallal, 1980; Tallal et al., 1993). While the specific claims of a temporal processing deficit have been contested numerous times, its implication that auditory perceptual impairments would result in degraded phonological representations has, until recently, been largely accepted (see Studdert-Kennedy & Mody, 1995; Mody, Studdert-Kennedy & Brady, 1997; Brady, 1997; Laasonen, Service & Virsu, 2001; but see Nittrouer, 1999; Bretherton & Holmes, 2003; Nittrouer, Shune & Lowenstein, 2011). Furthermore, the theory has received support from a substantial number of studies on auditory processing, including tasks investigating tone frequency discrimination (e.g., Ahissar, Protopapas, Reid & Merzenich, 2000; France et al., 2002; McAnally & Stein, 1996; Witton et al., 1998; Witton, Stein, Stoodler, Rosner & Talcott, 2002), categorical perception of speech contrasts involving stop consonants (Mody et al., 1997; Adlard & Hazan, 1998; Serniclaes, Sprenger-Charolles, Carré & Demonét, 2001; van Beinum, Schwippert, Been, van Leeuwen & Kuijpers, 2005), similarity judgments of speech and nonspeech stimuli differing with respect to rapidly changing acoustic cues (Vandermosten et al., 2010), and neurophysiological responses to auditory stimuli, especially speech (see Rosen, 2003, for a review, and the ERP chapter of the present thesis [Chapter 2]). The case for an established deficit in speech perception in developmental dyslexia and its role in phonological processing, and subsequently in reading, is not yet widely accepted by the scientific community (see Nittrouer, 1999; Rosen, 2003; Ramus, White & Frith, 2006; Hazan, Messaoud-Galusi, Rosen, Nouwens & Shakespeare, 2009).

Unimpaired phonological representations but deficits in access

The hypothesis of poor phonological representation quality as a fundamental perceptually-based deficit in dyslexia implies that it is not something that can be readily influenced or recovered (at least, not beyond the first few years of life) but only compensated for to some extent. The relative paucity of behavioural investigations into the manifestations of phonological deficits in reading may then partly be due to the assumption that a phonological deficit affects reading from the outset. In this context, visual word studies may be seen as providing little room for experimental insight since any phonological manipulations of stimuli would need to be teased apart from a baseline phonological deficit affecting reading globally (Ramus, personal communication).[2] Thus, investigation of phonological deficits has dominantly fallen within the auditory or spoken modality but it has not yielded strong evidence for degraded phonological representations in dyslexia. In a review of auditory tasks they had designed to specifically tap phonological representations in dyslexic adults, Ramus and Szenkovits (2008) concluded that there was no strong evidence that task performance reflected degraded phonological representations. Instead, they referred to several of these studies as evidence of intact phonological sensitivity. Specifically, dyslexic adults were found to show:

1) Normal phonological similarity effects. When participants had to discriminate between two sequences of two to seven auditorily–presented nonwords, increasing

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[2] There is another likely reason relating to the difficulty of disentangling phonological effects from those of other reading-related processes and state-related effects on behavioural measures.

phonetic similarity of the nonwords within a sequence (e.g., minimal change nonwords differed by one phonetic feature, [taz] vs. [taʒ]; in the maximum change nonwords shared no phonetic features. [taz] vs. [gum]) produced a decrease in performance of similar magnitude as that observed in normal readers, indicating that, functionally, dyslexics were not less sensitive to relative phonological structure.

2) Similar difficulties as normal readers in the discrimination and repetition of non-native speech sounds (Korean) compared to native speech sounds (French; Soroli, Szenkovits & Ramus, 2010).

3) Similar spontaneous voicing assimilations as controls when reading French sentences aloud (i.e., voicing in which the final phoneme of a word is altered to accommodate the voicing of the next; e.g., "cape grise" [kapgriz] becomes [kabgriz]).

4) Intact repetition priming for subliminally presented auditory words (after Kouider & Dupoux, 2005, with skilled readers).

Ramus and Szenkovits concluded from these studies that the phonological difficulty may instead concern working memory processes engaged in accessing phonological representations since the only divergence in group performance emerged when working memory load was increased. Agreement regarding working memory involvement in manifestations of phonological impairment can be found elsewhere. For instance, tone frequency discrimination deficits in dyslexia have been found to emerge as a function of task demands rather than stimulus properties (Banai & Ahissar, 2006; Ahissar, 2007). Meanwhile, evidence of generalized working memory span deficits found across verbal, nonverbal, and spatial stimuli in dyslexia weakens the case for specific verbal working memory impairments stemming from a core phonological deficit (see Menghini, Finzi, Giovagnoli & Vicari, 2011).

Summary: Phonological deficit theories in reading

The potentially critical role of working memory in mediating phonological impairment, which is relevant in the case of the behavioural literature in support of a core phonological deficit, is truly problematic as regards the assumptions of the phonological representations hypothesis. Indeed, it remains largely unclear if there is a perceptual basis to decoding difficulties grounded in a core phonological or auditory processing deficit that is independent from working memory operations, or whether phonological impairment is dependent upon attentional/memory demands.

Theoretical Perspectives: Visual processing dysfunction

Since written words are presented visually, it seems critical to exhaustively investigate visual processing in dyslexia. Any abnormalities in sensitivity to the orthographic content of a word will likely impact all subsequent stages of reading. Despite the obvious relevance of visual integration processes, potential deficits in the visual aspect of processing written words has received far less attention than the auditory aspect.

The magnocellular theory of dyslexia

Research on visual processing factors underlying reading began to flourish following observations from post-mortem analysis of five individuals with a history of dyslexia who displayed abnormal cells in the magnocellular layers of the dorsal lateral geniculate nucleus (LGN; Galaburda, 1993; Galaburda & Livingstone, 1993). Thalamic magnocells are part of the dorsal visual pathway, which receive axonal input from retinal ganglion cells and project to visual cortex and, ultimately, to superior parietal cortex through medial temporal areas (Shapley, 1990). Magnocells' specific properties, as suggested by observations of behavioural changes following lesions to macaque LGN (Merigan, Byrne & Maunsell, 1991), have enabled psychophysical investigation of magnocellular function using stimuli that tap these properties (see Figure 1; Galaburda & Livingstone, 1993).

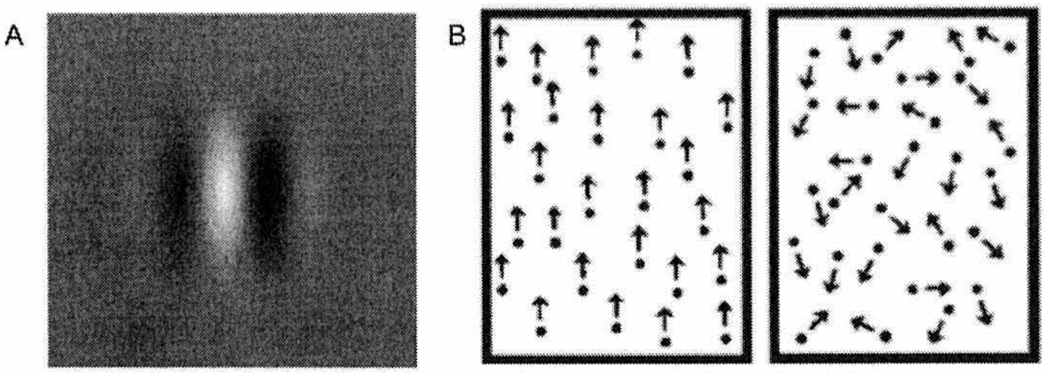

Figure 1. Stimuli typically used in psychophysical tests of magnocellular function. LGN Magnocells are neurons with large receptive fields that respond in a rapid, transient fashion, prefer low spatial frequencies and are fairly sensitive to low contrast stimuli. A shows a low contrast, low luminant visual grating typical of various magnocellular tasks. Tasks may include judging which is the faster of a pair of moving gratings, angle of orientation, or detection when rapidly displayed. B is an illustration of the extreme conditions of a random dot kinematogram, with 100% coherent motion on the left and no coherent motion on the right. Thresholds are measured for lowest coherence detection for intermediary conditions.

This has provoked a large behavioural literature devoted to testing dyslexic individuals' behavioural sensitivity to dynamic visual (nonverbal) stimuli as indicators of magnocellular and visual dorsal stream function (Lovegrove, Martin & Slaghuis, 1986; Vidyasagar, 1999). Differences between dyslexic and control readers have been found in experiments testing coherent motion sensitivity using random dot kinematograms (e.g., Cornelissen, Richardson, Mason & Stein, 1995; Talcot et al., 2001); contrast sensitivity of low spatial frequency gratings (e.g., Lovegrove, Bowling, Badcock & Blackwood, 1980; Martin & Lovegrove, 1984; Evans, Drasdo & Richards, 1994; Slaghuis & Ryan, 2006); spatial frequency doubling illusions (Pammer & Wheatley, 2001; Buchholz & McKone, 2004; Kevan & Pammer, 2008a, 2008b, 2010); flicker fusion sensitivity (Chase & Jenner, 1993; Talcott et al., 1998) and temporal order judgment (Slaghuis, Twell & Kingstone, 1996).

Abnormal performance in behavioural tests of magnocellular function has resulted in several explanations of developmental dyslexia. A view that posits impairment specific to sensory visual processing is that visual magnocellular function affects eye movement control via posterior parietal cortex (PPC), since PPC (involved in eye movement control, visuospatial attention and peripheral vision) receives dorsal stream projections from the magnocellular layers of the LGN ('the magnocellular theory of dyslexia'; Stein & Walsh, 1997; Stein, 2001). In this view, the resulting binocular and visual perceptual instability would produce unstable perception of letter strings, which would in turn impair orthographic decoding. The link between dynamic visual sensitivity and orthographic skill is supported by significant correlations between coherent motion detection or frequency doubling thresholds with orthographic measures such as word-pseudohomophone discrimination and irregular word reading (Castles & Coltheart, 1993; Talcott et al., 2000; Kevan & Pammer, 2008a, 2008b, 2010; see also Kinsey, Hansen & Chase, 2006, for electrophysiological links). Indeed, in 10-year-old children varying in reading ability, motion detection thresholds have been shown to account for up to 25% of irregular word reading variance (Talcott et al., 2000).

Unstable text perception has implications for reading overall in terms of deficient orthographic input, but it is too broad to explain specific decoding difficulties. However it is compatible, for instance, with the experience of misordering and reversal of letters that is commonly reported in dyslexic readers (e.g., Orton, 1925; see Kriss & Evans, 2007, for an overview on the high co-occurrence of Meares-Irlen syndrome in dyslexia), and with correlations between spatial sequencing of text-like objects and reading performance in children (Pammer, Lavis, Hansen & Cornelissen, 2004b) and adults (Pammer, Lavis, Cooper, Hansen, & Cornelissen, 2005). These are reading-relevant difficulties that do not readily converge with predictions of phonological or auditory hypotheses. Hypotheses that have alternatively linked magnocellular abnormalities with higher levels of processing due to dysfunction along the dorsal visual stream implicate visuo-attentional processes as a primary deficit; this view will be introduced in more detail in the section on attention deficits.

A caveat of magnocellular deficit hypotheses, beyond the issue of many failed replications (Victor, Conte, Burton & Nass, 1993; Walther-Müller, 1995; Johannes, Kussmaul, Munte & Mangun, 1996) and the observation of 'magnocellular deficits' in only a minority of dyslexic readers (Skoyles & Skottun, 2004), is that in most cases the deficient performance could be explained by a deficit in attention. The specificity of group differences in task performance in relation to impaired magnocellular function has been questioned in terms of (a) the tasks' usual requirement of comparisons to a referent, (b) the possibility that deficits are due to perceptual noise exclusion, or (c) the overall level of task demands (Ben-Yahudah, Sackett, Malchi-Ginzberg, & Ahissar, 2001; Stuart, McAnally & Castles, 2001; Amitay, Ben-Yehuda, Banai & Ahissar, 2002; Ben-Yahudah & Ahissar, 2004; Sperling, Lu, Manis & Seidenberg, 2005).

Summary: Visual processing deficits in reading

The visual perception literature should contend clearer implications for perceptual orthographic, rather than phonological, impairments. The relative unreliability of the behavioural deficits of dyslexic individuals in magnocellular tasks is perhaps the largest argument against the idea that magnocellular dysfunction produces visual processing deficits in dyslexia. However, the unreliability of magnocellular deficits could be due to issues of measurement (in)sensitivity (e.g., in terms of statistical power and scale of measurement; see, for instance, Chase & Stein's (2003) reply to Amitay et al.'s (2002) critique of magnocellular deficits). Whether or not magnocellular dysfunction makes a critical contribution to reading and dyslexia, and whether it is effectively gauged in the tasks used, there is enough evidence to suggest that dynamic visual processing is affected independent of the validity of magnocellular deficit theories. Certainly, correlations of magnocellular measures such as visual motion sensitivity and the frequency doubling illusion with orthographic skill suggest that visual processes taxed by magnocellular tasks are relevant to reading, but this need not be specific to dyslexia and is indeed observed reliably in control readers. Furthermore, the interpretation of magnocellular dysfunction operating via stability of text perception make sense, since this ought to have the greatest impact on irregular word reading, where recognition from degraded orthographic input will not be accurately supported by phonological information. Beyond implications for initial orthographic input, there is also another aspect of reading that is normally implicated in phonological accounts that is relevant here (Castles & Coltheart, 2004): GPC failures could arise from processing abnormalities at the level of graphemes (i.e., the visual level) or could arise at the level of visual-auditory connections (Rey, Ziegler & Jacobs, 2000; Whitney & Cornelissen, 2007), rather than necessarily stem from phonemic processing. If overall perceptual quality of orthographic input is impaired, as the visual magnocellular deficit hypotheses suggests, then this may contribute to GPC failure during decoding instead of, or in combination with, phonological impairment.

Theoretical Perspectives: Attentional impairments

Partly in response to both the increasing evidence against a core deficit in phonological representations (Ramus & Szenkovits, 2008; Blomert, Mitterer & Paffen, 2004; Banai & Ahissar, 2006) and evidence of possible magnocellular-driven dorsal stream dysfunction (cf., previous section), a relatively new literature has developed emphasizing attentional processes in the manifestations of phonological impairment and reading difficulty. These studies have looked at a range of processing affected by attention ranging from orthographic processing (the visuo-attentional span hypothesis: Valdois et al., 2004; Bosse, Tainturier, Valdois, 2007) or letter sequencing (Vidyasagar & Pammer, 2010) to more general attention or working memory processes thought to interact with reading (sluggish attentional shifting: Hari & Renvall, 2001; attentional engagement deficits: Facoetti et al., 2006, 2008, 2010; or attentional filtering difficulties: Roach & Hogben, 2007, 2008; Geiger et al., 2008). They vary with respect to the proposed neural origin of attentional impairment and the extent to which the deficit is considered to be automatic or under voluntary control.

The visual attention span deficit hypothesis

The visual attention span deficit hypothesis (Bosse et al., 2007), for instance, focuses on selective attention. This hypothesis distinguishes itself from the others by it attempts to differentially account for surface and phonological dyslexic profiles. It is based on a model of polysyllabic word reading (Ans, Carbonnel & Valdois, 1998) which, like the dual route model of reading (Coltheart et al., 2001), postulates two routes for reading: global (i.e., direct/lexical) or analytic (i.e., decoding-based/sublexical). Importantly, these processing modes are considered to differ with respect to the size of the visual attention window used for processing. For global mode processing, the focal window encompasses the whole letter string, whereas it is reduced in the analytic mode, typically to syllabic level information. This model differs from Coltheart et al. (2001)'s word recognition model insofar as the global procedure is always implemented first, with the analytic procedures only adopted when the global procedure has failed. In this context, a selective visual attention span (VAS) deficit would affect reading by reducing the number of letters that can be processed in parallel. A reduced VAS should particularly impact global reading procedures, which, in turn, would particularly impair irregular word reading that requires whole string recognition (as found in surface dyslexia). It should also, however, affect analytic (i.e., decoding) procedures if the VAS deficit interferes with processing digraphs and trigraphs (see Figure 2 for illustration of one of the VAS report tasks used).

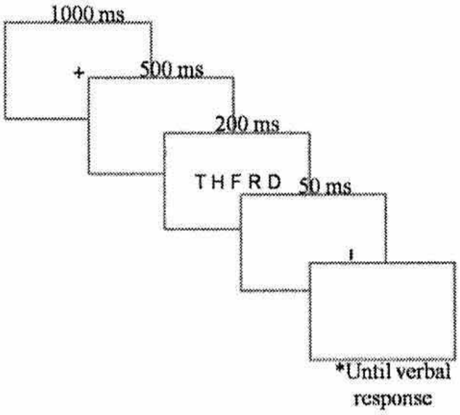

Figure 2. Illustrative trial of the partial report task used to measure visual attention span (VAS). VAS is assessed in terms of accuracy across partial and full report tasks each consisting of rapidly presented 5-letter consonant strings (displayed for 200 ms). In the partial report task, a line probe indicates the letter to be reported; in the full report task, all five letters have to be reported.

Valdois and colleagues have shown that VAS predicts reading performance independently from phonological skills in French and English dyslexic children (Bosse et al., 2007), and in normally developing children (Bosse & Valdois, 2009). Tasks using non-orthographic stimuli have shown that deficits are not specific to letter stimuli and can be conceived as deficient multi-element processing (Lassus-Sangosse, N'guyen-Morel, & Valdois, 2008; Dubois et al., 2010). The authors attribute VAS deficits to underlying functional activity within the left superior parietal lobe; based on functional magnetic resonance imaging (fMRI) testing of children who have a VAS deficit (Peyrin, Lallier & Valdois, 2008; Peyrin, Démonet, N'guyen-Morel, Bas & Valdois, 2011) and the commonly reported parietal involvement in selective attention. Unfortunately, it is not clear from the VAS model if the focal attentional processes they suggest to be involved would be in operation at the point in time that parallel access to letter strings first occur.

Attentional shifting deficits

Dysfunctional parietal cortex mediation of letter string processing in dyslexia has also been proposed in relation to attentional shifting (Facoetti, Ruffino, Peru, Paganoni & Chelazzi, 2008; Hari & Renvall, 2001) and focal attention mechanisms (Vidyasagar & Pammer, 2010); each with subtly different implications for reading. Deficient automatic, exogenous orienting processes have been proposed as the source of the reading impairment, both in terms of 'sluggish attentional shifting' (Hari & Renvall, 2001; see also Facoetti et al., 2008, 2010; Ruffino et al., 2010) or as a general weakness in automatic engagement of attention, in both the visual and auditory modalities (e.g., Buchholz & Aimola Davies, 2008; Facoetti et al., 2003b, 2003c; Petkov, O'Connor, Benmoshe, Baynes & Sutter, 2005). In the visual domain, evidence for sluggish or impaired attentional shifting (SAS) has come from mainly two sources of evidence. First, using attentional blink tasks (e.g., Hari, Valta & Uutela, 1999; Lacroix et al., 2005; Lallier, Donnadieu, Berger & Valdois, 2010; Lallier, Donnadieu & Valdois, 2010), (a) a longer blink has been reported in dyslexic participants ('prolonged dwell time'; Hari et al., 1999) suggesting sluggish disengagement of attention, and (b) T1 identification (i.e., recognition of the first stimulus) has been shown to be less accurate due to greater backward masking effects, also pointing to a deficit in attentional engagement (Facoetti et al., 2008). Secondly, using visuospatial tasks testing covert orienting of attention, the effect of a brief peripheral visual cue, supposed to improve target detection via exogenous orienting mechanisms, has been shown to be weaker in dyslexic participants despite intact cue and target detection when tested separately (Buchholz & Aimola Davies, 2007; Facoetti et al., 2001, 2006, 2010; Roach & Hogben, 2004; but see Roach &

Hogben, 2007, 2008). In the auditory domain, smaller auditory stream segregation thresholds in dyslexia (i.e., participants require a longer interval between high and low pitch sounds to perceive them in a single alternating stream; Helenius et al., 1999) and spatial cueing disadvantages in an auditory 'spatial attention' task (using tones to the left or right ear; Facoetti et al., 2010) have been taken as an indication that attentional shifting deficits are stimulus-driven and multisensory. Deficient automatic engagement and disengagement of attention is thought to impact reading because of the sequential attentional shifts required during text scanning (Hari & Renvall, 2001; Facoetti et al., 2006, 2008). Based on correlations between spatial cueing advantages and pseudoword reading, Facoetti and colleagues have proposed that an attentional engagement deficit specifically affects poor phonological decoders (Facoetti et al., 2006, 2008, 2010). The authors suggest that, in addition to a selective impairment of attentional engagement with spelling-to-sound mapping during sublexical reading, auditory orienting deficits would affect speech segmentation development (Facoetti et al., 2008, 2010; Menghini et al., 2010; Ruffino et al., 2010). They have proposed that these dysfunctions would be explained neurobiologically by abnormal processing within temporoparietal junction (Facoetti et al., 2008, 2010), which is strongly linked with attentional engagement processes (Corbetta & Shulman, 2002, 2008). More specifically, Hari and Renvall (2001) have further proposed that reading deficits stem from dysfunctional automatic attentional capture supported by parietal networks, which they regard as a 'pathophysiological link' between magnocellular pathology and deficits in rapid stimulus sequencing. Importantly, while it remains unclear why serial attentional engagement processes in sublexical analysis should be necessarily automatic and involuntary rather than focal and voluntary, they constitute a strong hypothesis as regards decoding impairments and the involvement of attention.

Dorsal stream dysfunction in visuospatial attention

Vidyasagar squarely places reading deficits in the realm of focal attention (Vidyasagar, 2001, 2004; Vidyasagar & Pammer, 1999, 2010). Following the suggestion that words are not usually read as wholes, but sequentially by individual letter or small groups of letters (Peli & Tillman, 2007), and considering the hypothesis that 'magnocellular deficits' may arise anywhere along the dorsal visual pathway leading to parietal cortex, Vidyasagar & Pammer (2010; see also Vidyasagar, 1999, 2001, 2004) have proposed that it is the parietal mechanisms involved in the smooth flow of attentional focus within visual fixations that lead to impaired orthographic input when disrupted (see Figure 3).

Instead of phonological processing as the core reading deficit, they posit that abnormal visual attentional mechanisms may underlie reading difficulties via disrupted coding of letter sequences. Vidyasagar and colleagues point out that phonological awareness itself may be at least partially dependent on the integrity of the visual system involved in grapheme-phoneme conversion. Therefore, while this hypothesis shares features with other hypotheses in terms of attentionally mediated dysfunction and subsequent deficient processing of a letter string, its emphasis is on the effective recognition of letter sequences. Thus, it differs from other theories insofar as phonological impairment is considered incidental and there is no distinction made between processing or reading outcome for words that would normally be associated with either a lexical or a sublexical strategy (e.g., familiar words vs. pseudowords).

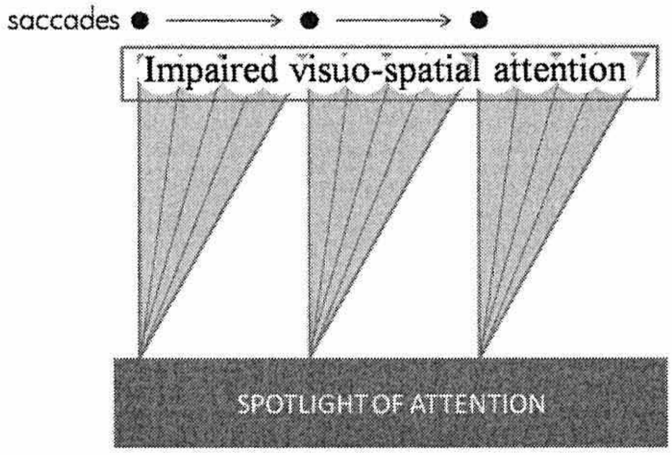

Figure 3. Figure adapted from Vidyasagar & Pammer (2010) on the role of visuo-spatial attention in reading. They locate the deficit in dyslexia in dorsal stream attention mechanisms controlling the sweep of attentional spotlight within periods of visual fixation (lasting approximately 250 ms, incorporating approximately 7-8 letters). It is proposed that this mechanism is critical for processing letter sequences, such that dorsal stream dysfunction would impact efficient letter sequencing.

Other observations on attentional impairments in dyslexia

Beyond these theoretical frameworks, attentional processes have been put forward in alternative accounts of deficient performance in psychophysical and spatial tasks, which would have been otherwise taken as indices of perceptual dysfunction. These perspectives do not make specific claims or predictions about reading, but have implications regarding reading impairments in several ways: (a) Deficient attentional selection, i.e., a difficulty in selecting task-relevant information that may affect the filtering of relevant orthographic and/or phonological information during reading. This is based largely on observations that spatial cuing performance is under flexible cognitive control, determined by the use of informational value of cues, and not necessarily related to orienting mechanisms in normal readers (Roach & Hogben, 2007, 2008; see also

Geiger et al., 2008); (b) reduced working memory resources, which have long been hypothesised to affect dyslexic readers (e.g., Menghini et al., 2011; see Brady, 1986; Berninger, Raskind, Richards, Abbott, & Stock, 2008; Jorm, 1983, for reviews) and may be as much a cause as a consequence of phonological and reading impairments (see Ramus & Szenkovits, 2008; Banai & Ahissar, 2006, for evidence of phonological deficits dependent on working memory load); or (c) difficulties in making comparisons to a referent. This point has been made based on deficits observed specifically in retain-and-compare experimental designs in dyslexia. It has been suggested that such difficulty could interfere with reading acquisition due to difficulties 'learning the regularities' of language (Ben-Yehudah et al, 2004; Ahissar, Lubin, Putter-Katz & Banai, 2006; Banai & Ahissar, 2010).

While the literature differs with regard to the specific attentional or working memory mechanisms that are implicated in dyslexia, there is notable convergence regarding the deficient attentional processes interfering with serial decoding of letter strings (see Laycock & Crewther, 2008, or Pammer, Hansen, Holliday & Cornelissen, 2006, for reviews on how the dorsal visual pathway may mediate attentional processes in reading; but see Skottun & Skoyles, 2006, for a critique). Given that most existing models of word reading do not make a special mention of attention (with the exception of Ans et al.'s, 1998 model of polysyllabic reading), it seems relevant to address how and when attention influences reading in normal and disordered reading. In a dedicated review paper, Shaywitz and Shaywitz (2008) made made a case for the importance of attention in the phenomenology of dyslexia. They noted in particular: (a) the high prevalence of comorbidity with attentional disorders in dyslexia since children with reading difficulties are at least three times more likely to have symptoms of attentional deficits than their normal reading peers (Willcutt & Pennington, 2000); (b) reports of beneficial effects of psychostimulants on reading performance in children with dyslexia and ADHD (Grizenko, Bhat, Schwartz, Ter-Sttepanian, & Joober, 2006; Keulers, Hendriksen, Feron, Wassenberg, Wuismen-Frerker et al., 2007); (c) a likely role of attention and memory in the automatisation of reading processes (see Logan, 1997); and, finally, (d) an accumulating functional literature linking attention, the inferior parietal cortex (frequently found to be underactive in dyslexia), and reading (Shaywitz & Shaywitz, 2008).

Piecing the literature together: Can all the hypotheses be valid simultaneously?

Point (d) above raised by Shaywitz and Shaywitz (2008) provides an avenue for future research in the field of dyslexia: examining the commonalities between reading processes and generic cognitive and neurobiological mechanisms and how they interact. Investigations using cognitive neuroscience methods such as event-related potentials (ERPs; described in the next chapter), functional neuroimaging (e.g., fMRI) and transcranial magnetic stimulation (TMS), to name only a few, enable us to test various theories in this way. So far, the neurocognitive research in dyslexia indicates, to some extent, that each of the dyslexia theories described may have useful explanatory power (Pernet, Andersson, Paulesu, & Démonet, 2009; see also Menghini et al., 2011, who encourage a multifactorial view of dyslexia based on batteries of behavioural tasks). For instance, the phonological hypotheses have gained particular support from functional studies of the superior temporal gyrus, which has been shown as underactive during reading tasks in developmental dyslexics (Paulesu et al., 2001; Salmelin & Helenius, 2004; Richlan, Kronbichler & Wimmer, 2009), as well as observations of abnormal activation in left inferior frontal gyrus (Hoeft et al., 2007, 2011; Richlan et al., 2009), which is implicated in effortful phonological analysis (Fiez, Balota, Raichle & Petersen, 1999; Mechelli, Gorno-Tempini & Price, 2003; Thierry, Ibarrola, Démonet & Cardebat, 2003; Graves, Desai, Humphries, Seidenberg & Binder, 2010). Hypotheses regarding visual processing of orthographic information find support in the study of the ventral occipitotemporal cortex, which is associated with abstract orthographic perception (Moore & Price, 1999; Cohen et al., 2002; Binder, Medler, Westbury, Liebenthal & Buchanan, 2006) and consistently underactivated during reading in dyslexic children and adults (Salmelin & Helenius, 2004; Richlan et al., 2010; van der Mark et al., 2009). Finally, deficits in attentional engagement and difficulties in GPC processes in reading are particularly linked to the temporoparietal cortex (e.g., for GPC involvement, see: Borowsky et al., 2006; Levy et al., 2009; Graves et al., 2010; for attention engagement see Corbetta & Shulman, 2002, 2008; Ravizza, Hazeltine, Ruiz & Zhu, 2011); this region is consistently underactivated in dyslexic individuals during reading, irrespective of level of compensation (Hoeft, 2007, 2011; see also Richlan et al., 2009).

In sum, there appears to be a case for independent, but interactive contributions from each of the domains of phonology, orthography and attention in reading, which makes good intuitive sense, because that is what reading essentially is: An attentionally demanding conversion of visual signs into language sounds. Each of these processes is likely to be weighted differently based on the particular experience of the dyslexic reader. Could one of these aspects of processing be responsible for driving deficits in other domains / at other levels? If, indeed, a phonological deficit is at the core of the reading impairment in dyslexia –a position that remains influential but challenged– then understanding interactions between phonological processing, orthographic and attentional factors will help understanding how it is expressed in reading and spelling difficulties. The present research aims to shed more light on these interactions through the use of event-related potentials.

Chapter Two

Overview of ERP Research

All of the empirical work presented in this thesis is based on behavioural measures and event-related potentials (ERPs). This chapter presents a general overview of the ERP technique and its interpretation in the investigation of cognitive processes; starting with the methods for recording and analysis, followed by a description of the biological underpinnings of the measured signal, and then by a section on the applications of ERPs in the study of reading and dyslexia.

ERP principles: recording and analysis

Electroencephalography (EEG) is the recording of the spontaneous electrical activity of the brain measured non-invasively using electrodes set on the scalp. Due to the weakness of electrical signals from the brain in comparison to electrical signals present in the environment, at least three electrodes are needed to record EEG activity: A recording electrode, a ground electrode and a reference electrode. The EEG signal at a recording electrode site corresponds to the difference in electrical potential between the recording site and the ground relative to the difference between the reference electrode and the ground electrode. Modern EEG systems record scalp activity from a number of sites (generally 16-512) distributed over the scalp in reference to one ground and one reference electrode, with electrodes positioned according to the 10/20 convention (American Electroencephalographic Society, 1994). In the present research 37 channels were used in total (with the exception of Study 2, which used a 32 channel array), including electrodes to monitor eye movement that were placed on either side of the eyes and above and below the left eye; see Figure 4. Since electrodes do not directly touch the scalp (due for instance to their plastic mounting and other barriers such as hair, dead skin, and grease), an electroconductive bridge is established between scalp and electrodes with the application of electrolytic gel containing a mild abrasive. This step is taken to ensure that electrical impedance (effectively the resistance between scalp and electrode) is low (typically below 5 KΩ). The signals at each electrode are amplified and can be sampled every millisecond (or higher, although it is unusual).

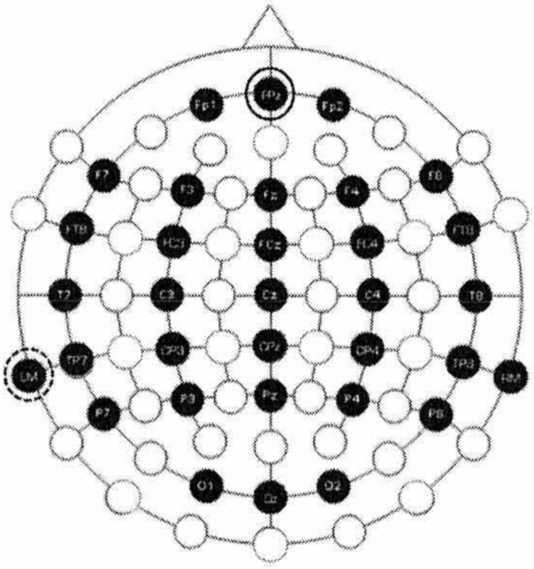

Figure 4. Electrode array used in the present research, arranged according to 10/20 convention. The ground electrode and online reference are indicated by solid and dashed rings respectively. Additional electrodes monitor eye movement (not shown).

The most common exploitation of EEG in cognitive neuroscience is the technique of ERPs. Individual ERPs are computed by cutting EEG data into defined time windows time-locked to each presentation of stimuli (called epochs), and by averaging the EEG epochs. The rationale is that ongoing EEG activity unrelated to the presentation of the stimulus, which can be positive or negative, will average out to zero with sufficient trials given that it is, by definition, unrelated to the stimulus, leaving brain activity time-locked to the stimulus, which ought to index specific processing responses.

There are several additional technical steps to improve signal-to-noise ratio, which include digital filtering of the EEG data and artifact rejection. These steps primarily help reduce contamination from exogenous electrical noise and artifacts such as eye movements (Brunia, 1989; Gratton, Coles & Donchin, 1989; Picton et al., 2000). A re-referencing procedure is usually also used in order to estimate a non-arbitrary zero value to reference the voltage measurements. For instance, the present research used the left mastoid as online reference, which, like any singular electrode, may be affected by periodic localized electrical artifacts. By re-referencing the recordings offline to an average of the left and right mastoid channels, a common choice in neurolinguistics, the effect of localized artifacts at the reference are diminished and spurious topographical asymmetries due to unilateral referencing are corrected.

The next step is to average individual ERPs together in each experimental condition to generate so-called grand-averages. These provide the final waveforms that are presented in ERP papers. If peak analyses are not defined on an a priori basis, the grand-averages can be inspected visually to select time windows and electrodes for analysis. Analysis parameters for each ERP peak are then used to take measures of amplitude (mean amplitude over a period of time is recommended over instantaneous peak amplitude from baseline; Luck, 2005) and latencies from the individual ERP data. These can then be subjected to statistical analyses depending on the objectives of the study.

ERPs are characterised by a series of positive and negative peaks, often referred to as components. These peaks generally follow a labeling convention of P or N to denote their positive or negative polarity and a number referring to their serial position in the waveform (for example, P1, N1, P2). However, these labels are not purely descriptive and peaks are generally labeled in accordance with established classifications based on their topography, latency, and typical eliciting conditions. For instance, the P1 is characterized as the first reliable positive peak found for visually presented stimuli over posterior electrode sites, typically peaking around 100 ms after stimulus onset (Mangun, 1995). It is usually followed by an N1 peak over the same scalp region. By contrast, an initial negative peak elicited in the same conditions over frontal electrodes will not be referred to as an N1, but may be labeled with further qualification, such as a 'frontal N1', or simply described without a label. As an alternative to serial position numbering, peaks are also sometimes described according to their polarity and average (rounded) peak latency, e.g., N250, P300.

Beyond a general principle that early peaks can provide insight into automatic, sensory processing of stimuli as compared to later ones, which are more associated with processing that is under the control of attention and modality-independent (Picton & Hillyard, 1998; Polich, 1993), their functional significance will vary depending on the task. That is, across tasks peaks will not necessarily reflect the same brain activity. Therefore, an appropriate use of ERPs consists of examining modulations of a given peak between experimental condition within a given task in order to determine relative differences in processing and to base interpretation on previous findings. Conclusions based on group differences in overall amplitude, for instance, can only be tentative because these may be driven by random individual differences in overall ERP magnitude, or by greater latency variation in one group resulting in smaller amplitudes, rather than by genuine group differences that are functionally meaningful (Picton et al., 2000). In fact, when comparing different groups representing particular populations (e.g., dyslexic individuals), one should rely exclusively on interactions between the group factor and other independent variables of interest, and ensure that these interactions are not spuriously driven by overall differences in amplitude between groups.

There are other important considerations that apply when interpreting ERP data. Firstly, ERP data can only be used to make correlational inferences rather than causational ones. This is because the neural response measured is elicited indirectly by psychological tasks (i.e., the processing of the stimuli) and the factors determining the ERP signal cannot be resolved absolutely. Secondly, it should be borne in mind that averaging can result in waveforms that do not necessarily (and actually rarely) resemble those for individual trials. For instance, if individual waveforms are bimodally distributed with regard to their amplitude or latency, the averaged waveform will fall between the two modes, and consequently fail to capture the actual amplitude or latency of any of the individual trials. Therefore, in order to obtain a representative average, the experimental design should incorporate a sufficient number of trials with a high-level of interstimulus consistency between experimental conditions. Thirdly, a given component can reflect a number of subcomponents indexing different processes and originating from different neural assemblies (e.g., what is typically referred to as an N2 as compared to the Mismatch Negativity; MMN). These can often only be differentiated by the eliciting experimental design, and interpretation should proceed accordingly.

Biological underpinnings of the EEG signal

The activity detectable at the scalp is thought to be a summation of postsynaptic potentials of mainly cortical pyramidal neurons firing together in synchrony. EEG amplitudes therefore index short-range coherence of membrane potentials between large groups of hundred of thousands or millions of neurons. The EEG is not thought to index action potentials as they are too brief for synchronous firing across large areas of cortex. A large number of neurons firing synchronously are necessary for any signal variation to be detectable on the scalp since the skull strongly attenuates electrical conduction. Conduction through the skull and also through the underlying meninges and cerebrospinal fluid also smears the signal such that a voltage recorded at a particular electrode site cannot be used to locate the neural source. A given signal registered at the surface of the scalp may be explained by an infinite number of source configurations, a difficulty known as the inverse problem (see Luck, 2005). As such, there is no clear spatial correspondence between ERPs observable at the scalp and underlying cortical activity. Gross judgments of topography such as the laterality of an effect or its anterior-posteriority are, however, broad enough to be considered acceptable in the literature (see for e.g., Evans & Federmeier, 2007; Grossi, Savill, Thomas, & Thierry, 2010; Potts & Tucker, 2001; Spironelli & Angrilli, 2009), even though the relationship to cortical sources should always remain tentative. The increasing use of concurrent functional neuroimaging with EEG recordings (see Ritter & Villringer, 2006, for a review) and the use of comparable eliciting experimental tasks with magnetoencephalography (MEG) are likely to improve our understanding of the correspondence between topographical ERP data and underlying neural sources in the future.

Spatial resolution is the main disadvantage of ERPs in comparison with other cognitive neuroscience techniques such as functional brain imaging. The spatial resolution of ERPs is (probably) in the order of the centimetre (Luck, 2005) compared to the now sub-millimetre range of Functional Magnetic Resonance Imaging (fMRI). Despite this, ERPs have many advantages in terms of cost, non-invasiveness and, most importantly, temporal resolution. As mentioned above, ERPs have a temporal resolution in the order of the millisecond whereas that of other neuroimaging techniques (aside from MEG) is too low to resolve processes underlying behavioural effects reflected in reaction times, which are usually in the order of several hundred milliseconds. Therefore, it is only possible to determine the timing of various cognitive processes and the stages at which experimental manipulations affect a particular condition with temporally sensitive techniques like ERPs and MEG. The next section will provide a selective review of the use of ERPs in elucidating stages of visual word recognition, from which insight into processes in normal and impaired reading have been and can be gleaned.

Selective review of ERP insights into the interplay of orthographic and phonological processing during visual word recognition

Used in conjunction with behavioural data, ERPs have helped track the time course of neural processes involved in a range of cognitive processes, including stimulus evaluation, decision-making, response preparation and execution (see Key, Dove & Maguire, 2005, for an overview). Recognizing a printed word involves a series of cognitive processes, which, according to models of visual word recognition, include print perception, orthographic analysis, lexical access, and retrieval of semantic and phonological representations. This processing stream can unfold with or without grapheme-phoneme conversion processes depending on the type of stimulus and the task at hand (see for example, Coltheart, Rastle, Perry, Langdon & Ziegler, 2001; Figure 5). Given the speed of word recognition – an average reader comfortably reads 250 words per minute, i.e., an average of 4 words per second (Carver, 1982) – ERPs are an ideal tool (a) for tracking these operations in word reading, particularly those that occur between initial sensory input and access to meaning, and (b) to help understand the interplay of such representation levels within the context of broader concurrent cognitive processes.

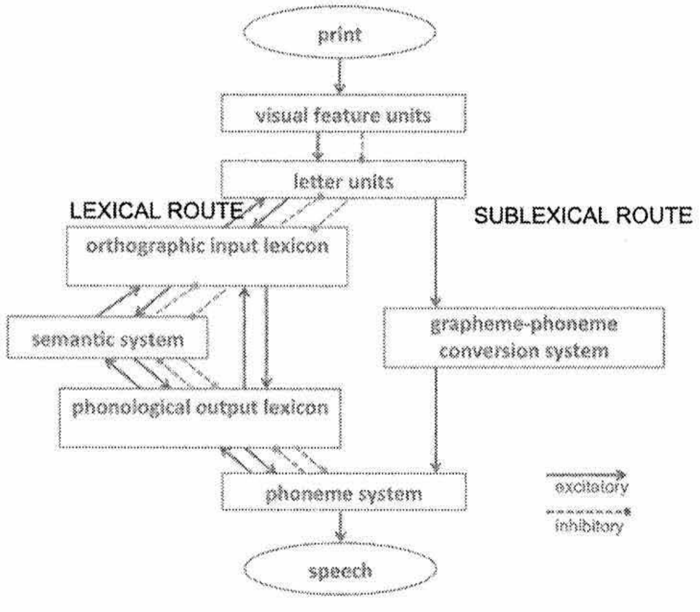

Figure 5. Adapted diagram of the stages of processing in reading hypothesised by the Dual Route Cascaded model of visual word recognition (Coltheart et al., 2001). Recognition of familiar words is thought to normally operate via the lexical route. Pseudowords and unfamiliar word reading, on the other hand, is thought to occur via the sublexical route.

ERPs can also be used to study when, and in which circumstances, word recognition in dyslexia deviates from that of normal readers. This section gives an overview of the stages of word recognition in normal reading as revealed by ERP data and is followed by a selective review of the ERP literature in dyslexia.

ERP tracking of visual word recognition processes in normal reading

As is the case subsequent to any visual presentation, the earliest modulations following the presentation of a word stimulus in normal readers make up the P1-N1 complex. The P1-N1 complex is particularly sensitive to orthographic stimuli (maximal at around 150-170 ms after stimulus onset and starting as early as 100 ms; Hauk, Davis, Ford, Pulvermüller & Marslen-Wilson, 2006). ERPs in this time range distinguish between orthographic (i.e., words, pseudowords, consonant strings) and non-orthographic stimuli (e.g., symbol strings).

The N170, in particular, is thought to index whole-string integration processes given its sensitivity to word-likeness (Bentin, Mouchetant-Rostaing, Giard, Echallier & Pernier, 1999; Maurer, Brem, Bucher & Brandeis, 2005; Zhang et al., 2010), that is, it indexes a relative tuning to 'visual aspects of print' (Maurer et al., 2005, Maurer et al., 2006; Xue, Jiang, Chen, & Dong, 2008). For instance, Bentin et al. (1999) showed that orthographic stimuli (words, pseudowords and consonant strings) elicited a larger N170 than non-orthographic stimuli (alphanumeric strings and symbols) during an irrelevant font size discrimination task. Similarly, Maurer and colleagues (2005, 2006) have shown evidence that the N170 response can act as an index of print sensitivity, based on modulation by print experience. They tested normally reading children and adults on a one-back task in which stimuli consisted of words, pseudowords, symbols, and pictures, in which children were tested (a) during kindergarten, prior to formal reading instruction but when letter categorisation was already acquired and (b) again, nearly two years later in second grade, after they had received formal reading training. Maurer et al. found that the difference in the N170 peak global field power between words and symbols increased significantly between kindergarten and second grade. Adults, on the other hand, showed a relatively reduced tuning for print modulation compared to second grade children, that is, a reduced difference between words and symbols, and no difference between words and pseudowords, which the authors interpreted as being due to a greater reliance on the coarse visual characteristics of print in learners than in adults (Maurer et al., 2006). It has been further argued that N170 modulations to word frequency index a logographic processing strategy or stage in reading (Simon, Petit, Bernard & Rebaï, 2007). Such a strategy is thought to dominate early phases of reading acquisition (Frith, 1985). Masked repetition priming studies have provided evidence suggesting that modulations peaking around this 150 ms range are primarily related to visual feature processing (see Grainger & Holcomb, 2009). This has been shown in tasks comparing prime-target pairs when repetitions are presented in the same case (Petit, Midgley, Holcomb & Grainger, 2006; see also Sauseng, Bergmann & Wimmer, 2004, using a simple silent reading task) or same font (Chauncey, Holcomb & Grainger, 2008) as compared to word repetitions differing in terms of case or font. At this point (N1 range), reading processes seem to be at a relatively rudimentary stage of orthographic processing influenced by whole-form visual familiarity. Accordingly, most N1 range distinctions between orthographic stimuli could be accounted for based on visual form/familiarity. These include ERP modulations driven by changes in written length (Assadollahi & Pulvermüller, 2003; Hauk, Pulvermüller, Ford, Marslen-Wilson, & Davis, 2009), orthographic neighbourhood size (Hauk & Pulvermüller, 2009); lexical frequency (Assadollahi & Pulvermüller, 2003; Hauk & Pulvermüller, 2004; Hauk, Pulvermüller, Ford, Marslen-Wilson, & Davis, 2009; Sereno, Rayner & Posner, 1998, Sereno, Brewer, O'Donnell, 2003; Simon et al., 2007) and lexical status, i.e., words versus consonant strings and pseudowords (Coch & Mitra, 2010; Maurer et al., 2005; Sauseng et al., 2004).

More specified fine-grained orthographic processing, for instance in terms of sensitivity to the relative similarity of stimuli in terms of orthography, tends to be revealed slightly later, between 150-250 ms (e.g., Carreiras, Perea, Vergara & Pollatsek, 2009; Grainger, Kiyonaga & Holcomb, 2006). For instance, Carreiras et al. investigated the time course of orthographic masked priming effects from primes differing in orthographic similarity but matched for phonological similarity to target words (e.g., conal-CANAL vs. konal-CANAL). They found significant orthographic priming within the 150-250 ms window. Based on such evidence, it appears that it is within the 150-250 ms window that fine-grained orthographic analysis of a letter string is detectable, and orthographic processing becomes abstract in terms of location-, size-, and font-invariance (see Dien, 2009; Grainger & Holcomb, 2009).

The P2-N2 range is then considered to see the transition from fine-grained orthographic analysis to mapping of a phonological form to the letter string, implemented approximately 250 ms post stimulus onset (Grainger & Holcomb, 2009; Dien, 2009). More specifically, P2 modulations, which onset approximately 200 ms post stimulus onset and, depending on task, are found over frontocentral (referred to as the P2a) or occipitoparietal electrode sites (referred to here as the posterior P2), have been considered sensitive to the correspondence between orthography and phonology (Bles, Alink & Jansma, 2007; Hsu, Tzai, Lee, & Tzeng, 2009). Integration of phonological information derived from orthography-phonology mapping is implicated shortly after, and indexed by modulations of the frontocentral N2, typically peaking at around 250 ms. There is substantial evidence that by the stage of processing indexed by the frontocentral N2 peak, visual word recognition is influenced by the phonological code of stimuli. Consistent with implications of the N2 as sensitive to stimulus discrimination and mismatch detection (Folstein & van Petten, 2008), phonological integration attenuates N2 amplitude relative to phonological priming, with greater amplitudes for less phonologically acceptable or expected stimuli. This effect is found in the case of phonological integration of orthographically unfamiliar pseudoword stimuli and it has been observed with masked priming (Ashby & Martin, 2008; Holcomb & Grainger, 2006; Grainger et al., 2006), in rhyme and lexical decision tasks (Bentin et al., 1999; Kramer & Donchin, 1987), sentence reading (Vissers, Chwilla & Kolk, 2006), and phoneme decision (Proverbio, Vecchi & Zani, 2004). For instance, when a word is highly expected in the context of a written sentence, an orthographically unexpected homophonic word will elicit N2 amplitudes which are not different to that elicited by the expected word (Vissers et al., 2006). Although Vissers et al.'s (2006) study focussed on P600 modulations to incorrect spellings rather than implicit stages of phonological integration, when words highly expected in the sentence context were replaced with pseudohomophones, N260 amplitudes were not significantly different (Vissers et al., 2006). Given that (a) the replaced words were highly predicted by the sentence and therefore should have been orthographically primed and (b) processing in this range is sensitive to orthographic similarity of stimuli (e.g., Kramer & Donchin, 1987; Carreiras et al., 2009), the absence of N260 modulation due to orthographic mismatch suggests that phonological priming can yield a greater, overriding influence on processing in the N2 range as compared to orthographic information. However, where studies have included additional orthographic manipulations, N2 phonological integration is not impervious to orthographic expectations (Newman & Connolly, 2004; Niznikiewicz & Squires, 1996). Therefore it seems that, in general, the N2 is affected by relative phonological and orthographic expectancies, reflecting the ongoing or recent process of orthographic-phonological mapping.

Integration of visual and auditory representations occurring in this N2 window has recently been demonstrated at the level of individual letters using an unconventional auditory mismatch negativity (MMN) paradigm (Froyen, van Atteveldt, Bonte & Blomert, 2008; Froyen, van Atteveldt & Bonte, 2009). The MMN is a modulation of the auditory N2 reliably elicited over frontocentral electrodes when a series of unattended repeated auditory stimuli is interrupted by an oddball stimulus and is thought to index preattentive change detection (Näätänen, 1992; but is sensitive to phonotactic knowledge, e.g., Winkler et al., 1999). Froyen et al. (2008, 2009) found that the change from a standard spoken vowel sound /a/ to an oddball vowel sound /o/ elicited an MMN (while participants were engaged in an easy, irrelevant task of responding to a specified picture shown between trials) which increased in amplitude by the simultaneous presentation of the mismatching visual letter ‘a’. Furthermore, when they created temporal lag between the presentation of letter and oddball sound, MMN amplitude reduced accordingly. This is good evidence for visual and auditory integration in the N2 range, and it is consistent with orthographic-phonological mapping. However, in this particular study, the direction of the auditory-visual match was in the opposite direction to that of a reading context and is probably not indicative of letter-sound mapping processes, nor easily extendable to correspondences at the graphemic or syllabic level.

Nonetheless, access to phonology from print has been shown to modulate ERPs as early as in the P2 range. The bulk of the evidence for this comes from studies using non-alphabetic stimuli (Chen, Fu, Iversen, Smith, & Matthews, 2002; Meng, Jian, Shu, Tian, & Zhou, 2008; Zhang, Zhang, & Kong, 2009; Kong, Zhang, Kang, Du, Zhang, & Wang 2010). For instance, when the phonetic radical of Chinese characters is manipulated, characters that are phonologically similar (rhyming) or identical (homophonic) to expected characters elicit a larger posterior P2 than phonologically unrelated ones. This has been shown using characters without orthographic overlap and therefore interpreted as indexing early lexical (i.e., direct) phonological access (Kong et al., 2010). Considering the ERP literature as a whole, this is early in terms of a phonologically driven effect, probably because of the logographic nature of Chinese. In Chinese, graphemes represent meaningful syllabic information rather than sublinguistic phonological units (DeFrancis, 1989; Seidenberg, 1985). Furthermore, phonetic consistency is low (for example, only 23% of compound characters in elementary school Chinese are phonologically regular; Shu, Anderson, Wu & Xuan, 2003). This may encourage particular reliance on direct phonological access, which may be faster than phonological analysis of alphabetic stimuli. This consideration aside, rapid whole-string (Braun, Hutzler, Ziegler, Dambacher & Jacobs, 2009) and syllabic-level (Ashby &

Martin, 2008; Carreiras, Vergara & Barber, 2005) phonological effects from 'sublexical' stimuli have been reported with alphabetic stimuli in this time range. Braun et al. (2009), for example, have shown such phonological effects as early as 150 ms post stimulus onset with alphabetic stimuli by comparing ERPs elicited by pseudohomophones with orthographic control pseudowords in a lexical decision task.

Overall, it remains unclear when exactly normal readers access whole string phonology. Such representations are probably not retrieved instantly and it is beyond the scope of this review to ascertain the precise timing of phonological retrieval and the mechanism by which lexical or sublexical analysis influence P2 and N2 ERP modulations. However, there is reasonable evidence to suggest that orthography-to-phonology conversion essentially spans the P2 and N2 ranges of ERPs.

The most studied ERP peak across cognitive domains is the P3, or P300 (Hruby & Marsalek, 2003). Overall, the P3 is associated with stimulus-driven attentional engagement and working memory updating processes (Polich, 2007). A distinction is made between a frontal P3a, which reflects the engagement of focal attention by unexpected or salient nontarget events, and a generally centroparietal P3b, which is linked to attentional processing of target stimuli, and is thought to index updating in working memory (Donchin & Coles, 1988) and/or the 'joint operation of attention and working memory' (Kok, 2001). P3 is most commonly elicited in tasks with rare target and oddball stimuli. However, P3-type modulations are found in other experimental contexts, including in tasks in which visual word stimuli are manipulated for their phonological content (in terms of similarity: e.g., Carreiras et al., 2009; Kramer & Donchin, 1987; Polich, McCarthy, Wang & Donchin, 1983; and phonological match:

e.g., Grainger et al., 2006), and orthographic content (in terms of similarity: e.g., Carreiras et al., 2009; Kramer & Donchin, 1987; and orthotactic information: e.g., Mariol, Jacques, Schelstraete & Rossion, 2008). P3 amplitudes can also be modulated by semantic/conceptual manipulations (e.g., Watson, Azizian, Berry & Squires, 2005). For instance, stimuli that are conceptually the same but in a different presentation modality to a target also increase P3 amplitudes (e.g., the word 'globe' will elicit a large P3 when the target is a picture of a globe and vice versa, Watson et al., 2005; see also Dorjee, Devenney & Thierry, 2010). Therefore, with regard to language, P3 amplitudes can be seen as an index of attentional responses to perceptual or semantic similarity (see also Azizian, Freitas, Parvaz & Squires, 2006; Azizian, Freitas, Watson & Squires, 2006), with its amplitude being increased with perceived similarity or relevance of a stimulus in a given context. Therefore, in the case of visual word processing, P3 amplitudes can give a useful indication of relative attentional allocation to a given linguistic variable.

The next language-relevant ERP modulation relevant in the domain of word recognition mechanisms is the N400 wave; an event primarily related to semantic processing. The N400 is the most widely studied ERP index of semantic integration, particularly studied in the domain of language processing (see Kutas & Federmeier, 2011, for a review). It is a large negative wave starting approximately 250 ms post stimulus onset in the auditory modality and slightly later in the visual modality and typically peaking at around 400 ms and modulated by semantic expectancies. N400 amplitude is increased by violations of semantic expectation (as in "The pizza was too hot to *sing*") and modulated by cloze probability (the probability of occurrence of a word within a sentence in relation to its semantic context). For instance, N400 amplitude elicited by words such as "palms" in the context “they wanted to make the resort look more exotic, so they planted *palms* in the alley” would be of weak amplitude as compared as the N400 elicited by words such as “*pines*” or “*tulips*”, which would elicit progressively larger N400s (Federmeier & Kutas, 1999). Furthermore, N400 modulations are not only observed in sentence contexts (e.g., Kutas & Hillyard, 1980; 1984; van Berkum, Hagoort & Brown, 1999; Hagoort, Hald, Bastiaansen & Petersson, 2004) but also single word contexts, when words prime another in meaning (Bentin, McCarthy & Wood, 1985; Benton, Kutas & Hillyard, 1993) or when an individually presented word belongs to a given, target semantic category. Importantly, N400 is not only sensitive to semantic violation, but also other expectancy violations in language, including phonological expectancy, such as in the case of nonrhyming stimuli in rhyme judgment tasks (Rugg, 1984; Rugg & Barrett, 1987), or orthographic expectancy, such as in the case of manipulations of orthographic similarity of a stimulus to a target word (Lazslo & Federmeier, 2010). In other words, N400 amplitude is generally sensitive to processes of stimulus integration and decision-making (e.g., Bentin et al., 1999; Brown & Hagoort, 1993; Chwilla, Brown & Hagoort, 1995; Connolly & Phillips, 1994) and subject to influence from attention and memory and has been recently theorised to reflect stimulus-driven activity in long-term memory systems induced while meaning is dynamically constructed (Laszlo & Federmeier, 2010).

Finally, another ERP wave often reported in studies of reading is the P600. The P600 has similar characteristics to the P300, and is often considered to be part of the P300 family (see Coulson, King & Kutas, 1998a, 1998b; but also Osterhout, McKinnon, Bersick & Corey, 1996; Osterhout & Hagoort, 1999). It is generally observed when a stimulus stands out within the focus of attention and/or is difficult to integrate and triggers stimulus reanalysis and reprocessing (Kolk, Chwilla, van Herten, & Oor 2003; Kolk & Chwilla, 2007; Martin, Dering, Thomas & Thierry, 2009; Van De Meerendonk, Kolk, Chwilla & Vissers, 2009; Van de Meerendonk, Indefrey, Chwilla & Kolk, 2011; Van De Meerendonk, Kolk, Vissers & Chwilla, 2010; Vissers, Chwilla & Kolk, 2006; Vissers, Kolk, Van de Meerendonk, & Chwilla, 2008). It has been associated with syntactic violations and their subsequent re-evaluation (accordingly, it is sometimes called a syntactic positive shift, SPS, Osterhout & Holcomb, 1992; see also Friederici, Hahne & Mecklinger, 1996, Friederici, Steinhauer & Frisch, 1999, Hagoort, Brown & Groothusen, 1993; Hahne & Friederici, 2002, Thierry et al., 2008). Recently, however (as hinted by early works showing that a P600 is elicited by unexpected font size, Kutas & Hillyard, 1980), it has been described in the case of other expectancy violations that do not depend on syntactic integration but require double-checking (Kolk et al., 2003; Münte, Heinze, Matzke, Wieringa, & Johannes, 1998; van de Meerendonk et al., 2009, 2010, 2011). For instance, P600 modulations can be elicited by incorrect spellings of phonologically acceptable words (van de Meerendonk et al., 2011; Vissers et al., 2006; see also Liu, Jin, Wang & Xin, 2011). P600 is also elicited by certain kinds of semantic plausibility violations in the context of weakly meaningful or implausible sentences, such as "The fox that hunted the poacher stalked through the woods" (van Herten, Kolk & Chwilla, 2005; see also Kim & Osterhout, 2005; Kolk et al., 2003; Kuperberg, Kreher, Sitnikova, Caplan & Holcomb, 2007; van Herten, Chwilla & Kolk, 2006), or simply when a sentence is untrue (e.g., a P600 has been observed for written sentences inaccurately describing a pictured spatial array; Vissers et al., 2008). Therefore, P600 responses are broadly indicative of the extent to which a stimulus is reattended to check it has been correctly perceived (Kolk et al., 2003).

Summary: an ERP profile of the stages of word recognition

Overall, ERPs elicited by words in a reading context offer insights into various stages of stimulus integration. A timeline of visual word processing is starting to emerge, distinguishing stages of print perception, sensitivity to orthographic properties, phonological integration, semantic integration and monitoring. This processing time line is schematically illustrated in Figure 6.

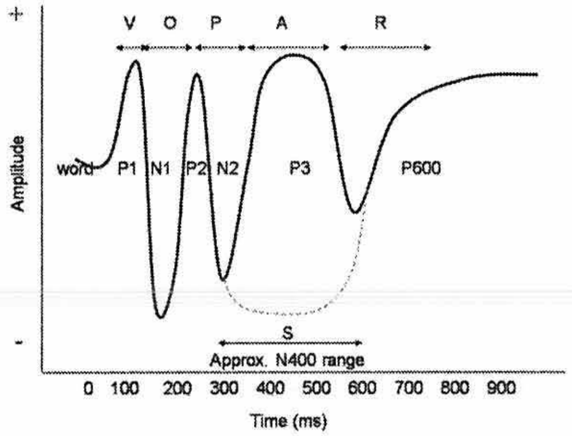

Figure 6. A stylised ERP wave to illustrate the approximate time course of visual word processing based on the current literature. The dotted line indicates the approximate range of the N400 wave, which temporally overlaps the P3. V = Visual word form processing; O = Orthographic analysis; P = Phonological analysis; A = overt attentional engagement, indexed by P3a and P3b; S = Semantic integration; R = Reanalysis

ERP insights into visual word recognition (i.e., reading) in dyslexia

Considering that reading difficulty is the definitive core deficit characterizing developmental dyslexia, ERP research into the mechanisms underlying visual word recognition in dyslexic individuals is surprisingly scarce. Indeed, recent reviews of the electrophysiological literature covering visual and auditory processing in dyslexia (Lyytinen et al., 2005; Schulte-Körne & Bruder, 2010) do not even address visual word processing. In the case of auditory processing, efforts have largely focused on the mismatch negativity (MMN; cf., previous section), and taken MMN amplitudes as an index of phonological sensitivity. In the visual domain, efforts have largely concentrated on the effects of motion and contrast sensitivity on P1 and N1 modulations, to investigate possible magnocellular dysfunction (in Schulte-Körne & Bruder, 2010) or nonverbal visual attentional processes (e.g., Lallier et al., 2010). To our knowledge, there is no published review on the time course of visual word integration in developmental dyslexia.

Given the rich ERP literature on visual word recognition in normal readers, however, there is scope to test hypotheses about relative orthographic and phonological processing during reading in dyslexia. The following selective review of ERP research carried out with dyslexic readers demonstrates the usefulness of ERPs for testing existing theoretical perspectives on dyslexia and provides the impetus for the research in the present thesis.

ERP investigations of phonological effects during visual word recognition in dyslexia

ERP studies investigating phonological processing of visual word stimuli provide little support for an early deficit in phonological activation in dyslexia. Experiments based on phonological manipulations in visual word stimuli generally show differences in modulation between dyslexic and control groups from the N400 range onwards. These differences are largely confined to rhyme judgment tasks, in which dyslexic individuals typically show attenuated or delayed N400s (Ackerman, Dykman & Oglesby, 1994; McPherson, Ackerman, Holcomb & Dykman, 1998; Rüsseler, Becker, Johannes & Münte, 2007). For example, McPherson et al. (1998) tested dyslexic and normal reading adolescents on visual and auditory word rhyming tasks. In both tasks, stimuli were monosyllabic word pairs manipulated orthogonally for rhyming status (rhyme, nonrhyme) and orthographic similarity (neighbour, non-neighbour). Dyslexic participants who had been labelled as 'dysphonetic' on the basis of relatively poor nonword reading showed no significant phonological priming in the N400 range, unlike controls and 'phonetic' dyslexic readers who had better nonword performance and whose phonological priming attenuation of N400 amplitudes fell between the other groups. Studies such as these have been put forward as electrophysiological evidence of deficient phonological processing in dyslexia (Rüsseler et al., 2007). However, both due to the modulations of interest occurring in the N400 range and given the specific demands of rhyming judgment, it is unclear whether these differences may have been affected by or even due to differences in attentional involvement and/or working memory capacity between groups. Indeed, in McPherson et al.'s word task, each word was displayed for 800 ms and there was a 1300 ms interval separating two words to be rhymed. These are long inter-stimulus intervals in which to hold phonological information in working memory. Differences in N400 amplitude may therefore have stemmed from faster memory decay in developmental dyslexic rather than weaker/deficient phonological representations.

Evidence for group differences in the earliest stages of phonological analysis (P2/N2 range based on the literature in normal readers) would be stronger evidence for a fundamental phonological deficit affecting reading in dyslexia. Several studies have reported such modulations before the N400 range (Wimmer, Hutzler & Wiener, 2002; Breznitz & Misra, 2003; Meyler & Breznitz, 2005; Meng, Tian, Jian & Zhou, 2007).

Wimmer et al. (2002) reported ERP data in dyslexic readers showing smaller early negative amplitudes over the left frontal scalp at a latency of 100 ms (which they refer to as an N1) during a lexical decision task. Even though the authors interpreted this effect as an indication of a deficit in activating phonological codes, they did not analyse N1 modulations over occipitoparietal sites where the N1 is usually maximal and they did not report a group by condition interaction. Therefore, this study in fact lacked evidence for a deficit in phonological code activation: (a) Performance on a lexical decision task is not directly relevant to phonological processing (Pseudowords may be discarded on a purely visual/orthographic basis: Balota & Chumbley, 1984; Besner & Johnston, 1989); (b) Functional interpretation of effects over left frontal sites in the N1 range was not predictive and in fact the focus on this region rather than typical sites of maximal N1 amplitude is unjustified; (c) Group differences in amplitude were not qualified by significant interactions with experimental manipulation and therefore claims regarding differences between groups in terms of processing may have been confounded by spurious group differences (cf., ERP principles section).

In several papers, Breznitz and colleagues (Breznitz & Meyler, 2003; Breznitz & Misra, 2003; Meyler & Breznitz, 2005) have presented P2 and P3 range differences between adult dyslexic and control readers in visual word tasks as evidence of deficient orthographic and phonological representations, and their integration. In one set of studies Breznitz & Misra (2003) reported that dyslexic participants show (a) longer overall P2 latencies during lexical decision than their control peers and (b) greater differences in P3 target latency between auditory (consonant sounds and pure tones) and visual (letters and shapes) oddball detection tasks. They discussed these results in terms of temporal asynchrony of orthographic and phonological coding, which they give as an account of word recognition deficits in dyslexia. However, the only differences between groups were greater P3 peak latency differences between tasks, in the absence of a control task. Furthermore, neither lexical decision (which can be performed on the basis of orthography), nor detection of the sound /d/ in a stream of /b/ necessarily test phonological representations. To infer that greater peak latency differences between unrelated visual and auditory tasks may index asynchronous integration of orthographic and phonological information is therefore highly speculative. In a further set of studies, Meyler & Breznitz (2005) claimed to show evidence for deficient orthographic and phonological representations in dyslexic readers on the basis of smaller overall P2 and P3 amplitudes during lexical discrimination of word-pseudohomophone pairs and lexically-based phonological discrimination of pseudohomophone-pseudoword pairs, respectively. Again, the group differences reported were not validated by adequate control conditions and inferences about specific stimulus representations remain questionable. Furthermore there was no evidence that stimuli were controlled in terms of length, orthotactic and phonotactic properties. As it stands, the global task differences may still reflect spurious group differences in ERP amplitudes.

Meng et al. (2007) studied Chinese dyslexic children during sentence reading and studied ERP modulations in the P200 (posterior P2) and N400 windows. They presented participants with moderate cloze-probability sentences (between 71% and 76%) ending either in two-character compound words that formed the best completion or nonword compounds formed by introducing radicals that were either homophonic and orthographically dissimilar to that of the best completion word, or orthographically similar but phonologically unrelated. The dyslexic group showed no differences between experimental conditions in either the P200 or N400 ranges. The experimental manipulation had no differential effect on P200 amplitudes or latency between groups. The only significant group by condition interaction was found in the N400 range, in which the dyslexic group failed to display a modulation, whilst control participants showed a graded N400 response, with homophonic stimuli eliciting the largest N400 amplitudes. This lack of N400 modulation in the dyslexic group may have indexed deficient access to phonological information but at a relatively late stage of processing. However, the direction of N400 effects in control readers was opposite to what would be expected if homophonic stimuli had been integrated as phonologically acceptable (e.g., Newman & Connolly, 2004). This may be due to the logographic (i.e., visual) nature of Chinese characters leading to orthographic dissimilarity of the homophonic stimuli being the driving effect behind the N400 modulation. This possible interpretation of the results underlines the difficulty in disentangling phonological from orthographic effects without resorting to orthogonal manipulation of the two factors and in the absence of significant group by condition interactions. This study also raises the question of the comparability of developmental dyslexia in logographic and alphabetic languages.

In sum, the rare studies on visual word recognition in dyslexia do not make a strong case for phonological processing differentially affecting reading prior to the N400 range.

ERP investigations of visual word recognition in dyslexia: Orthographic findings

There is evidence for globally reduced early responsivity to orthographic stimuli in dyslexia during reading. This evidence comes from findings of reduced N170 differentiation of words from symbol strings (Maurer et al., 2007), and smaller N170 and P1 amplitudes overall during visual lexical decision tasks in dyslexia (Dujardin et al., 2011; Kast, Elmer, Jancke & Mayer, 2010; Taroyan & Nicolson, 2009). For instance, in comparison with their study in normal reading children (see Maurer et al., 2005, 2006; described earlier), Maurer et al. (2007) found that children who had been identified at risk of dyslexia during kindergarten, and had been classified as dyslexic by the time of follow up in second grade, showed a substantially smaller change in N170 differentiation of words and symbols post training as compared to normal readers. This observation led the authors to suggest that dyslexic children manifest deviant print-specific plasticity that may affect grapheme-phoneme conversion or result in an orthographic processing deficit independent from phonological processing.

ERP data in the N170 time range have recently been taken to indicate specific impairment in letter-sound associations in developmental dyslexia, which may account for downstream decoding difficulties (Froyen, Willems, & Blomert, 2010; see Ziegler, Peche-Georgel, Dufau & Grainger, 2010, for similar suggestions based on behavioural evidence). Specifically, Froyen et al. (2010) reported that dyslexic children show no letter mismatch modulation in an audiovisual paradigm in which normal readers show an amplified MMN upon simultaneous presentation of an oddball vowel and a mismatching letter (as described in the previous section). However, this data could be explained by generically smaller MMN responses in dyslexic individuals irrespective of letter presentation, which has been suggested by other MMN studies (see Bishop, 2007 for a review), or by a lack of orientation to the letter form (see below) given that it is task-irrelevant.

Consistent with Maurer et al.'s (2007) findings, Helenius and colleagues (Helenius, Tarkiainen, Cornelissen, Hansen & Salmelin, 1999a) found weaker modulation of activity in the left inferior occipito-temporal cortex by letter strings in dyslexic readers using MEG in the same time range as the MMN (~ 150 ms). In addition, further evidence for a generally abnormal response to orthographic stimuli comes from reduced ERP responses prior to presentation of a visual word stimulus (smaller contingent negative variation, CNV, during sentence reading; Bergmann et al. [2005], and in rhyming, Ackerman et al. [1994]) and smaller P3 to visual word stimuli (nouns) compared to pictures of the same referent (Holcomb, Ackerman & Dykman, 1985; Silva-Pereyra et al., 2001). In other words, orthographic processing difficulties may generally relate to attenuated responses to visual word material.

However, with regard to insight into dyslexic readers' relative sensitivity to the orthographic content within a letter string (i.e., fine-grained orthographic sensitivity rather than general responsivity to written stimuli per se), there are no existing ERP studies to judge. Therefore, it is unclear if orthographic information might differentially impair early reading processes in dyslexia.

ERP findings in dyslexia: Relevant deficits outside the reading context

So far, this review of developmental dyslexia studies of reading using ERPs has shown that dyslexic readers may be (a) generally less automatically drawn to orthographic stimuli than their normal reading peers, and (b) initially unimpaired in perceiving phonological information during reading but manifesting abnormal processing once attention and working memory are engaged. The final section of this selective overview describes ERP evidence for attentional processing differences, and includes ERP insights for reading from tasks that do not involve a visual word context. This includes visual ERP investigations of magnocellular dysfunction hypotheses, relevant to orthographic processing; the substantial auditory ERP literature, relevant to phonological processing, and an array of studies showing P3 range processing differences, which implicate abnormal attentional engagement.

Evidence for differences in basic visual processing in dyslexia

ERP investigation of visual processing in dyslexia inspired by theories of magnocellular and dorsal visual pathway dysfunction have contributed some evidence supporting early visual processing differences between developmental dyslexic participants and normal reading controls. For instance, dyslexic individuals show delayed and smaller P1 responses and longer N1 latencies to coherent motion stimuli but not static visual perception (Schulte-Korne, Bartling, Deimel, & Remschmidt, 2004). Mixed evidence for differences in contrast sensitivity effects in the P1-N1 range has been obtained (see Schulte-Körne & Bruder, 2010). In their review of the literature, Schulte-Körne & Bruder (2010) relate these ERP differences to impaired magnocellular function, which would in turn affect visual and visuospatial attention (see Chapter One; also Boden & Giaschi, 2007). Magnocellular dysfunction would involve primarily the posterior parietal cortex where magnocellular projections culminate. However, the extent to which early visual ERPs elicited by the tasks used are capable of tapping these functions, and therefore support the case for the magnocellular deficit theory overall or its manifestation in visual and attentional processing of a letter string, remains controversial (e.g., Skottun, 2000).

Evidence for auditory processing deficits in dyslexia

A comprehensive review of this ERP literature is beyond the scope of this thesis (see Schulte-Körne & Bruder, 2010, for a recent overview, or Bishop, 2007, for a specific discussion of research on the mismatch negativity response in dyslexia). However, the overall findings are naturally relevant to research on reading dysfunction. The overall pattern of findings in the investigation of auditory processing difficulties in dyslexia is by no means consistent (Bishop, 2007). Numerous studies have found reduced auditory mismatch negativity (MMN) responses to speech in dyslexic participants (typically to a change in phoneme, e.g., /da/-/ga/; Kraus et al., 1996; Schulte-Körne et al., 1998), and to tone frequency (e.g., Baldeweg, Richardson, Watkins, Foale & Gruzelier, 1999, Kujala, Belitz, Tervaniemi & Näätänen, 2003; Stoodley, Hill, Stein, & Bishop, 2006; but not tone duration, see Schulte-Körne & Bruder). Attenuated MMN responses have been observed across ages, from pre-reading children at risk of dyslexia (Molfese, 2000; Maurer et al., 2003) through to adulthood (Stoodley et al., 2006). These results are often taken as electrophysiological evidence of impaired rapid auditory temporal processing, which is thought to impact reading via speech processing impairment, leading to under-specified phonological representations (see Bishop, 2007). If this is the case, it is unclear why corresponding differences in early phonological processes in reading have not yet been reported in dyslexia. However, the premise of the MMN effects demonstrating speech or rapid auditory processing deficits is based on the MMN as an index of perceptual (i.e., auditory/phonological) sensitivity, which may be an erroneous assumption. For instance, when performance in an MMN eliciting task is compared to responses in active (i.e., attended) tasks using the same stimuli, dyslexic participants tend to show normal sensitivity to the physical properties of the stimuli. Stoodley et al. (2006) found that high-functioning dyslexic adults showed an attenuated MMN to 20 Hz frequency-modulated (FM) 1kHz oddball tones within a passive oddball paradigm (but not to 5 Hz or 240 Hz FM tones)[3]. Importantly, when the same stimuli were used to test psychophysical detection thresholds, dyslexics performed as well as controls. Given that the MMN is a preattentive response (Näätänen, 1992), reduced amplitudes may reflect, for example, a dispositional processing indifference to certain (perhaps verbal) stimuli or differences in automaticity (e.g., Nicolson, Fawcett & Dean, 2001) rather than index relative insensitivity to the physical properties of the auditory stimuli.

A role of attention (e.g., task orientation) on differences in auditory processing between dyslexic and control groups has been suggested in auditory studies in the P3 range using speech (Fosker & Thierry, 2005) and tone stimuli (Rüsseler, Kowalczuk, Johannes, Wieringa & Münte, 2002). For example, Fosker and Thierry (2004) found that dyslexic adults performing an irrelevant lexical decision task failed to show a P3a (automatic nontarget detection) to phonological oddballs (spoken words with a change in initial phoneme to /g/ or /p/, from standards beginning with /r/ or /b/), whereas control participants showed P3a to both the deviants (see also Corbera, Escera & Artigas, 2006, for reduced P3a to tone oddballs). Critically, when Fosker & Thierry (2005) asked

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[3] The authors reasoned that the specific attenuation for 20 Hz FM was indicative of the 20 Hz time frame as being important in the perception of stop consonants. This is circular since, according to temporal processing hypotheses, the direction of auditory deficits ought to be an impact on speech perception, rather than from it.

participants to actively detect the phonological oddballs, the P3 became indistinguishable between groups. The authors suggested that the absent P3a modulation in the irrelevant oddball task in the dyslexic group may relate to a relative failure in shifting attention to phonological cues.

Findings such as these revitalise the question of potential differences in phonological processing in dyslexia: Phonological impairments in dyslexia may be a result of a failure in attentional orientation to phonological information rather than sensitivity to it. This would fit with the behavioural literature showing deficits in phonological task performance, which is attention-dependent and under the control of working memory factors, whereas early differences are not seen.

A number of ERP studies across auditory and visual domains have shown smaller ERP amplitudes in the time window of the P3, which indicates differences in attentional responses (see Polich, 2007) either across task (Barnea, Lamm, Epstein & Pratt, 1994; Erez & Pratt, 1992; Lallier et al., 2010), or to verbal relative to nonverbal material (e.g., Holcomb et al., 1985; Silva-Pereyra et al., 2001, 2003; Taylor & Keenan, 1999). In light of (a) the evidence in support of attentional deficits in dyslexia, and (b) the lack of existing ERP evidence showing a particular insensitivity to the orthographic or phonological content of visual word stimuli prior to processing stages linked to attention, the importance of investigating attentional factors in reading dysfunction is emphasised.

Overview of ERP insights for reading in dyslexia

Overall, the selective review presented in this section enables us to consider two main theoretical accounts for developmental dyslexia: (1) Dyslexic participants may overall be less engaged with, or less prone to, attentional engagement with visual word stimuli, and (2) Evidence for deficient phonological processing in reading is only seen at a time point concurrent with attentional and working memory processes, and not at a perceptual stage. There is also indication from the literature outside of a reading context that suggests a possible role of attention/orientation in mediating deficient stimulus processing in dyslexia (e.g., Lallier et al., 2010).

The core questions that stem from this literature review are:

a) If there is a core phonological deficit in dyslexia, why is it not found earlier in the ERP waveform?

b) If visual word processing, including particular phonological decoding, is initially normal and prompts difference at a fairly late stage of processing, when and what is dysfunctional?

c) Is there evidence of reduced sensitivity to orthographic information? Are processing differences better explained by attentional or top-down effects on stimulus engagement?

Aims and hypotheses of the present research

This PhD research takes steps to answering the above questions with experiments using carefully controlled orthographic and phonological stimulus sets in order to track the time-course of processing in dyslexia. The following four empirical chapters (Chapters Three to Six) present four studies. Each of them tests two alternate experimental hypotheses with regard to phonological processes: either (a) From the earliest effects of phonological manipulations in control readers (e.g., in the N2 range) dyslexic readers will show reduced phonological priming effects, indexed by group by condition interactions, which would be consistent with a basic deficit in phonological representations in dyslexia; or (b) Early phonological effects will not significantly differ between groups, and differences will emerge at later, post-perceptual stages of processing in relation to attention and working memory effects (i.e., approximately the P3/N400 ranges). The latter outcome would be consistent with the existing ERP evidence in dyslexia showing no clear processing differences in early perceptual stages.

General hypotheses regarding orthographic processing across tasks, on the other hand, are not possible since ERP modulations due to orthographic manipulations should vary with task context. For instance, some task manipulations will give indications of sensitivity to sublexical orthographic content, whereas others will relate to lexical accuracy; these may differentially tap impaired and intact orthographic processing in dyslexia.

The first three studies (Chapters Three to Five; published in *Brain Research*, *NeuroReport* and *Frontiers in Psychology* respectively) target the earliest phonological modulations of the ERP that should be observable within a reading context. The first of these specifically examines the interplay of orthographic and phonological information in dyslexia using a pseudoword-word priming paradigm. It is expected that effects of both phonological and orthographic priming should be observable within the N2 range, and that any differences between dyslexic and normal readers in terms of relative sensitivity to phonological or orthographic information should be manifest from this time range. The second and third studies tackle this question within a more natural reading context. The first of these (Study 2) sets out to establish the automaticity of phonological access in reading in normal readers, even when it is unhelpful, by focussing on N2 modulations. Study 3 uses this as a foundation to test automatic phonological integration in dyslexia and how this interplays with orthographic expectations. The final study (Study 4; submitted for publication) turns the spotlight on attentional processes. Using an adapted oddball task designed to elicit P3a peaks to pseudohomophone stimuli (i.e., to stimuli similar to those used in the previous studies testing early phonological integration), the intention is to elicit processing differences between dyslexic and normal readers in a late time window associated with the reorientation of attention. That is, processing differences stemming from dysfunctional attentional processes should be detectable since the P3a indexes the onset of stimulus-driven focal attention. By comparing these attention-based effects with earlier stimulus processing in the same task and across verbal and nonverbal contexts, and also by relating ERP modulations to performance on behavioural measures, the studies should overall give a clearer picture of the timeline of deficits in reading in dyslexia.

Chapter Three

Reading for sound with dyslexia: Evidence for early orthographic and late phonological integration deficits

Paper published in *Brain Research*, volume 1385, April 2011, pages 192-205.

The published article is provided in the Appendix.

Abstract

Deteriorated phonological representations are widely assumed to be the underlying cause of reading difficulties in developmental dyslexia, however existing evidence also implicates degraded orthographic processing. Here, we used event-related potentials whilst dyslexic and control adults performed a pseudoword-word priming task requiring deep phonological analysis to examine phonological and orthographic priming, respectively. Pseudowords were manipulated to be homophonic or non-homophonic to a target word and more or less orthographically similar. Since previous ERP research with normal readers has established phonologically driven differences as early as 250 ms from word presentation, degraded phonological representations were expected to reveal reduced phonological priming in dyslexic readers from 250 ms after target word onset. However, phonological priming main effects in both the N2 and P3 ranges were indistinguishable in amplitude between groups. Critically, we found group differences in the N1 range, such that orthographic modulations observed in controls were absent in the dyslexic group. Furthermore, early group differences in phonological priming transpired as interactions with orthographic priming (in P2, N2 and P3 ranges). A group difference in phonological priming did not emerge until the P600 range, in which the dyslexic group showed significantly attenuated priming. As the P600 is classically associated with online monitoring and reanalysis, this pattern of results suggest that during deliberate phonological processing, the phonological deficit in reading may relate more to inefficient monitoring rather than deficient detection. Meanwhile, early differences in perceptual processing of phonological information may be driven by the strength of engagement with orthographic information.

Introduction

Developmental dyslexia is a disorder found in both children and adults characterised by literacy abilities below those expected given their general abilities and adequate motivation. The primary cause of difficulty in developmental dyslexia (henceforth dyslexia) is disputed (see Ramus, 2003), and probably multi-factorial (Menghini et al., 2010; Pennington, 2006) however a dysfunction of phonological processing is widely thought to be at the core of the deficit (Lyon et al., 2003; Snowling, 2000). A persistent hypothesis is that dyslexic individuals have weak and/or coarsely coded phonological representations (Adlard & Hazan, 1998; Boada & Pennington, 2006; Brady, 1997; Elbro, 1996; Goswami, 2000; Hulme & Snowling, 1992; Metsala, 1997; Morais, 2003; Snowling, 2000; Swan & Goswami, 1997). These are suggested to impact reading by interfering with automatic grapheme-phonemic conversion required for skilled reading (Morais, 2003; Morais & Kolinsky, 1994).

However, a convergence of recent research has also indicated that orthographic processing may be compromised in dyslexia and contribute to difficulties with reading (e.g., Bosse et al., 2007; Maurer et al., 2007; Vidyasagar & Pammer, 2010). Vidyasagar and Pammer (2010), for example, suggest that defects in the dorsal stream of the visual system may be the core deficit in dyslexia. This hypothesis is built on numerous studies showing dyslexic group performance to be weaker for behavioural indices of visual magnocellular function (see Laycock & Crewther, 2008; Schulte-Körne & Bruder, 2010, for recent reviews). In their perspective, focal visuo-spatial attention weaknesses affect scanning of orthographic strings resulting in poor orthographic inputs, which in turn affect grapheme-phoneme mapping. A similar perspective (Hari & Renvall, 2001;

Facoetti et al., 2006, 2008), derived primarily from observations of a prolonged attentional blink and slower spatial cued-detection in dyslexia, hypothesises that sluggish automatic engaging and disengaging of attention impairs the visual selection of graphemes, and subsequent decoding. In support of the association between attentional shifting and decoding ability, orienting performance has been found to significantly correlate with nonword reading (Facoetti et al., 2006, 2008, 2010).

Further implications of reduced orthographic sensitivity in dyslexia come from Valdois and colleagues (e.g., Bosse et al., 2007; Valdois, et al., 2004; Dubois, De Micheaux, Noel & Valdois, 2007), who separately describe a visual attentional span (VAS) deficit. VAS refers to the number of items in a visual string that can be processed simultaneously and has been shown to be smaller in subsets of dyslexic participants and to impact reading independently from phonological problems. It is suggested that a reduced visuo-attentional window would impair whole word processing and thus particularly affect irregular word reading (Bosse & Valdois, 2009).

These hypotheses have differing implications for the point(s) at which dyslexic readers' visual word recognition ought to be affected. Recording event-related potentials (ERP) can offer insight here. ERP investigations have had a positive contribution on our understanding of the time course and stages of normal visual word recognition: from initial processing of visual input, through orthographic analysis, phonological mapping and subsequent working memory integration (see Dien, 2009; Grainger & Holcomb, 2009). As such, ERPs present an ideal tool to enable description of the temporal course of the deficit(s) in dyslexia and clarify the case for early degraded orthographic inputs and/or phonological representations, or difficulties relating to later integrative processing.

However, modulations of the N400 wave are rather late to index impaired sensitivity to phonology, and are more likely to relate to the deep processing and decision-making related to integration of the phonological stimuli, rather than a marker of sublexical processes (e.g., Bentin et al. 1999; Brown & Hagoort, 1993; Chwilla et al., 1995; Connolly & Phillips, 1994). ERP studies with normal readers have shown that phonological manipulations can reliably modulate the ERP wave from 250 ms after stimulus onset in a range of tasks (masked priming: Ashby & Martin, 2008; Holcomb & Grainger, 2006; Grainger et al., 2006; rhyme and lexical decision: Bentin et al., 1999; rhyming decision: Kramer & Donchin, 1987; sentence reading: Savill, Lindell, Booth, West & Thierry, 2011 [Study 2]; phoneme decision: Proverbio et al., 2004). Furthermore, amplification of the N2 peak elicited by phonological mismatch is well established: An effect referred to as the Phonological Mismatch/Mapping Negativity (PMN), typically observed when the expected final word of a sentence is replaced with a phonologically dissimilar, unexpected stimulus, has been shown with auditory stimuli (e.g., Connolly & Phillips, 1994; D'Arcy, Connolly, Service, Hawco, Houlihan, 2004; Diaz & Swaab, 2007; Newman & Connolly, 2009; Newman, Connolly, Service & McIvor, 2003), and similar effects have been shown in visual contexts (Connolly, Phillips & Forbes, 1995; Newman & Connolly, 2004; Savill et al., 2011). The lack of studies reporting differences in phonological effects between dyslexic and normal readers in this earlier time range, within the context of reported findings within the later N400 range, seems to favour integration/working memory accounts of phonological dysfunction in a reading context, rather than degraded phonological sensitivity.

The ERP literature on visual word processing in developmental dyslexia has, however, shown early discriminatory ERP profiles between dyslexic and normal readers. These differences have been found during stages related to processing visual/orthographic input (see Coch & Mitra, 2010; Dien, 2009; Grainger & Holcomb, 2009; Hauk et al., 2006; Kast et al., 2010; Parviainen, Helenius, Poskiparta, Niemi & Salmelin, 2006) prior to phonological analysis, within 150 ms of stimulus onset (Maurer et al., 2007; Helenius et al., 1999a; Taroyan & Nicolson, 2009; Wimmer et al., 2002). These early group differences, found in naming, one-back and lexical decision tasks, have been shown to be letter-string specific (Helenius et al., 1999a; Maurer et al., 2007), and have been observed at the word form level, e.g., absent left-lateralised P1 amplitude differences between words and pseudowords observed in dyslexic readers (Taroyan & Nicolson, 2009). Such findings of reduced orthographic activation are comparable with the varied literature implicating visual/visuo-attentional factors underlying dyslexic word processing difficulties, which share the implication of a weaker orthographic percept (Bosse et al., 2007; Facoetti et al., 2008; Hawelka, Huber & Wimmer, 2006; Hawelka & Wimmer, 2005; Jones, Branigan & Kelly, 2008; Pammer & Vidyasagar, 2005; Salmelin, Service, Kiesilä, Uutela & Salonen, 1996; Vidyasagar, 2004; Vidyasagar & Pammer 2010). Given the suggestion that early reduced attention or sensitivity to orthographic and/or whole word perceptual differences may interfere with later phonemic mapping (e.g., Cestnick & Coltheart, 1999; Facoetti et al., 2006, 2008; Vidyasagar & Pammer, 2010), and provide the basis of reading difficulties observed in dyslexia, it would be instructive to consider the relative contribution of orthographic and phonologic effects in phonological analysis during reading in dyslexia.

Our study was designed to disentangle sensitivity to phonological and orthographic information in dyslexic and normal readers using ERPs. The cognitive chronometry afforded by ERPs allowed us to distinguish detection and decoding from attentional and working memory processes. We used a 2 x 2 design, similar to that of Grainger et al. (2006), except we did not use masked priming. We created pseudoword-word pairs controlled for phonological and orthographic similarity in order to produce four experimental conditions, e.g., in the case of the word *horse* as target, primes could be *horce* (P+O+), *hauce* (P+O-), *horle* (P-O+) and *hiele* (P-O-, where 'P' denotes homophony and 'O' denotes orthographic neighbourhood with the paired word). To examine dyslexic readers' sensitivity to phonological manipulations, participants were asked to decide whether the presented pseudoword prime and the following target word sounded the same. This design allowed examination of the participants' overt phonological processing abilities in time, and potential interactions with orthographic processing.

We hypothesised that if poor phonological task performance is due to weak phonological sensitivity in dyslexia, dyslexic participants ought to show reduced phonological priming from the earliest point at which the ERP indexes phonological effects. More specifically, we would expect a relatively larger N2 to P+ stimuli (that is, less N2 attenuation for weaker phonological expectations) and smaller differences between P+ and P- amplitudes than in controls. In contrast, if phonological sensitivity in reading is intact, phonological priming effects at stages of stimulus processing and discrimination (i.e., in the P2/N2 and P3 ranges) should be of similar magnitude to those found in control readers. In this situation, it is possible that processes of integration or reanalysis may instead be the source of error in phonological tasks, in which case ERPs should differ in a later time-window, i.e., that of the N400 or beyond.

Regarding orthographic effects, we reasoned that if sensitivity to orthographic information at the whole string level is decreased in dyslexia, we should observe reduced modulation by orthographic similarity from the N1 onwards in the dyslexic group. Crucially, we were interested to see the extent to which orthographic and phonological effects would interact. If, for example, orthographic sensitivity had a greater impact on phonological analysis in dyslexic than control readers, we would expect significant interactions of group with orthographic and phonological priming from the P2/N2 range onwards.

Method

Participants

Sixteen high-functioning developmental dyslexic adults (mean age 21.63 years; 8 males) and 16 control adults (mean age 21.19 years, 9 males) participated in our experiment that had been approved by Bangor University's Ethics Committee. Data from four control participants had previously been discarded due to technical failure or insufficient number of trials. All participants were undergraduate or postgraduate students at Bangor University and were right-handed, native speakers of English with normal or corrected-to-normal vision, and no self-reported neurological impairment or comorbid difficulties. Dyslexic volunteers were recruited from Bangor University's Dyslexia Unit and through advertisement on the University's Participant Panel; all had a diagnosis of dyslexia from an educational psychologist. The rationale for testing high-functioning dyslexic adults is that observable deficits that persist into adulthood, even in the context of a normal reading level, can help to identify core deficits common to developmental dyslexia across abilities (see for e.g., Bruck, 1992; Gallagher, Laxon, Armstrong & Frith, 1996; Ingvar, Trampe, Greitz, Eriksson, Stone-Elander & Euler, 2002; Jones et al., 2008; McCrory, Mechelli, Frith & Price, 2005; Miller-Shaul, 2005; Paulesu et al., 1996; Szenkovits & Ramus, 2003; Wilson & Lesaux, 2001). Furthermore, the advantages of testing university students is that (a) they form a fairly homogenous sample with similar levels of print exposure; (b) it minimizes the likelihood of potential comorbidity, and (c) individuals are more likely to actively engage with attentionally demanding psycholinguistic tasks (see also Szenkovits & Ramus, 2003, for a similar rationale).

Table 1. *Group performance on psychometric subtests*

Measure	Controls (*n*=16)		Dyslexics (*n*=16)		
	Mean	*SD*	*Mean*	*SD*	*t*
Age (years)	21.19	4.40	21.63	4.72	-0.27
DAST One-minute Reading	110.25	9.25	92.06	14.92	4.14**
DAST Nonsense Passage	93.94	4.19	88.69	6.34	2.76*
DAST Rapid Naming (s)	24.56	5.67	32.13	9.47	-2.74*
WAIS Digit Span	12.25	2.67	9.81	3.92	2.06*
WIAT Pseudoword Reading	105.63	6.51	98.44	12.32	2.06^a
WRAT Reading	114.19	4.31	104.63	9.38	3.71**
WRAT Spelling	104.44	8.05	93.63	16.78	2.32*

Note. WAIS, WIAT and WRAT scores are age-scaled. $*p < .05$; $**p < .01$; $^a p = .051$

Performance on a battery of literacy related behavioural measures, taken from the DAST (Nicolson & Fawcett, 1998), WRAT-3 (Jastak & Wilkinson, 1993) WAIS-III (Wechsler, 1997) and WIAT (Wechsler, 2005) confirmed that the individuals in the dyslexic group, although of similar academic ability and showing a reading level within the normal range, were significantly poorer than the control group across measures, with the exception of the WIAT's untimed pseudoword reading task for which differences in accuracy fell just outside of significance. Corresponding results are shown in Table 1.

Stimuli

Word stimuli were 60 four- or five-letter long English words selected from the MRC Psycholinguistic database (Coltheart, 1981). Each word (e.g., "HORSE") was paired with four pseudowords, each belonging to one of four priming conditions: P+O+, in which the prime differed from the target word by only one letter and was a homophone of the target (e.g., "horce"; mean orthographic similarity score, 0.89); P+O-, in which the prime was homophonic to the target but had reduced orthographic overlap ("hauce"; mean orthographic score, 0.52); P-O+, in which the prime was a non-homophonic pseudoword created by changing the same letter as in the P+O+ condition ("horle"; mean orthographic score, 0.89); and P-O-, in which the prime was not a homophone of the target but had the same orthographic overlap as in the P+O- condition ("hiele", mean orthographic score, 0.52). Orthographic similarity between each prime and target was measured using *Normalized Edit Distance* (NED; see Lambert, Lin, Chang & Gandhi, 1999), for which the minimum number of edits between stimuli (i.e., substitutions, deletions or additions) is divided by the longer string length (in this study prime and targets were the same length). The NED was subtracted from one to produce a similarity rather than dissimilarity score. For instance, "HORSE" and "hauce" are separable by a minimum edit of three: substitution of 'O', 'R' 'and 'S' with 'A', 'U' and 'C': $1 - (3 \div 5) = 0.4$. As we were interested in orthographic similarity between primes and targets, rather than effects of orthographic neighbourhood size of the stimuli, number of neighbours (NN) was controlled across conditions (Mean NN: P+O+ 3.60; P+O- 3.70; P-O+ 3.82; P-O- 3.43). Constrained bigram and trigram frequencies of each prime verified there were no significant differences in orthographic frequency across prime conditions. The full list of critical prime-target pairs can be found in the Appendix.

Twenty-four further stimulus pairs were created as fillers to prevent a strategy of making a decision before presentation of the second stimulus based on recognition of whether the prime was a pseudohomophone and promote comparison of prime and target. Fillers consisted of six primes from each of the four conditions paired with mismatching word stimuli.

Procedure

Participants made phonological decisions to pseudoword-word pairs presented visually in sequence. They decided whether the target word sounded the same as the prime. In a given trial participants looked at a fixation cross displayed for 1000 ms, followed by a prime presented in lower case and displayed for 200 ms. The target was separated from the prime by a variable inter-stimulus interval (ISI) of 200, 260, 320, 380, 440 or 500 ms, during which the screen was blank. For a given target, the ISI was constant across conditions and frequency of ISIs was controlled across the experiment. The word target was subsequently presented in upper case for a further 200ms, and was followed by an inter-trial fixed interval of 3000 ms (Figure 7). Participants responded by pressing one of two designated keyboard keys (yes/no response). For the duration of the task, participants were seated comfortably in a dimly lit, sound-attenuated room in front of a projector screen. All stimuli were presented at eye-level at the centre of the screen, with stimulus strings subtending a maximum visual angle of 3.7° to ensure that the word stimulus was close to foveal vision. Stimuli were presented in black Arial font, in the centre of a white background and were presented pseudo-randomly across four trials blocks, such that there was the same number of trials from each condition in each block, with rest breaks in between. Trials were presented and behavioral performance was recorded by E-Prime (Psychology Software Tools, Inc., Pittsburgh, USA). The testing session lasted approximately 15 minutes.

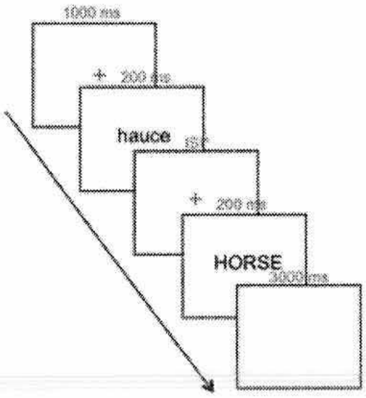

Figure 7. A single trial. Words were presented with each priming pseudoword condition, and critical trials were interspersed with non-priming fillers. *Variable ISI (controlled across prime conditions) of 200, 260, 320, 380, 440 or 500 ms.

ERP Processing

The EEG was recorded with Synamps DC-amplifiers (NeuroScan, Sterling, VA, USA) from 36 Ag/AgCl electrodes, placed in an EasyCap (www.easycap.de) according to the 10-20 system. Bipolar recordings from electrodes set above and below the left eye recorded vertical eye movement. Electrode impedance was maintained below 5 kΩ. The online reference was the left mastoid and FPz served as the ground electrode. EEG activity was band-pass filtered on-line between 0.1 and 200 Hz and sampled at 1 KHz. The EEG was re-filtered off-line with a 30 Hz band-pass zero-phase shift low pass digital filter (48 dB/octave). Eye blinks were mathematically corrected using the algorithm provided by Scan 4.3 (Neuroscan, Inc.): A model eye-blink was computed from a minimum of 50 individual blinks, and, when the variance of the model at each recording channel was below 0.001 (which was the case in every participant), the amplitude of the model was subtracted from each channel proportionally to the overall size of the eye-blink at each recording site in the continuous EEG recording, which is more conservative than the method proposed by Gratton, Coles & Donchin (1983). Visual inspection of the EEG identified remaining artefacts to be manually rejected. The continuous EEG was sliced into epochs ranging from -100 to 1000 ms after the onset of the target word. Epochs with voltage exceeding ±75 μV were automatically rejected. Only corrected trials were included. There was a minimum of 30 valid epochs per condition in each participant (Control group epochs: P+O+ *M*= 49.00, *SD*= 7.88; P+O- *M*= 44.19, *SD*= 8.41; P-O+ *M*= 42.63, *SD*= 9.65; P-O- *M*= 48.07, *SD*= 9.55; Dyslexic group epochs: P+O+ *M*= 48.56, *SD*= 6.79; P+O- *M*= 42.31, *SD*= 8.54; P-O+ *M*= 41.13, *SD*= 8.75; P-O- *M*= 47.44, *SD*= 8.27). Baseline correction was performed in reference to pre-stimulus activity, and individual averages were digitally re-referenced to the average of the mastoid electrodes. Individual averages defined by the prime condition were computed and used to produce grand-mean averages for the dyslexic and control group. ERP data were collected simultaneously to behavioural data.

ERP data analysis

Main ERP components were identified based on their deflection, topography and latency.

Time windows for analysis of each component were defined on the basis of the mean global field power produced by all electrodes taken together across the scalp. The same windows were used in all conditions and both groups: 85–115 ms for the P1; 150–180 ms for the N1; 150-220 ms for the P2; 250-320 for the N2; 260-360 ms for the P3; and 450–670 ms for the P600. Peak detection was time-locked to the electrode of maximal amplitude for each component: O2 for the P1; P8 for the N1; FCz for the P2 and N2, CPz for the P3 and P600. Similarly, mean amplitudes were measured at electrodes chosen based on their maximum sensitivity: O1, O2, P7 and P8 electrodes for the P1; O1, O2, P7 and P8 for the N1; F3, F4, Fz, FC3, FC4, FCz for the P2 and N2; C3, C4, Cz, CP3, CP4, CPz, for the P3 and P600. Mean amplitudes and peak latencies were subjected to 2 x 2 x 2 x electrode mixed analyses of variance (ANOVAs). Within-subject factors were phonological similarity (homophonic, non-homophonic) and orthographic similarity (orthographic neighbour, non-neighbour) and electrodes and a between subjects factor of group (control, dyslexic). Behavioural data was analysed with a three-way mixed ANOVA with within subjects factors of phonological similarity (homophonic, non-homophonic) and orthographic similarity (orthographic neighbour, non-neighbour); and a between subjects factor of group (control, dyslexic).

Results

Behavioural results

Correct response reaction times were significantly faster to homophonic than non-homophonic pairs, *F*(1, 30) = 50.86, $p < .001$. Orthographic neighbouring stimuli also resulted in faster reaction times, *F*(1, 30) = 5.51, $p < .05$, but reduced accuracy, *F*(1, 30) = 6.94, $p < .05$. Furthermore, phonological and orthographic similarity significantly interacted for both accuracy, $F(1, 30) = 111.52, p < .001$, and reaction time, $F(1, 30) = 96.05, p < .001$. This was due to decreased accuracy and increased reaction times for 'mixed' primes (i.e., P+O- and P-O+ stimuli) as compared to non-mixed ones. A trend for an interaction between group, phonological priming and orthographic priming interaction for accuracy, $p = .09$, related to the dyslexic group showing a greater relative deficit in accuracy to the mixed cues, compared to controls (see Figure 8). A significant main effect of group on reaction times indicated that responses were generally slower from the dyslexic group, $F(1, 30) = 4.76, p < .05$.

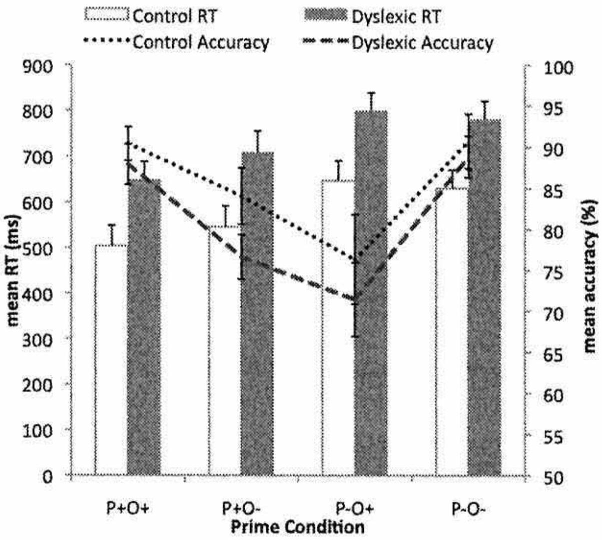

Figure 8. Mean reaction time and accuracy (Error bars represent 1 standard error)

Event-related potential results

P1

No significant effects were observed in the P1 range.

N1

There was a significant interaction between orthographic similarity and group on N1 mean amplitudes, *F*(1, 30) = 5.18, $p < .05$, driven by significant amplification of N1 to orthographically neighbouring (O+) stimuli in the control group only (see Figure 9). N1 peak latencies were significantly delayed overall in the dyslexic group, *F*(1, 30) = 5.99, $p < .05$ (Peak latency: control group *M*= 159 ms; dyslexic group *M*= 166 ms)[4]. A non-significant trend for orthographic neighbour modulation of N1 latency was also observed, with O- primed words tending to elicit an earlier N1 peak ($p = .07$).

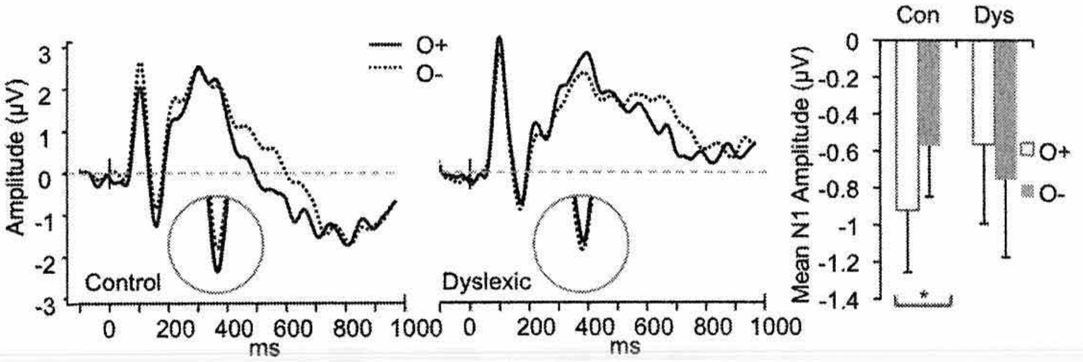

Figure 9. Orthographic priming modulations of target N1 amplitude (Linear derivation of O1, O2, P7 and P8 electrodes).

P2

No main effects were observed with respect to P2 mean amplitudes. However an interaction of phonological similarity, orthographic similarity and group significantly affected P2 amplitude, *F*(1, 30) = 5.58, $p < .05$. This interaction was driven by the

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[4] To investigate possible effects of having different peak latencies in the groups (which was the case for N1), we ran a second analysis with slightly different intervals for each of the two groups. This analysis yielded the same qualitative result as the analysis using common intervals and is not reported here.

dyslexic group showing a significantly amplified response to P-O- primed words compared to P-O+.

A main effect of phonological similarity indicated that homophonic stimulus pairs significantly delayed P2 latencies, $F(1, 30) = 3.41, p < .05$. Phonological similarity also interacted with group, $F(1, 30) = 4.32, p < .05$, which related to only the control group showing a later peak for P+ stimuli.

N2

A main effect of phonological similarity showed that non-homophonic words significantly amplified the N2 peak relative to homophonic words, $F(1, 30) = 36.20, p < .001$. No interaction of group with phonological similarity was observed. However, mean amplitudes were modulated by a three-way interaction of group, phonological similarity and orthographic similarity, $F(1, 30) = 8.45, p < .01$. The source of this interaction related to the relative attenuation of P-O+ and P-O- primed words: whilst homophonic words (P+O+ and P+O- primed) elicited a significantly attenuated response relative to non-homophonic words (P-O+ and P-O- primed), P-O+ words were also significantly attenuated relative to P-O- in the control group; the dyslexic group, on the other hand, showed similar amplification of N2 to non-homophonic words (P-O+ and P-O- primed), however they only significantly differed from P+O+ primed words, and not P+O- (see Figure 10).

N2 peak latencies were significantly shorter to homophonic words, $F(1, 30) = 12.80, p < .001$, and to orthographically neighbouring words, $F(1, 30) = 15.47, p < .001$. Furthermore, a trend for an interaction between group, phonological similarity and orthographic similarity, $p = .09$, indicated that peak latencies were significantly longer to P-O- primed words compared to all other priming conditions in the dyslexic group, whilst in the control group P-O- and P+O- peak latencies were not significantly different.

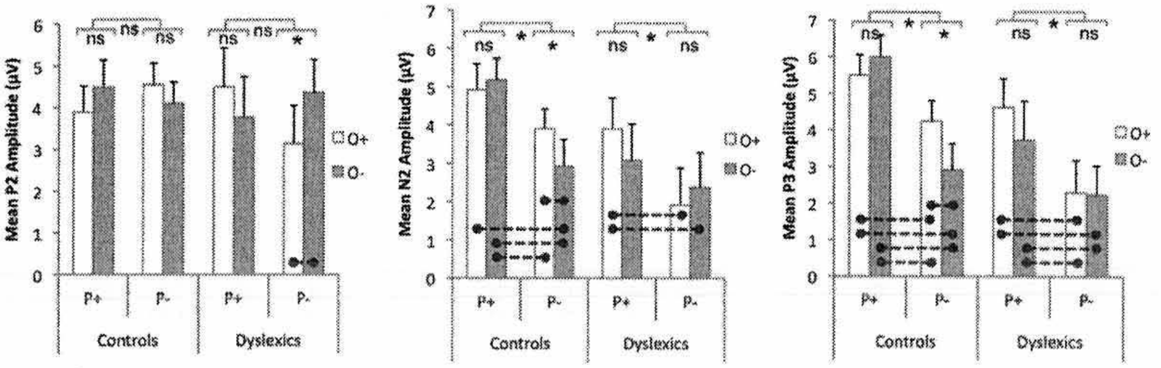

Figure 10. The three-way interactions spanning the P2, N2 and P3 peaks. * Condition effect is $p < .05$. Dotted lines depict significant pair-wise comparisons.

P3

Phonological similarity, $F(1, 30) = 38.01, p < .001$, and orthographic similarity, $F(1, 30) = 4.26, p < .05$, significantly amplified P3 target word peaks. A three-way interaction of group, phonological similarity and orthographic similarity, $F(1, 30) = 8.17, p < .01$, was due to differences in group responses to P-O+ primed words: Whilst P+O+ and P+O- were significantly amplified relative to P-O+ and P-O- priming conditions in both groups, the P-O+ primed targets were significantly amplified compared to P-O- in controls only. P3 peak latencies were significantly affected by both phonological similarity, $F(1, 30) = 8.94, p < .01$, for which P+ primed stimuli elicited later peaks, and by an interactive effect of phonological and orthographic similarity, $F(1, 30) = 4.79, p < .05$, which related to a significantly shorter P3 peak latency for P-O- primed stimuli compared to the homophonic stimuli (P+O+ and P+O-).

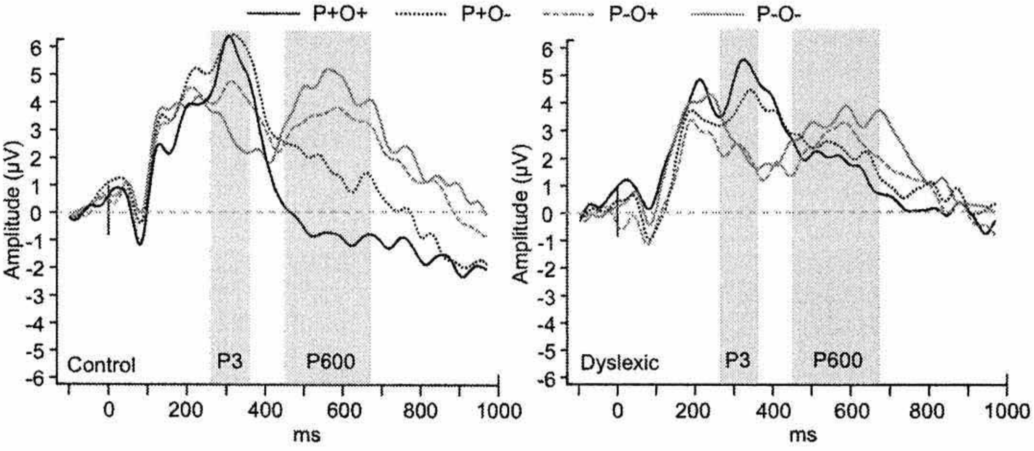

Figure 11. P3 and P600 target word modulations for each prime condition (Linear derivation of C3, C4, Cz, CP3, CP4 and CPz electrodes).

P600

Non-homophonic, $F(1, 30) = 15.00, p < .001$ and orthographic non-neighbour stimulus pairs, $F(1, 30) = 14.38, p < .001$, elicited significantly larger P600 amplitudes than homophonic and orthographically neighbouring pairs, respectively. Participant group was found to significantly interact with both phonological similarity, $F(1, 30) = 6.05, p < .05$, which showed that phonological priming modulations of P600 amplitude were significant for the control group only (see Figures 11 and 12); and with orthographic similarity, $F(1, 30) = 4.73, p < .05$, for which significant priming effects were also only in the control group (Figure 11).

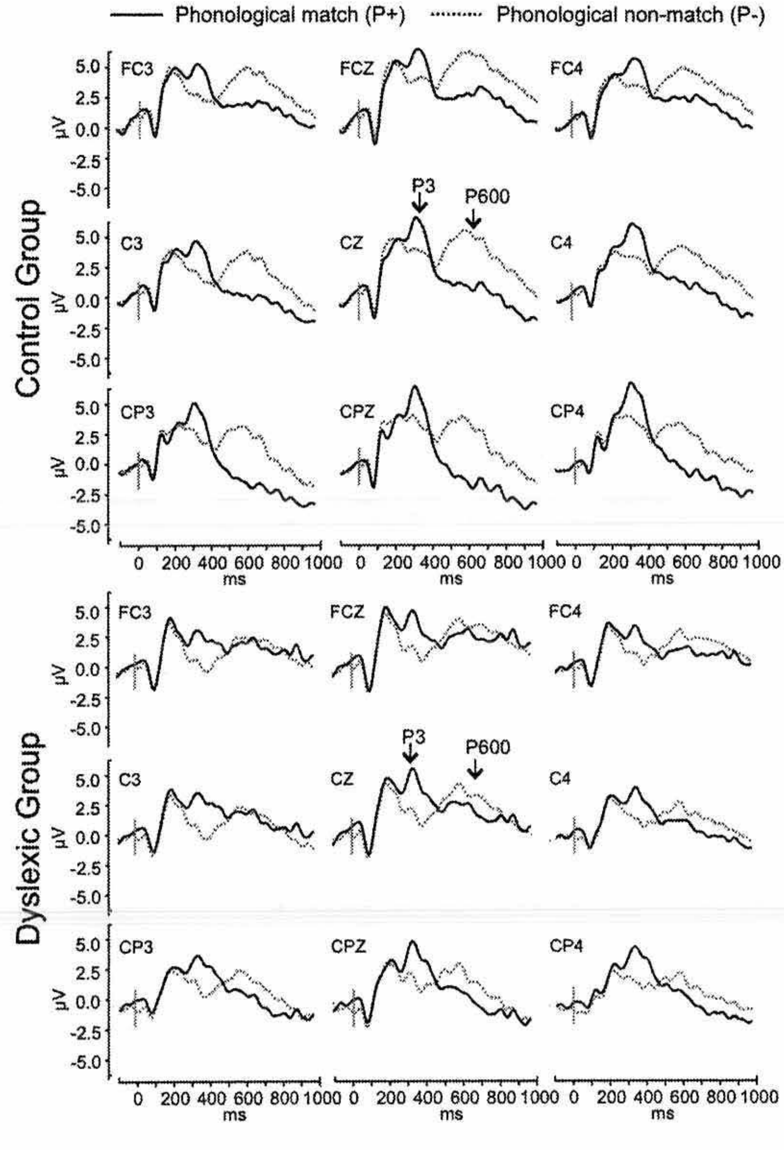

Figure 12. Averaged phonological priming effects across central electrodes, depicting the diffuse P600 attenuation in the dyslexic group (P+ is P+O+ and P+O- combined; and P- is P-O+ and P-O-).

A further three-way interaction of group, phonological and orthographic similarity, $F(1, 30) = 4.65, p < .05$, indicated that the significant differences in P600 amplitude present in the controls (P+O+ significantly attenuated compared to all, and significant differences between P+O- and the P- stimuli) were absent in the dyslexic group, for whom only amplitude differences between the P-O+ and P-O- stimuli reached significance. P600 latencies were only modulated by a main effect of phonological similarity, $F(1, 30) = 11.64, p < .05$.

Difference waves showing priming main effects across each reported ERP epoch are provided in Figure 13.

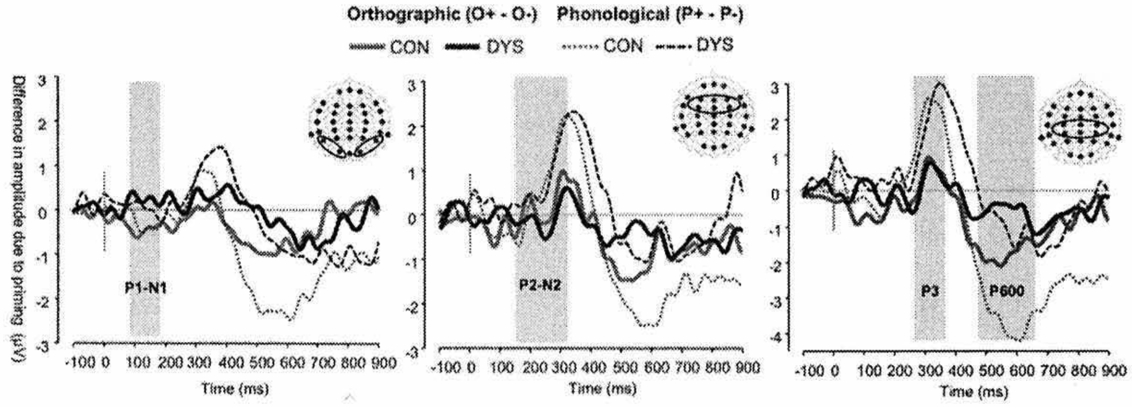

Figure 13. Orthographic and phonological priming difference waves at analysed electrode sites. A: linear derivation (LDR) of O1, O2, P7 and P8. B: LDR of F3, F4, Fz, FC3, FC4 and FCz. C: LDR of C3, C4, Cz, CP3, CP4 and CPz. CON = Control. DYS = Dyslexic.

Discussion

This study aimed at dissociating phonological and orthographic priming effects during a phonological awareness task performed on letter strings by dyslexic participants and matched controls. Our main findings were (a) main effects of phonological and orthographic priming on reaction times in both the groups; (b) N1 increase by orthographic priming in the control group only; (c) a main effect of phonological priming in the N2 and P3 range in both the participant groups; (d) a set of three way interactions with group spanning the P2, N2 and P3 peaks; and (e) a reduced P600 modulation by phonological priming in the dyslexic group only. These will be discussed in turn.

Behavioural insights

The dyslexic group, as expected, performed the task significantly slower overall. Beyond this, no significant group interactions emerged in behavioural data. However, priming significantly improved performance overall and showed the expected interaction between phonological and orthographic priming such that orthographic neighbourhood facilitated recognition of phonologically primed stimuli and degraded recognition of non-matched stimuli, and vice versa for less orthographically informative cues across group. Importantly, a trend for a three-way interaction with group indicated that the significantly deleterious effect of mixed priming on accuracy was larger in the dyslexic group. In the context of a priming manipulation in which differences between all conditions were subtle and the task was designed to avoid high error, it is perhaps not surprising that reaction time or accuracy measures in isolation did not distinguish between the groups.

The use of orthographic cues: reviewing early ERP group differences

The earliest condition modulation of the ERP was found for the N1 peak, where targets primed by orthographic neighbours elicited significantly amplified peaks in the control group only. This is consistent with previously reported effects in the N1 range in controls (Hauk et al., 2009) and other orthographic variables have been shown to modulate the N1, such as written length (Assadollahi & Pulvermüller, 2003; Hauk et al., 2009), frequency (Assadollahi & Pulvermüller, 2003; Hauk & Pulvermüller, 2004; Hauk et al., 2009; Sereno, Rayner & Posner, 1998; Sereno, Brewer, O'Donnell, 2003) and lexical status, e.g., words versus consonant strings (Coch & Mitra, 2010; Compton, Grossenbacher, Posner & Tucker, 1991; Hauk et al., 2006; Maurer et al., 2005; McCandliss, Posner & Givon, 1997; Sauseng, Bergmann & Wimmer, 2004). The absence of an N1 orthographic priming effect in our dyslexic group, along with a significant latency delay, indicates that orthographic cues were processed less efficiently/slower in dyslexic participants. This would be consistent with previous reports of attenuated P1 or N1 to orthographic stimuli (Helenius et al., 1999; Kast et al., 2010; Maurer et al., 2007) and reduced activation in left occipitotemporal areas involved in orthographic identification and integration, as shown by functional brain imaging studies (Blau et al., 2010; Brunswick, McCrory, Price, Frith & Frith, 1999; Cao, Bitan, Chou, Burman & Booth, 2006; Kronbichler et al., 2006; Liu et al., 2010; McCrory et al., 2005; Richlan et al., 2010; Salmelin et al., 1996; Van der Mark et al., 2009, 2010; Wimmer et al., 2010).

With respect to existing literature, perceptual difficulties at the word form level have been proposed to impact reading in different ways: Valdois and colleagues (e.g., Bosse et al., 2007; Lassus-Sangosse et al., 2008; Peyrin et al., 2011; Valdois et al., 2004), for instance, have suggested that subsets of dyslexic readers have a smaller attentional window impacting the scanning of letter strings, which may affect subsequent grapheme perception and integration, and contribute to downstream phonological decoding difficulties. Poor left-to-right scanning has also been suggested as the route to impaired reading in dyslexia due to deficient processing along the dorsal visual pathway, which is suggested to degrade orthographic input and impact awareness of grapheme-phoneme correspondence (Cestnick & Coltheart, 1999; Vidyasagar & Pammer, 2010). Whilst our study was primarily aimed at addressing the interaction of orthographic and phonological information, rather than orthographic/visual word form perception per se, our data indicates that orthographic information is not accessed as readily in compensated dyslexic adults as it is in normal readers.

Further, we found significant three-way interactions of group with phonological and orthographic similarity in the P2, N2 and P3 ranges: (a) A three-way modulation affecting P2 amplitude showed a significantly amplified response in the P-O- relative to P-O+ condition in the dyslexic group only; (b) Differences in the N2 range showed the following ordering of conditions in the control group: P+O- weaker than P-O+ and P-O- and P-O+ weaker than P-O-; and (c) An interaction in the P3 range induced by responses in P-O+ condition being greater than in the P-O- condition in the control group only.

Overall, three-way interactions between group, phonological, and orthographic priming may have been expected if we assume that dyslexic readers have degraded phonological representations. However, we observed significant main effects of phonological priming in the absence of a group interaction in ERP amplitudes from the N2 range through to the P3 range. We interpret this as a sign that early phonological access in our dyslexic participants may not have been functionally deficient. It must be kept in mind that this is not a null effect since phonological priming was significant in both of our groups.

By contrast, the three-way interactions listed above seem to have arisen primarily from weaker and/or possibly qualitatively different effects of orthographic similarity in the dyslexic group. Starting with the P2, which was the earliest peak where effects of mismatch between orthographic and phonological representations might have been expected (Bles et al., 2007; Braun et al., 2009; Hsu et al., 2009; Potts, 2004), the dyslexic group showed an amplified response in the P-O- condition, perhaps because this is the point at which orthographic processing kicked in for the dyslexic participants, whereas in the case of the control group, orthographic similarity of the target word may have been resolved as early as the N1 window (cf. N1 effect which was both delayed and reduced in dyslexic participants). In other words, in the case of dyslexic participants, orientation to orthographic *dissimilarity* of the stimuli in a pair would have helped phonological discrimination but not helped the detection of homophony (i.e., no differences between P+O+ and P+O-).

The following N2 interaction may relate to reduced orthographic cueing in the dyslexic group (since P-O+ elicited weaker N2 amplitude than P-O- in the controls) and perhaps a slight phonological processing weakness since P+O- was not significantly different from the P- conditions.

The third interaction, in the P3 range, continued to show reduced orthographic similarity effects in the dyslexic group: The interaction was due to the lack of difference between P-O+ and P-O- stimulus pairs in the dyslexic group as was the case in the N2 range. In other words, orthographic similarity may have failed to capture dyslexic participants' attention, perhaps because their focusing on phonological form may have limited distraction by orthographic information.

Together, these results show that stimuli were essentially distinguished on the basis of their phonological status. Moreover, dyslexic participants were less influenced by orthographic similarity than controls over and above phonological priming, with orthographic priming differences evident from the N1 to the P3 through the N2 range. A possible explanation is that the dyslexic group may have had weaker orthographic input at the whole-stimulus level (e.g., see literature on visuo-attention span, Valdois et al., 2004; and dorsal visual pathway hypotheses, Vidyasagar & Pammer, 2010) or managed to focus more exclusively on phonological similarity. Future studies in which phonological judgments are explicitly emphasized by the task ought to clarify whether group differences in orthographic processing are driven by reduced access of orthographic information in dyslexic readers or emerge from relative streamlining of attention to the phonological level when participants are required to focus on phonology.

P600: Late differences in phonological processing

The dyslexic group showed a significantly reduced main effect of phonological similarity within the P600 range. P600 mean amplitude was significantly attenuated in the dyslexic group for both phonological and orthographic as compared to the control group. Across groups, the strongest increase in P600 amplitude was found for the least related stimuli (P-O-), with progressively reduced amplitudes for 'P-O+' and 'P+O-', and 'P+O+' stimuli. Typically, the P600 component is triggered by linguistic incongruence that is not based on semantic integration (Kolk & Chwilla, 2007) and has been proposed to index a process of reanalysis (Van de Meerendonk et al., 2010; Vissers et al., 2008). The reduced P600 differentiation between conditions suggests that stimulus relatedness may have been less salient and/or subject to limited reanalysis at this late reprocessing stage in the dyslexic group. Whatever difficulty or difference is driving the attenuation elicited by the dyslexic group in this task, it is unlikely to relate to sensitivity to phonological manipulations within the orthographically controlled stimuli, since no marked differences were found in the N2 and P3 ranges.

Is a reprocessing dysfunction exacerbating performance deficits in overtly phonological tasks in dyslexia?

The significant P600 attenuation possibly indexes a deficient strategic response during an overt verbal task. Recent accounts of the phonological deficit in dyslexia have focussed on working memory demand rather than perceptual deficits relating to weak phonological representations (Banai & Ahissar, 2006; Ramus & Szenkovits, 2008). For instance, a series of experiments by Ramus and colleagues targeting predictive effects of weak or fuzzy phonological representations using speech-based auditory tasks repeatedly failed to find significant differences between dyslexic and control listeners (see Ramus & Szenkovits, 2008). In the same vein, Banai and Ahissar (2006) showed that dyslexic participants only manifest phonological deficits while performing complex ordinal or parametric judgments of auditory phonological stimuli, but were not hindered in judgements of the same stimuli when they required simple (i.e., same-different) discriminations. Together the latter two studies suggest that task demand, e.g., the level of short-term memory involvement and time constraints, determines access to phonological representations and subsequent observed behavioural deficits in phonological tasks. Our task required maintenance of the phonological form of consecutively presented pairs of stimuli, which arguably placed similar processing demands on the participants. Thus it may be that our observed P600 effects are the result of depleted working memory resources precluding phonological integration and reappraisal. Studies that have previously reported differences in P600 amplitude in dyslexic populations have attributed similar late ERP differences to conscious and strategic rather than automatic linguistic processes. Rispens and colleagues (2004, 2006), for instance, demonstrated that Dutch dyslexic participants showed no significant P600 modulation to auditorily presented sentences containing plural noun phrase structure violations. As an earlier measure of automatic syntactic parsing – an early left anterior negativity (ELAN), found approximately 200ms after violation – was unaffected, the authors suggested that their P600 differences indicated dyslexic deficits in more controlled and strategic linguistic processes involved in syntactic revision (Rispens, 2004), which may reflect some form of reprocessing failure. Within the visual word domain, studies considering the electrophysiological basis of word learning in dyslexia (Schulte-Körne, Deimel, Bartling & Remschmidt, 2004) and recognition memory for visually-presented words (Rüsseler, Probst, Johannes & Münte, 2003) have also shown intact early word recognition and discriminative ERP effects, with only diminished responses at the stage of conscious recollection/retrieval in the P600 range. Schulte-Körne et al. (2004), for example, studied dyslexic and control children's recognition of previously learned four-letter pseudowords and complex graphic symbols using ERPs. In the context of accurate behavioural performance and normal P300 effects, they found that the recognition ERP correlate – the P600 – was significantly attenuated specifically for the pseudowords, compared to graphic symbols and control group responses. Whilst the authors related their finding to an impairment in visual recognition due to the limited phonological demand of the pseudowords; their results could also be interpretable as a strategic processing and/or working memory failure elicited by stimuli requiring phonological analysis in the dyslexic participants, despite intact recognition.

Some form of reduced maintenance and integration of phonological information could also account for findings of existing ERP studies using phonological tasks with visual word stimuli, which typically report reduced N400 modulations from dyslexic readers (Ackerman et al., 1994; McPherson et al., 1998; Rüsseler et al., 2007). This would fit with associations of the N400 with working memory (e.g. Gunter, Wagner & Friederici, 2003) and decision-making processes related to stimulus integration (Brown & Hagoort, 1993; Connolly & Phillips, 1994; Chwilla et al., 1995; Holcomb, 1993). Our task did not elicit an N400 response, but instead a P600. This may be due to the differences in task demand between word rhyming judgment, in which such N400 phonological differences have typically been observed, and in this study, a homophone judgment. Kolk and colleagues (Kolk et al., 2003; Kolk & Chwilla, 2007; Van De Meerendonk et al., 2009) suggest that the N400 wave indexes lexical integration of an unexpected linguistic event (e.g., to a rhyme mismatch) but that if the unexpected event is perceptually uncertain (e.g., with complex sentences or, perhaps, brief presentations of unfamiliar pseudowords, as in the case of our homophone judgment task) integration indexed by the N400 will not occur and a veridicality check indexed by the P600 will occur instead. Thus the specificity of our P600 effect needs to be clarified: It is unlikely to be a downstream net result of weaker phonological priming in the dyslexic group, both because (a) earlier modulations indicated similar magnitudes of phonological priming between groups and (b) the likely outcome of a weaker phonological percept would be uncertainty and thus larger, rather than significantly smaller, P600 amplitudes. If we nonetheless adopted this interpretation our data would indicate that the dyslexic group responded more confidently than the control group, which is highly unlikely. Thus the hypothesis of a performance monitoring/reanalysis deficit is more likely. The question of whether this deficient monitoring is specific to phonological task performance or indicative of a more general trend cannot be determined from this study and will require further investigation.

Converging evidence for a phonological monitoring failure comes from recent ERP studies examining dyslexic error-related negativities – a negative fluctuation typically found 100ms post an erroneous response (Horowitz-Kraus & Breznitz, 2008, 2009). Horowitz-Kraus and Breznitz (2008) reported reduced differentiation between error-related negativities and correct-related negativities from dyslexic readers compared to controls during performance of a lexical decision task, which they suggested could relate to inefficient error monitoring. The P600 effects observed here may be a pre- (or peri-) response correlate of this inefficient monitoring. Unfortunately, it was not possible to run analyses of error-related responses because of the very low rate of errors. However, future studies could address if reduced differentiation of error/correct-related negativities post-response may relate to prior atypical performance monitoring, and furthermore whether these monitoring deficits are specific to performing a phonological task.

The role of attention in manifestations of the phonological deficit?

An important consideration with our task is that attention was explicitly focused on the phonological relationship between stimuli in a pair. The only ERP difference between groups in phonological priming effects (irrespective of orthographic cues) were observed in response monitoring. It may be that we would have observed early differences in phonological priming effects if attention had not been oriented to phonology and/nor engaged in a phonological task. If this were the case, the pervasive phonological deficit would probably not be due to a significantly reduced ability to perceive phonological manipulations, but rather a relative failure in attentional capture. This would fit with the auditory ERP literature typically showing reduced phonological modulations in oddball tasks in which the oddball is task-irrelevant (Fosker & Thierry, 2004; see Bishop, 2007, for a review of MMN studies) versus normal P3 phonological modulations when participants are asked to attend to the oddball (Fosker & Thierry, 2005; Rüsseler et al., 2002). Deficits switched by attention to phonological information may explain much of the conflicting data regarding phonological processing difficulties in developmental dyslexia: Reduced voluntary orientation to phonological information, possibly exacerbated in the case of reading by reduced orthographic sensitivity and subsequently disrupted graphemic-phonemic mapping on the one hand; and limited processing capacity for deliberate phonological analysis on the other.

Conclusions

This study provides electrophysiological evidence for early sensitivity to subtle phonological manipulations of visual pseudoword stimuli, but reduced sensitivity to whole form orthographic information during phonological analysis in dyslexic readers. A failure in stimulus integration and reprocessing, indexed by a significantly less discriminative P600 may account for the weaker performance of dyslexic participant in homophonic judgement. The phonological deficit, in pseudoword reading at least, might thus be better conceived in line with Ramus and Szenkovits' (2008) conclusion regarding the recruitment of controlled, metacognitive processes in phonological analysis. Further research should determine the specificity of reduced orthographic effects in dyslexia and clarify the role of phonology in deliberate and implicit word recognition. Tasks which selectively manipulate the focus on phonological and orthographic information and the degree of attentional demand required should help to clarify the relative perceptual and executive aspects of reading deficits in dyslexia.

Chapter Four

Literate humans sound out words during silent reading

Nicola Savill, Annukka Lindell, Alison Booth, Gemma West, and Guillaume Thierry

Paper published in *NeuroReport*, Volume 22, February 2011, pages 116-120.

The published article is provided in the Appendix.

Abstract

Whether humans spontaneously sound out words in their mind during silent reading is a matter of debate. Some models of reading postulate that skilled readers access the meaning directly from print but others involve print-to sound transcoding mechanisms. Here, we provide evidence that silent reading activates the sound form of words before accessing their meaning by comparing event-related potentials induced by highly expected words and their homophones. We found that expected words and words that sound the same but have a different orthography (homophones and pseudohomophones) reduce scalp activity to the same extent within 300 ms of presentation compared with unexpected words. This shows that phonological access during silent reading, which is critical for literacy acquisition, remains active in adulthood.

Introduction

Studies that have tested phonological effects during single word reading have shown brain activity modulations as early as 100ms after stimulus onset (Ashby, 2010; Ashby, Sanders & Kingston, 2009; Braun et al., 2009; Wheat, Cornelissen, Frost & Hansen, 2010), suggesting a fundamental role for phonology. However, whether phonological information is spontaneously retrieved when accessing semantic information while reading is open to debate (Coltheart, Curtis, Atkins & Haller, 1993; Lukatela & Turvey, 1994; Taft & van Graan, 1998). To test whether the phonological form of written words is activated during silent reading, we measured the N2 and N400 peak amplitudes of event-related potentials (ERPs), which reflect the degree of phonological and semantic mismatch, respectively, between a word and the context in which it appears (Connolly &

Phillips, 1994; Kutas & Hillyard, 1980; Näätänen, 1990; Ziegler, Benraiss & Besson, 1999). For example, in the spoken sentence 'an eagle is a bird of flare', the word 'flare' would elicit larger N2 and N400 compared with 'prey' as it is neither phonologically nor semantically expected in the sentence context (Connolly & Phillips, 1994). As the N2 is sensitive to the phonological expectation about words, significant reduction in its amplitude for both an expected word and its homophone (HO) relative to an unexpected word in visually presented sentences would provide strong evidence that the sound form of words is retrieved during silent reading.

Most of the existing ERP studies investigating this question have not found convincing evidence for phonological involvement in accessing the meaning of written words. In the case of single word reading, one ERP study (Ziegler et al., 1999) testing phonological access in a semantic categorization task found no differences in the N400 between homophones of category exemplars (e.g. 'meet' for the category of food) compared with orthographic controls (e.g. 'melt'). In the context of behavioural data showing higher error rates in the homophone condition (HOs were more likely to be accepted as correct category members than orthographic control items), the conclusion was that the phonological effects occur after semantic integration indexed by the N400. However, the possibility was raised that the increased processing demands of reading sentences for meaning might entail greater phonological involvement (Ziegler et al., 1999).

Earlier sentence reading studies have examined phonological activation by replacing semantically primed final words with unexpected words sharing initial phonemes (Connolly, Phillips & Forbes, 1995), homophones (Niznikiewicz & Squires, 1996; Ren, Lui & Han, 2009), or pseudohomophones (PHs) (pseudowords homophonic to a real word; Newman & Connolly, 2004). Some studies have found evidence for phonological effects in semantic integration indexed by the N400 (Newman & Connolly, 2004; Ren et al., 2009), whereas other studies have not (Connolly et al., 1995; Niznikiewicz & Squires, 1996). Furthermore, these studies have found only weak phonological reductions in the N2 range in an early stage and, moreover, concluded that the N2 modulations in reading are primarily related to orthographic violation (Newman & Connolly, 2004). However, these results have provided only limited insight with regard to spontaneous phonological activation in silent reading, because they have either (i) not used a controlled task (e.g. no behavioural monitoring in the case of Connolly et al., 1995; Newman & Connolly, 2004; Ren et al., 2009); (ii) not used sentences with high cloze probability (in Niznikiewicz & Squires, 1996), and/or (iii) not controlled cloze probability across experimental conditions (i.e., they used different sentence contexts across conditions in Connolly et al.,1995, and Newman & Connolly, 2004). Cloze probability is the numerical probability of a given word to be selected to complete a given sentence context (e.g. the cloze probability of 'prey' in the sentence starting 'An eagle is a bird of prey' is close to 1).

Indirect evidence for phonological activation in sentence reading comes from a study on misspellings (Vissers et al., 2006), in which expectancy was manipulated by presenting low-cloze and high-cloze probability sentences containing a congruent word or its pseudohomophone. In the N2 time range (N270), differences between words and pseudohomophones were found in the context of low-cloze sentences but not in that of high-cloze sentences. Although the aim of the study was to investigate the processing of misspellings, this result is compatible with phonological mediation in silent reading, as pseudohomophones, when highly constrained by sentence context, are phonologically expected. In the same study, words and PHs also reduced ERP amplitudes in the N400 range when presented in a high-cloze probability sentence (Vissers et al., 2006), suggesting that phonological activation during silent reading may extend into the window of semantic integration (Newman & Connolly, 2004; Kutas & Hillyard, 1984).

Here, we tested whether participants who read silently for meaning would show phonological processing of stimuli that are orthographically and semantically inappropriate but phonologically expected, when reading highly constrained sentences. Our main question was whether homophones and pseudohomophones presented at the end of a highly constrained sentence would reduce the amplitude of the N2 peak relative to totally unexpected endings (Connolly & Phillips, 1994; Kramer & Donchin, 1987). Our predictions were as follows: if retrieval of the phonological form of written words is spontaneous during silent reading, we should observe a reduced N2 peak in all conditions except for totally unexpected completions. In addition, retrieval of the phonological form of a homophone or pseudohomophone was expected to activate the semantic representation of the best completion (BC) and thus, similarly reduce the subsequent N400 (Kutas & Hillyard, 1980, 1984).

Materials and methods

Participants

Fifteen undergraduate students participated in the partial fulfilment of a course requirement (11 women and 4 men, with a mean age of 19.3 years, range: 18–24 years) in our study, approved by the Bangor University's Ethics Committee. All had normal or corrected-to-normal vision and were native speakers of English.

Stimuli

To ensure that the best completion stimuli were highly predictable from the preceding sentence context, a separate group of 37 participants completed a series of sentences that were missing the final word with their most likely ending (e.g. 'Rob looked at his watch to check they' elicited the response 'time'). Sentences were included on the basis of their percentage predictability: each had a minimum of 0.80 cloze probability, with an average cloze probability of 0.84 for the final best completion stimuli.

There were four experimental conditions: the best completions (e.g., 'time'); homophones of the best completion (e.g., 'thyme'); pseudohomophones of the best completion (orthographically legal pseudowords homophonic to the best completion, e.g., 'tyme'); and unrelated (UN, words unrelated to the sentence context, e.g. 'skull'). BC, HO and UN word lists were matched for lexical frequency (mean log=1.13±0.7), concreteness (mean=465±99), length (mean=4.6±1) and grammatical class (Coltheart, 1981). The sentences ranged from five to 12 words in length.

Of the four stimulus conditions, three provided endings that were incongruent with the sentence whereas only one (best completion) provided a congruent completion. To avoid spurious P300 effects prompted by unbalanced proportion between the best completion and other experimental conditions, we created a filler best completion condition (Courchesne, Hillyard & Galambos, 1975). These fillers consisted of sentences with congruent endings but had no corresponding HO or PH equivalents and were not analysed. The complete stimulus set consisted of a total of 240 words: 40 words in each of the four critical experimental conditions (BC, HO, PH, UN) and 80 words in the filler BC condition. The critical sentence stimuli are give in the Appendix.

Procedure

Participants were comfortably seated in a darkened, and acoustically shielded room. A high-resolution cathode ray tube monitor was centred approximately 100 cm from the participants' eyes. They were instructed to fixate at the centre of the screen and to minimize eye and body movements throughout the ERP recording. The participants were asked to indicate whether the final word was congruent or incongruent with the preceding sentence by pressing either the 'F' or 'J' keys (with the left and right index fingers, respectively). Response side was alternated between blocks and counterbalanced across participants. The 240 stimuli were divided into four blocks of 60 trials. In each trial, the sentence was presented one word at a time for 200 ms with an inter-stimulus interval of 300ms. After the presentation of the final word, the participants had 2 s to respond. Each word subtended a maximum visual angle of 4 x 0.8°. Individual reaction times for correct responses were averaged as a function of the experimental condition. Incorrect responses and non-responses were coded as errors.

Electroencephalography recording and analysis

Electroencephalography (EEG) data were recorded (1 kHz sampling rate; SynAmps 2 amplifiers; Neuroscan Inc., El Paso, USA) from 32 Ag/AgCl electrodes in reference to Cz (impedance <11 kΩ). The electrodes were placed in accordance with the International 10–20 System at the frontal (Fp1, Fp2, Fz, F3, F4, F7, F8), central (C3, C4), temporal (T7, T8), parietal (Pz, P3, P4, P7, P8) and occipital (O1, O2) sites, with additional electrodes in the anterior frontal (AFz), frontotemporal (FT9, FT10), frontocentral (FC1, FC2, FC5, FC6), centralparietal (CP1, CP2, CP5, CP6) and parietooccipital (PO9, PO10) locations. Electrodes above and below the left eye monitored eyeblink activity. EEG signal was filtered online between 0.1 and 100 Hz and was refiltered offline using a zero-phase shift using a 20 Hz cutoff low pass. Neuroscan software (Scan 4.2) was used to mathematically correct the eyeblinks. Epochs ranged from – 100 to 1000 ms after the final word onset. Baseline correction was made with reference to 100 ms prestimulus activity. At least 30 correct response epochs were obtained for each experimental condition (acceptance of BCs, rejections for the remainder) for each participant.

Individual averages, which were digitally re-referenced to the global average reference, were averaged to produce the grand average ERPs. Mean amplitudes were measured at electrodes FC1, FC2 and Fz between 250 and 350 ms for the N2 and CP1, CP2 and Pz between 350 and 500 ms for the N400. For both the peaks, individual mean amplitudes and peak latencies for each condition were subjected to repeated measures analyses of variance with within-subject factors of condition (BC, HO, PH, UN) and electrodes (three electrodes).

Results

Behavioural data

Repeated measures analysis of variance indicated that experimental conditions significantly affected the reaction times, $F(3,14)=6.57$, $p < 0.05$, with PH stimuli eliciting faster responses compared with other conditions (all $p < 0.05$; Figure 14). Error rates also differed among the experimental conditions, $F(3,14)=12.25$, $p < .01$ (Figure 14). Both BC and PH conditions yielded lower error rates than the HO and UN conditions (all $p < 0.05$). Differences between BC and PH on the one hand and between HO and UN on the other hand were nonsignificant (all $p > 0.1$).

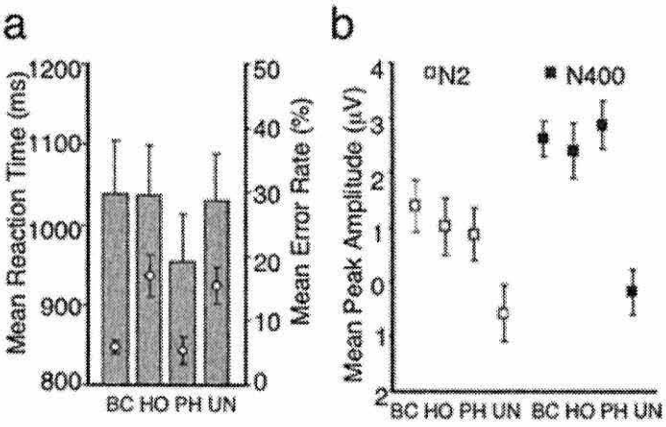

Figure 14. a. Reaction times for correct trials (bars) and error rates (circles) in the 4 experimental conditions. b. Mean peak amplitude of the N2 and N400 in the 4 experimental conditions. BC: Best Completion, HO: Homophone, PH: Pseudohomophone, UN: Unexpected Completion. Error bars depict the standard error of the mean in all cases.

Electrophysiological Data

The P1 and N1 components elicited by words in the final position peaked at 115 and 223 ms, respectively, and were unaffected by experimental conditions either in amplitude or latency. The N2 peaked at 317 ms over the frontal area, and was maximal at Fz. The N400 was a broad negative wave maximal across centroparietal electrodes.

N2 peak latency was insensitive to experimental conditions ($p > 0.1$), but its mean amplitude was affected by experimental conditions, $F(3,14)=7.81, p < 0.05$ (Figure 15). Post-hoc t-tests indicated that the N2 elicited by the UN condition was larger compared with all other conditions: BC–UN: $t(14)=2.03$, $p < 0.05$; HO–UN: $t(14)=2.82$, $p < 0.05$; PH–UN $t(14)=2.70$, $p < 0.05$, whereas differences among BC, HO and PH considered in pairs were non-significant.

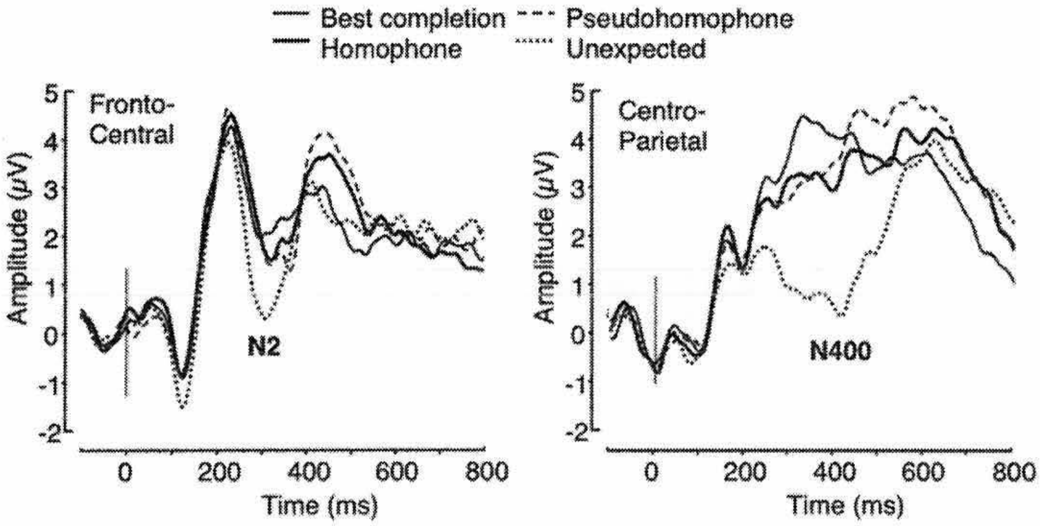

Figure 15. ERP waves over the fronto-central region (linear derivation of electrodes FC1, FC2 and Fz) and centro-parietal region (linear derivation of electrodes CP1, CP2 and Pz) averaged across the 15 participants.

The N400 amplitude was modulated by experimental conditions, $F(3,14)=21.26$, $p < 0.05$. Post-hoc comparisons showed that the N400 component was significantly more negative for the UN condition than in the other three experimental conditions (BC–UN $t(14)=6.24$, $p < 0.05$; HO–UN $t(14)=5.67$, $p < 0.05$; PH–UN $t(14)=8.57$, $p < 0.05$). The BC, HO and PH conditions showed a substantially reduced wave and there were no differences among them ($p > 0.05$; Figure 15). Owing to the absence of peak in the N400 range of BC, HO and PH conditions, no latency analysis was carried out in the N400 range.

Discussion

This study investigated online phonological activation during silent reading and its implication in semantic integration mechanisms. We found that unexpected sentence completions prompted an N2 effect. As predicted, the N2 amplitude was significantly reduced for phonologically congruent completions (whether orthographically expected or not) compared with unexpected completions. Furthermore, a large amplitude N400 indexing violation of semantic expectancy was found only in the unexpected completion condition whereas the N400 elicited by phonologically congruent sentence completions (BC, HO, and PH) was substantially reduced and non-discriminative. Thus, in a context in which orthographic and semantic expectations were maximal and despite the fact that phonological retrieval was detrimental to the task at hand, as HO and PH had to be judged as incorrect completions, participants systematically accessed the sound form of the printed word within 300 ms. Furthermore, the N400 reduction observed for all homophone conditions indicates that phonological activation of the BC sound form triggered semantic access.

From a behavioural point of view, we found that orthography discriminated between the expected and homophonic completions. Error rates were higher in the HO condition than in other conditions. Moreover, participants were faster and more accurate in rejecting PHs than any other stimulus type. As both HO and PH conditions shared phonological representations with BCs, orthography is the only basis on which correct rejections could be made. Therefore, different performances in the two homophonic conditions were probably due to relative differences in orthographic familiarity (Lukatela & Turvey, 1994): PHs were orthographically unfamiliar, making it easier to reject them than HO, which were real words.

It may be argued that amplitude reductions observed in the N2 and N400 ranges could have been prompted by orthographic rather than phonological similarity among BC, HO and PH conditions (Coltheart, Patterson & Leahy, 1994). However, orthographic similarity is unlikely to account for the degree of attenuation observed here because (i) as HOs and PHs were correctly rejected and BC words were accepted, the N2 reduction found in former conditions should not have been as pronounced as that seen in the BC condition if this decision had been made based on orthography alone; (ii) nonhomophonic pseudowords usually elicit larger N400 amplitudes than PHs, even when they are matched for orthographic similarity with word targets (Briesemeister, Hofmann, Tamm, Kuchinke, Braun & Jacobs, 2009) (orthographically driven effects have even been found as early as 150 ms; Braun et al., 2009); and (iii) unexpected orthographic neighbours of highly expected words have been shown to elicit significantly larger N400 waves than expected sentence completions (Lazslo & Federmeier, 2009). As in this study, HOs and PHs were less than 60% orthographically similar to BC words (HO mean similarity=0.59 [based on normalized edit distance; Lambert, Lin, Chang, & Gandhi, 1999] SD 0.18; PH normalized edit distance 0.55, SD 0.20) one would have expected larger N400 amplitudes if the effect had been driven by orthographic similarity.

Overall our results seem inconsistent with earlier studies showing larger N2 peaks to HOs (Niznikiewicz & Squires, 1996; Ren et al., 2009) and PHs (Newman & Connolly, 2004) compared with semantically congruent words. However, in our study, sentence cloze probability was manipulated so as to make the phonological priming effects particularly strong (see also Vissers et al., 2006), which we assume led to automatic phonological activation overriding the effects of orthographic expectation until after the window of semantic integration. We speculate that the earlier conflicting findings with regard to phonological integration indexed by the N2 may be accounted for by the absence of strong phonological expectations of the reader (Connolly et al., 1995; Newman & Connolly, 2004; Niznikiewicz & Squires, 1996; Ren et al., 2009). In this situation, phonological activation may be at a subthreshold level and vulnerable to interference from mismatch responses elicited by dissonant orthographic forms. This would result in the observed increased N2 modulations (Connolly et al., 1995; Newman & Connolly, 2004; Niznikiewicz & Squires, 1996), indexing early conflicts between orthographic and phonological processing (Kramer & Donchin, 1987; Newman & Connolly, 2004). Such a conflict would presumably reduce phonological integration and subsequent semantic access triggered by the stimulus (Ziegler et al., 1999).

Conclusion

Despite being correctly rejected as inappropriate sentence completions, HOs and PHs seem to elicit N2s and N400s of similar amplitude to those elicited by predictable words. This result provides new evidence that while final meaning selection may be constrained by orthography, phonological information is accessed and mediates semantic access during sentence reading.

Chapter Five

Electrophysiological evidence for impaired attentional engagement with phonologically-acceptable misspellings in developmental dyslexia

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The published article is provided in the Appendix.

Abstract

Event-related potential (ERP) studies of word recognition have provided fundamental insights into the time-course and stages of visual and auditory word form processing in reading. Here, we used ERPs to track the time-course of phonological processing in dyslexic adults and matched controls. Participants engaged in semantic judgments of visually presented high-cloze probability sentences ending either with (a) their best completion word, (b) a homophone of the best completion, (c) a pseudohomophone of the best completion, or (d) an unrelated word, to examine the interplay of phonological and orthographic processing in reading and the stage(s) of processing affected in developmental dyslexia. Early ERP peaks (N1, P2, N2) were modulated in amplitude similarly in the two groups of participants. However, dyslexic readers failed to show the P3a modulation seen in control participants for unexpected homophones and pseudohomophones (i.e., sentence completions that are acceptable phonologically but are misspelt). Furthermore, P3a amplitudes significantly correlated with reaction times in each experimental condition. Our results showed no sign of a deficit in accessing phonological representations during reading, since sentence primes yielded phonological priming effects that did not differ between participant groups in the early phases of processing. On the other hand, we report new evidence for a deficient attentional engagement with orthographically unexpected but phonologically expected words in dyslexia, irrespective of task focus on orthography or phonology. In our view, this result is consistent with deficiency in reading occurring from the point at which attention is oriented to phonological analysis, which may underlie broader difficulties in sublexical decoding.

Introduction

During the last decade, the reading difficulties experienced by individuals with developmental dyslexia have been consistently associated with a deficit in phonological processing (e.g., Ramus, 2002; Snowling, 2000). More specifically, weak phonological coding capacity would be responsible for weak phonological representations of words and, in turn, for difficulties in the learning of grapheme–phoneme correspondences necessary to decode unfamiliar words, for a deficit in constraining phonological analysis and segmentation, and, finally, for poor performance in phonological awareness tasks (Fowler, 1991; Manis et al., 1997; Snowling, 2000; Swan & Goswami, 1997; Vellutino et al., 2004).

However, evidence for weak phonological representations in developmental dyslexia is limited (see Ramus, 2002; Blomert et al., 2004; Ramus & Szenkovits, 2008) and largely derived from auditory tasks testing sensitivity to speech or acoustically modified stimuli within the context of tasks taxing working memory resources, and which usually require discrimination from a referent (see Ahissar et al., 2006; Banai & Ahissar, 2006, for a discussion). This has prompted alternative proposals of mechanisms that contribute to phonological processing impairments involving working memory during phonological access (Blomert et al., 2004; Menghini et al., 2011; Ramus & Szenkovits, 2008), attentional engagement with phonological information (Facoetti et al., 2006, 2008, 2010; Hari et al., 1999; Hari & Renvall, 2001; Ruffino et al., 2010), visuo-attentional processes engaged in orthographic analysis (e.g., Ans et al., 1998; Bosse et al., 2007; Valdois et al., 2004; Vidyasagar & Pammer, 2010) or perceptual filtering (Roach & Hogben, 2007, 2008; Geiger et al., 2008), or a combination of such more generic cognitive processes (e.g., Menghini et al., 2010, 2011; Pennington & Bishop, 2009).

Behavioural studies are limited in the extent to which they can provide information in support of or against the hypotheses presented above, not only with respect to the magnitude of the impairment but also with regard to the exact point in time when word recognition is affected. Event-related potentials (ERPs) allow us to plot the millisecond-by-millisecond time-course of visual word recognition processes (see Grainger & Holcomb, 2009) and provide a functional interpretation of deficient cognitive mechanisms based on existing knowledge of specific electrophysiological markers (Brandeis & Lehmann, 1986, 1994). We chose to use this technique to study the locus of the phonological deficit in dyslexia within a reading context. If reduced sensitivity to phonological information is the source of reading difficulties in dyslexia (as predicted by degraded phonological representations) then, from the moment that ERPs discriminate visual word stimuli such as pseudowords on the basis of their phonological properties, any differences between dyslexic and control readers should be manifest.

We know from ERP studies with normal, skilled readers that phonologically manipulated stimuli can reliably modulate the N2 peak, which occurs at least 100 ms before the N400 window. For instance, masked primes varied in phonological similarity to a target word elicit a graded amplification of N2 (N260: Grainger et al., 2006; Holcomb & Grainger, 2006). Furthermore, N2 amplitude has been shown to increase as a function of relative phonological and orthographic similarity of visually presented word rhyme pairs[5] (Kramer & Donchin, 1987). A modulation of the N2 elicited by phonological mismatch is also observed when the expected final word of a sentence is replaced with a phonologically dissimilar, unexpected stimulus. This effect has been shown using both auditory (also known as the phonological mismatch/mapping negativity, PMN; Connolly & Phillips, 1994; D'Arcy et al., 2004; Diaz & Swaab, 2007; Newman & Connolly, 2009) and visual (Connolly et al., 1995; Savill et al., 2011 [Study 2]) presentation. Furthermore, orthographic stimuli that are phonologically similar or even identical to an expected stimulus can show N2 attenuation similar to the expected stimulus congruent with their phonological acceptability (e.g., Briesemeister et al., 2009; Savill & Thierry, 2011b [Study 1]; Savill et al., 2011; Vissers et al., 2006).

Looking at earlier influences of phonological information embedded in words, studies with normal readers have also reported phonological effects in reading within the P2 range. For instance, rhyming visual word pairs have been shown to increase P2 amplitudes relative to non-rhyming pairs (Barnea & Breznitz, 1998; Kong et al., 2010). Other studies have shown effects of phonetic consistency of Chinese characters radicals read silently as early as 170 ms post-stimulus onset (Hsu et al., 2009; Lee, Tsai et al., 2007). Given that phonetic consistency relates to the frequency of the phonological mapping to a character, Hsu et al. (2009) hypothesized that the P2 is sensitive to variations in the mapping between orthography and phonology. A similar conclusion was reached by Bles et al. (2007) in an ERP study examining the passive effects of word

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[5] In this study, the N2 peak was largest to non-rhyming orthographically dissimilar word pairs "shirt-witch"; smallest to rhyming and orthographically similar pairs "match-patch," and of intermediate amplitude to non-rhyming, orthographically similar "catch-watch," and rhyming, orthographically dissimilar pairs "blare-stair."

cohort size reduction in which participants simply monitored for change in letter colour. The authors found that reduction in cohort size, which was achieved by letter-by-letter presentation, correlated with reduction in P2 amplitude. They proposed that the P2 is modulated by the inhibition of competing stimuli based on phonological or orthographic information. Consistent with this view, recent studies comparing pseudohomophones or homophones with words or pseudowords have also found modulations of the P2 peak (Kong et al., 2010; Meng et al., 2008; Zhang et al., 2009) with onset of difference found as early as 150 ms after stimulus onset (Braun et al., 2009; Sauseng et al., 2004). Braun et al. (2009), for example, found that pseudohomophones elicited greater P150 amplitudes as compared to orthographically similar pseudowords during a lexical decision task. They proposed that P2 (or, as they call it, P150) modulations in amplitude index the conflict between the unfamiliar orthographic representation of pseudohomophones and their familiar phonological representation, such that P2 amplitude is increased with increased competition. Interestingly, such interaction between phonological and orthographic information is delayed when the primes are not consciously perceived, in which case ERP modulations are found later, e.g., in or beyond the N250 range (Ashby & Martin, 2008; Grainger et al., 2006). Therefore, if phonological representations are impaired in dyslexia, it is reasonable to expect group differences in the P2–N2 range in relation to phonology–orthography interactions during reading.

However, most of the previous electrophysiological studies with dyslexic participants have shown differential effects between groups for phonological manipulation in visually presented words fairly late in the processing stream, i.e., from within the so-called N400 range. The N400 wave is a large negative deflection typically elicited in linguistic tasks involving violations of semantic expectation in sentence (e.g., Kutas & Hillyard, 1980, 1984; see also Hagoort et al., 2004; van Berkum et al., 1999) and single word priming contexts (Bentin et al., 1985, 1993), but is also elicited by other forms of expectancy violation in language, such as mismatching stimuli in rhyming tasks (Rugg, 1984; Rugg & Barrett, 1987). Studies reporting N400 differences between dyslexic and control readers with respect to phonological processing of visual word stimuli are confined to studies of rhyme judgment, in which dyslexic individuals typically show an attenuated N400 (Ackerman et al., 1994; McPherson et al., 1998; Rüsseler et al., 2007). Such observations have been taken as electrophysiological evidence of phonological processing difficulties in dyslexia (Rüsseler et al., 2007). N400 differences observed in rhyme judgment, however, can be influenced by anomalies in domain-general cognitive processes including working memory (e.g., Gunter et al., 2003), integration (Holcomb, 1993), inhibition (Gunter et al., 2003), and/or decision-making processes (Brown & Hagoort, 1993; Chwilla et al., 1995; Connolly & Phillips, 1994; Holcomb, 1993). This is particularly relevant, because rhyming judgment is a fairly complex, abstract task reliant on working memory for retrieval, maintenance, and segmentation of the phonologic representation of the first stimulus into onset and rime and comparison with the rime of the following target (Besner, 1987). This means that we ought to consider earlier modulations elicited by phonological and orthographic interactions in reading.

Recently, we investigated early phonological effects in dyslexic adults making homophony judgments on visual word stimuli (Savill & Thierry, 2011b [Study 1]). By comparing responses to words primed by pseudowords orthogonally manipulated for orthographic and phonological similarity, we found that, like controls, dyslexic adults showed early phonological priming effects in the N2 and P3 ranges (attenuated N2 and increased P3). Main effects of phonological priming only showed differences between groups in the P600 range, a stage of stimulus re-evaluation. We did, however, find that the interactive effects of orthographic and phonological priming differed between groups for peaks spanning the P2, N2, and P3 ranges, following reduced orthographic priming effects in the N1 range in the dyslexic group. These results indicate that the processing of orthographic information and its later integration with phonological information is problematic in dyslexia, rather than sensitivity to phonological information per se; at least within the context of a demanding meta-linguistic homophony judgment task.

To determine whether processing differences between dyslexic and unimpaired readers are present from the onset of reading-related phonological analysis or whether differences emerge after phonological access has taken place in a more natural reading context, we decided to record ERP modulations elicited by phonological and orthographic priming during sentence reading. This study expands on a task that has previously been shown to elicit phonological modulations of the N2 in normal readers (Savill et al., 2011 [Study 2]). To adapt the task for use with dyslexic participants, we increased the size of the stimulus set from Savill et al. (2011) and created high-cloze probability sentences (e.g., "Clare went on a diet to lose ___") ending either in (a) its expected best completion word ("weight"), (b) a word homophonic to the expected word ("wait"), (c) a pseudohomophone of the expected word ("wate"), or (d) an unexpected word ("string"). Since three of the four conditions were phonologically very close, and should have been primed by each sentence context phonologically, this enabled us to see how phonological representations were accessed from different, unexpected orthographic forms in dyslexic readers.

We were primarily interested to see whether dyslexic readers would show reduced early effects of phonological manipulations in the N2 range (i.e., less N2 attenuation, following phonologically reduced N2 amplitudes seen in Grainger & Holcomb, 2009; Savill et al., 2011; Vissers et al., 2006). We also anticipated that mismatching orthographic and phonological information (i.e., in the case of phonologically matched but orthographically incorrect homophones and pseudohomophones) would induce conflict during lexical access and increase P2 mean amplitude (Bles et al., 2007; Braun et al., 2009; Hsu et al., 2009) and we investigated whether such modulation would be different in dyslexic readers (we did not test this in Savill et al. (2011) due to the paper's focus on phonological main effects). Furthermore, since previous ERP studies of visual word processing in dyslexic participants have predominantly shown effects of phonological manipulations in the N400 range, we investigated whether group differences would also/alternatively appear at later, post-perceptual stages of processing.

In order to test automatic versus controlled phonological processing, we tested participants using two different tasks performed on the same stimuli: a semantic-judgment task we termed "ortho-semantic" focusing on orthography following Savill et al. (2011) ("is the final word the best way to complete the sentence?"); and a task we named "phono-semantic," which demanded focus on phonological form ("does the final word of the sentence sound like the best way to complete the sentence?"). We predicted that ERPs would provide evidence for a phonological deficit in reading in one of two ways:

(i) If the phonological deficit affecting reading in dyslexia has its source in degraded phonological representations and/or deficiency in extracting phonological information from written stimuli, dyslexic participants should show reduced sensitivity to phonological information and thus should display reduced phonological priming in response to homophones and pseudohomophones in both tasks. Therefore, we expected reduced N2 amplitude decreases for these conditions relative to the unrelated condition in dyslexic participants as compared to matched controls.

(ii) Alternatively, if we can find no evidence of group differences in early stimulus evaluation stages, but differences manifest later in processing (e.g., beyond 300 ms post-stimulus onset), this would indicate that the deficit in dyslexia is not apparent during decoding and/or perception phases, but related to more integrative, attention-regulated, stages of phonological analysis which involve working memory and re-evaluation mechanisms.

Finally, the use of two tasks enabled us to test the potential role of overt attention to phonology during reading. Indeed, if the processes at work are under the voluntary control of the participants, attending to orthography ("ortho-semantic" task), and phonology ("phono-semantic" task) should yield different patterns across tasks and, what is more, interact with participant group.

Materials and Methods

Participants

Twelve adult participants with developmental dyslexia (six females, mean age 20.8 years) and 12 control adults (six females, mean age 22.9 years) participated in this study approved by the local Ethics committee of Bangor University. Participants were all students at Bangor University and had given informed consent to participate. All were right-handed according to the Edinburgh handedness inventory and native English speakers with normal or corrected-to-normal vision. Our dyslexic participants had a confirmed diagnosis of developmental dyslexia from an educational psychologist and were recruited through the university's Dyslexia Unit or through advertisement via the university's participant panel and were paid for participation. The dyslexic group consisted of high-functioning individuals who had compensated for their difficulties such that their reading level was within a normal range but at a level inconsistent with their academic ability.

Table 2. *Group performance on psychometric subtests.*

	Control group (*n*=12)		Dyslexic group (*n*=12)		*t*
	M	*SD*	*M*	*SD*	
Age (years)	22.92	6.13	20.75	1.29	1.20
Reading (WRAT; untimed[a])	115.58	6.10	102.83	11.34	3.43**
One minute reading (DAST)	117.25	11.99	96.17	15.68	3.70**
Pseudoword reading (WIAT[a])	114.67	5.55	90.17	14.62	5.43***
Nonsense passage (DAST)	95.58	3.87	82.67	9.46	4.38**
Spelling (WRAT[a])	108.42	5.71	96.33	5.60	5.23***
Rapid naming (DAST; s)	25.08	3.75	31.58	10.19	-2.07*
Digit span (WAIS[a])	11.75	2.34	9.08	2.35	2.78*

Note. Raw scores are reported unless otherwise stated. [a] standardised scores.

*$p < .05$. **$p < .01$. ***$p < .001$

Performance on a series of subtests taken from the Dyslexia Adult Screening Test (DAST; Nicolson & Fawcett, 1998), Wide Range Achievement Test (WRAT-3; Jastak &

Wilkinson, 1993), Wechsler Individual Achievement Test (WIAT-II; Wechsler, 2005), and Wechsler Adult Intelligence Scale (WAIS-III; Wechsler, 1997) showed that the dyslexic group performed significantly poorer than the control group across reading and spelling measures (Table 2).

Stimuli

To allow for the possibility of a greater loss of experimental trials from performance error due to testing dyslexic participants, we created additional stimuli to expand the stimulus set used by Savill et al. (2011). High-cloze sentences for which the best completion had an existing semantically unrelated homophone were created (e.g., "Clare went on a diet to lose ____": best completion is "weight"; homophone is "wait"). These were supplemented with filler high-cloze sentences for which the final word had a unique phonological form. All sentences were normed by 26 native English speakers who completed them with the most expected word. Sentences selected for the study had at least 92% terminal word agreement. Pseudohomophones of the target word were created to form the pseudohomophone condition (e.g., "wate") and a word semantically unrelated to the sentence stem was chosen for the unrelated condition (e.g., "string"). The final stimulus set consisted of 48 test sentences, shown once with their best completion, a homophone of the best completion, a pseudohomophone of the best completion, and an unrelated stimulus. A further two sets of 96 filler sentences were created: (a) a set of sentences ending with best completion words to be used in one of the tasks ("ortho-semantics") and (b) a set of sentences ending with unrelated homophones or pseudohomophones to be used in the other task ("phono-semantics"). The purpose of the fillers was to ensure equally probable yes or no responses in both tasks: In the ortho-semantic task a yes response was expected for best completions (48 items) and fillers (96 items) with homophones (48), pseudohomophones (48) and unrelated (48) requiring a no response; and for the phono-semantic task a yes response was expected for best completions (48), homophones (48), and pseudohomophones (48), with a no for unrelated (48), and filler items (96). Word lengths varied between 3 and 10 letters (terminal word $M = 4.9$, $SD = 1.3$) and terminal words did not significantly differ in length across conditions ($p > 0.2$). Kucera–Francis written frequency and concreteness of the sentence final words were controlled between best completion, homophone and unrelated conditions ($p > 0.1$). All pseudohomophones used were piloted in the 26 participants mentioned above to verify pronunciation was homophonic to the target word. Finally, the orthographic properties of the pseudohomophone stimuli did not differ from the other conditions in terms of constrained bigram and trigram counts and averaged orthographic neighbour frequency (verified by http://www.neuro.mcw.edu/mcword/, Medler and Binder, 2005) and were similar in orthographic overlap with best completion words as the homophones were (according to their normalized edit distance, see Lambert et al., 1999). A list of the stimuli used is given in the Appendix.

Procedure

Participants were seated comfortably in a dimly lit, sound-attenuated room in front of a projector screen. They were instructed to fixate the center of the screen and perform one of two tasks: (a) in the "ortho-semantic" task, they were asked to press a designated key for final words which were expected according to the sentence context and another for any other ending; (b) in the "phono-semantic" task, they were asked to press a key for final words that sounded like the expected completion of sentences and another key for phonologically inadequate endings. Sentences were presented using EPrime (Psychology Software Tools, Inc., Pittsburgh, USA) at the centre of the screen, at eye-level, one word at a time, subtending a maximum angle of 3.7°, in black Times New Roman font on a white background. Experimental trials were presented in pseudo-random order across five blocks such that filler and test trials were evenly distributed. Each test trial consisted of a fixation cross displayed for 200 ms, individual words in lower case displayed for 200 ms and separated by 300 ms inter-stimulus intervals featuring a fixation cross (Figure 16). After presentation of each final word the screen remained blank for a fixed period of 2000 ms to allow for participant response. A further 1000 ms separated trials. Task order and response sides were counterbalanced between participants.

The EEG data was recorded from 37 Ag/AgCl electrodes, placed in an elastic cap according to the extended 10–20 system, using Nuamps amplifiers (NeuroScan™, Sterling, USA). The online reference was the left mastoid and FPz served as the ground electrode. Electrodes positioned above and below the left eye recorded vertical eye movement. Electrode impedance was maintained below 5 kΩ. Recordings were band-pass filtered off-line between 0.1 and 30 Hz using a zero-phase shift digital filter. Eye blinks were mathematically corrected using the correction provided by Edit 4.3 (NeuroScan™, Sterling, USA). The continuous EEG was sliced into epochs ranging from −100 to 1000 ms after the onset of the target word. Epochs with voltage exceeding ±75 μV were automatically rejected. After baseline correction in reference to pre-stimulus activity, individual averages were re-referenced to the average of the mastoids. Individual averages were computed from correct trials in experimental condition (more than 35 epochs from each task for each case) and averaged together to produce grand-mean averages. Behavioural data were collected simultaneously to ERP data.

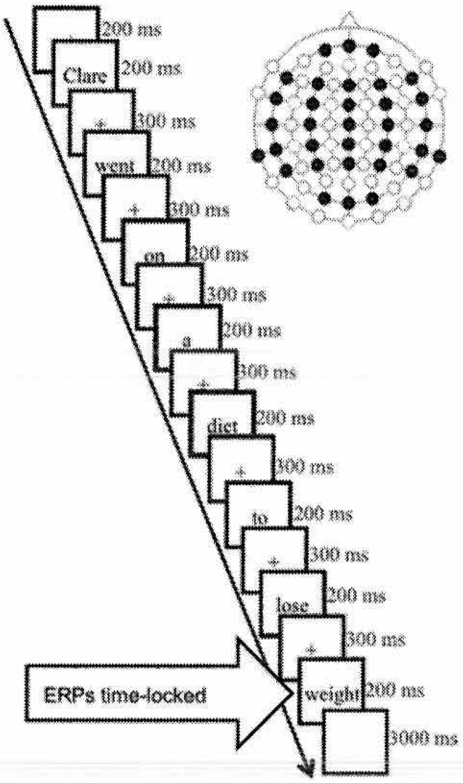

Figure 16. Schematic of a single trial.

Data Analysis

Time windows for mean amplitude analyses were defined for the control group on the basis of mean global field power, expectations from previous experiments using similar stimuli (e.g., Connolly et al., 1995; Thierry et al., 2008; Savill et al., 2011; Vissers et al., 2006) and visual inspection of topographic distribution of ERP modulations (Luck, 2005). The expected P1/N1/P2/N2 peaks were observed, followed by a visible P3a peak in the control group only. Windows of analysis for the control group were 80–110 ms for the P1; 140–170 ms for the N1; 160–210 for the P2; 250–350 ms for the N2, 350–450 ms for the P3a; and 470–670 ms for the P600.

To determine appropriate time windows for mean amplitude analyses in the dyslexic group, automatic peak detection was performed on large temporal windows encompassing each peak to check for significant group differences in overall peak latency (70–110 ms for the P1; 130–180 ms for the N1; 160–230 ms for the P2; 250–370 ms for the N2, 340–470 ms for the P3a; and 470–700 ms or the P600). Peak detection was time-locked to the electrode of maximal amplitude for each observed peak: O2 for the P1; P7 for the N1; and FCz for the P2, N2, and P3a. As both the P2 peak and the P600 peak were found to peak significantly later in the dyslexic group, with a delay of approximately 16 and 26 ms respectively, the analysis windows were adjusted to 180–230 ms for P2 mean amplitudes and to 500–700 ms for P600 mean amplitudes in the dyslexic group. No other peaks showed a significant delay and so for all other peaks the same analysis window was used as for the control group.

Mean amplitudes were measured at electrodes selected a priori based on classical topography of main components and checked for maximal sensitivity based on visual inspection: O1, O2, P7, and P8 electrodes for the P1; O1, O2, P7, and P8 for the N1; FC3, FC4, FCz, and Cz for the P2, N2, and P3a peaks and Cz, CP3, CP4, CPz for the P600.

Mean ERP amplitudes and peak latencies were subjected to a mixed ANOVA with task ("ortho-semantic," "phono-semantic"), sentence condition (best completion, homophone, pseudohomophone, unrelated), and electrode as within-subject factors, and participant group (control, dyslexic) as between-subject factor. Error rates and reaction times (RTs) were also analyzed by means of a mixed ANOVA with task and condition as within-subject factors and participant group as between-subject factor. Greenhouse–Geisser corrections of degrees of freedom were applied where appropriate.

Results

Behavioural Data

Statistical analyses revealed a main effect of group on both accuracy, $F(1, 22) = 4.40$, $p = 0.05$, and RTs, $F(1, 22) = 13.79$, $p < 0.01$, such that dyslexic participants were overall less accurate and slower than matched controls (Figure 17). Sentence condition significantly influenced performance accuracy, $F(3, 66) = 17.34$, $p < 0.001$ and correct RT, $F(3, 66) = 14.07$, $p < 0.001$. Accuracy was significantly lower for homophone endings than any other condition. RTs, meanwhile, were significantly faster for pseudohomophone endings, and unrelated endings elicited significantly slower reaction times than best completions. There was also a near-significant group by condition interaction with respect to accuracy ($p = 0.08$), relating to poorer accuracy in the homophone condition in the dyslexic group compared to the other conditions. Task also interacted significantly with condition in terms of accuracy, $F(3, 66) = 6.09$, $p < 0.01$. Post hoc analyses showed that this interaction was driven by significantly poorer accuracy in the homophone condition in the “ortho-semantic” task, compared with no differences between conditions in the “phono-semantic” task. Task interacted significantly with condition also in terms of RT, $F(3, 66) = 5.35$, $p < 0.01$. Post hoc tests showed that pseudohomophones elicited significantly faster RTs compared to all other conditions in the "ortho-semantic" task, whereas in the "phono-semantic" task only the unrelated words elicited slower RTs than the other conditions. A trend for a task by group interaction on accuracy ($p = 0.08$) was driven by a trend in the dyslexic group to perform less accurately in the "ortho-semantic" task compared to the "phono-semantic" task ($p = 0.09$), whilst the control group showed no significant difference between tasks ($p = 0.69$).

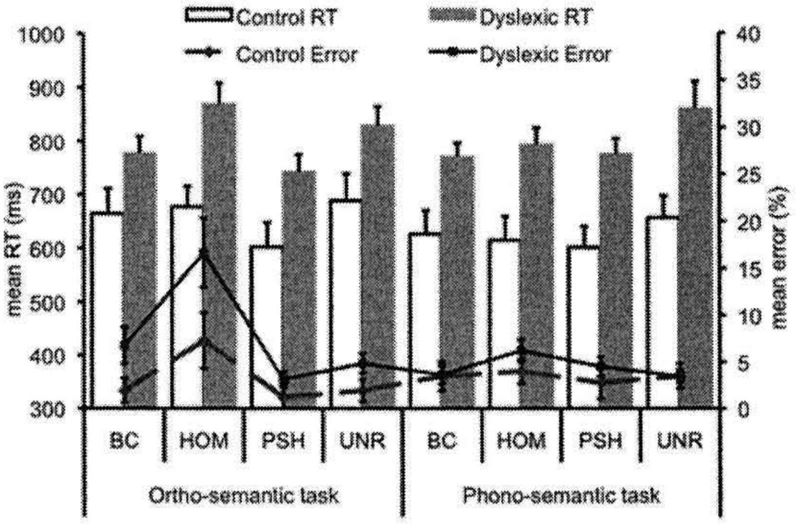

Figure 17. Behavioural data for both tasks. Error bars represent 1 standard error. BC, best completion; HOM, homophone; PSH, pseudohomophone; UNR, unrelated.

Event-Related Potential Results

No significant task effects were observed on ERP peak latencies or mean amplitudes, therefore valid EEG epochs for each trial of both tasks were averaged together to increase statistical power (accepted epochs $M = 83.20$, $SD = 11.42$; no significant differences between condition or group). All results reported below relate to the combined task averages.

No significant differences in P1 mean amplitude or latency were found between groups or conditions. The N1 tended to be smaller in the dyslexic group, as indicated by a group effect on N1 mean amplitudes, $F(1, 22) = 4.34, p < 0.05$ (see Figure 18). No significant experimental modulations of the N1 were observed.

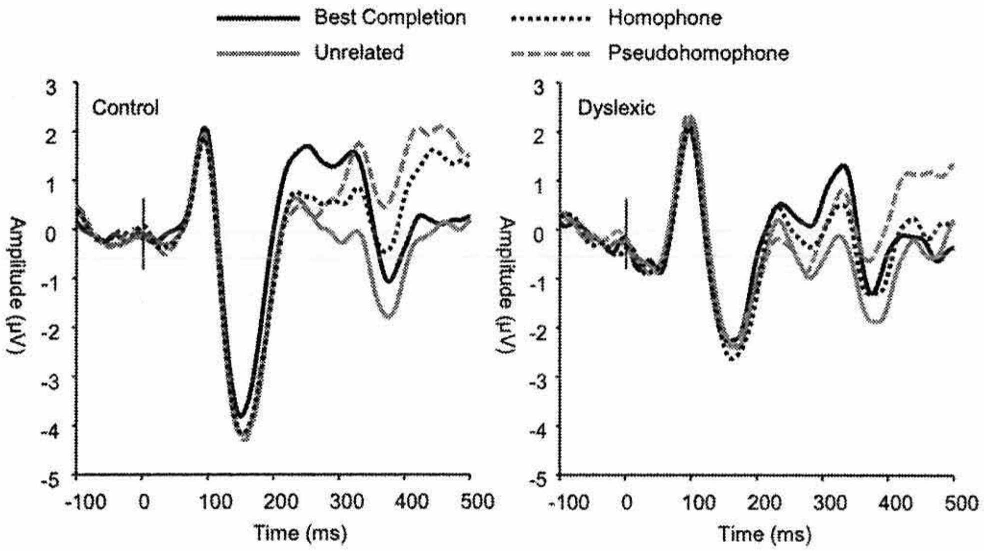

Figure 18. Group effect on N1 amplitude. Linear derivation of O1, O2, P7, and P8 electrodes.

The P2 was significantly modulated by sentence condition, $F(3, 66) = 5.54, p < 0.01$. Post hoc tests showed that this effect was driven by the homophone and pseudohomophone conditions eliciting significantly larger responses compared to the unrelated condition (both $p < 0.01$). No significant group differences on mean amplitude were found (all $p > 0.50$. P2 peak latency was also significantly affected by sentence condition, $F(3, 66) = 5.50, p < 0.01$), such that the unrelated condition elicited shorter latencies relative to the other conditions (all $p < 0.05$). Analyses also showed a main effect of group, $F(1, 22) = 7.01, p < 0.05$, indicating significantly longer P2 latencies overall in the dyslexic group (control $M = 183$ ms; dyslexic $M = 199$ ms).

Sentence condition significantly modulated mean N2 amplitude, $F(3, 66) = 36.55, p < 0.001$ (Figure 19) such that unrelated words elicited greater negativity in this range compared to all other sentence conditions (all $p < 0.001$). N2 latencies were also significantly modulated by sentence condition, $F(3, 66) = 3.21, p < 0.05$, due to the unrelated condition eliciting significantly shorter latencies than the homophone and pseudohomophone conditions ($p < 0.05$). No group differences were found in the N2 range (condition × group amplitude, $p = 0.77$; latency, $p = 0.30$).

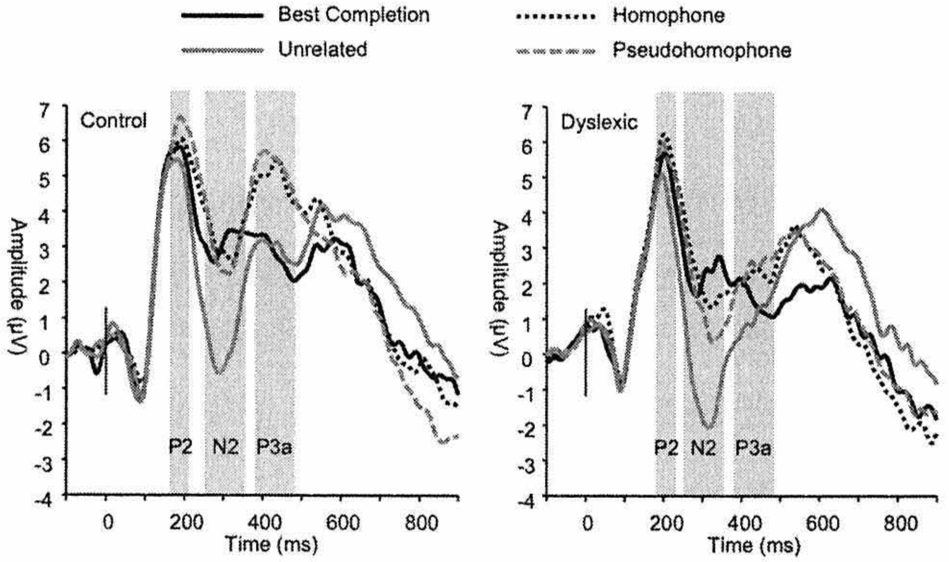

Figure 19. Group grand averages showing P2, N2, and P3a peaks based on a linear derivation of FC3, FC4, FCz, and Cz electrodes. Time windows for mean amplitude analyses are marked by the grey bars.

The frontocentral P3 was significantly modulated by sentence condition, $F(3, 66) = 12.72, p < 0.001$. This effect related to significantly larger P3a amplitudes elicited in the homophone and pseudohomophone conditions relative to the best completion and unrelated conditions (each $p < 0.01$). The condition effect was qualified by a main effect of group on P3a amplitude, confirming that the P3a was significantly larger in the control group, $F(1, 22) = 15.11, p < 0.001$ (Figures 19 and 20), and by a significant interaction of group and condition, $F(3, 66) = 3.19, p < 0.05$. Subsequent group-wise analyses showed that the control group showed a strong condition effect in the same direction as the observed overall condition effect, $F(3, 33) = 11.32, p < 0.001$, showing significant differentiation of pseudohomophone and homophone conditions from best completion and unrelated conditions (all $p < 0.01$), while the dyslexic group showed an effect driven only by smaller amplitudes to the unrelated condition compared to each other condition, $F(3, 33) = 4.51, p < 0.05$.

A trend for P3a peak latency differences induced by experimental condition was also found ($p = 0.06$), such that the best completion condition elicited significantly shorter latencies compared to the unrelated condition.

The P600 wave was also significantly modulated by sentence condition, $F(3, 66) = 8.03$, $p < 0.001$ (see Figure 21), irrespective of group. Pairwise comparisons showed that this effect was due to significantly attenuated amplitudes for the best completion condition relative to each of the other conditions, respectively (all $p < 0.01$). Pairwise comparisons did not show significant differences in P600 amplitude between homophone, pseudohomophone, and unrelated conditions (all $p > 0.20$). P600 peak latency was also significantly affected by sentence condition, $F(3, 66) = 11.36, p < 0.001$, such that the homophone and pseudohomophone conditions elicited shorter latencies relative to the best completion and unrelated conditions (all $p < 0.01$). Analyses also showed a main effect of group on P600 latency, $F(1, 22) = 4.56, p < 0.05$, indicating significantly longer P600 latencies overall in the dyslexic group (control $M = 540$ ms; dyslexic $M = 576$ ms).

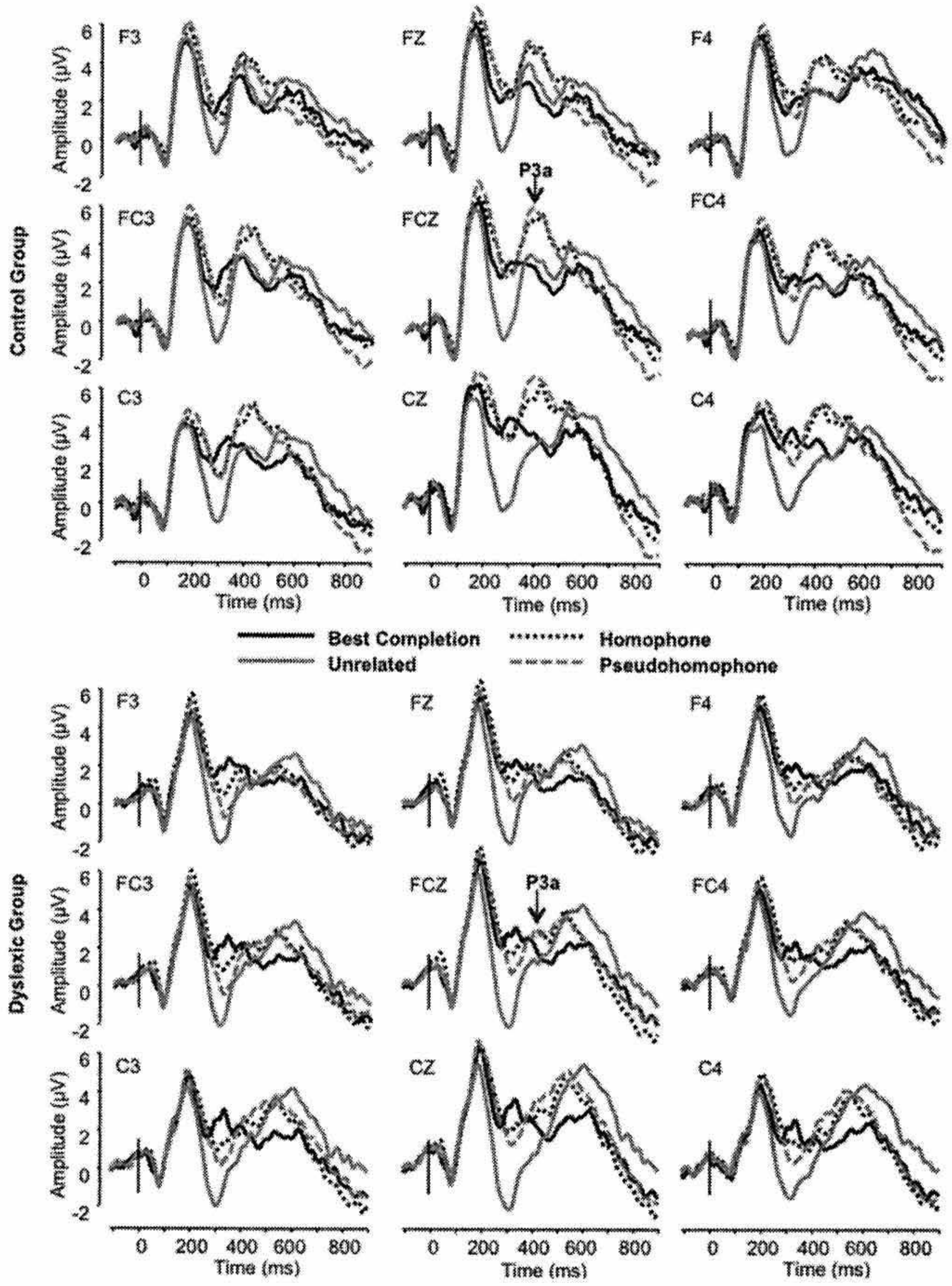

Figure 20. Grand averages of frontocentral electrodes showing the diffuse group difference in P3a modulation.

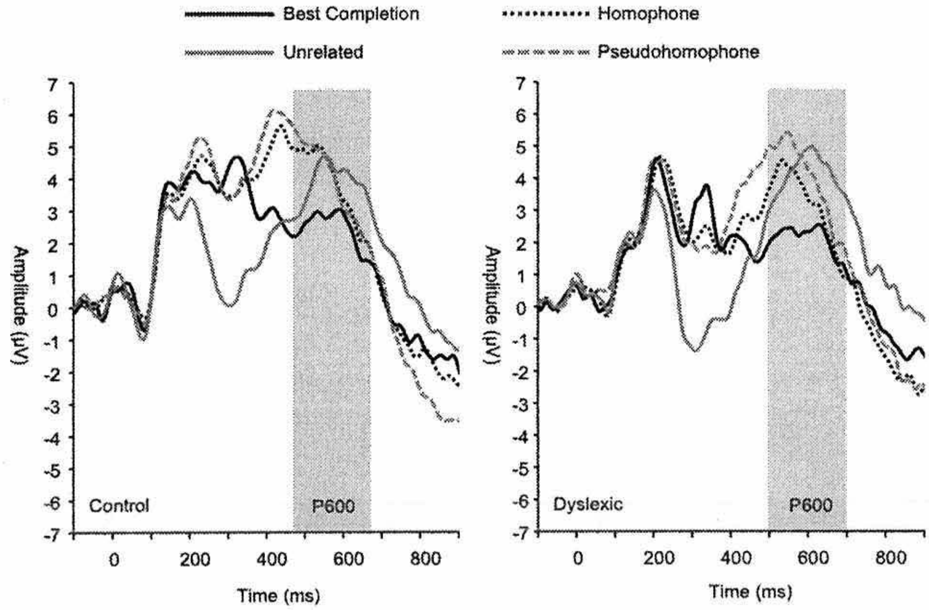

Figure 21. Group grand averages showing the P600 peak, marked by the grey bar. Linear derivation of CP3, CP4, CPz, and Pz electrodes.

Bivariate correlations performed on mean amplitudes of ERP peaks for each experimental condition with their respective behavioural data are given in Table 3.

Table 3. *Significant correlations between individual mean amplitudes and behavioural data for each condition.*

	N1	P2	N2	P3a	P600
BC Accuracy					
HOM Accuracy	-.406*				
PSH Accuracy					
UNR Accuracy					
BC RT				-.656**	
HOM RT			-.414*	-.595**	
PSH RT			-.427*	-.743**	
UNR RT				-.532**	

Note. Values are Pearson *r* coefficients ($n = 24$). * $p < .05$; ** $p < .01$ (two-tailed)

Discussion

This study aimed at detecting differences between individuals with developmental dyslexia and matched controls in orthographic/phonological integration mechanisms using ERPs.

We found early significant ERP modulations by orthographic and phonological priming in both the participant groups. However, despite poorer behavioural performance in the dyslexic group for the "ortho-semantic" and the "phono-semantic" variants of the task, ERP analyses failed to show any significant group differences in experimental effects before the P3 range and no task-specific effects were found. N1 amplitude was generally smaller in the dyslexic group but no experimental effects within or between groups were observed. P2 and N2 amplitude were both significantly affected by the experimental manipulation but these effects did not interact with group. By contrast, the P2 peak was significantly delayed in the dyslexic group as compared to the control group, but again there was no group by condition interaction. Moreover, in the P3 range, pseudohomophone and homophone stimuli elicited a significant, albeit late, frontocentral P3a in control participants but failed to elicit a similar peak in this time window in the dyslexic group. The subsequent P600 wave peaked later in the dyslexic group but P600 amplitudes, which were increased to orthographically incorrect sentence completions, did not significantly differ between groups.

In this discussion we address the main result of our study, i.e., the differential P3a modulation in the two groups, first, and then we make observations regarding results in the N1, P2, N2, and P600 ranges.

P3a: Deficient orthographically/phonologically driven orientation of attention in dyslexia?

We interpret the increase in P3a mean amplitude triggered by the homophone and pseudohomophone stimuli as a correlate of automatic attentional capture in the control group, because these stimuli had a "special" status: They were either the wrong completion which sounded like the correct completion in the "ortho-semantic" task or they were the correct completion but only in terms of phonology in the "phono-semantic" task. This special status prompted a P3a response that was not found for unambiguous targets or completely unrelated completions.

Critically, dyslexic participants failed to show this P3a modulation. The P3a is traditionally conceived as a response evoked over frontocentral areas of the scalp by the engagement of working memory following shifts in the orientation of attention (Squires et al., 1975; see also Donchin & Coles, 1988; Knight, 1997; Polich, 2007). It is classically elicited by deviant non-target stimuli in the context of an oddball paradigm (Courchesne et al., 1975; Daffner et al., 2000; Debener et al., 2005; Katayama & Polich, 1996a, 1996b; Knight, 1984; Sawaki & Katayama, 2006, 2007, 2008; Spencer et al., 1999, 2001; Simons et al., 2001) and has been shown to be modulated by the degree of difficulty involved in discriminating distracters from targets (Cormerchero & Polich, 1998; Hagen et al., 2006; Polich & Comerchero, 2003). The P3a indexes automatic engagement of focal attention during stimulus evaluation (e.g., Katayama & Polich, 1998) for further processing of a stimulus as a potentially important signal (e.g., Daffner et al., 2000) and is thought to reflect context updating (Kok, 2001). In other words, our results suggest that normal readers automatically oriented their attention to these special, phonologically acceptable but orthographically unexpected stimuli, whereas dyslexic participants did not. This could stem from a visual–phonological integration failure or a general failure in orienting of attention to phonologically relevant material, possibly leading to deficient engagement of working memory, rather than a deficit in the perceptual decoding of orthographic and/or phonological information.

Previous studies have indeed reported reduced or absent P3a in participants with developmental dyslexia, using phonologically manipulated speech and tone oddball stimuli (Fosker & Thierry, 2004; Hämäläinen et al., 2008; Rüsseler et al., 2002). Fosker and Thierry (2004), for instance, found that the P3a elicited by phonological oddballs during an auditory lexical decision task in adult control participants was not found in the dyslexic group. However, when phonological oddballs were brought into the focus of attention, dyslexic participants produced P3b modulations comparable with controls (Fosker & Thierry, 2005). Rüsseler et al. (2002) have shown similar attentional modulations of dyslexic oddball effects on the P3 with tone stimuli. Anomalous frontal P3a-like modulations have also been shown in dyslexic adults engaged in tasks requiring shifts in spatial attention (Wijers et al., 2005). Overall, such results have led to the idea of impaired shifts and/or capacity for automatic attentional capture by phonological information rather than impaired phonological processing abilities.

This interpretation links with the literature derived from tasks with rapidly presented stimuli that propose disordered automatic orienting of attention (e.g., Facoetti et al., 2008) and sluggish attentional shifting in dyslexia (Hari & Renvall, 2001). Slow capture of attention has previously been observed in non-linguistic cued-detection and T2 detection in attentional blink tasks using visual and auditory stimuli in dyslexic children and adults (Brannan & Williams, 1987; Buchholz & Aimola Davies, 2007; Hari et al., 1999; Facoetti et al., 2003a, 2003b, 2006, 2008, 2010; Lallier et al., 2010). Sluggish shifting of attention has also been reported in dyslexic individuals using auditory or visual stream segregation tasks (Helenius et al., 1999b; Lallier et al., 2009; Petkov et al., 2005). With respect to reading, sluggish attentional capture has been found to significantly predict non-word reading performance (Cestnick & Coltheart, 1999; Facoetti et al., 2006, 2010). Facoetti et al. (2008) hypothesized that a deficit in automatic attention could impact decoding due to deficient engagement and disengagement with each letter/grapheme. Such a deficit, along with the absence of the P3a in our dyslexic group, is unlikely to relate to a general deficit in automatic attention, as dyslexic participants have shown intact automatic orientation of attention in non-rapid tasks using nonverbal stimuli (Facoetti et al., 2008, 2010).

Although we did not test sluggish attentional shifting (since SOA was longer than 200 ms, e.g., Lallier et al., 2009), the present results are congruous with such interpretations derived from studies of visuospatial attention in decoding and whole word reading. In general terms, our data, which indicate a reduced tendency to react to, rather than detect, a mismatch between orthography and primed lexical phonological representations in dyslexia, are consistent with a deficit in engagement of attention with phonological information when it is not supported by expected orthographic mappings. In relation to visual attention hypotheses regarding developmental dyslexia, this could be due to a deficit in attentional engagement and disengagement with each letter/grapheme (Facoetti et al., 2008); and/or to under-specified orthographic representation in the lexicon of dyslexic individuals (Bosse et al., 2007; Lallier et al., 2010; Lassus-Sangosse et al., 2008;

Prado et al., 2007). Alternatively, the absent P3a response in the dyslexic group could reflect a wider impairment in attentional filtering that could reduce their filtering of incorrect orthographic and/or relevant phonological stimuli. Roach and Hogben (2007, 2008) propose that such impairment would stem from a relative failure in uncertainty reduction in dyslexic individuals.

Importantly, the deviation in processing seems to be related to attentional capture rather than perceptual encoding or phonological access per se, since the dyslexic group studied here activated and accessed phonological lexical forms similarly to the control group (P2–N2 complex) as shown by the amplified response to homophones and pseudohomophones in the P2 range (see below, P2–N2 discussion). Furthermore, the significant correlations with RTs indicate that the attentional processes engaged in visual word analysis indexed by the P3a impact processing efficiency. How could this relate to reading difficulties more broadly? We suggest that a general weakness in engaging attention with orthographic–phonological correspondences could affect sensitivity to spelling and spelling errors, which in turn would impede the acquisition of accurate and stable lexical representations. Furthermore, our results are compatible with recent hypotheses of deficient working memory in relation to phonological analysis rather than perceptual encoding (e.g., Banai & Ahissar, 2006; Ramus & Szenkovits, 2008; Menghini et al., 2011).

A review of the neuroimaging literature in relation to P3a origins, orthographic–phonological mapping, and functional correlates of developmental dyslexia offers interesting insights into the neuroanatomical substrates likely to be involved in the process under study.

Firstly, patient and neuroimaging data have shown that temporoparietal cortex (TPJ) is fundamentally involved in P3 generation (both the P3a and P3b) with additional involvement from prefrontal areas in the case of the novelty P3a (Bledowski et al., 2004; Knight, 1984; Knight, Scabini, Woods & Clayworth, 1989; Linden, 2005; Polich, 2007; Yamaguchi & Knight, 1991). The inferior parietal areas, in particular, have been implicated in attentional orienting based on stimulus relevance (Downar, Crawley, Mikulis & Davis, 2001; Kiehl, Laurens, Duty, Forster & Liddle, 2001; Serences et al., 2005).

Secondly, left inferior parietal areas have been specifically implicated in the integration of orthographic and phonological information (Booth et al., 2002, 2004, 2007; Bitan et al., 2007; Borowsky et al., 2006; Chen et al., 2002; Cao et al., 2006; Nakamura et al., 2006; Graves et al., 2010; Newman & Joanisse, 2011) and more generally in sublexical decoding processes (e.g., Jobard, Crivello & Tzourio-Mazoyer, 2003; Levy et al., 2009; Graves et al., 2010), phonological judgments (Hartwigsen, Baumgaertner, Price, Koehnke, Ulmer & Siebner, 2010; Stoeckel, Gough, Watkins & Devlin, 2009), and verbal working memory involvement (see Ravizza et al., 2011). Note that inferior frontal areas have also been shown to be significantly activated during phonological tasks in which working memory load is high (e.g., Graves et al., 2010; Nixon et al., 2004; Strand et al., 2008; Thierry et al., 2003).

Thirdly, temporoparietal areas have consistently been shown to be underactivated in dyslexic readers (e.g., Hoeft et al., 2007; see Richlan et al., 2009 for a review) and inferior frontal areas frequently show abnormal activation (with greater activity associated with greater behavioural compensation; e.g., Hoeft et al., 2011 etc.). For instance, consistent with our interpretation, Cao et al. (2006, 2008) found reduced activations in left inferior parietal lobe of dyslexic children performing rhyme judgments on stimuli with conflicting orthographic and phonological information (e.g., pint-mint, jazz-has versus press-list, gate-hate), and reduced functional connectivity between left inferior parietal lobe and left inferior frontal and fusiform gyri.

This convergence of functional data regarding the TPJ and inferior frontal cortex in terms of (a) generation of the P3a, (b) phonological analysis in reading, and (c) loci of abnormal activation in dyslexia, provide empirical support for a functional link between attention, phonological processing in reading, and developmental dyslexia. Therefore, the P3a effects in the present study support the existence of a physiological relationship between attentional orienting mechanisms and phonological sublexical processing in reading; a relationship likely to be dysfunctional in developmental dyslexia.

N1: Reduced orthographic sensitivity in dyslexia?

Significant differences in visual word form processing between dyslexic and control readers in the P1–N1 range, thought to be letter-string specific, have previously been reported (Helenius et al., 1999a; Maurer et al., 2007; Savill & Thierry, 2011b; Taroyan & Nicolson, 2009; Wimmer et al., 2002). In the present study, however, the only significant effect in the N1 range was an overall reduction in amplitude in the developmental dyslexic participants as compared to controls. This could be taken as a sign of reduced general sensitivity to orthographic stimuli (Maurer et al., 2005). However, the observation of smaller N1 overall may simply reflect greater latency variation in the dyslexic group yielding smaller average amplitudes (control N1 latency *SD* = 12.58;

dyslexic latency *SD* = 15.04; see Picton et al., 2000). Alternatively, other random between–group differences unconnected to stimulus processing may have affected N1 amplitudes between groups. Overall, global N1 differences that are not qualified by an interaction with experimental conditions ought to be interpreted cautiously. Whilst reduced N1 amplitudes may index some form of reduced orthographic input in the dyslexic group that might contribute to the effects we observe downstream, such data alone can provide little supporting evidence of differential sensory integration mechanisms in developmental dyslexia and normal reading.

Intact phonological representations (P2 and N2) but slow processing (P2 and P600) in dyslexia?

Both participant groups showed similar amplification of the P2 in the homophone and pseudohomophone conditions relative to the unrelated condition, as well as similar attenuation of N2 mean amplitude in the homophone and pseudohomophone conditions relative to the unrelated condition, irrespective of task. This suggests that dyslexic readers' phonological representations of the anticipated word were well specified and that grapheme–phoneme conversion mechanisms allowed extraction and identification of the stimuli's phonological form not significantly different from that observed in control participants. This absence of differences between groups in the pattern of P2 and N2 mean amplitudes across experimental conditions suggests that a deficit in early sensitivity to phonological information may not be the main source of the persistent phonological deficit in reading, at least in the case of high-functioning dyslexic adults. Furthermore, a study similar to ours with Chinese dyslexic children using a sentence paradigm in which the second character of two-character Chinese words was replaced with homophonic or orthographically similar characters also failed to find group differences in P2 amplitude, but instead revealed P2 latency effects and later N400 modulations (Meng et al., 2007). The elicitation of earlier P2 latencies for homophonic replacements as compared to baseline in both groups suggests that early phonological extraction from orthography was intact in the dyslexic participants tested.

The P2 has been reported to be affected by stimulus salience in relation to task relevance (Kieffaber & Herrick, 2005; Potts, 2004; Potts & Tucker, 2001). In contrast to P3 modulations, it is not, however, thought to index orienting of attention (Potts, 2004). Thus, finding only group differences in the latency of the P2 suggests that the dyslexic group successfully identified the phonologically salient but semantically and orthographically incongruent homophones and pseudohomophones, albeit slower than controls. The significant P2 differentiation of the incorrect orthographic completions on the basis of phonological match (homophones and pseudohomophones versus unrelated conditions) discourages an alternative interpretation of the later P3a group difference being simply due to a general lack of orientation to orthographic form in the dyslexic group. Indeed, the later significant increases in P600 amplitude to incorrect orthographic completions relative to the best completion seen in both groups (in line with previous observations of P600 increases to misspellings in highly constrained sentences; Vissers et al., 2006) shows that the dyslexic group was sufficiently sensitive to orthographic form for incorrect forms to elicit stimulus re-evaluation. Furthermore, as homophones and pseudohomophones elicited the largest P2 amplitudes (rather than the best completion) in both groups, which is compatible with interpretations of frontal P2 amplitudes as sensitive to orthographic–phonological mapping and to competition between phonological and orthographic information, the absence of a later amplitude increase to the same stimuli within the P3a range in the dyslexic group suggests that the incorrect orthographic–phonological conflict was detected early but did not engage attention. In addition, ERP effects in the N2 range showed phonological integration in the dyslexic group (indexed by attenuated N2 amplitudes) comparable to both the normal readers in the present study and those tested in Savill et al. (2011). This also corroborates recent results in dyslexic readers (Savill & Thierry, 2011b) and, on the basis of its occurrence immediately before the P3a window over the same electrodes, suggests that the emergence of dysfunctional phonological responses in reading coincides with the failure of attentional engagement.

The only group difference we observed prior to P3a amplitude effects was the finding that P2 latencies were longer overall for the dyslexic group. This P2 latency delay suggests that the initiation of phonological mapping may have been delayed, which, in turn, could account for the differences observed downstream in the P3a range. In the absence of a P3a peak in the dyslexic group, we cannot infer whether attentional engagement processes were progressively delayed, however the observation of P600 modulations involved in orthographic monitoring also peaked later in the dyslexic group suggesting that word recognition may be slowed down throughout the processing window. This finding is consistent with that of Breznitz and colleagues, who found evidence for slower speed of processing during various forced-choice visual and auditory tasks, indexed by delayed P2 and P3 latencies in dyslexic readers (Breznitz & Meyler, 2003; Breznitz & Misra, 2003). These authors put forward the hypothesis of a temporal asynchrony between visual and auditory perceptual systems in dyslexia, which would affect word recognition because it requires synchronization of orthographic and phonological codes. Their and our data converge regarding the implication of slower engagement with orthographic and phonological code integration, in a context of intact perceptual analysis. However, our study differs in that it uses homophonic visual word stimuli and the consequent observation of a relative lack of attentional specificity in the context of orthographically inappropriate, but phonologically acceptable, stimuli. This contributes to the accumulating evidence supporting the key role of attentional processing in dyslexia and underlines the usefulness of techniques such as ERPs in the characterization of orthographic and phonological processing and, critically, the assessment of their interactions during reading.

Conclusion

In this study, we attempted to establish a link between the phonological deficit in dyslexia and visual word recognition using a reading task in a sentence context. The absence of a P3a modulation in dyslexic participants suggests that a failure to attend either to the correspondence between orthography and phonology, or to phonological relevance more generally, may be critical in the emergence of dyslexic symptoms, which may be exacerbated by slower initiation of ortho-phonological integration. By contrast, the absence of group differences in experimental effects in earlier time-windows immediately before the P3a peak (P2–N2 range) both suggests that early phonological extraction from orthographic stimuli may be intact and that dysfunction in sublexical analyses relating to phonological integration might not emerge until stages of attentional capture. However, one must be cautious before discarding earlier sensory integration mechanism deficits on the basis of null interactions. Future studies will further explore deficient orienting to orthographic forms and sensitivity to phonological information in relation to reading and the specificity of deficient orienting mechanisms in developmental dyslexia.

Chapter Six

Developmental dyslexia at the core? Deficient interactions between attention and phonological analysis in reading

Nicola J. Savill and Guillaume Thierry. Paper submitted for publication.

Abstract

Whilst there is general consensus that phonological processing is deficient in developmental dyslexia, recent research also implicates visuo-attentional contributions. Capitalising on the P3a wave of event-related potentials as an index of attentional capture, we tested dyslexic and normal readers on a novel variant of a visual oddball task to examine the interplay of orthographic-phonological integration and attentional engagement. Targets were animal words (10% occurrence). Amongst nontarget stimuli were two critical conditions: pseudohomophones of targets (10%) and control pseudohomophones (of fillers; 10%). Pseudohomophones of targets (but not control pseudohomophones) elicited a large P3 wave in normal readers only, revealing a lack of attentional engagement with these phonologically salient stimuli in dyslexic participants. Critically, both groups showed similar early phonological discrimination as indexed by posterior P2 modulations. Furthermore, phonological engagement, as indexed by P3a differences between pseudohomophone conditions, correlated with several measures of reading. Meanwhile, an analogous experiment using coloured shapes instead of orthographic stimuli failed to show group differences between experimental modulations in the P2 or P3 ranges. Overall, our results show that, whilst automatic aspects of phonological processing appear intact in developmental dyslexia, the breakdown in pseudoword reading occurs at a later stage, when attention is oriented to orthographic-phonological information.

Introduction

Impaired decoding of visually unfamiliar words or pseudowords is one of the key characteristics of developmental dyslexia (in an alphabetic language; see Rack, Snowling & Olson, 1992). Since pseudowords do not have an entry in the lexicon that can be directly accessed from print, pseudoword recognition requires sublexical decoding (that is, breaking down the letter string into its graphemes to map and blend their corresponding sounds). In the context of behavioural evidence indicating phonological processing weakness in dyslexia (see Vellutino, Fletcher, Snowling & Scanlon, 2004, for a review), one of the dominant hypotheses accounting for pseudoword reading deficiency is the existence of weaker and/or poorly specified phonological representations (e.g., Adlard & Hazan, 1998; Boada & Pennington, 2006; Morais, 2003; Snowling, 2000; Swan & Goswami, 1997). Degraded phonological representations are thought to impact reading in general by interfering with the acquisition and use of grapheme-phoneme correspondence (GPC) rules (Morais, 2003; Morais & Kolinsky, 1994). However, successful pseudoword decoding also requires accurate orthographic processing, intact graphemic parsing, integration of visual and phonological information both at the grapheme and/or letter string level, and for all to be present in the context of adequate attentional engagement, motivation, and working memory resources (e.g., Guthrie & Wigfield, 1999; Lepola, Poskiparta, Laakkonen & Niemi, 2005; Lien, Ruthruff, Cornett, Goodin & Allen, 2008; O'Malley, Reynolds, Stolz & Besner, 2008; Reynolds & Besner, 2006; Shaywitz & Shaywitz, 2008). It is perhaps not surprising then, that corresponding differences in orthographic processing (Bosse et al., 2007; Hawelka, Huber & Wimmer, 2006; Maurer et al., 2007; Pitchford, Ledgeway & Masterson, 2009; Valdois et al., 2004;

Vidyasagar & Pammer, 2010), visuo-attentional processing (Bosse et al., 2007; Facoetti et al., 2003a, 2006, 2010; Facoetti et al., 2003b, 2008; Hawelka et al., 2006; Hawelka & Wimmer, 2005; Lassus-Sangosse et al., 2008; Valdois et al., 2004; Pammer, Lavis, Hansen & Cornelissen, 2004b; Roach & Hogben 2007, 2008; Romani, Tsouknida, di Betta & Olson, 2011; Vidyasagar & Pammer, 2010), symbol-sound mapping (e.g., Ziegler, Pech-Georgel, Dufau & Grainger, 2010), and working memory involvement (e.g., Banai & Ahissar, 2006; Menghini et al., 2011; Ram-Tsur, Faust & Zivotofsky, 2008; Ramus & Szenkovits, 2008) have also been reported.

On the basis of most of the latter observations, authors have challenged the primacy of the phonological deficit; often emphasising the potential role of attention. For instance, deficits in exogenous visual attention have been reported in behavioural studies of visuospatial processing, such as the Posner paradigm, in which dyslexic individuals typically show reduced reaction time (RT) advantages from valid spatial cues as compared to uncued or nonvalid stimuli (Brannan & Williams, 1987; Facoetti et al. 2003a, 2003b, 2006; Jones, Branigan, & Kelly, 2008; Roach & Hogben, 2004; 2007, 2008) and from poorer stimulus detection in attentional blink tasks (Buchholz & Aimola Davies, 2007; Facoetti et al., 2008; Ruffino et al., 2010). Furthermore, performance in these tasks have been found to correlate with pseudoword reading measures (Facoetti et al., 2006, 2008), which has led to the hypothesis that stimulus-driven engagement of attention is weaker or slower in dyslexic individuals who manifest deficient phonological awareness (e.g., Buchholz & Aimola Davies, 2008; Facoetti et al., 2006, 2010; Hari & Renvall, 2001; Ruffino et al., 2010). Reading difficulties would then arise because of impaired visuo-attentional mechanisms controlling letter sequence scanning, affecting orthographic inputs, and impacting subsequent phonological mapping (e.g., Facoetti et al., 2006, 2008; Pammer et al., 2006; Ruffino et al., 2010; Valdois et al., 2004; Vidyasagar & Pammer, 2010). Alternatively, a general impairment in attentional filtering has been put forward, in which difficulties relate to selecting task-relevant sensory information (Roach & Hogben, 2007, 2008; see also Geiger et al., 2008).

These hypotheses of decoding dysfunction in dyslexia are based on behavioural studies mostly outside a reading context. Such studies are essential for theory development and for identifying characteristics of developmental dyslexia but are limited in their insight into the relative and interactive contributions of attention, orthography and phonology in reading. Using event-related brain potentials (ERPs), processing in dyslexia in one or more of these stages of reading can be studied with exquisite temporal resolution.

Based on results from studies with skilled readers, we know that manipulations of whole-word phonology can reliably modulate ERP waves within approximately 250 ms of stimulus onset, in the early P2-N2 ranges (Braun et al., 2009; see Dien, 2009, or Grainger & Holcomb, 2009, for reviews). If, for example, phonological representations are impaired in dyslexia, which ought to impact reading both via deficient grapheme-phoneme decoding and subsequently weakened phonological percept, then phonological manipulations of visual word stimuli should affect dyslexic and normal readers differently in the early processing windows. Since ERP studies of visual word processing in dyslexia had not reported phonological effects earlier than in the N400 window (where differences could equally be attributed to attentional or working memory factors as much as perceptual differences), we specifically targeted phonological processing in the P2-N2 range in developmental dyslexics (Savill & Thierry, 2011b). Dyslexic adults, engaged in judgements regarding the homophony of written words with a preceding pseudoword, displayed similar phonological modulations as normal readers in this early time range. Interestingly, reduced phonological modulations in the dyslexic group emerged later, in the P600 range, which we interpreted as a sign of deficient monitoring of phonological information rather than that of a fundamental deficit in extracting phonological information from print. Recently, we estimated a potential temporal onset for weaker phonological engagement in dyslexia in the P3a range i.e., between 350 and 450 ms (Savill & Thierry, 2011a [Study 3]). In a sentence reading context, we found that, unlike controls, dyslexic adults do not show a P3a response to homophones and pseudohomophones (homophonic pseudowords) of predictable sentence endings despite earlier phonological priming effects in the P2a (frontocentral P2 peak; see Potts, 2004) and N2 ranges. We interpreted this pattern as evidence of impaired attentional engagement with stimuli that are phonologically relevant but orthographically unexpected, whilst perceptual phonological processing appears intact. In the present study, we set out to test the robustness of our previous findings using a P3a-eliciting paradigm. We developed a novel visual oddball paradigm that incorporates a range of words along with pseudohomophones to test the P3a-eliciting capacity of orthographic-phonological incongruities. The rare, target stimuli were animal nouns, making up 10% of the stimuli shown (TARG). Filler stimuli were words from seven other semantic categories consisting of the same number of exemplars (totalling 70% of the stimulus set, FILL). The critical P3a-eliciting nontarget consisted of pseudohomophones of the animal names used as targets (10% of the stimulus set), i.e., pseudohomophones of targets (PSHT). Finally, we also included a rare, nontarget control condition, which consisted of pseudohomophones of one of the filler semantic categories (food words, PSHF) and which were therefore irrelevant. We created this latter condition in order to (1) test whether the pseudohomophone status in itself would be enough to elicit a P3a (whether or not the pseudoword is a homophone of an animal name); (2) provide a measure of phonological engagement with phonologically relevant versus irrelevant pseudohomophones; and (3) provide a control condition for the phonological duplication of stimuli (since targets were phonologically duplicated too).

On the basis of our previous study (Savill & Thierry, 2011a), in which we showed that dyslexic adults fail to manifest a P3a in response to the phonological content of unanticipated orthographic forms, we predicted that PSHT stimuli would elicit a significant P3a in the control group only as compared to control conditions. Furthermore, given that visual stimuli presented in an unprimed continuous stream can modulate P2 amplitudes based on semantic manipulations (e.g., Kissler, Herbert, Winkler & Junghofer, 2009, Martin-Loeches, 2007; Moscoso del Prado Martín, Hauk & Pulvermüller, 2006), lexical properties (e.g., Costa, Strijkers, Martin & Thierry, 2009; Strijkers, Costa & Thierry, 2010), and phonological effects (Braun et al., 2009; Kong et al., 2010; Meng et al., 2008; Zhang et al., 2009), we anticipated ERPs modulations also in the P2 range here. To see whether oddball effects in the main experiment would generalise to the processing of nonverbal stimuli, participants were also tested on a nonverbal control version of the experiment, which used a set of coloured shapes mimicking the relationships between conditions in the word version (conditions were labelled TARG-S, FILL-S, PSHT-S, PSHF-S).

Method

Participants

Fourteen adults with a diagnosis of developmental dyslexia (7 males; mean age 22.57 years) and 14 age-matched control adults (7 males; mean age 23.14 years) took part in the experiments approved by Bangor University's ethics committee.

Table 4. *Literacy and cognitive measures*

Measure	Control (n=14)		Dyslexic (n=14)		t (26)
	M	*SD*	*M*	*SD*	
Age (years)	23.14	4.50	22.57	5.35	0.31
Reading (untimed; WRAT[a])	114.79	4.17	101.50	8.36	5.32***
One Minute Reading (DAST)	118.57	12.50	91.86	18.40	4.49***
Spelling (untimed; WRAT[a])	108.79	7.86	94.21	10.28	4.21***
Two Minute Spelling (DAST)	36.71	2.16	28.64	4.73	5.80***
Nonsense Passage Reading (DAST)	95.79	2.75	79.07	14.13	4.35**
Phon. Segmentation (max=12; DAST)	11.21	0.80	10.14	1.70	2.13*
Pseudoword Reading (WIAT[a])	110.29	5.58	92.29	12.56	4.90***
Rapid Naming (s; DAST)	24.75	5.09	29.91	7.47	-2.13*
Spoonerisms (max=3; DAST)	2.93	0.27	1.93	1.21	3.03**
Digit Span (WAIS[b])	11.00	3.53	9.14	2.60	1.59
Matrix Reasoning (WAIS[b])	14.43	1.51	13.93	2.02	0.74

[a] Based on standard scores; [b] age-scaled scores

* $p < .05$; ** $p < .01$; *** $p < .001$;

All were right-handed with normal or corrected-to-normal vision, reported no attentional difficulties or comorbidities and were students recruited via Bangor University's dyslexia unit or participant panel. Performance on subtests taken from the Dyslexia Adult

Screening Test (DAST; Nicolson & Fawcett, 1998), Wide Range Achievement Test (WRAT-3; Jastak & Wilkinson, 1993), Wechsler Individual Achievement Test (WIAT-II; Wechsler, 2005) and Wechsler Adult Intelligence Scale (WAIS-III; Wechsler, 1997) showed that the dyslexic group were significantly impaired compared to the control group on measures of literacy and phonological skill, but did not differ in nonverbal reasoning and digit span performance (see Fosker & Thierry, 2004, 2005 for a similar profile). Table 4 details group performance on the measures used.

Stimuli

Word task: Twenty-five English words were selected (from the MRC Psycholinguistic database) as exemplars for each of eight semantic categories (animals, food items, clothing, tools, nature, jobs, furniture items and body parts). Kucera-Francis written frequency, concreteness, imageability, length, number of syllables, orthographic neighbourhood density (OND), and constrained bigram and trigram frequencies were controlled across semantic category. Animal words were allocated as target stimuli (TARG) and the remaining semantic categories acted as filler items (FILL). Pseudohomophones (homophonic pseudowords) of the words from two of the categories were also created: animals (pseudohomophones of targets; PSHT) and food items (pseudohomophones of fillers; PSHF). Pseudohomophones did not differ in length from their exemplars and the PSHT and PSHF conditions were also controlled for their orthographic similarity to their exemplar, and for OND, and constrained bigram and trigram frequencies (http://www.neuro.mcw.edu/mcword/, Medler & Binder, 2005). See the Appendix for a full summary of stimulus characteristics.

Shape task: Target stimuli were 25 unicoloured squares (TARG-S). Relevant rare nontargets were 25 bicoloured squares (PSHT-S) while the rare nontarget controls were 25 bicoloured triangles (PSHF-S). The standard fillers consisted of 25 unicoloured shapes belonging to each of 7 geometric forms (triangle, circle, parallelogram, trapezoid, kite, pentagon, hexagon; FILL-S). Stimuli were created in Adobe Illustrator CS3 and each shape was matched for number of pixels and coloured in one of 5 isoluminant shades of blue. The second shade embedded in the rare nontarget stimuli occupied the same number of pixels in each case (see Figure 22 for sample stimuli). The final 25 colours (blues, yellows, greens, pinks and purples) were created by adjusting the hue value in 5 steps for each shape in Adobe Photoshop CS3.

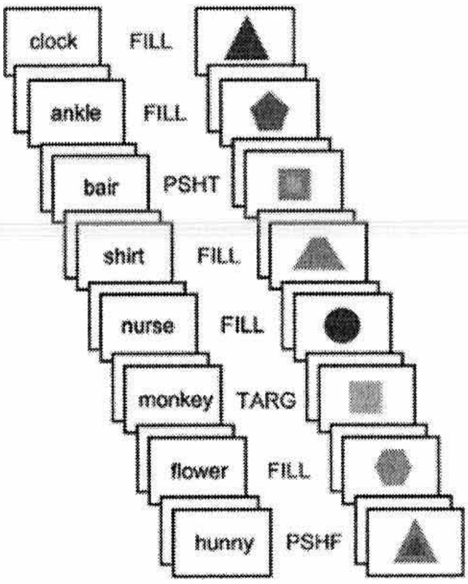

Figure 22. Experimental design: Example of 8 consecutive trials in the word task (left) and the shape task (right). Response targets were animal words in the word task and single-coloured squares in the shape task.

Design

The experiment adapted a traditional oddball design, which was analogous for both word and nonverbal tasks. In both tasks, targets (animal words / unicoloured squares), relevant nontargets (animal pseudohomophones / bicoloured squares) and non-relevant nontargets (food word pseudohomophones / bicoloured triangles) were each presented 10% of the time. Stimuli taken from across 7 other categories (non-animal words / unicoloured non-square shapes) constituted the remaining 70%. Both word and nonverbal tasks used a repeated measures mixed design with within-subjects factors of stimulus (TARG/-S, FILL/-S, PSHT/-S, PSHF/-S) and electrode and between-subjects factor of group (control, dyslexic).

Procedure

Participants were seated in a sound attenuated, dimly lit room and asked to keep eye and head movement to a minimum. Stimuli were centrally presented on a 40" high resolution LED screen (75 Hz refresh rate) with word stimuli in black lower case Arial font on a white background (Word stimuli: max. visual angle of 3.44° x 0.41°; shape task: 2.79° x 3.00°). In a given trial, a blank screen was displayed for 150 ms, followed by the stimulus, which was shown for 200 ms. Participants had 1250 ms in which to make a response during which the screen was blank, and remained blank for a further 250 ms in the word version. Participants were asked to make a button press as soon as a target stimulus was presented (i.e., an animal word or single-coloured square), and to withhold a response to all other stimuli. Stimuli were presented semi-randomly using E-Prime (Psychology Software Tools, Inc., Pittsburgh, USA) such that stimulus categories were represented evenly across each block and each stimulus was shown once in both halves of the experiment. There were 500 trials in total, presented across four blocks. Task order was counterbalanced across participants.

Data Acquisition

Electrophysiological (EEG) data were continuously recorded at a rate of 1kHz from 37 Ag/AgCl electrodes placed according to the 10-20 system in an elastic cap (impedances < 5 kΩ). Recordings were in reference to the left mastoid with FPz serving as the ground electrode. Eye movement was monitored by electrodes positioned above and below the left eye. EEG recordings were filtered online between 0.1 and 200 Hz and re-filtered offline using a zero-phase shift band-pass between 0.1 and 30 Hz. Eye blinks were removed using the correction procedure provided by Edit 4.3 (NeuroScan). EEG epochs ranged from -100 to 1000 ms after the onset of stimulus. Epochs with voltage exceeding ± 75 μV were automatically rejected. After baseline correction in reference to pre-stimulus activity, individual averages were re-referenced to the average of the left and right mastoids and computed for each experimental condition (30+ trials in each case) and averaged together according to participant group to produce grand-mean averages.

Data Analysis

In both tasks, a typical P1/N1 complex was observed followed by an early frontal P2 (P150) peak and a later observable P2 at posterior sites. These were followed by a diffuse P3 peaking over central midline sites and which was visibly earlier in the shape task than the word task. Epochs for mean amplitude analyses were defined based on visual inspection of ERP modulations (Luck, 2005) and apriori expectations from previous experiments using similar stimuli (e.g., Savill & Thierry, 2011a). Windows of analysis were 80 – 115 ms for the P1; 140 – 180 ms for the N1; 140 – 200 ms for the frontal P2; from 210 – 240 ms for the posterior P2; 270 – 350 ms for the N2 and, in the case of the P3a, 370 – 670 ms in the word task and 280-580 ms in the shape task. Peak detection was time-locked to the electrode of maximal amplitude for each component: O1 for the P1; P7 for the N1; FCz for the frontal P2 (P150) and N2, Pz for the posterior P2 and Cz for the P3a. Mean amplitudes were measured at electrodes chosen on their maximum sensitivity: O1, O2, P7 and P8 electrodes for the P1 and N1; and FC3, FC4, FCz, C3, C4, Cz for the frontal P2, N2 and P3a and CP3, CP4, CPz and Pz for the posterior P2. Greenhouse-Geisser correction of degrees of freedom was applied where relevant.

Results

Word Task

Behavioural Results: Mean reaction time and hit rates to animal words did not differ between groups ($t(26) = 0.14, p = 0.89$; control RT = 568 ± 59 ms; dyslexic RT = 566 ± 57 ms and $t(26) = 1.69, p =.10$; control accuracy = 97% ± 3%; dyslexic accuracy = 94% ± 6%). PSHT stimuli elicited significantly more false alarms as compared to PSHF and FILL, however this did not significantly differ between groups ($p = .10$; Correct rejections: PSHT: Control = 88.86%; Dyslexic = 82.86%; PSHF: Control = 100%; Dyslexic = 100%; FILL: Control = 99.98%; Dyslexic = 99.73%).

ERP Results: There were no significant modulations of the P1, N1, or frontal P2 peaks. The P2 over occipitoparietal electrodes was significantly modulated by experimental condition, $F(3, 78) = 9.04, p < .001$ (see Figure 23). Pairwise comparisons showed that posterior P2 mean amplitudes were increased to the TARG and PSHT conditions relative to FILL and PSHF, with no difference between TARG and PSHT or FILL and PSHF, respectively. No group differences or latency effects were observed in the P2 range.

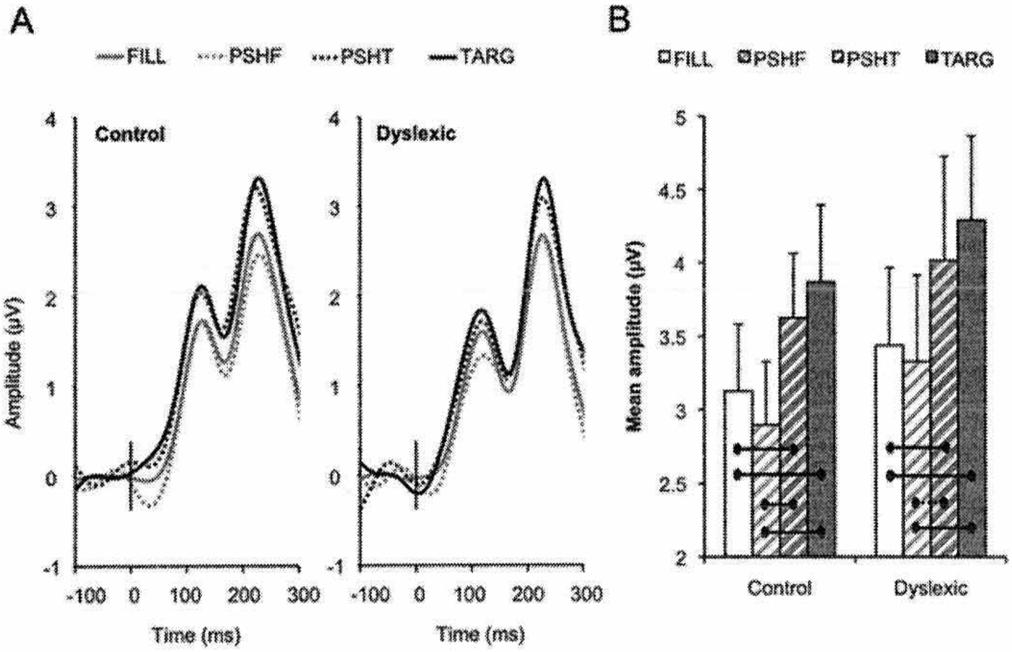

Figure 23. (A) Group grand-averages over occipitoparietal electrodes showing posterior P2 modulation in the word task. Linear derivation of electrodes P3, P4, Pz, O1, O2 and Oz; (B) Group mean amplitudes for each experimental condition averaged across posterior P2 electrodes between 210 and 240 ms post stimulus onset. Connecting lines depict significant pairwise comparisons at $p < .05$ (dotted connector, $p = .053$).

In the P3a range, a significant effect of condition on mean amplitudes was observed over frontocentral electrodes, $F(3, 78) = 23.80, p < .001$. Pair-wise comparisons showed that TARG and PSHT elicited larger amplitudes than FILL and PSHF conditions, with TARG eliciting greater amplitudes than PSHT. This was qualified by a main effect of group, $F(1, 26) = 4.43, p < .05$, and further by an interaction between group and condition, $F(3, 78) = 4.12, p < .05$. The group effect indicated smaller P3a amplitudes overall in the dyslexic group. The group by condition interaction showed that the P3a elicited by PSHT in control readers was significantly larger than PSHF and FILL conditions and did not differ in amplitude from TARG; whereas the dyslexic group showed no discernable separation of PSHT, PSHF and FILL, with only TARG eliciting significantly larger amplitudes (see Figure 24).

P3a latency analyses showed no condition effect but P3a peak latencies were longer overall in the dyslexic group, $F(1, 26) = 10.52, p < .01$; control = 521 ± 80 ms; dyslexic = 580 ± 77 ms).

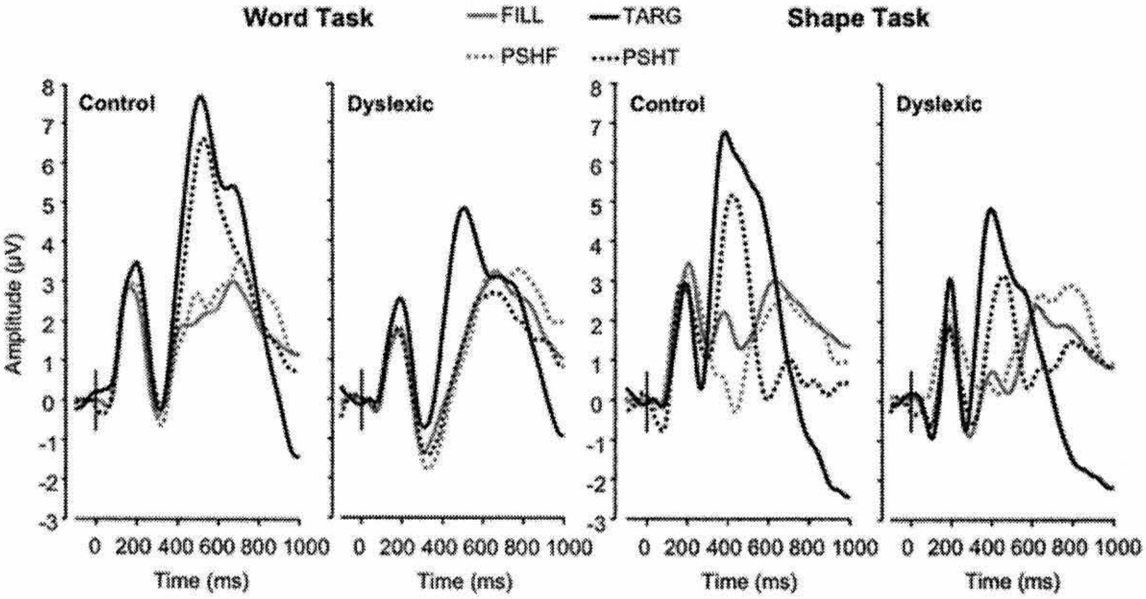

Figure 24. Group grand averages over frontocentral electrodes showing P3 modulations in the word and shape tasks. Linear derivation of electrodes FC3, FC4, FCz, C3, C4, and Cz.

Shape Task

Behavioural Results: Mean reaction time and proportion of correct hits to target squares did not differ between groups (reaction time: $t(26) = 0.62, p = .54$; control = 413 ± 56 ms; dyslexic = 402 ± 41 ms; accuracy: $t(26) = 1.38, p =.18$; control = 99.6% ± 0.9%; dyslexic = 99.0% ± 1.3%). Both groups correctly withheld behavioural responses to 100% of the PSHF-S and FILL-S stimuli; however this significantly differed from PSHT-S, which were correctly rejected at a rate of 97.6% overall, $F(2, 52) = 23.26, p < .001$, and significantly less so in the dyslexic group, $F(2, 52) = 11.59, p < .01$ (control = 99.3%; dyslexic = 95.9%).

ERP Results: PSHF-S stimuli elicited larger P1 amplitudes, $F(3,78) =18.08, p < .001$, and earlier P1 and N1 peaks, $F(3,78) = 9.67, p < .001$ and $F(3, 78) = 11.14, p < .001$ respectively, compared to the other conditions. P1 and N1 also peaked earlier to PSHF-S than FILL. Frontal P2 latencies were significantly affected by condition, $F(3,78) = 7.11$, $p < .001$, because the peak elicited by target stimuli was delayed. No significant amplitude modulations were observed for the N1 or frontal P2 peaks.

Posterior visual P2 peak mean amplitudes were significantly modulated by condition, $F(3, 78) = 18.29, p < .001$, such that all conditions were significantly different from each other, with PSHF-S showing the largest P2 (PSHF-S>PSHT-S>FILL-S>TARG-S). No group differences for the P2 peak were observed.

As expected, condition significantly modulated P3a amplitudes, $F(3, 78) = 36.08, p < .001$ (Figure 24). Pair-wise comparisons showed that TARG-S elicited a larger P3 compared to all conditions and PSHT-S was significantly larger than PSHF-S and FILL-S. A main effect of group showed that P3a amplitudes were generally smaller in the dyslexic group, $F(3, 78) = 5.53, p < .05$. No significant group interaction or P3a latency effects were observed. In other words the pattern observed in the P3a range was not different between groups.

Table 5. *Significant correlations between the standardised language measures and amplitude modulations of the posterior P2 and P3a peaks.*

	TARG – PSHT Orthographic discrimination		TARG-S – PSHT-S Unicolour discrimination	
	P2 (post.)	P3a	P2 (post.)	P3a
WRAT reading	-	-	-	-
WRAT spelling	-	-	-	-
Two min. spelling	-	-	-	-
One min. reading	-	-	-	-
Pseudoword reading	-	-	-	-
Nonsense Passage	-	-	-	-
Rapid Naming	-	-	-	-
Digit span	.426*	-	-	-
Matrix reasoning	-	.400*	-	-
	PSHT – PSHF Phonological relevance		PSHT-S – PSHF-S Relevance detection	
	P2 (post.)	P3a	P2 (post.)	P3a
WRAT reading	-	-	-	-
WRAT spelling	.434*	.384*	-	-
Two min. spelling	-	-	.415*	-
One min. reading	-	.477*	-	-
Pseudoword reading	-	.371a	-.368a	-
Nonsense Passage	-	.407*	-	-
Rapid Naming	-	-.538**	-	-
Digit span	-	-	-	-
Matrix reasoning	-	-	-	-

Note. Pearson *r* values reported; * $p < .05$; ** $p < .01$; $^{a}p < .07$ (two-tailed)

Bivariate correlations performed on the differences in posterior P2 and P3a amplitudes elicited by PSHT relative to PSHF with our diagnostic language measures are shown in Table 5.

Discussion

This study examined attentional engagement by the phonological content of orthographic stimuli in dyslexic and normal-reading adults and compared this with engagement with nonverbal stimuli, using P3a modulations of event-related potentials elicited in visual oddball tasks as the index of choice.

The results of our main experiment indicated that incorrect spellings of semantically defined target words failed to significantly engage attention in dyslexic participants over and above irrelevant filler words and irrelevant misspellings. This was manifested by the dyslexic group showing similarly attenuated P3a ERP responses to pseudohomophone targets, pseudohomophone fillers, and fillers, which were, in turn, significantly smaller than the P3 elicited by target words. This differed from normal readers, who, in the context of larger P3 amplitudes overall, showed the anticipated pattern of increased P3a amplitudes to pseudohomophone targets such that they were of the same magnitude as those elicited by target words and larger than filler conditions.

Importantly, we can infer from the P3a being elicited by pseudohomophone targets and not pseudohomophone fillers that the control group response was underpinned by phonological processing rather than orthographic familiarity or lexicality. Furthermore, in normal readers these phonological effects were strongly prepotent since ERPs to pseudohomophone targets were of the same magnitude as those elicited by targets; even though they were discriminated on an orthographic basis in a similar time window (average response time to targets = 570 ms). Thus, although dyslexic participants showed normal P3 responses to targets (i.e., similar amplitude increase to animal words), they showed little or no attentional engagement with the orthographically unfamiliar stimuli irrespective of their phonological relevance.

In our nonverbal control task, on the other hand, the dyslexic group showed a clear P3a response to the nonverbal equivalent of the pseudohomophone targets, and the pattern of difference between conditions was similar between groups. This shows that the differences found were task-specific. Furthermore, we found significant correlations between ERP modulations in the verbal task and performance in reading, spelling and rapid naming tasks, while corresponding correlations were absent in the nonverbal shape task. This lends support to the hypothesis of an attentional deficit in accessing or processing the correspondence between orthographic and phonological form and/or phonologically relevant information (e.g., Facoetti et al., 2006, 2008, 2010; Ramus & Szenkovits, 2008; Vidyasagar & Pammer, 2010; Ziegler et al., 2010). Event-related potentials, however, provide insights into early processing stages after stimulus presentation, enabling us to also determine whether P3a effects are the consequence of early perceptual differences in stimulus processing or purely attention-dependent. Crucially, the P3a group differences in the word task emerged after similar ERP modulations in the P2 range for target words and pseudohomophone targets in the two groups. Specifically, the posterior P2 peak was significantly larger for targets and pseudohomophone targets as compared to filler stimuli in both the dyslexic and control groups, with no significant differences between target words and pseudohomophone targets. Since phonological access is the only route by which pseudohomophone targets and pseudohomophone fillers can be discriminated, both groups showed rapid phonological discrimination on the basis of semantic information irrespective of orthographic/lexical status. The timing of this effect (peaking at 220 ms) is comparable with several ERP studies showing early phonological extraction from orthographic stimuli (Braun et al., 2009; Hsu et al., 2009; Kong et al., 2010; Meng et al., 2008; Zhang et al., 2009) and is consistent with most current estimates for the timing of semantically-driven lexical access (e.g., Costa et al., 2009; Moscoso del Prado Martin et al. 2006; Strijkers et al., 2010). The case for these P2 modulations in both of our participant groups reflecting rapid phonologically-mediated semantic discrimination is compelling given the variety of possible exemplars for each semantic category, and the orthographic variability of stimuli within (but controlled across) each category, unlikely based solely on low-level physical properties. Such "normal" early phonological effects before attentional engagement are in agreement with our recent observations in dyslexic adults performing sentence reading and homophone judgment tasks (Savill & Thierry, 2011a; 2011b).

Is the attentional engagement deficit in dyslexia specific to orthographic stimuli?

Given that hypotheses of an attentional engagement deficit in dyslexia are based on observations of impaired spatial and nonspatial attentional cuing, usually with nonverbal stimuli, it is reasonable to expect dyslexic participants would also show reduced attentional capture by the PSHT-S condition in the shape task. Whilst we did not find interactions between group and other experimental factors, P3 amplitude was nonetheless reduced overall in the dyslexic group, as they were in the word task. Similar observations have been made before (Barnea et al., 1994; Dhar, Been, Minderaa &

Althaus, 2008, 2010; Holcomb et al., 1985; Lovrich & Stamm, 1983; Meyler & Breznitz, 2005; Taylor & Keenan, 1990) but not consistently (Giorgewa et al., 2002; Silva-Pereyra et al., 2001, 2003, 2010; Stelmack, Saxe, Noldycullum, Campbell & Armitage, 1988). It is possible that the overall reduction in P3a amplitude indexes a generalized deficit in frontal attention allocation mechanisms. On the other hand, since the verbal and nonverbal tasks were qualitatively matched, the nonverbal stimulus conditions may have been too distinct to capture subtle relationships between PSHT-S and TARG-S stimuli (as hinted by the P1 range modulations). Alternatively, attentional processing may be qualitatively different for stimuli that are not words. For example, dyslexic participants have been shown to display larger nontarget P3s during an active oddball task, and larger target P3s in a passive task in an oddball design when discriminating between two single letters, which the authors discuss in terms of altered allocation of attention in visual classification (Rüsseler, Johannes, Kowalczuk, Wieringa & Münte, 2003; see also Silva-Pereyra et al., 2010).

Nonetheless, the lack of a group by condition interaction in the shape task indicates that attentional engagement mechanisms may be particularly relevant to processing orthographic stimuli. Specific deficits in attentional processing of orthographic strings are supported by two ERP studies that tested reading-impaired (RI) children in an oddball context. First, an early ERP study (Holcomb et al., 1985) showed that unexpected visual distractors within a target detection task elicited smaller P3s in RI children when targets were words as compared to nonverbal symbol strings, and as compared to children with or without attention deficits. Second, stimulus-driven differences in P3 amplitude have similarly been observed in forced-choice semantic categorisation (Silva-Pereyra et al., 2001). In this case, when RI children had to rapidly decide whether a presented stimulus was an animal or not (presented 22% of the time), they did not show a significant P3 when the stimuli were words. They did, however, show P3 responses similar to normal readers within the same paradigm when the stimuli were line drawings. Along with our observation of significant correlations between language measures and P3a modulations in the word task, but not in the shape task, these data suggest that attentional engagement particularly interacts with visual word processing in dyslexia. Therefore, reduced responsiveness to visual words may be as much part of the deficit in dyslexia as it may be a long-term practical consequence.

Understanding the temporal dynamics of reading is key

The phonological modulations of the posterior P2 that we observed in both the groups were as early as those reported for whole-string phonology in previous ERP studies (e.g., Barnea & Breznitz, 1998; Braun et al., 2009; see Dien, 2009). These early phonological responses appear to be normal in the dyslexic group prior to the P3a differences between groups, which suggests the existence of temporally dissociable phonological processing stages and/or streams; one which involves rapid, automatic phonological access that is relatively intact in dyslexics and is separate from later decoding processes affected by deficient attentional engagement. Behavioural (e.g., Frost, 1998) and MEG data (Cornelissen et al., 2009; Wheat, Cornelissen, Frost & Hansen, 2010) have implicated that serial decoding processes can be preceded by an early phase of automatic phonological access. For instance, recent applications of MEG have shown lexically-driven activations in a similar time range as our P2 modulations within the left inferior frontal gyrus (IFG; BA 44, within 200 ms; Cornelissen et al., 2009; Pammer et al., 2004a), and in particular, phonologically-related oscillations in BA 44 as early as 100 ms, using pseudohomophone masked primes (Wheat et al. 2010). Interestingly, Cornelissen and colleagues (Cornelissen et al., 2009; Pammer et al., 2004a; Wheat et al., 2010) have found these IFG responses to occur shortly after activations in mid occipital gyrus (within 100 ms of stimulus onset), and prior to modulations of both ventral occipitotemporal cortex (vOTC; associated with abstracted orthographic analysis: e.g., Binder, Medler, Westbury, Liebenthal & Buchanan, 2006; Cohen et al., 2002; McCandliss, Cohen & Dehaene, 2003; Moore & Price, 1999) and left temporoparietal regions (left TPJ, associated with phonological analysis; see Graves, Desai, Humphries & Seidenberg & Binder, 2010; Hartwigsen et al., 2010; Jobard et al., 2003; Levy et al., 2009; Pugh et al. 2000; Sandak, Mencl, Frost & Pugh, 2004; Stoeckel et al., 2009). Whilst our ERP data are insufficient to speculate on the precise functional significance of early phonological activations, they are consistent with intact phonological access within 200 ms of stimulus onset and later impairments involving cortical areas typically associated with reading.

TPJ dysfunction has been speculated as the neurofunctional cause of attentional engagement deficits in dyslexia (e.g., Facoetti et al., 2010; Ruffino et al., 2010). Taking together (a) our current understanding of P3 neural generators, (b) neuroimaging data in relation to phonological analysis in reading, (c) patterns of abnormal activation in developmental dyslexia, and (d) the temporal series identified by MEG, the left TPJ –and to a lesser extent the left IFG– is likely to have a key role in the generation of the P3 effect observed here.

Firstly, TPJ involvement (which MEG studies have shown activated after 300 ms during word recognition; Pammer et al., 2004a) appears to be requisite to P3 generation (i.e., both P3a and P3b; see Bledlowski et al., 2004a, 2004b; Knight et al., 1989; Linden, 2005; Soltani & Knight, 2000; Polich, 2007; Yamaguchi & Knight, 1991) with additional involvement of inferior and dorsolateral prefrontal cortex in the case of novelty effects (Clark, Fannon, Lai, Benson & Bauer, 2000; Corbetta, Patel & Shulman, 2008; Corbetta & Shulman, 2002; Daffner et al., 2000, 2003; Kiehl et al., 2001; Lee, Park, Kang, Kang, Kim & Kwon, 2007; McCarthy, Luby, Gore & Goldman-Rakic, 1997). TPJ activation, on the other hand, is modulated by the relevance of a stimulus (e.g., its phonological relevance; e.g., Clark et al., 2000; Cristescu, Devlin & Nobre, 2006; Doricchi, Macci, Silvetti & Macaluso, 2010; Downar et al., 2001, 2002; Fjell, Walhovd, Fischl & Reinvang, 2007; Kiehl et al. 2001; McCarthy et al., 1997; Serences et al., 2005) and, within inferior parietal cortex (IPL) in particular, is implicated in stimulus-driven attentional orienting (see Corbetta & Shulman, 2002; Corbetta et al., 2008 for reviews).

Secondly, TPJ and left posterior IFG are understood to be involved in phonological decoding during reading (e.g., Borowsky et al., 2006; Das, Padakannaya, Pugh & Singh, 2011; Graves et al., 2010; Jobard et al., 2003; Levy et al., 2009; Pugh et al., 2000; Sandak et al., 2004). For example, left IPL is implicated in orthographic-phonological integration at the whole string level (e.g., Bitan et al., 2007; Booth, 2002; Booth et al, 2003, 2004; Booth, Cho, Burman & Bitan, 2007) and hypothesised to be part of a sublexical reading pathway *en route* to left posterior IFG (Borowsky et al., 2006, Jobard et al., 2003; Levy et al., 2009) involved in effortful phonological integration (Fiez et al., 1999; Graves et al., 2010; Mechelli et al., 2003; Thierry et al., 2003).

Thirdly, there is substantial functional evidence for underactive TPJ and abnormal IFG activations during decoding and phonological tasks in developmental dyslexic readers (typically found alongside underactivation of vOTC in relation to abstract orthographic processing; Paulesu et al., 1996; Pugh et al., 2000; Rumsey et al., 1997; see Richlan et al., 2009, or Gabrieli, 2009, for reviews).

Fourth, a recent proposal that the left TPJ facilitates maintenance of verbal material in working memory (e.g., Awh et al., 1996; Baddeley, 2003; Paulesu, Frith & Frackowiak, 1993) via a mechanism of automatic orienting of attention to verbal material (see Ravizza et al., 2011; see also Chien, Ravizza & Fiez, 2003; Ravizza, Delgado, Chein, Becker & Fiez, 2004) is also consistent with our interpretation of the P3a group differences (see also Savill & Thierry, 2011a) as an index of group differences in attentional orientation to phonological information.

In sum, our P3 ERP data provide additional support for a functional link between attentional orienting mechanisms, phonological decoding, and developmental dyslexia, subtended by temporoparietal cortex involvement and the pathway to inferior frontal cortex.

However, it remains unclear at this stage, how attentional engagement actually affects reading. Is it (a) serial engagement / disengagement of attention across a letter string (e.g., Facoetti et al., 2008; Vidyasagar & Pammer, 2010); (b) globally reduced attentional orientation to the correspondence between orthographic and phonological information, or to phonological information in general, during reading (see Savill & Thierry 2011a, 2011b); (c) impaired attentional selection of perceptual information (Roach & Hogben, 2008) or (d) inefficient working memory engagement during decoding (e.g., Berninger et al., 2008; Menghini et al., 2011; Swanson & Ashbaker, 2000)?

Conclusions

In this study we use a P3-eliciting oddball paradigm to characterise attentional capture by incorrect spellings of phonologically relevant material using pseudohomophones. Consistent with previous results, we failed to see a deficit in rapid sublexical decoding (Savill & Thierry, 2011a). In addition, we observed (1) a failure in attentional engagement with phonologically-relevant stimuli in dyslexic readers, possibly underpinned by temporoparietal junction dysfunction; (2) early intact phonological access in a context of spontaneous, uncued word recognition; (3) correlations between attentional engagement and behavioural measures of reading and spelling; and (4) specificity of these effects to the case of word-like stimuli. With greater understanding of the spatiotemporal dynamics of phonological activation in reading and its interactions with orthographic processing and attention, further studies will help to unravel the determinants of reading performance in developmental dyslexia and hopefully pave the way to efficient remediation strategies.

Chapter Seven

General Discussion

General Summary

The studies in the present thesis investigated sensitivity to phonological information in written words in dyslexic and normal adult readers using event-related potentials. There were two broad aims: 1) to track the time course of deficient phonological processing in reading in dyslexia, and 2) to characterise interactive effects of orthographic and phonological information during reading.

In the first study (Chapter 3) high task demands were deliberately placed on phonological analysis, via homophony judgements of pseudoword-word pairs orthogonally manipulated for their phonological and orthographic similarity, in order to reveal phonological processing differences between groups. Despite their putative difficulties with phonological processing, dyslexic readers showed significant early (i.e., N2 range) sensitivity to homophony of visual word stimuli similar to that found in normal readers that was manifested by attenuated amplitudes to words preceded by a pseudohomophone, as compared to those preceded by a non-homophonic pseudoword. Group differences in phonological priming did not emerge until ERP indices of reanalysis in the P600 range.

The second study (Chapter 4) conducted with normal readers investigated if N2 integration of phonologically primed stimuli (cf., Study 1, and see Holcomb & Grainger, 2009, for a review of ERP word priming studies in normal readers) is also observable within a more natural sentence reading context. This study showed that sentence completions phonologically matched to expected words but orthographically unexpected (i.e., homophones and pseudohomophones) produce similar N2 modulations as best completion words, suggesting full-blown phonological integration. These phonologically expected stimuli also led to semantic integration, since N400 amplitudes were attenuated to a similar extent as for expected words relative to unrelated words. This phonologically-mediated semantic integration occurred despite the inappropriate sentence completions being correctly rejected. This study laid the foundations to test sentence-based phonological integration in developmental dyslexic readers in the third study (Chapter 5), alongside a new group of control readers.

Study 3 looked beyond phonologically primed integration of homophones and pseudohomophones to examine the time at which phonologically acceptable stimuli are differentiated in relation to their orthographic appropriateness. This study yielded two important findings: 1) Like control participants, dyslexic readers showed significantly attenuated N2 amplitudes in response to homophones and pseudohomophones of best completions words, indicating intact phonological integration of the stimuli in a sentence context; but 2) ERPs indexing the processing of the same stimuli significantly differed in pattern between dyslexic and normal readers in the P3a range. The orthographically unexpected homophone and pseudohomophone completions elicited a significantly increased P3a response as compared to best completion words and unrelated words in the control group only. Significant correlations between individual mean amplitudes for each ERP peak and reaction times also showed that P3a range processing had the strongest relationship with behavioural performance. Importantly, these differences did not seem to stem from an earlier failure to detect incorrect spellings since both groups showed increased frontal P2a activity to orthographically unexpected stimuli relative to unrelated words. Furthermore, in the P600 range, significant amplitude increases distinguished orthographically incorrect and correct completions in both the participant groups.

The fourth and final study (Chapter 6) set out to test the hypothesis based on the previous studies that deficient phonological processing in reading occurs from the point of attentional engagement. An adapted oddball design targeted P3a generation in spontaneous word processing, in the absence of a priming context. In this study, pseudohomophones of semantically defined target stimuli elicited the predicted P3a peak in control readers only. The inclusion of a critical pseudohomophone control condition strengthened the interpretation of the P3a response to pseudohomophones as being phonologically-driven, since only the target (not the control) pseudohomophones elicited a P3a response in control readers, ruling out the alternative interpretation that the effect may have been driven by orthographic unfamiliarity. The importance of the visual word context on group differences in orienting was tested by means of a nonverbal control task, which elicited similar P3a modulations in both the participant groups. Moreover, these effects could not be attributed to weaknesses in detecting the phonological content of animal pseudohomophones, since the pseudohomophones generated similar posterior P2 amplitudes to animal words, which were increased relative to irrelevant stimuli in both dyslexic and normal readers.

Together, these studies in high functioning dyslexic adults show a general, consistent pattern that has not been previously reported: (a) Early, intact phonological analysis of written words at the whole-word level irrespective of orthographic familiarity, single word or sentence context or lexical status, found prior to the engagement of attention; and (b) Deficient phonological processing in reading emerging at the point of attentional capture indexed by the P3a (though observable after the P3a in the case of Study 1). This pattern of effects can be interpreted as a general failure of attentional orientation to phonologically appropriate stimuli, which would impact reading at the behavioural level. In other words, phonologically, at least, the deficit in reading appears to be attentionally mediated and not purely perceptual.

The interaction of attention and phonology in reading in dyslexia

Can attentional engagement account for reading dysfunction in developmental dyslexia? This research has provided strong evidence for deficient orientation of attention in reading in high-functioning developmental dyslexic readers. Irrespective of the extent to which orienting is involuntary, deficient attentional orienting to phonological information is likely to result in less efficient initiation of working memory engagement with phonological information, and thus impact subsequent phonological monitoring processes (e.g., as seen in the P600 differences reported in Study 1). Reduced engagement with phonological information should affect reading efficiency globally. For instance, in addition to sublexical reading, lexical reading (i.e., the reading strategy associated with direct retrieval of a word's phonological form from the lexicon), may be affected by reduced attention orienting in reading via (1) attentional constraints on the strength of the associations learnt between orthographic and phonologic representations of a given lexical item, and (2) inefficient access to phonological representations on subsequent presentations. Here, distinctions between the effects of phonological processing on dual route reading efficiency may not be appropriate given evidence that sublexical reading skills benefit lexical reading processes (but not vice versa; Gough & Walsh, 1991; Stuart

& Masterson, 1992; Share, 1995). Deficient phonological engagement should affect both.

A deficit in phonological orienting does not require the development of new hypotheses for reading impairment in dyslexia. The mechanisms by which impaired phonological representations have been implicated in explaining deficient decoding in developmental dyslexia (see Snowling, 2000) should equally apply if the deficit is at the attentional rather than the perceptual level, and the difficulty is in accessing phonological information rather than sensitivity to it. Segmentation, the use of grapheme-phoneme mapping, blending, and maintenance in verbal working memory, all require attentionally mediated phonological access (and, with the exception of verbal working memory, are also orthographically mediated). Therefore, sublexical analysis in reading would be greatly affected by reduced orientation to, and engagement with, phonological information.

However, we do not contend that deficient reading in dyslexia can be entirely explained by automatic orienting mechanisms; whether these are in orienting to phonological information in general or to orthographic-phonological correspondences. Three reasons for this are the following:

1) The limited understanding of the precise attentional processes underlying P3a generation discourages attempts to explain reading difficulty in dyslexia entirely in terms of automatic involuntary attention. There is good evidence that the P3a is triggered by automatic attention capture (see Polich, 2007) however it is likely that P3a amplitudes do not index entirely automatic processes. For instance, P3a

amplitudes can be modulated by voluntary attention prompted by stimulus pre-cues (Chong et al., 2008; Sussman, Winkler & Schröger, 2003) and by working memory load (SanMiguel, Corral & Escera, 2008), and can be enhanced by P3b-related voluntary attentional processes (e.g., Debener et al., 2005). It has been suggested that the P3a indexes decision about the allocation of further attentional resources to a novel stimulus (e.g., Daffner et al., 1998) or indicates a signal from the executive system to 'think differently' (Barcelo, Periañez, & Knight, 2002); also implying non-automatic processes. Therefore it is not clear to what extent voluntary and decision making mechanisms, as well as involuntary orienting, should be accommodated as explanations of attentional involvement in reading difficulty (see also Roach & Hogben, 2008, for a relevant discussion of problems with distinctions between exogenous and endogenous attention processes in dyslexia).

2) Not all reading difficulties experienced in dyslexia can be explained by phonological mechanisms. This is particularly so in the case of surface dyslexia, for which the greatest deficits are in reading reliant on whole word recognition (e.g., exception words) and where phonological task performance may be unimpaired (see Valdois et al., 2004; Bosse et al., 2007). As we did not test individuals with this profile it is not clear whether deficient attentional engagement in reading would apply only in individuals with phonological processing difficulties. That said, existing behavioural studies indeed indicate that attentional orienting deficits are specific to individuals with phonological decoding impairments (Facoetti et al., 2006, 2010).

3) We used lexically unusual homophones and (lexically nonexistent) pseudohomophones. These are not representative of ordinary word reading, and differences in orienting only related to these phonologically relevant but incorrect stimuli. Target P3 responses to correct words were not impaired. The relevance of attentional orienting to processing ordinary word stimuli needs to be understood in normal readers before broad conclusions can be drawn about attentional mediation of reading deficits in dyslexia.

If the differences we see in orienting to the phonological content of stimuli in dyslexia are not confined to the orthographic context, then the present findings share common ground with the hypothesis (based on auditorily-presented phonological tasks) that phonological impairment in dyslexia is not in the quality of phonological representations, but based instead in deficient working memory access to them (Ramus & Szenkovits, 2008). Likewise, established behavioural deficits in phonological awareness tasks used in diagnoses of dyslexia (which are, after all, attentionally mediated metaphonological tasks), could manifest through deficient working memory engagement with phonological representations, as opposed to fundamental weaknesses in phonological sensitivity (e.g., Snowling, 2000; Swan & Goswami, 1997), or auditory processing (e.g., Tallal, 1980, 2004; Witton et al., 1998; Goswami et al., 2002).

Aside from being consistent with hypotheses of working memory mediation of phonological access, our observations add to the case made in Shaywitz and Shaywitz's (2008) review on the importance of investigating attentional processes in reading, especially in the case of dyslexia (refer to general introduction for details). Our findings fit within a broad trend of recent behavioural dyslexia research implicating deficits at the level of attentional processing. These include (1) research indicating the possible contribution of a smaller visual-attention span (i.e., the number of letters that can be simultaneously detected and subsequently reported; e.g., Valdois et al., 2004), which is particularly relevant to irregular word reading difficulties and also implicated in the encoding of letter strings for sublexical analysis (Bosse et al., 2007; Valdois et al., 2004); (2) studies investigating spatial cuing deficits, which indicate impaired attentional filtering of perceptual information involved in uncertainty reduction and optimising task performance (Roach & Hogben, 2007, 2008); and (3) hypotheses of deficient or sluggish serial attentional engagement mechanisms involved in the processing of a letter string (Facoetti et al., 2008; Hari & Renvall, 2001; Vidyasagar & Pammer, 2010). In some form or other, each of these perspectives indicate deficient attentional engagement (c.f., Facoetti et al., 2008; Hari & Renvall, 2001; Vidyasagar & Pammer, 2010; Shaywitz & Shaywitz, 2008) or diminished attentional capacity (cf., Valdois et al., 2004; Bosse et al., 2007; Shaywitz & Shaywitz, 2008) in dyslexia that could stem from deficient involuntary or voluntary attentional mechanisms and initiation of working memory involvement. At the same time, however, the listed studies each implicate attentional mechanisms relying on visual rather than phonological processes, and are primarily based on studies involving non-orthographic stimuli (or, at least, non-legal orthographic strings in the case of the visuo-attention span studies). This raises the question of the generalisability of attentional orienting deficits in dyslexia. In Study 4, the investigation of attentional orienting to nonverbal stimuli yielded no evidence of differences in processing between groups. By comparison with the word task, this has been taken as evidence that attentional orienting difficulties are pronounced in a reading context. As mentioned in the discussion in Chapter 6, it may be that there is, however, a broader impairment in automatic attentional orienting in dyslexia that would be detectable in the nonverbal domain using stimuli that are more complex or with conditions that differ more subtly. If successful sublexical decoding is somewhat reliant on attentional orienting mechanisms, then it would not be surprising that stimuli read sublexically would show greater impairment than found in distinguishing stimuli on the basis of shape. The interaction of sublexical and attentional orienting mechanisms (or perhaps the necessity of orienting mechanisms for sublexical analysis?) is consistent with neurobiological data from studies investigating orthographic-phonological analysis, stimulus-driven attentional orienting, and phonological judgement. Support for the critical role of this interaction also comes from studies investigating the neural generators of the P3 ERP, which have implicated the left TPJ and the left IFG (see discussion in chapters 5 and 6). Relevant to our data from high-functioning dyslexic readers, the left TPJ is consistently found to be underactive during reading in these individuals, irrespective of relative compensation for reading difficulties (Hoeft et al., 2007, 2011). The consistent implication of these regions underpinning functions relevant to P3a group differences in phonological processing during word reading both provides neurobiological support for the possible interaction of orienting and phonological processes in reading, and indicates a likely functional source for the relative orienting weakness of dyslexic participants in the word task.

Intact, rapid, automatic phonological access from pseudowords in dyslexia: A challenge for a fundamental phonological deficit in dyslexia?

Each of the dyslexia studies presented in this thesis have shown ERP effects of early phonological access from visual word stimuli prior to stimulus-driven engagement of attention that are not different in dyslexic and control participants. These early phonological effects in the P2 and N2 ranges were comparable in amplitude and topography between groups. As discussed in Study 4, this is evidence for rapid access to phonological form from print. Assuming that ERPs would be sensitive enough to detect phonological integration deficits, this suggests that rough phonological analysis may be relatively unimpaired in dyslexic readers prior to attentionally driven decoding/phonological engagement. This view is difficult to reconcile with the hypothesis that phonological processing differences in dyslexia are essentially driven by basic impairment in phonological representations. Critically, rapid –and apparently automatic– phonologically-driven stimulus discrimination was observed with pseudoword stimuli that, theoretically, relies heavily on sublexical analysis. A stage of automatic phonological access prior to and distinct from effortful decoding is not accounted for within traditional characterisations of sublexical reading in classical models of word reading (for e.g., see Coltheart et al., 2001). A suggestion for possible modifications to the dual route model of reading to incorporate developmental aspects of word decoding is given in Figure 25, with phonological dysfunction in reading located at the onset of attentional engagement. The possible neurobiological pathways underpinning these processes are addressed in the discussion of Study 4. New research efforts to test the existence of distinguishable stages of sublexical analysis in normal readers would provide a reference point both for determining the extent to which early phonological processing may be normal in dyslexia, and the relationship between early phonological access and behaviour.

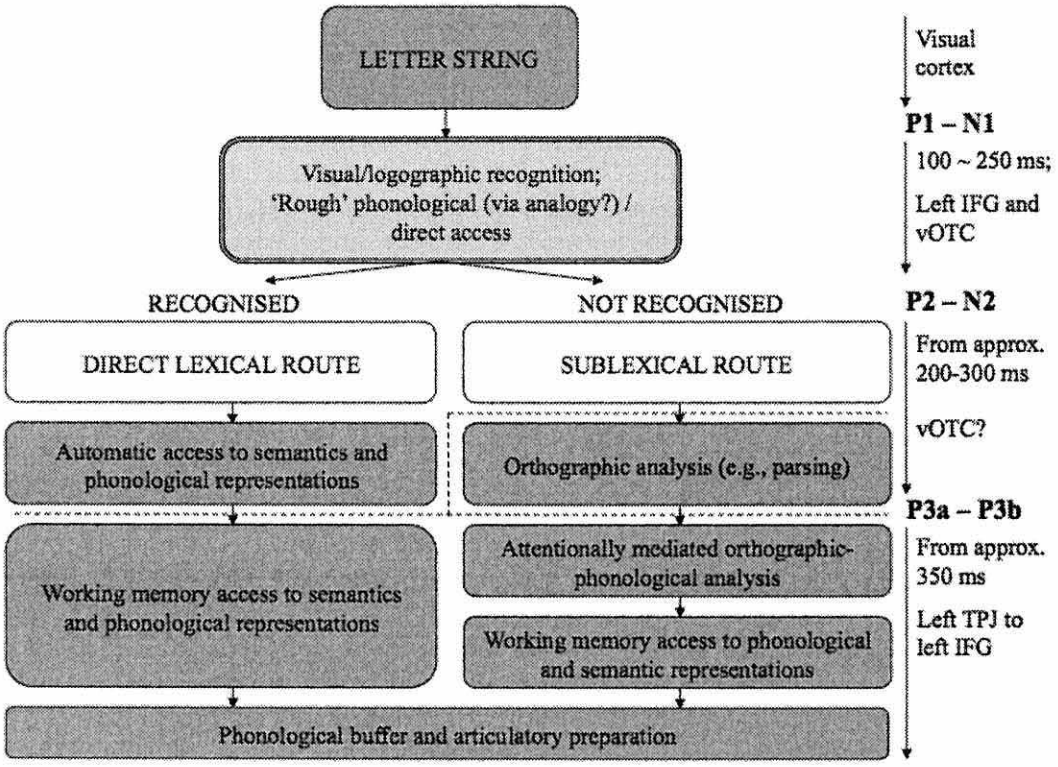

Figure 25. A proposal for the integration of ERP and MEG data into a dual route model of reading. The lightest grey box indicates the main amendment allowing for rapid preattentive phonological access, and a stage at which dyslexic readers appear unimpaired. Dotted lines indicate suggested onsets of phonologically-based reading dysfunction in developmental dyslexia.

With regard to word level phonological analysis, to our knowledge, the P2 effects in Study 4 provide the earliest unprimed ERP effects of whole-word phonology from visual word stimuli – and phonologically-mediated semantic access – reported so far. The use of an unpredictable stimulus sequence seems a particularly fruitful paradigm when studying the speed of word recognition and semantic processing in single word reading.

Is orthographic sensitivity deficient in dyslexia? Does the use of orthographic information contribute to deficient phonological analysis in reading?

Based on reduced N1 amplitudes (in Studies 1 and 3), dyslexic readers seem to show less engagement with orthographic stimuli than their normal reading peers. In Study 1, where orthographic and phonological information were varied orthogonally, we observed that the orthographic similarity of a word to its priming pseudoword did not significantly modulate the N1 in dyslexic readers. This relative indifference to orthographic similarity seems to have had knock-on effects on later interactions with phonological similarity such that phonological discrimination appeared less efficient in the dyslexic group. However, later main effects of orthographic priming (seen in the P3b range) were similar to those seen in control readers. Thus the earlier orthographic differences could reflect either weaker orthographic perception or more top-down differences in orienting to orthographic forms. In other words, dyslexic readers may be more efficient at filtering out orthographic similarity information in order to successfully perform phonological tasks, rather than displaying an orthographic impairment per se.

Indeed, dyslexic readers showed no differences in orthographic discrimination. That is, in Studies 3 and 4, where differences in sensitivity to orthographic form could be assessed in terms of weaker ERP differentiation of correct and incorrect/unfamiliar spellings, dyslexic readers showed orthographic discrimination similar to controls (cf., P2 modulations in both studies and P600 increases to unprimed sentence completions). Furthermore, the perception of orthographic information was sufficiently fine-grained to allow not only successful behavioural discrimination of words from their homophones

(Study 3) and pseudohomophones (Studies 3 and 4), but also rapid sublexical access to phonological information as indexed by significant P2 modulations (Study 4).

However, the observation of reduced sensitivity to orthographic similarity in Study 1 without differences in orthographic discrimination of (a) stimuli that are orthographically incorrect and dissimilar from highly primed orthographic forms (Study 3) and (b) real words from pseudohomophones (Study 4) is also compatible with an underlying impairment in the quality of simultaneous access to whole letter strings (as suggested by observations of a smaller visual attention span in dyslexia; Bosse et al., 2007; Valdois et al., 2004). In the absence of existing ERP studies testing dyslexic participants on fine-grained manipulations of orthographic information (beyond a lexical basis), it is premature to infer whether reduced orthographic effects in the N1 range are (a) the manifestation of a subtle perceptual level weakness in whole string orthographic processing, or (b) due to task-driven top down mechanisms suppressing orientation to orthographic information. Further ERP studies manipulating relative orthographic similarity (for example in homophony judgement or identity priming) and attentional load should help to identify whether developmental dyslexics have a perceptual or attentional difficulty with orthographic information at the word level.

Going beyond pseudohomophones: Limitations

The studies presented here made extensive use of pseudohomophones and therefore relied heavily on sublexical decoding to investigate the timing of phonological retrieval while controlling the orthographic characteristics of the stimuli. However, pseudohomophones are special, nonlexical stimuli. The processes underlying dyslexic readers' reduced orienting response to these orthographically unfamiliar stimuli may not readily extend to the processing of lexical stimuli. It remains therefore unclear if the present findings can be extrapolated to mechanisms at work when reading real regular and irregular words.

The nature of pseudohomophone stimuli presents another concern regarding generalisability: The creation of pseudohomophone stimuli was substantially helped by the natural irregularity and opacity of the English language, which offers multiple orthographic entries for a given phonological form. While this is an advantage in designing tightly controlled stimuli, it is also likely to be a disadvantage insofar as it is unclear if and how the findings here would apply to languages with more transparent and consistent orthographies, where such stimuli will be rare.

Another concern relating to the use of homophones and pseudohomophones is the extent to which group differences in P3a responses in Studies 3 and 4 can be attributed to the relative orientation to phonological over orthographic information. Pseudohomophones were controlled for their orthographic similarity with their word counterpart across conditions in each task. This, however, limited our ability to also control for the orthographic similarity of non-homophonic items with target stimuli (e.g., in Study 4, although PSHT and PSHF stimuli were both similarly close to their word counterparts in terms of orthography, PSHF stimuli were not as orthographically similar to target stimuli as PSHT stimuli). Some of the concerns regarding the confound of relative orthographic similarity were addressed in the discussion of Study 2, with regard to discounting the role of orthographic similarity in the observed N400 effects (cf., page 116). Beyond those points, it simply makes sense that the phonological content of pseudohomophones would have significantly contributed to P3a modulations given that it had influenced processing in the earlier P2 and N2 ranges. Put another way, early phonological access, which has previously been studied behaviourally (e.g., Frost, 1998; Lukatela & Turvey, 1994), with ERPs (Braun et al., 2009; Savill et al., 2011; Vissers et al., 2006), and with MEG (Wheat et al., 2010), has been shown to sustain semantic access (Lukatela & Turvey, 1991; Luo, Johnson & Gallo, 1998) through to semantic integration in the N400 range (Savill et al., 2011; Vissers et al., 2006). It seems reasonable to posit that P3a modulations, in a concurrent time range to the N400, should also be influenced by phonological content. However, based on observations from the present studies it is not possible to rule out, for instance, that over and above the effects of homophony, the P3a responses may have been driven by orientation to a conflict between the relatively greater orthographic similarity of target items as compared to fillers and their incorrect semantic/lexical representations. Therefore, it cannot be excluded that reduced sensitivity to orthographic form and/or lexical knowledge in dyslexia may have contributed to reducing P3a responses to homophones. However, given that the largest P2a amplitudes in dyslexic participants were observed for orthographically incorrect homophones and that they showed significant differentiation of correct and incorrect sentence completions in Study 3, it is unlikely that the differences in orthographic discrimination explain P3a group differences. Nonetheless, future inclusion of further orthographic controls may clarify the extent to which attentional orienting in reading, and its depletion in dyslexia is affected by orthography. Ideas for such studies are described below in the section entitled 'future directions'.

The choice of testing university students with a diagnosis of developmental dyslexia may be regarded as another limitation of our studies. These participants have obviously compensated to some degree for their reading difficulties and have attained a reading proficiency within a normal range. However, there are a number of reasons why testing this population may actually be seen as an advantage. First, reading experience is relatively homogenous in the student population. Second, they have been diagnosed as dyslexic on the basis of thorough examination (Bangor University has a Dyslexia Unit). Third, their behavioural profile in terms of residual weaknesses in measures of pseudoword reading and spelling was available. Fourth, group differences observable in the current studies can help identify core dysfunction in dyslexia which are dissociable from relative reading level (see also reasons listed in Study 1). However, the high-functioning status of the participants leads to the question of whether the same pattern of results would be found in dyslexic individuals who have persistently poor reading, or in children with dyslexia. It is possible that intact early phonological access seen here in high-functioning dyslexic adults may be an index (or cause) of their relatively well-compensated reading. Clearly, the generalisability of early phonological access to other dyslexic populations needs to be investigated further. Similar attentional orienting differences, on the other hand, are likely to be observable across levels of reading proficiency because (1) it is unlikely that an attentional orienting deficit would develop only in high functioning dyslexics; and (2) there is a hypothetical link between attentional orienting differences and TPJ underactivation; since TPJ dysfunction is suggested to be a persistent marker of dyslexia irrespective of levels of compensation (unlike activation in left IFG, which varies with compensation level; Hoeft et al., 2007, 2011).

Implications and future directions

This PhD research has provided, for the first time, electrophysiological evidence of deficient attentional processes in reading, and has given indication that orienting may be critical in the manifestation of phonological impairment of reading. This represents a fruitful arena for future research on the relationship between attentional processes and reading / phonological processing.

In relation to the suggested underactivation of left temporoparietal cortex (as discussed in Studies 3 and 4), it would be interesting to test dyslexic and normal readers on tasks that compare attentional orienting that is phonologically driven or not with functional neuroimaging, and to see whether differences in activation are specific to orthographic/verbal material. Not only would insights from such investigation (for example using an event-related fMRI adaptation of the oddball tasks in Study 4) help to further elucidate the cognitive and neural underpinnings of attentional impairments affecting reading in developmental dyslexia, but, alongside ERP data (or MEG), it would help to break down the cognitive and spatiotemporal profile of sublexical processing in normal reading. This would help determine the extent to which attentionally mediated sublexical analysis can be separated from rapid phonological activation indexed by P2 modulations and similar effects found in MEG studies with normal readers (Wheat et al., 2010). The investigation of relative differences in left TPJ modulation depending on orientation to verbal or nonverbal stimuli, under voluntary or involuntary control, would also test the validity of Ravizza et al.'s (2011) proposal that left TPJ involvement in verbal working memory relates to automatic orienting to verbal information; and therefore the suggestion that underactive TPJ indeed accounts for automatic orienting failures to phonological information in developmental dyslexia.

More broadly, this PhD project lends electrophysiological support for the research agenda put forward by Shaywitz and Shaywitz (2008), who have suggested that future investigations need to focus on the role of attentional processes in the manifestations of reading difficulties and how these may be modified to help remediate reading. Significant advances could be made with a convergent approach comparing tasks in which critical stimuli are attended or unattended, verbal or nonverbal, visual, auditory, or reliant on audiovisual integration, and where differences are considered in the context of their spatiotemporal processing course within the brain. For instance, one broad question arising from this thesis that would benefit from a multi-task approach is why deficits in auditory processing in dyslexia, which have long been proposed as the basis of the phonological deficit and are supported by a wealth of ERP studies showing reduced mismatch negativities (MMNs) to auditory oddballs, do not manifest themselves here in terms of an early weakness in phonological processing during reading. Similarly, the present ERP data emphasises the need for further consideration of whether differences in auditory processing in dyslexia might also be accounted for by attentional rather than perceptual factors (see Fosker & Thierry, 2005 and Rüsseler et al., 2003, for previous implications of attentional modulation of auditory oddball responses).

Suggested future studies

The first study could build directly on the experimental design and results of the oddball word task in Study 4. The objective would be to distinguish the relative contribution of orthographic similarity to pseudohomophone effects and their involvement in the P3a response (or lack thereof). In this version of the oddball word task, the number of critical conditions would be altered to include orthographic control conditions, while preserving the ratio of target and homophonic conditions relative to phonologically irrelevant stimuli. That is, in addition to the target words, pseudohomophones of target words and pseudohomophones of filler stimuli used in the present research (still each 10% occurrence), orthographic controls would be included for both pseudohomophone conditions (each 10%; non-homophonic pseudowords with identical orthographic overlap to target words as in the respective pseudohomophones). The remaining 50% of stimuli would consist of irrelevant words. With this design, ERP amplitudes to pseudohomophones of target stimuli would be expected to be significantly larger than those for orthographic controls and filler words. An additional task variant would adjust the instruction to responding when stimuli sound the same as an animal name irrespective of spelling. This should elicit a target P3 to pseudohomophones instead of a nontarget P3a, which would help to determine whether the group differences in P3a effects are specific to automatic and involuntary orienting mechanisms.

Another study could specifically investigate rapid and intact phonological access from pseudohomophones that this research has shown in dyslexic as well as normal readers. An existing paradigm that seems to be an obvious choice to investigate preattentive access to phonological information in words, away from possibly overlapping and cancelling effects of stimulus driven orienting mechanisms, is masked phonological priming. Indeed it is surprising, considering the vast phonological masked priming literature (see Rastle & Brysbaert, 2006, or Dimitropolou, Duñabeitia & Carreiras, 2011, for overviews), that there are no ERP masked priming studies in dyslexia (a PubMed internet search 18th May 2011 using the search terms "dyslexia ERP masked priming" yielded no results; "dyslexia masked priming" yielded one study which found no group differences in morphological processing). A possible explanation for such a gap in the literature is that masked phonological priming effects would tap into rapid preattentive phonological skills that are intact in dyslexia rather than deficient stimulus-driven attentional processing and therefore such studies have yielded non-results, which we know to be particularly difficult to publish. Presumably, null effects of group would not be an interesting finding to report if evidence of impaired phonology was expected. This observation indicates an interesting avenue for investigation: Comparing the effects of masked and unmasked phonological priming in dyslexia. If attentional orienting is the source of the problem (particularly if the deficit concerns orienting to the correspondence of orthographic and phonological information), then group differences in the P3 range should be observable only for consciously detectable stimuli in the unmasked version, while early phonological priming should be similar between conditions. Furthermore, an initial effort to test whether analogy might be a way in which phonology can be rapidly accessed from 'sublexical' stimuli could incorporate the comparison of pseudohomophone primes derived from high frequency exception words (e.g., 'bight') with orthographically consistent pseudohomophones (e.g., 'brane') and orthographic control pseudowords (e.g., 'binst', 'brank').

Overall contribution

This PhD research draws attention back to the reading context in developmental dyslexia. It provides consistent evidence that, in well-compensated dyslexic adults, phonological processing deficits affecting reading emerge from the point of attentional engagement. These studies illustrate the substantial value of ERPs in delineating the time-course of word reading, and enabling investigation of relative and interactive contributions of phonological and orthographic processes. In particular, these studies have shown how ERP investigation can help achieve a broad overview of difficulties in visual word processing in dyslexia. There has been an over-reliance within the field of dyslexia research on inferences from behavioural measures that fail to distinguish between perceptual and higher-level phases of processing. This has contributed to widespread adoption of the hypothesis that fundamentally impaired perceptual phonological representations affect reading in dyslexia. In the present project, ERPs showed rapid, automatic and intact phonological sensitivity in reading in dyslexia, and deficient phonological processing only once attention is engaged, two phases that could not be dissociated on the basis of behavioural testing alone. Furthermore, a possible neurobiological framework regarding how this pattern of dysfunction emerges has been put forward by identifying convergent results from studies of P3 generation, attentional orienting, orthographic-phonological analysis, and relative underactivations during reading in dyslexia. By attempting to place ERP observations of phonological and orthographic processing in the context of what is known about perceptual and attentional processes, both in terms of timing and neurophysiologically, this research has provided new physiological constraints for future explanations of the reading deficit in developmental dyslexia.

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Appendices

Appendix 1: Pseudoword and word stimuli (Study 1)

Ortho: Orthographic similarity to target (Normalized Edit Distance; Lambert et al., 1999)

Target	P+O+		P+O-		P-O+		P-O-	
	Prime	Ortho	Prime	Ortho	Prime	Ortho	Prime	Ortho
BROAD	brord	0.90	brawd	0.65	brold	0.90	brend	0.65
CAUSE	cauze	0.90	corze	0.40	cauge	0.90	corge	0.40
CEASE	sease	0.95	seece	0.40	vease	0.95	veuke	0.40
CLIFF	kliff	0.95	cliph	0.70	bliff	0.95	clipe	0.70
CLIMB	clime	0.95	clyme	0.65	climm	0.95	clume	0.65
CLOAK	cloac	0.95	cloke	0.70	cloaf	0.95	clorl	0.70
COACH	koach	0.95	coche	0.65	noach	0.95	tothe	0.65
COAL	coll	0.83	kole	0.25	coul	0.83	loke	0.25
COPE	kope	0.92	coap	0.58	yope	0.92	coaf	0.58
CORE	kore	0.92	coor	0.58	zore	0.92	coze	0.58
CORK	corc	0.92	cauk	0.50	corb	0.92	cisk	0.50
CORN	korn	0.92	kawn	0.50	rorn	0.92	woan	0.50
COURT	kourt	0.95	corte	0.65	wourt	0.95	doart	0.65
CREEK	creec	0.95	creac	0.70	creeg	0.95	creng	0.70
CROW	croe	0.83	kroh	0.58	crod	0.83	frop	0.58
CRUDE	krude	0.95	crood	0.45	grude	0.95	graim	0.45
CUFF	kuff	0.92	cuph	0.58	suff	0.92	sump	0.58
CYST	syst	0.92	sist	0.58	nyst	0.92	wust	0.58
DAWN	daun	0.83	dorn	0.50	drin	0.83	deln	0.50
DEER	dier	0.83	dere	0.58	drer	0.83	dern	0.58
DIVE	dyve	0.83	deiv	0.25	duve	0.83	demb	0.25
DRINK	drinc	0.95	drync	0.65	drinp	0.95	dranp	0.65
EASE	eaze	0.83	eeze	0.50	eabe	0.83	elge	0.50
FAIL	feil	0.83	fale	0.50	flil	0.83	farf	0.50
FALL	faul	0.83	forl	0.50	farl	0.83	frul	0.50
FLOOR	florr	0.90	phlor	0.45	floir	0.90	splor	0.45
FLOW	floe	0.92	phlo	0.25	flod	0.92	phod	0.25
GERM	jerm	0.92	jurm	0.58	herm	0.92	hirm	0.58
GOAT	goht	0.83	gote	0.58	gont	0.83	goce	0.58
GOOSE	gooce	0.90	geuce	0.40	gooke	0.90	gawfe	0.40
GUARD	ghard	0.90	garde	0.60	geard	0.90	gombe	0.60
GUIDE	geide	0.90	ghyed	0.20	gaide	0.90	gnane	0.20
HAWK	hawc	0.92	hork	0.50	hawp	0.92	henk	0.50
HORSE	horce	0.90	hauce	0.40	horle	0.90	hiele	0.40
HYMN	himn	0.83	himm	0.50	homn	0.83	hame	0.50
JAIL	jeil	0.83	jale	0.58	jaul	0.83	jarv	0.58
KEEP	kiep	0.83	kepe	0.58	krep	0.83	kesh	0.58
LOOP	loup	0.83	lupe	0.25	lorp	0.83	lurp	0.25
MOUSE	mowse	0.90	mowce	0.65	molse	0.90	molge	0.65

PHASE		phaze	0.90	faize	0.20	phabe	0.90	grulp	0.20
RHYME		rhime	0.90	wrime	0.45	rhame	0.90	spame	0.45
SCORE		skore	0.90	schor	0.65	slore	0.90	scelm	0.65
SCREW		screu	0.90	skroo	0.40	scren	0.90	sprut	0.40
SEAL		seel	0.83	ceel	0.50	seul	0.83	derl	0.50
SHEEP		sheap	0.90	shepe	0.70	shelp	0.90	sherm	0.70
SHOE		shoo	0.92	sheu	0.58	shom	0.92	shig	0.58
SHORE		shorr	0.95	shawe	0.65	shorg	0.95	shate	0.65
SKUNK		scunk	0.90	scunc	0.65	saunk	0.90	stune	0.65
SORE		sorr	0.92	soor	0.58	sork	0.92	sowt	0.58
TALL		tawl	0.83	torl	0.50	tarl	0.83	thol	0.50
THIEF		theef	0.90	theaf	0.65	thref	0.90	thulf	0.65
TRAIN		trein	0.90	trane	0.70	troin	0.90	trawp	0.70
WALL		wawl	0.83	worl	0.50	wahl	0.83	wewl	0.50
WEEK		weec	0.92	weac	0.58	weef	0.92	weab	0.58
WHEEL		wheal	0.90	weale	0.60	wheul	0.90	wouge	0.60
WHITE		whyte	0.90	wight	0.20	whote	0.90	weabe	0.20
WORE		worr	0.92	wour	0.58	worg	0.92	woag	0.58
WORSE		werse	0.90	wirce	0.60	warse	0.90	warze	0.60
YOUTH		yooth	0.90	yuthe	0.60	yopth	0.90	yaud	0.60
Ortho.	***M***	**P+O+**	**0.89**	**P+O-**	**0.52**	**P-O+**	**0.89**	**P-O-**	**0.52**
	SD		0.04		0.14		0.04		0.14
N.Neigh.	***M***		**3.60**		**3.08**		**3.18**		**3.43**
	SD		2.34		3.40		2.82		3.26

Appendix 2: Critical sentence stimuli (Study 2)

	BC	HO	PH	UN	Cloze (%)
A deal is made between a buyer and a	seller	cellar	sela	ache	88
A female sheep is a	ewe	you	yoo	tap	82
A fruit sometimes used to describe a woman's figure is a	pear	pair	pare	garlic	71
A stack of hay is called a	bale	bail	bayel	brute	38
Alert! Alert! Return immediately to	base	bass	baice	yell	41
All these corridors, I felt like I was lost in a	maze	maize	mays	polish	88
An eagle is a bird of	prey	pray	prai	flare	100
Andrew broke his leg and therefore was in a lot of	pain	pane	payn	mince	100
Anti-war activist want world	peace	piece	peece	approach	100
As soon as the crew had boarded, the boat set	sail	sale	sayel	pouch	71
At football today, Nick didn't bother to pass the	ball	bawl	baul	dog	100
Before walking up the garden path, Edmond had to open the	gate	gait	gayt	bone	97
Bruce gave his rotweiler a thick, juicy	steak	stake	stayk	robin	62
Drink cans are made of aluminium or	steel	steal	stiel	beaver	26
Emily combed Syvia's beautiful	hair	hare	haer	window	97
Goliath was strong but David was	weak	week	weec	narrow	21
Heather sang the song with her whole heart and	soul	sole	sowl	next	100
I took psychology as my major and criminology as my	minor	miner	myna	clamour	82
If you are in debt, you may need to take out a	loan	lone	lown	open	100
In front of the hotel is a beautiful sandy	beach	beech	beetch	train	100
Jim put a belt on to keep his trousers around his	waist	waste	wayst	skull	97
John looked stressed, his boss told him to take a	break	brake	brayk	weigh	65
Linda was nine months pregnant, she was about to give	birth	berth	burth	plane	100
Noah loaded all the animals into his	ark	arc	arq	ram	85
Old mother Hubbard's cupboard was	bare	bear	bair	mass	71
Rob looked at his watch to check the	time	thyme	tyme	thwart	100
Sandpaper can be graded from fine to	coarse	course	korce	short	82

She left the church after singing the last	hymn	him	hem	register	91
Susan got some lozenges because her throat was	sore	soar	sawe	dawn	97
Symbols of Wales are the dragon, the daffodil and the	leek	leak	leec	blanket	88
The children were excited by the roller coaster at the	fair	fare	phare	rapid	91
The jockey put the saddle on his	horse	hoarse	hauce	music	100
The length of time a king is on the throne is described as his	reign	rain	wrayn	outset	97
The moon shines at	night	knight	nyte	face	100
The old woman knew many stories, but only one fairy	tale	tail	tayel	east	82
The postal service in Britain is run by the Royal	mail	male	mayel	sting	97
The shop did not have the shoes in Anne's	size	sighs	seiz	act	100
The son inherits his father's possessions because he is the rightful	heir	air	aeir	frail	94
They watched the car until it was out of	sight	site	syte	broke	97
William was unsure whether he was wrong or	right	rite	ryte	unit	88
	BC	**HO**	**PH**	**UN**	**84.71**
Average Concreteness	467.08	459.28	NA	470.05	
Average log frequency	1.13	1.16	NA	1.10	

Appendix 3: Critical sentence stimuli (Study 3)

Sentence stem	**BC**	**HOM**	**PSH**	**UNR**	**Cloze (%)**
Anti-war activists want world	peace	piece	peece	heavy	100
Emily combed Sylvia's beautiful	hair	hare	heyr	window	97
The moon shines at	night	knight	nyte	face	100
The dog was wagging its	tail	tale	tayl	yell	100
Baking bread involves kneading the	dough	doe	dow	unit	100
Instead of hands, cats have	paws	pause	porze	tap	92
There are seven days in a	week	weak	weec	desk	100
Marie wasn't sure which dress to	wear	where	wair	register	96
The prisoner was locked in his	cell	sell	sel	germ	96
An eagle is a bird of	prey	pray	prai	flare	100
Pierre recommended a bottle of French red	wine	whine	wighn	boat	100
The jockey put the saddle on his	horse	hoarse	hauce	music	100
Pectorals and triceps are both types of	muscle	mussel	mussle	dawn	100
The gas man visited to read the	meter	metre	meater	prune	96
The little boy did as he was	told	tolled	toled	short	100
Clare went on a diet to lose	weight	wait	wate	string	100
The police quickly arrived at the murder	scene	seen	sene	ram	96
Groups work best if they work as a	team	teem	tiem	spice	100
The lecturer used a microphone so everyone could	hear	here	hier	point	100
Susan got some lozenges because her throat was	sore	soar	sawe	brute	97
Rob looked at his watch to check the	time	thyme	tyme	thwart	100
More troops were recruited to fight in the	war	wore	worr	mass	96
The bride's father proudly walked her down the	aisle	isle	ighl	fairy	100
The children were scared when they heard the lion	roar	raw	rore	cook	96
Umbrellas are used to stop getting wet from the	rain	rein	reyn	biscuit	100

At football today, Nick didn't bother to pass the	ball	bawl	baul	dog	100
In front of the hotel is a beautiful sandy	beach	beech	beetch	train	100
They watched the car until it was out of	sight	site	syte	broke	97
The shop did not have the shoes in Anne's	size	sighs	seiz	act	100
Heather sang the song with her whole heart and	soul	sole	sowl	next	100
Gerard had over one hundred vintage wines in his	cellar	seller	sella	ache	92
Kelly was annoyed at how much mess her kids had	made	maid	meyed	east	100
Pete took the lift to his office on the fifth	floor	flaw	flore	cost	100
The postal service in Britain is run by the Royal	mail	male	mayel	sting	97
Linda was nine months pregnant, she was about to give	birth	berth	burth	plane	100
Rita tried to find the supermarket till with the shortest	queue	cue	quew	rapid	96
The defendant was relieved that the jury was on his	side	sighed	syed	pouch	100
The son inherits his father's possessions because he is the rightful	heir	air	ehr	frail	94
Andrew broke his leg and therefore was in a lot of	pain	pane	payn	mince	100
Jim put a belt on to keep his trousers around his	waist	waste	wayst	skull	97
Before walking up the garden path, Edmond had to open the	gate	gait	gayt	bone	97
When Lucy went to the seaside she took her bucket and	spade	spayed	spaid	garlic	92
The plumber came to fix the pipe that had sprung a	leak	leek	leec	blanket	96
They played eye-spy in the car to stop the children from getting	bored	board	borde	moral	96
If you are in debt, you may need to take out a	loan	lone	lown	open	100
She set her alarm clock to go off very early in the	morning	mourning	mawning	power	100
Sally put a lot of sugar in her coffee as she liked it really	sweet	suite	swete	urban	100
The length of time a king is on the throne is described as his	reign	rain	wrayn	outset	97

Appendix 4: Controlled sentence completion properties (Study 3)

	BC	HOM	PSH	UNR
Number of letters	4.54	4.54	4.44	5.00
Kucera-Francis Frequency[a]	117.90	71.42	NA	91.36
Concreteness[a]	475.22	436.12	NA	469.33
Constrained Bigram Count[b]	42.87	57.35	39.11	50.38
Constrained Trigram Count[b]	10.35	11.24	7.57	8.76
Orthographic Neighbour Freq.[b]	68.53	116.91	49.89	33.43
Orthographic Similarity to BC[c]	1.00	0.59	0.55	NA

Note. Average values given. [a] According to the MRC Psycholinguistic Database (Coltheart, 1981); [b] According to http://www.neuro.mcw.edu/mcword/ (Medler & Binder, 2005); [c] Calculated according to Normalized Edit Distance (Lambert et al., 1999).

Appendix 5: Properties of words and pseudohomophones by category (Study 4)

Word Cat.		K-F F.	Letters	Phon.	Syll.	Orth. N.	C. Bi. F.	C. Tri. F.
Animal	*M*	**16.72**	**4.64**	**3.60**	**1.32**	**7.52**	**1854.56**	**229.99**
	SD	25.08	1.25	0.91	0.48	7.23	1396.39	447.64
Food	*M*	**13.28**	**5.12**	**3.84**	**1.44**	**5.12**	**1408.13**	**214.45**
	SD	12.10	1.05	0.94	0.51	5.04	1101.63	231.94
Tools	*M*	**17.44**	**4.88**	**3.76**	**1.32**	**5.80**	**1086.06**	**213.38**
	SD	22.63	1.24	0.93	0.48	4.92	703.97	237.93
Jobs	*M*	**26.92**	**5.48**	**4.04**	**1.52**	**4.16**	**1444.56**	**209.19**
	SD	27.35	1.12	1.06	0.51	4.84	988.62	211.02
Body Parts	*M*	**27.24**	**4.92**	**3.64**	**1.28**	**5.04**	**1195.04**	**151.57**
	SD	20.37	1.15	0.99	0.46	4.77	788.51	179.67
Nature	*M*	**28.80**	**4.80**	**3.88**	**1.24**	**6.16**	**1394.80**	**272.16**
	SD	26.46	0.82	0.97	0.44	5.79	1142.76	501.95
Household	*M*	**28.88**	**5.12**	**4.04**	**1.44**	**4.92**	**1492.90**	**288.80**
	SD	32.76	1.09	0.98	0.51	4.96	1385.61	388.17
Clothing	*M*	**19.68**	**4.80**	**3.80**	**1.20**	**7.84**	**1374.36**	**160.08**
	SD	19.08	1.35	1.15	0.41	6.71	1362.23	154.30
F		1.71^{ns}	1.31^{ns}	$.067^{ns}$	1.37^{ns}	1.34^{ns}	0.99^{ns}	0.56^{ns}

Pseudo-homophone		Letters	Orth. Sim.	Orth. N.	C. Bi. F.	Un. Bi. F.	C. Tri. F.	Un. Tri. F.
Animal (salient PSH)	*M*	**4.84**	**0.62**	**5.08**	**1417.98**	**16369.21**	**375.14**	**1211.01**
	SD	1.14	0.11	5.11	2000.55	8470.58	1391.17	1603.13
Food (non-salient PSH)	*M*	**5.04**	**0.62**	**3.04**	**972.27**	**13723.15**	**87.17**	**1125.87**
	SD	0.94	0.13	3.77	1000.27	8804.15	102.97	1043.28
t		-0.68^{ns}	0.03^{ns}	1.61^{ns}	1.00^{ns}	1.08^{ns}	1.03^{ns}	0.22^{ns}

Note. Based on 25 exemplars per category. K-F F. Kucera-Francis Written Frequency; Letters. Number of letters; Phon. Number of phonemes; Syll. Number of syllables; Orth. N. Number of orthographic neighbours; C. Bi. F. Constrained bigram frequency; C. Tri. F. Constrained trigram frequency; PSH. Pseudohomophone; Orth. Sim. Orthographic similarity to exemplar, based on normalised edit distance (Lambert et al., 1999); Un. Bi. F. Unconstrained bigram frequency; Un. Tri. F. Unconstrained trigram frequency.

Appendix 6: Supplementary Analyses

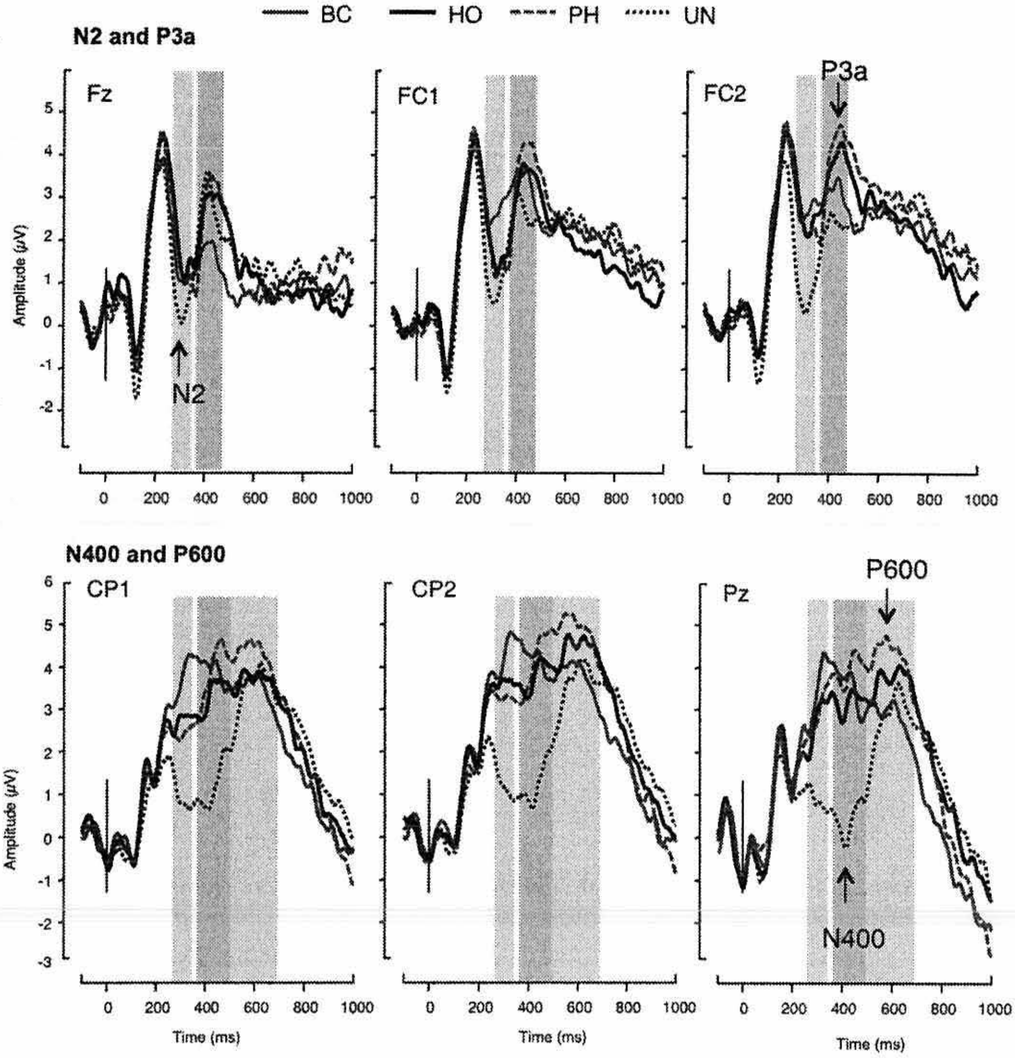
Study 2:

Following the focus on P3a modulations in the sentence study with dyslexic participants in Study 3, we revisited the sentence study data in Study 2 with skilled readers to test whether these replicated the P3a and P600 modulations observed in control readers. This study used a different electrode and recording array to the one used in Study 3 so the electrodes that corresponded most closely in terms of topography were analysed.

In the case of the P3a, these were Fz, FC1, FC2 and Cz, and for the P600 these were Cz, CP1, CP2 and Pz.

The P3a results showed a similar pattern as in Study 3: increased amplitudes to homophone and pseudohomophone stimuli relative to unrelated and best completions, $F(3, 42) = 5.20, p < .01$, however the difference between homophones and best completions did not reach significance in this case. P3a latency also showed an effect of condition, $F(3, 42) = 3.83, p < .05$. This was due to the P3a peak being detected earlier to unrelated completions compared to homophones and pseudohomophones.

For the P600, a significant condition effect was also observed, $F(3, 42) = 4.81, p < .05$. This was driven by significantly larger P600 amplitudes to pseudohomophones compared to best completions and unrelated items. No other amplitude comparisons were significant. P600 latencies were influenced by sentence condition, $F(3, 42) = 4.21, p < .05$. Pairwise comparisons showed that the condition effect was due to best completions eliciting an earlier P600 peak than homophone and unrelated items.



Supplementary Figure 1: Grand averages at individual electrode sites. N2 and P3a modulations are shown at Fz, FC1 and FC2. N400 and P600 effects are shown at CP1, CP2 and Pz.

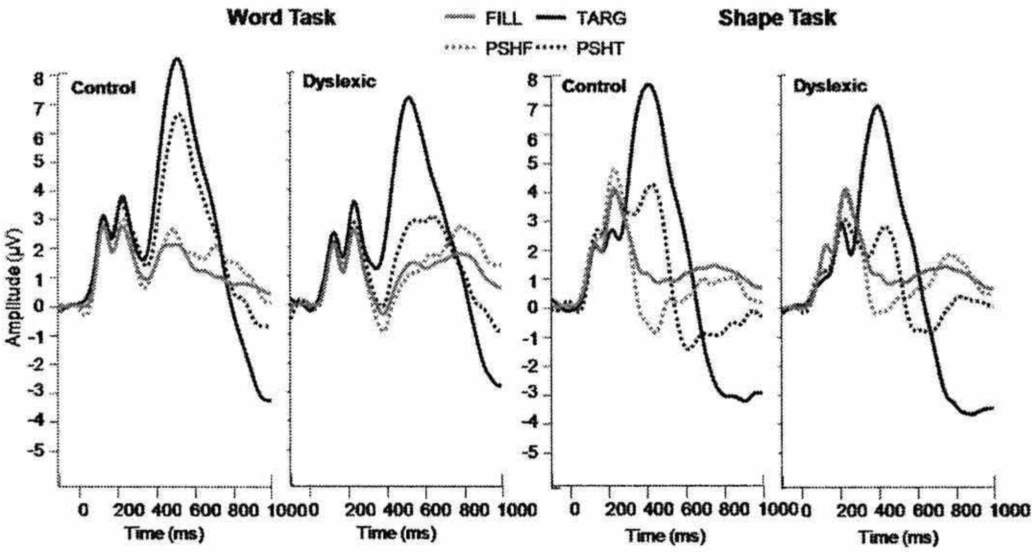
Summary

By finding a clear P3a to homophones and pseudohomophones it confirms that the effect we observed in controls in Study 3 is reliable. Regarding the P600, the significant increase only to pseudohomophones is different to our results, but not inconsistent with, the generally attenuated response to unrelated compared to all other conditions that we observed in Study 3. These results are similar to those of Vissers et al. (2006) who also looked at the effects of pseudohomophone (but not homophone or unrelated) sentence completions on P600 modulations. The finding that only the pseudohomohone and not the homophone condition elicited an increased response, despite both being rejected as incorrect would suggest that the double-checking response in this case is primarily driven by the orthographic familiarity rather than the 'lexical correctness' of the stimulus.

It may be we would also have found a subtle P600 increase to pseudohomophones in Study 3 had we not collapsed data with the phonological variant of the sentence task, in which participants were asked to accept all phonogically acceptable completions, irrespective of whether spellings were correct (and familiar). Nonetheless, we had observed no clear differences in ERP modulations elicited by the ortho-semantic (whether the sentence was semantically acceptable) and phono-semantic task modulations (whether the sentence was phonologically acceptable) during early analyses, which is why they were combined.

Study 4:

In the submitted paper, only P3a analyses are reported. Analyses were, however, run on P3 amplitudes across the scalp to consider P3b effects. An anteriority factor was included in analyses to distinguish between P3a and P3b modulations (anterior sites: FC3, FC4, FCz, C3, C4, Cz; and posterior sites: CP3, CP4, CPz, P3, P4, Pz). Indeed, in the case of the word task, we found a significant effect of condition on mean amplitudes broadly across the scalp, $F(3, 78) = 45.32, p < .001$. Pair-wise comparisons showed target words elicited larger P3 amplitudes than each other condition and target-pseudohomophones elicited larger amplitudes than the filler and filler-pseudohomophone conditions. This was qualified by a near significant main effects of group, $p = .051$, and further by significant interactions of anteriority x condition, $F(3, 78) = 21.70, p < .001$, and a group x anteriority x condition interaction, $F(3, 78) = 21.70, p < .001$. The group effect indicated smaller P3 amplitudes overall in the dyslexic group. The interaction of anteriority by condition showed that, whilst the direction of condition effects was the same across sites, target stimuli elicited relatively larger amplitudes over posterior electrode sites. Meanwhile, the three-way interaction of group by anteriority by condition confirmed the following pattern of results, which was what determined the decision to report only P3a effects: Over centroparietal electrodes, both dyslexic and control groups showed the same pattern of significant effects as the main condition effect, albeit with relatively greater (non-significant) separation of target pseudohomophone and target stimuli in the dyslexic group. Over frontocentral electrodes, on the other hand, controls showed significant amplification of the target pseudohomophone condition compared to the filler conditions that did not significantly differ from that for target stimuli; whereas the dyslexic group showed no separation of the filler conditions from the pseudohomophone target condition, with only the target condition eliciting a significantly increased/different response. A group x condition effect on P3 amplitudes across anterior and posterior sites was just outside of significance, $p = .06$, indicating that group differences were driven by frontocentral modulations. Supplementary Figure 2 shows that centroparietal target P3 responses were similar between groups, albeit with slightly smaller amplitudes in the dyslexic group.



Supplementary Figure 2. Group grand averages over centroparietal electrodes showing P3 modulations in the word and shape tasks. Linear derivation of electrodes CP3, CP4, CPz, P3, P4, and Pz.

The P3 peak in the shape task was also significantly modulated by condition, $F(3, 78) = 65.34$, $p < .001$. Pairwise comparisons showed that target shapes elicited a significantly increased P3 compared to all conditions and pseudo-target shapes were increased relative to the pseudo-filler and filler shapes. This was qualified by an interaction of anteriority by condition, $F(3, 78) = 20.75$, $p < .001$. Pairwise comparisons showed that the direction of effects were the same for anterior and posterior sites, however target amplitude was relatively increased over posterior electrodes. A non-significant trend for smaller P3 amplitudes overall in the dyslexic group was observed, $p = .06$. No significant group interactions were observed (all $p > .1$)

Summary:

Based on these results, the conclusions in the main paper remain: The main group differences were for nontarget attentional processing indexed by the P3a, while target detection was relatively unimpaired. The attenuated P3 response to PSHT stimuli was observable over centroparietal sites but was not significantly reduced compared to the control group response. We did, however, replicate the fairly reliable observation of smaller P3 amplitudes in dyslexic participants overall, which may be indicative of broad differences in attentional processing. Nonetheless, P3b amplitudes did not show group differences in experimental condition effects. Therefore, these data confirm that the important group differences in ERP modulations in Study 4 are centred on the attentional processes underlying the reported frontocentral modulations.

Appendix 7: Articles published from the present research

Study 1: Savill, N. J., & Thierry, G. (2011). Reading for sound with dyslexia: Evidence for early orthographic and late phonological integration deficits. *Brain Research, 1385*, 192-205.

Study 2: Savill, N., Lindell, A., Booth, A., West, G., & Thierry, G. (2011). Literate humans sound out words during silent reading. *NeuroReport, 22*, 116-120.

Study 3: Savill, N., & Thierry, G. (2011) Electrophysiological evidence for impaired attentional engagement with phonologically-acceptable misspellings in developmental dyslexia. *Frontiers in Psychology, 2*, 139.

The following pages are copies of the original articles

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BRAIN RESEARCH

Research Report

Reading for sound with dyslexia: Evidence for early orthographic and late phonological integration deficits

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ABSTRACT

Deteriorated phonological representations are widely assumed to be the underlying cause of reading difficulties in developmental dyslexia; however, existing evidence also implicates degraded orthographic processing. Here, we used event-related potentials whilst dyslexic and control adults performed a pseudoword-word priming task requiring deep phonological analysis to examine phonological and orthographic priming, respectively. Pseudowords were manipulated to be homophonic or non-homophonic to a target word and more or less orthographically similar. Since previous ERP research with normal readers has established phonologically driven differences as early as 250 ms from word presentation, degraded phonological representations were expected to reveal reduced phonological priming in dyslexic readers from 250 ms after target word onset. However, phonological priming main effects in both the N2 and P3 ranges were indistinguishable in amplitude between groups. Critically, we found group differences in the N1 range, such that orthographic modulations observed in controls were absent in the dyslexic group. Furthermore, early group differences in phonological priming transpired as interactions with orthographic priming (in P2, N2 and P3 ranges). A group difference in phonological priming did not emerge until the P600 range, in which the dyslexic group showed significantly attenuated priming. As the P600 is classically associated with online monitoring and reanalysis, this pattern of results suggest that during deliberate phonological processing, the phonological deficit in reading may relate more to inefficient monitoring rather than deficient detection. Meanwhile, early differences in perceptual processing of phonological information may be driven by the strength of engagement with orthographic information.

1. Introduction

Developmental dyslexia is a disorder found in both children and adults characterised by literacy abilities below those expected given their general abilities and adequate motivation. The primary cause of difficulty in developmental dyslexia (henceforth dyslexia) is disputed (see Ramus, 2003), and probably multi-factorial (Menghini et al., 2010; Pennington, 2006); however, a dysfunction of phonological processing is widely thought to be at the core of the deficit (Lyon et al., 2003; Snowling, 2000). A persistent hypothesis is that dyslexic individuals have weak and/or coarsely coded phonological representations (Adlard and Hazan, 1998; Boada and Pennington, 2006; Brady, 1997; Elbro, 1996; Goswami, 2000; Hulme and Snowling, 1992; Metsala, 1997; Morais, 2003; Snowling, 2000; Swan and Goswami, 1997). These are suggested to impact reading by interfering with

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automatic grapheme–phonemic conversion required for skilled reading (Morais, 2003; Morais and Kolinsky, 1994).

However, a convergence of recent research has also indicated that orthographic processing may be compromised in dyslexia and contribute to difficulties with reading (e.g., Bosse et al., 2007; Maurer et al., 2007; Vidyasagar and Pammer, 2010). Vidyasagar and Pammer (2010), for example, suggest that defects in the dorsal stream of the visual system may be the core deficit in dyslexia. This hypothesis is built on numerous studies showing dyslexic group performance to be weaker for behavioural indices of visual magnocellular function (see Laycock and Crewther, 2008; Schulte-Körne and Bruder, 2010, for recent reviews). In their perspective, focal visuo-spatial attention weaknesses affect scanning of orthographic strings resulting in poor orthographic inputs, which in turn affect grapheme–phoneme mapping. A similar perspective (Hari and Renvall, 2001; Facoetti, et al., 2006, 2008), derived primarily from observations of a prolonged attentional blink and slower spatial cued-detection in dyslexia, hypothesises that sluggish automatic engaging and disengaging of attention impairs the visual selection of graphemes, and subsequent decoding. In support of the association between attentional shifting and decoding ability, orienting performance has been found to significantly correlate with nonword reading (Facoetti et al., 2006, 2008, 2009).

Further implications of reduced orthographic sensitivity in dyslexia come from Valdois and colleagues (e.g., Bosse et al., 2007; Valdois et al., 2004; Dubois et al., 2007), who separately describe a visual attentional span (VAS) deficit. VAS refers to the number of items in a visual string that can be processed simultaneously and has been shown to be smaller in subsets of dyslexic participants and to impact reading independently from phonological problems. It is suggested that a reduced visuo-attentional window would impair whole word processing and thus particularly affect irregular word reading (Bosse and Valdois, 2009).

These hypotheses have differing implications for the point (s) at which dyslexic readers' visual word recognition ought to be affected. Recording event-related potentials (ERP) can offer insight here. ERP investigations have had a positive contribution on our understanding of the time course and stages of normal visual word recognition: from initial processing of visual input, through orthographic analysis, phonological mapping and subsequent working memory integration (see Dien, 2009; Grainger and Holcomb, 2009). As such, ERPs present an ideal tool to enable description of the temporal course of the deficit(s) in dyslexia and clarify the case for early degraded orthographic inputs and/or phonological representations, or difficulties relating to later integrative processing.

With respect to phonological manipulations, ERP studies using visual word stimuli tend to report differences between dyslexic and control readers in the N400 range; most of which demonstrate weaker amplitude modulations to rhyme match-mismatch (Ackerman et al., 1994; McPherson et al., 1998; Rüsseler et al., 2007). However, modulations of the N400 wave are rather late to index impaired sensitivity to phonology, and are more likely to relate to the deep processing and decision-making related to integration of the phonological stimuli, rather than a marker of sublexical processes (e.g., Bentin et al., 1999; Brown and Hagoort, 1993; Chwilla et al., 1995; Connolly and Phillips, 1994). ERP studies with normal readers have shown that phonological manipulations can reliably modulate the ERP wave from 250 ms after stimulus onset in a range of tasks (masked priming: Ashby and Martin, 2008; Holcomb and Grainger, 2006; Grainger et al., 2006; rhyme and lexical decision: Bentin et al., 1999; rhyming decision: Kramer and Donchin, 1987; sentence reading: Savill et al., 2011; phoneme decision: Proverbio et al., 2004). Furthermore, amplification of the N2 peak elicited by phonological mismatch is well established: An effect referred to as the phonological mismatch/mapping negativity (PMN), typically observed when the expected final word of a sentence is replaced with a phonologically dissimilar, unexpected stimulus, has been shown with auditory stimuli (e.g., Connolly and Phillips, 1994; D'Arcy et al., 2004; Diaz and Swaab, 2007; Newman and Connolly, 2009; Newman et al., 2003), and similar effects have been shown in visual contexts (Connolly et al., 1995; Newman and Connolly, 2004; Savill et al., 2011). The lack of studies reporting differences in phonological effects between dyslexic and normal readers in this earlier time range, within the context of reported findings within the later N400 range, seems to favour integration/working memory accounts of phonological dysfunction in a reading context, rather than degraded phonological sensitivity.

The ERP literature on visual word processing in developmental dyslexia has, however, shown early discriminatory ERP profiles between dyslexic and normal readers. These differences have been found during stages related to processing visual/orthographic input (see Coch and Mitra, 2010; Dien, 2009; Grainger and Holcomb, 2009; Hauk et al., 2006; Kast et al., 2010; Parviainen et al., 2006) prior to phonological analysis, within 150 ms of stimulus onset (Maurer et al., 2007; Helenius et al., 1999; Taroyan and Nicolson, 2009; Wimmer et al., 2002). These early group differences, found in naming, one-back and lexical decision tasks, have been shown to be letter-string specific (Helenius et al., 1999; Maurer et al., 2007), and have been observed at the word form level, e.g., absent left-lateralised P1 amplitude differences between words and pseudowords observed in dyslexic readers (Taroyan and Nicolson, 2009). Such findings of reduced orthographic activation are comparable with the varied literature implicating visual/visuo-attentional factors underlying dyslexic word processing difficulties, which share the implication of a weaker orthographic percept (Bosse et al., 2007; Facoetti et al., 2008; Hawelka et al., 2006; Hawelka and Wimmer, 2005; Jones et al., 2008; Pammer and Vidyasagar, 2005; Salmelin et al., 1996; Vidyasagar, 2004; Vidyasagar and Pammer, 2010). Given the suggestion that early reduced attention or sensitivity to orthographic and/or whole word perceptual differences may interfere with later phonemic mapping (e.g., Cestnick and Coltheart, 1999; Facoetti et al., 2006, 2008; Vidyasagar and Pammer, 2010), and provide the basis of reading difficulties observed in dyslexia, it would be instructive to consider the relative contribution of orthographic and phonologic effects in phonological analysis during reading in dyslexia.

Our study was designed to disentangle sensitivity to phonological and orthographic information in dyslexic and normal readers using ERPs. The cognitive chronometry afforded by ERPs allowed us to distinguish detection and decoding from attentional and working memory processes. We used a 2×2 design, similar to that of Grainger et al. (2006), except we did not use masked priming. We created pseudoword-word pairs controlled for phonological and orthographic similarity in order to produce four experimental conditions, e.g., in the case of the word *horse* as target, primes could be *horce* (P+O+), *hauce* (P+O–), *horle* (P–O+) and *hiele* (P–O–, where 'P' denotes homophony and 'O' denotes orthographic neighbourhood with the paired word). To examine dyslexic readers' sensitivity to phonological manipulations, participants were asked to decide whether the presented pseudoword prime and the following target word sounded the same. This design allowed examination of the participants' overt phonological processing abilities in time, and potential interactions with orthographic processing.

We hypothesised that if poor phonological task performance is due to weak phonological sensitivity in dyslexia, dyslexic participants ought to show reduced phonological priming from the earliest point at which the ERP indexes phonological effects. More specifically, we would expect a relatively larger N2 to P+ stimuli (that is, less N2 attenuation for weaker phonological expectations) and smaller differences between P+ and P– amplitudes than in controls. In contrast, if phonological sensitivity in reading is intact, phonological priming effects at stages of stimulus processing and discrimination (i.e., in the P2/N2 and P3 ranges) should be of similar magnitude to those found in control readers. In this situation, it is possible that processes of integration or reanalysis may instead be the source of error in phonological tasks, in which case ERPs should differ in a later time-window, i.e., that of the N400 or beyond.

Regarding orthographic effects, we reasoned that if sensitivity to orthographic information at the whole string level is decreased in dyslexia, we should observe reduced modulation by orthographic similarity from the N1 onwards in the dyslexic group. Crucially, we were interested to see the extent to which orthographic and phonological effects would interact. If, for example, orthographic sensitivity had a greater impact on phonological analysis in dyslexic than control readers, we would expect significant interactions of group with orthographic and phonological priming from the P2/N2 range onwards.

2. Results

2.1. *Behavioural results*

Correct response reaction times were significantly faster to homophonic than non-homophonic pairs, F(1, 30)=50.86, $p<.001$. Orthographic neighbouring stimuli also resulted in faster reaction times, F(1, 30)=5.51, $p<.05$, but reduced accuracy, F(1, 30)=6.94, $p<.05$. Furthermore, phonological and orthographic similarity significantly interacted for both accuracy, F(1, 30)=111.52, $p<.001$, and reaction time, F(1, 30)=96.05, $p<.001$. This was due to decreased accuracy and increased reaction times for 'mixed' primes (i.e., P+O– and P–O+ stimuli) as compared to non-mixed ones. A trend for an interaction between group, phonological priming and orthographic priming interaction for accuracy, $p=.09$, related to the dyslexic group showing a greater relative deficit in accuracy to the mixed cues, compared to controls (see Fig. 1). A significant main effect of group on reaction times indicated that responses were generally slower from the dyslexic group, F(1, 30)=4.76, $p<.05$.

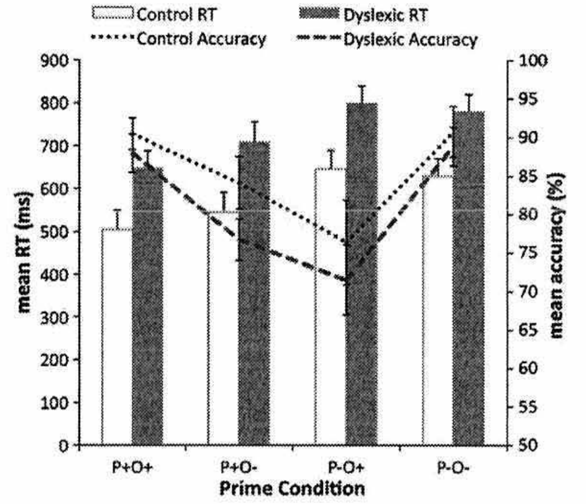

Fig. 1 – Mean reaction time and accuracy (error bars represent 1 standard error).

2.2. *Event-related potential results*

2.2.1. P1

No significant effects were observed in the P1 range.

2.2.2. N1

There was a significant interaction between orthographic similarity and group on N1 mean amplitudes, F(1, 30)=5.18, $p<.05$, driven by significant amplification of N1 to orthographically neighbouring (O+) stimuli in the control group only (Fig. 2). N1 peak latencies were significantly delayed overall in the dyslexic group, F(1, 30)=5.99, $p<.05$ (peak latency: control group M=159 ms; dyslexic group M=166 ms).[1] A non-significant trend for orthographic neighbour modulation of N1 latency was also observed, with O- primed words tending to elicit an earlier N1 peak ($p=.07$).

2.2.3. P2

No main effects were observed with respect to P2 mean amplitudes. However an interaction of phonological similarity, orthographic similarity and group significantly affected P2 amplitude, F(1, 30)=5.58, $p<.05$. This interaction was driven the dyslexic group showing a significantly amplified response to P–O– primed words compared to P–O+.

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[1] To investigate possible effects of having different peak latencies in the groups (which was the case for N1), we ran a second analysis with slightly different intervals for each of the two groups. This analysis yielded the same qualitative result as the analysis using common intervals and is not reported here.

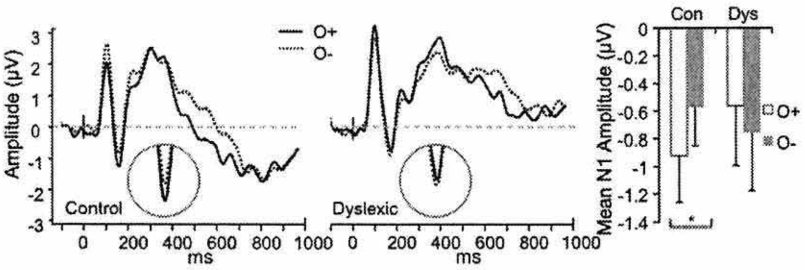

Fig. 2 – Orthographic priming modulations of target N1 amplitude (linear derivation of O1, O2, P7 and P8 electrodes).

A main effect of phonological similarity indicated that homophonic stimulus pairs significantly delayed P2 latencies, $F(1, 30)=3.41$, $p<.05$. Phonological similarity also interacted with group, $F(1, 30)=4.32$, $p<.05$, which related to only the control group showing a later peak for P+ stimuli.

2.2.4. N2

A main effect of phonological similarity showed that non-homophonic words significantly amplified the N2 peak relative to homophonic words, $F(1, 30)=36.20$, $p<.001$. No interaction of group with phonological similarity was observed. However, mean amplitudes were modulated by a three-way interaction of group, phonological similarity and orthographic similarity, $F(1, 30)=8.45$, $p<.01$. The source of this interaction related to the relative attenuation of P–O+ and P–O– primed words: whilst homophonic words (P+O+ and P+O– primed) elicited a significantly attenuated response relative to non-homophonic words (P–O+ and P–O– primed), P–O+ words were also significantly attenuated relative to P–O– in the control group; the dyslexic group, on the other hand, showed similar amplification of N2 to non-homophonic words (P–O+ and P–O– primed); however, they only significantly differed from P+O+ primed words, and not P+O– (see Fig. 3).

N2 peak latencies were significantly shorter to homophonic words, $F(1, 30)=12.80$, $p<.001$, and to orthographically neighbouring words, $F(1, 30)=15.47$, $p<.001$. Furthermore, a trend for an interaction between group, phonological similarity and orthographic similarity, $p=.09$, indicated that peak latencies were significantly longer to P–O– primed words compared to all other priming conditions in the dyslexic group, whilst in the control group P–O– and P+O– peak latencies were not significantly different.

2.2.5. P3

Phonological similarity, $F(1, 30)=38.01$, $p<.001$, and orthographic similarity, $F(1, 30)=4.26$, $p<.05$, significantly amplified P3 target word peaks. A three-way interaction of group, phonological similarity and orthographic similarity, $F(1, 30)=8.17$, $p<.01$, was due to differences in group responses to P–O+ primed words: Whilst P+O+ and P+O– were significantly amplified relative to P–O+ and P–O– priming conditions in both groups, the P–O+ primed targets were significantly amplified compared to P–O– in controls only (see Figs. 4 and 5). P3 peak latencies were significantly affected by both phonological similarity, $F(1, 30)=8.94$, $p<.01$, for which P+ primed stimuli elicited later peaks, and by an interactive effect of phonological and orthographic similarity, $F(1, 30)=4.79$, $p<.05$, which related to a significantly shorter P3 peak latency for P–O– primed stimuli compared to the homophonic stimuli (P+O+ and P+O–) (Fig. 5).

2.2.6. *P600*

Non-homophonic, $F(1, 30)=15.00$, $p<.001$ and orthographic non-neighbour stimulus pairs, $F(1, 30)=14.38$, $p<.001$, elicited significantly larger P600 amplitudes than homophonic and orthographically neighbouring pairs, respectively. Participant group was found to significantly interact with both phonological similarity, $F(1, 30)=6.05$, $p<.05$, which showed that phonological priming modulations of P600 amplitude were significant for the control group only, and with orthographic similarity, $F(1, 30)=4.73$, $p<.05$, for which significant priming effects were also only in the control group. A further three-way interaction of group, phonological and orthographic similarity, $F(1, 30)=4.65$, $p<.05$, indicated that the significant differences in P600 amplitude present in the controls (P+O+ significantly attenuated compared to all, and significant differences between P+O– and the P-stimuli) were absent in the dyslexic group, for whom only amplitude differences between the P–O+ and P–O– stimuli reached significance. P600 latencies were only modulated by a main effect of phonological similarity, $F(1, 30)=11.64$, $p<.05$ (see Figs. 4 and 5). Difference waves showing priming main effects across each reported ERP epoch are provided in Fig. 6.

3. Discussion

This study aimed at dissociating phonological and orthographic priming effects during a phonological awareness task performed on letter strings by dyslexic participants and matched controls. Our main findings were (a) main effects of phonological and orthographic priming on reaction times in both the groups; (b) N1 increase by orthographic priming in the control group only; (c) a main effect of phonological priming in the N2 and P3 range in both the participant groups; (d) a set of three-way interactions with group spanning the P2, N2 and P3 peaks; and (e) a reduced P600 modulation by phonological priming in the dyslexic group only. These will be discussed in turn.

3.1. *Behavioural insights*

The dyslexic group, as expected, performed the task significantly slower overall. Beyond this, no significant group

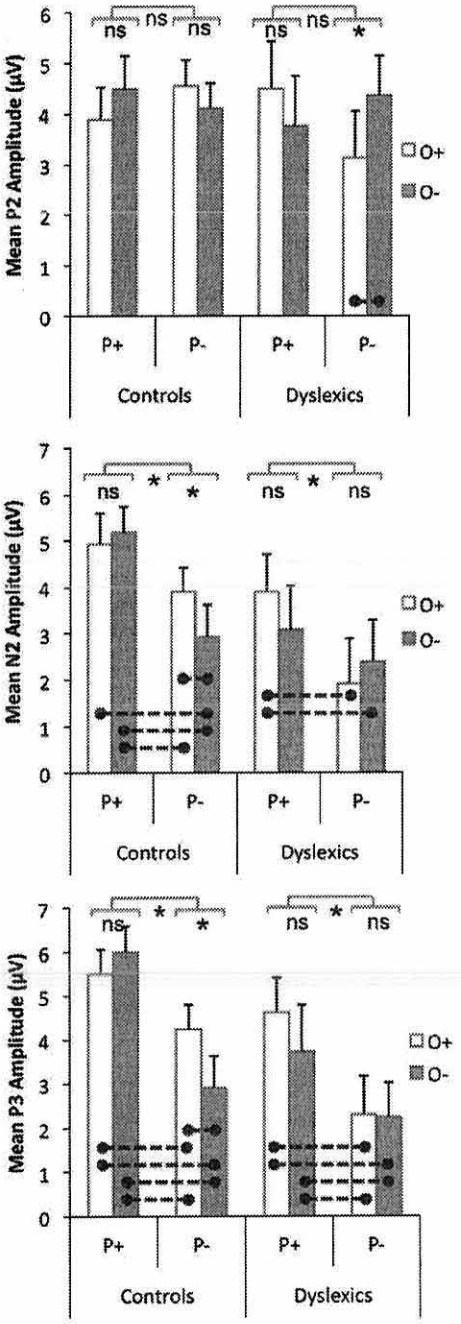

Fig. 3 – The three-way interactions spanning the P2, N2 and P3 peaks. * = Condition effect is $p < .05$. Dotted lines depict significant pair-wise comparisons.

interactions emerged in behavioural data. However, priming significantly improved performance overall and showed the expected interaction between phonological and orthographic priming such that orthographic neighbourhood facilitated recognition of phonologically primed stimuli and degraded recognition of non-matched stimuli, and vice versa for less orthographically informative cues across group. Importantly, a trend for a three-way interaction with group indicated that the significantly deleterious effect of mixed priming on accuracy was larger in the dyslexic group. In the context of a priming manipulation in which differences between all conditions were subtle and the task was designed to avoid high error, it is perhaps not surprising that reaction time or accuracy measures in isolation did not distinguish between the groups.

3.2. *The use of orthographic cues: Reviewing early ERP group differences*

The earliest condition modulation of the ERP was found for the N1 peak, where targets primed by orthographic neighbours elicited significantly amplified peaks in the control group only. This is consistent with previously reported effects in the N1 range in controls (Hauk et al., 2009) and other orthographic variables have been shown to modulate the N1, such as written length (Assadollahi and Pulvermuller, 2003; Hauk et al., 2009), frequency (Assadollahi and Pulvermuller, 2003; Hauk and Pulvermüller, 2004; Hauk et al., 2009; Sereno et al., 1998, 2003) and lexical status, e.g., words versus consonant strings (Coch and Mitra, 2010; Compton et al., 1991; Hauk et al., 2006; Maurer et al., 2005; McCandliss et al., 1997; Sauseng et al., 2004). The absence of an N1 orthographic priming effect in our dyslexic group, along with a significantly latency delay, indicates that orthographic cues were processed less efficiently/slower in dyslexic participants. This would be consistent with previous reports of attenuated P1 or N1 to orthographic stimuli (Helenius et al., 1999; Kast et al., 2010; Maurer et al., 2007) and reduced activation in left occipitotemporal areas involved in orthographic identification and integration, as shown by functional brain imaging studies (Blau et al., 2010; Brunswick et al., 1999; Cao et al., 2006; Kronbichler et al., 2006; Liu et al., 2010; McCrory et al., 2005; Richlan et al., 2010; Salmelin et al., 1996; Van der Mark et al., 2009, 2010; Wimmer et al., 2010).

With respect to existing literature, perceptual difficulties at the word form level have been proposed to impact reading in different ways: Valdois and colleagues (e.g., Bosse et al., 2007; Lassus-Sangosse et al., 2008; Peyrin et al., 2010; Valdois et al., 2004), for instance, have suggested that subsets of dyslexic readers have a smaller attentional window impacting the scanning of letter strings, which may affect subsequent grapheme perception and integration, and contribute to downstream phonological decoding difficulties. Poor left-to-right scanning has also been suggested as the route to impaired reading in dyslexia due to deficient processing along the dorsal visual pathway, which is suggested to degrade orthographic input and impact awareness of grapheme–phoneme correspondence (Cestnick and Coltheart, 1999; Vidyasagar and Pammer, 2010). Whilst our study was primarily aimed at addressing the interaction of orthographic and phonological information, rather than orthographic/visual word form perception per se, our data indicates that orthographic information is not accessed as readily in compensated dyslexic adults as it is in normal readers.

Further, we found significant three-way interactions of group with phonological and orthographic similarity in the P2, N2 and P3 ranges: (a) A three-way modulation affecting P2 amplitude showed a significantly amplified response in the P–O– relative to P–O+ condition in the dyslexic group only; (b) differences in the N2 range showed the following ordering of conditions in the control group: P+O– weaker than P–O+ and P–

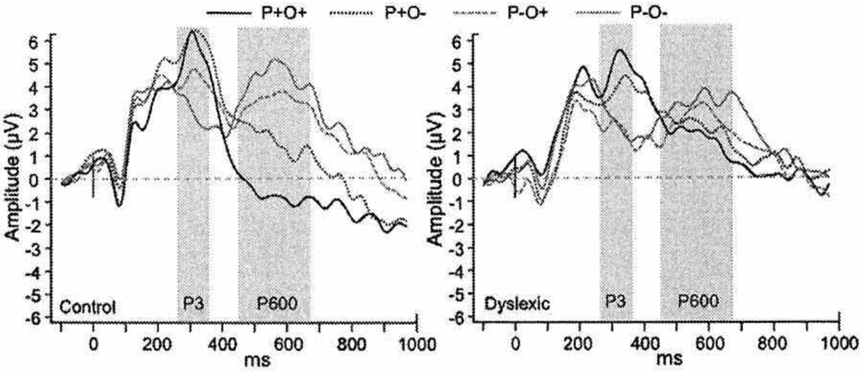

Fig. 4 – P3 and P600 target word modulations for each prime condition (linear derivation of C3, C4, Cz, CP3, CP4 and CPz electrodes).

O– and P–O+ weaker P–O–; and (c) an interaction in the P3 range induced by responses in P–O+ condition being greater than in the P–O– condition in the control group only.

Overall, three-way interactions between group, phonological, and orthographic priming may have been expected if we assume that dyslexic readers have degraded phonological representations. However, we observed significant main effects of phonological priming in the absence of a group interaction in ERP amplitudes from the N2 range through to the P3 range. We interpret this as a sign that early phonological access in our dyslexic participants may not have been functionally deficient. It must be kept in mind that this is not a null effect since phonological priming was significant in both of our groups.

By contrast, the three-way interactions listed above seem to have arisen primarily from weaker and/or possibly qualitatively different effects of orthographic similarity in the dyslexic group. Starting with the P2, which was the earliest peak where effects of mismatch between orthographic and phonological representations might have been expected (Bles et al., 2007; Braun et al., 2009; Hsu et al., 2009; Potts, 2004), the dyslexic group showed an amplified response in the P–O– condition, perhaps because this is the point at which orthographic processing kicked in for the dyslexic participants, whereas in the case of the control group, orthographic similarity of the target word may have been resolved as early as the N1 window (cf. N1 effect which was both delayed and reduced in dyslexic participants). In other words, in the case of dyslexic participants, orientation to orthographic dissimilarity of the stimuli in a pair would have helped phonological discrimination but not helped the detection of homophony (i.e., no differences between P+O+ and P+O–).

The following N2 interaction may relate to reduced orthographic cueing in the dyslexic group (since P–O+ elicited weaker N2 amplitude than P–O– in the controls) and perhaps a slight phonological processing weakness since P+O– was not significantly different from the P– conditions.

The third interaction, in the P3 range, continued to show reduced orthographic similarity effects in the dyslexic group: The interaction was due to the lack of difference between P–O+ and P–O– stimulus pairs in the dyslexic group as was the case in the N2 range. In other words, orthographic similarity may have failed to capture dyslexic participants' attention, perhaps because their focusing on phonological form may have limited distraction by orthographic information.

Together, these results show that stimuli were essentially distinguished on the basis of their phonological status. Moreover, dyslexic participants were less influenced by orthographic similarity than controls over and above phonological priming, with orthographic priming differences evident from the N1 to the P3 through the N2 range. A possible explanation is that the dyslexic group may have had weaker orthographic input at the whole-stimulus level (e.g., see literature on visuo-attention span, Valdois et al., 2004; and dorsal visual pathway hypotheses, Vidyasagar and Pammer, 2010) or managed to focus more exclusively on phonological similarity. Future studies in which phonological judgments are explicitly emphasized by the task ought to clarify whether group differences in orthographic processing are driven by reduced access of orthographic information in dyslexic readers or emerge from relative streamlining of attention to the phonological level when participants are required to focus on phonology.

3.3. *P600: Late differences in phonological processing*

The dyslexic group showed a significantly reduced main effect of phonological similarity within the P600 range. P600 mean amplitude was significantly attenuated in the dyslexic group for both phonological and orthographic as compared to the control group. Across groups, the strongest increase in P600 amplitude was found for the least related stimuli (P–O–), with progressively reduced amplitudes for 'P–O+' and 'P+O–', and 'P+O+' stimuli. Typically, the P600 component is triggered by linguistic incongruence that is not based on semantic integration (Kolk and Chwilla, 2007) and has been proposed to index a process of reanalysis (Van de Meerendonk et al., 2010; Vissers et al., 2008a,b). The reduced P600 differentiation between conditions suggests that stimulus relatedness may have been less salient and/or subject to limited reanalysis at this late reprocessing stage in the dyslexic group. Whatever difficulty or difference is driving the attenuation elicited by the dyslexic group in this task, it is unlikely to relate to sensitivity to phonological manipulations within the orthographically

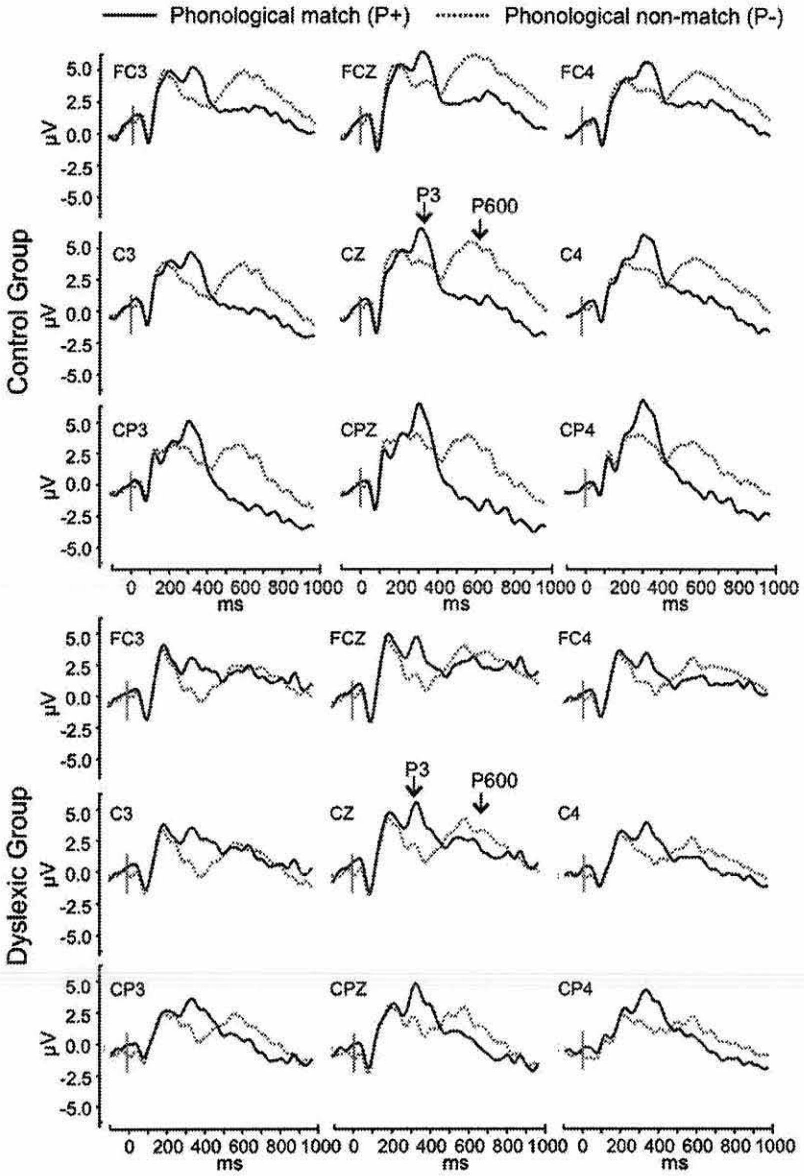

Fig. 5 – **Averaged phonological priming effects across central electrodes, depicting the diffuse P600 attenuation in the dyslexic group (P+ is P+O+ and P+O– combined, and P– is P–O+ and P–O–).**

controlled stimuli, since no marked differences were found in the N2 and P3 ranges.

3.4. *Is a reprocessing dysfunction exacerbating performance deficits in overtly phonological tasks in dyslexia?*

The significant P600 attenuation possibly indexes a deficient strategic response during an overt verbal task. Recent accounts of the phonological deficit in dyslexia have focussed on working memory demand rather than perceptual deficits relating to weak phonological representations (Banai and Ahissar, 2006; Ramus and Szenkovits, 2008). For instance, a series of experiments by Ramus and colleagues targeting predictive effects of weak or fuzzy phonological representations using speech-based auditory tasks repeatedly failed to find significant differences between dyslexic and control listeners (see Ramus and Szenkovits, 2008). In the same vein, Banai and Ahissar (2006) showed that dyslexic participants only manifest phonological deficits while performing complex ordinal or parametric judgments of auditory phonological stimuli, but were not hindered in judgements of the same stimuli when they required simple (i.e., same-different) discriminations. Together the latter two studies suggest that task demand, e.g., the level of short-term memory involvement and time constraints, determines access to phonological representations and subsequent observed behavioural deficits in phonological tasks. Our task required maintenance of the phonological form of consecutively presented pairs of stimuli,

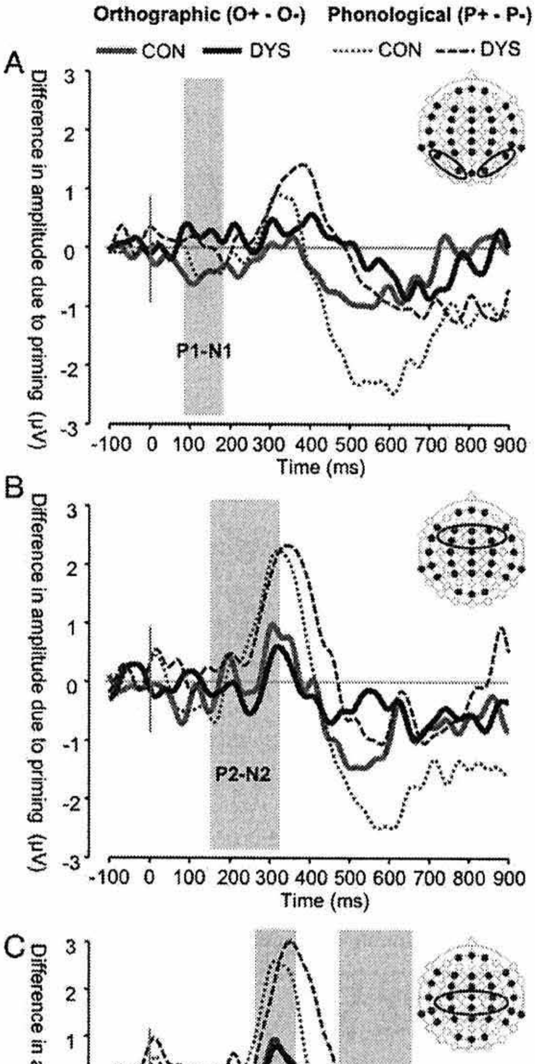

Fig. 6 – Orthographic and phonological priming difference waves at analysed electrode sites. (A) Linear derivation (LDR) of O1, O2, P7 and P8. (B) LDR of F3, F4, Fz, FC3, FC4 and FCz. (C) LDR of C3, C4, Cz, CP3, CP4 and CPz. CON = control. DYS = dyslexic.

which arguably placed similar processing demands on the participants. Thus it may be that our observed P600 effects are the result of depleted working memory resources precluding phonological integration and reappraisal. Studies that have previously reported differences in P600 amplitude in dyslexic populations have attributed similar late ERP differences to conscious and strategic rather than automatic linguistic processes. Rispens (2004) and Rispens et al. (2006), for instance, demonstrated that Dutch dyslexic participants showed no significant P600 modulation to auditorily presented sentences containing plural noun phrase structure violations. As an earlier measure of automatic syntactic parsing – an early left anterior negativity (ELAN), found approximately 200 ms after violation – was unaffected, the authors suggested that their P600 differences indicated dyslexic deficits in more controlled and strategic linguistic processes involved in syntactic revision (Rispens, 2004), which may reflect some form of reprocessing failure. Within the visual word domain, studies considering the electrophysiological basis of word learning in dyslexia (Schulte-Körne et al., 2004) and recognition memory for visually presented words (Rüsseler et al., 2003) have also shown intact early word recognition and discriminative ERP effects, with only diminished responses at the stage of conscious recollection/retrieval in the P600 range. Schulte-Körne et al. (2004), for example, studied dyslexic and control children's recognition of previously learned four-letter pseudowords and complex graphic symbols using ERPs. In the context of accurate behavioural performance and normal P300 effects, they found that the recognition ERP correlate – the P600 – was significantly attenuated specifically for the pseudowords, compared to graphic symbols and control group responses. Whilst the authors related their finding to an impairment in visual recognition due to the limited phonological demand of the pseudowords; their results could also be interpretable as a strategic processing and/or working memory failure elicited by stimuli requiring phonological analysis in the dyslexic participants, despite intact recognition.

Some form of reduced maintenance and integration of phonological information could also account for findings of existing ERP studies using phonological tasks with visual word stimuli, which typically report reduced N400 modulations from dyslexic readers (Ackerman et al., 1994; McPherson et al., 1998; Rüsseler et al., 2007). This would fit with associations of the N400 with working memory (e.g., Gunter, et al., 2003) and decision-making processes related to stimulus integration (Brown and Hagoort, 1993; Connolly and Phillips, 1994; Chwilla et al., 1995; Holcomb, 1993). Our task did not elicit an N400 response, but instead a P600. This may be due to the differences in task demand between word rhyming judgment, in which such N400 phonological differences have typically been observed, and in this study, a homophone judgment. Kolk and colleagues (Kolk et al., 2003; Kolk and Chwilla, 2007; Van de Meerendonk et al., 2010) suggest that the N400 wave indexes lexical integration of an unexpected linguistic event (e.g., to a rhyme mismatch) but that if the unexpected event is perceptually uncertain (e.g., with complex sentences or, perhaps, brief presentations of unfamiliar pseudowords, as in the case of our homophone judgment task) integration indexed by the N400 will not occur and a veridicality check indexed by the P600 will occur instead. Thus the specificity of our P600 effect needs to be clarified: It is unlikely to be a downstream net result of weaker phonological priming in the dyslexic group, both because (a) earlier modulations indicated similar magnitudes of phonological priming between groups and (b) the likely outcome of a weaker phonological percept would be uncertainty and thus larger, rather than significantly smaller, P600 amplitudes. If we nonetheless adopted this interpretation our data would indicate that the dyslexic group responded more confidently than the control group, which is highly unlikely. Thus the hypothesis of a performance monitoring/reanalysis deficit is more likely. The question of whether this deficient monitoring is specific to phonological task performance or indicative of a more general trend cannot be determined from this study and will require further investigation.

Converging evidence for a phonological monitoring failure comes from recent ERP studies examining dyslexic error-related negativities – a negative fluctuation typically found 100 ms post an erroneous response (Horowitz-Kraus and Breznitz, 2008, 2009). Horowitz-Kraus and Breznitz (2008) reported reduced differentiation between error-related negativities and correct-related negativities from dyslexic readers compared to controls during performance of a lexical decision task, which they suggested could relate to inefficient error monitoring. The P600 effects observed here may be a pre- (or peri-) response correlate of this inefficient monitoring. Unfortunately, it was not possible to run analyses of error-related responses because of the very low rate of errors. However, future studies could address if reduced differentiation of error/correct-related negativities post-response may relate to prior atypical performance monitoring, and furthermore whether these monitoring deficits are specific to performing a phonological task.

3.5. *The role of attention in manifestations of the phonological deficit?*

An important consideration with our task is that attention was explicitly focused on the phonological relationship between stimuli in a pair. The only ERP difference between groups in phonological priming effects (irrespective of orthographic cues) were observed in response monitoring. It may be that we would have observed early differences in phonological priming effects if attention had not been oriented to phonology and/nor engaged in a phonological task. If this were the case, the pervasive phonological deficit would probably not be due to a significantly reduced ability to perceive phonological manipulations, but rather a relative failure in attentional capture. This would fit with the auditory ERP literature typically showing reduced phonological modulations in oddball tasks in which the oddball is task-irrelevant (Fosker and Thierry, 2004; see Bishop, 2007, for a review of MMN studies) versus normal P3 phonological modulations when participants are asked to attend to the oddball (Fosker and Thierry, 2005; Rüsseler et al., 2002). Deficits switched by attention to phonological information may explain much of the conflicting data regarding phonological processing difficulties in developmental dyslexia: Reduced voluntary orientation to phonological information, possibly exacerbated in the case of reading by reduced orthographic sensitivity and subsequently disrupted graphemic-phonemic mapping on the one hand, and limited processing capacity for deliberate phonological analysis on the other.

4. Conclusions

This study provides electrophysiological evidence for early sensitivity to subtle phonological manipulations of visual pseudoword stimuli, but reduced sensitivity to whole form orthographic information during phonological analysis in dyslexic readers. A failure in stimulus integration and reprocessing, indexed by a significantly less discriminative P600, may account for the weaker performance of dyslexic participant in homophonic judgement. The phonological deficit, in pseudoword reading at least, might thus be better conceived in line with Ramus and Szenkovits' (2008) conclusion regarding the recruitment of controlled, metacognitive processes in phonological analysis. Further research should determine the specificity of reduced orthographic effects in dyslexia and clarify the role of phonology in deliberate and implicit word recognition. Tasks which selectively manipulate the focus on phonological and orthographic information and the degree of attentional demand required should help to clarify the relative perceptual and executive aspects of reading deficits in dyslexia.

5. Experimental procedures

4.1. *Participants*

Sixteen high-functioning developmental dyslexic adults (mean age 21.63 years; 8 males) and 16 control adults (mean age 21.19 years, 9 males) participated in our experiment that had been approved by Bangor University's Ethics Committee. Data from four control participants had previously been discarded due to technical failure or insufficient number of trials. All participants were undergraduate or postgraduate students at Bangor University and were right-handed, native speakers of English with normal or corrected-to-normal vision, and no self-reported neurological impairment or comorbid difficulties. Dyslexic volunteers were recruited from Bangor University's Dyslexia Unit and through advertisement on the University's Participant Panel; all had a diagnosis of dyslexia from an educational psychologist. The rationale for testing high-functioning dyslexic adults is that observable deficits that persist into adulthood, even in the context of a normal reading level, can help to identify core deficits common to developmental dyslexia across abilities (see for e.g., Bruck, 1992; Gallagher et al., 1996; Ingvar et al., 2002; Jones et al., 2009; McCrory et al., 2005; Miller-Shaul, 2005; Paulesu et al., 1996; Szenkovits and Ramus, 2005; Wilson and Lesaux, 2001). Furthermore, the advantages of testing university students is that (a) they form a fairly homogenous sample with similar levels of print exposure; (b) it minimizes the likelihood of potential comorbidity; and (c) individuals are more likely to actively engage with attentionally demanding psycholinguistic tasks (see also Szenkovits and Ramus, 2005, for a similar rationale). Performance on a battery of literacy related behavioural measures, taken from the DAST (Nicolson and Fawcett, 1998), WRAT-3 (Jastak and Wilkinson, 1993) WAIS-III (Wechsler, 1997) and WIAT (Wechsler, 2005) confirmed that the individuals in the dyslexic group, although of similar academic ability and showing a reading level within the normal range, were significantly poorer than the control group across measures, with the exception of the WIAT's untimed pseudoword reading task for which differences in accuracy fell just outside of significance. Corresponding results are shown in Table 1.

4.2. *Stimuli*

Word stimuli were 60 four- or five-letter long English words selected from the MRC Psycholinguistic database (Coltheart, 1981). Each word (e.g., "HORSE") was paired with four pseudowords, each belonging to one of four priming conditions: P+O+, in which the prime differed from the target word by only one letter and was a homophone of the target (e.g., "horce"; mean orthographic similarity score, 0.89); P+O–, in which the prime was homophonic to the target but had reduced orthographic overlap ("hauce"; mean orthographic score, 0.52); P–O+, in which the prime was a non-homophonic pseudoword created by changing the same letter as in the P+O+ condition ("horle"; mean orthographic score, 0.89); and P–O–, in which the prime was not a homophone of the target but had the same orthographic overlap as in the P+O– condition ("hiele"; mean orthographic score, 0.52). Orthographic similarity between each prime and target was measured using Normalized Edit Distance (NED; see Lambert et al., 1999), for which the minimum number of edits between stimuli (i.e., substitutions, deletions or additions) is divided by the longer string length (in this study prime and targets were the same length). The NED was subtracted from one to produce a similarity rather than dissimilarity score. For instance, "HORSE" and "hauce" are separable by a minimum edit of three: substitution of 'O', 'R' 'and 'S' with 'A', 'U' and 'C': 1 – (3÷5)=0.4. As we were interested in orthographic similarity between primes and targets, rather than effects of orthographic neighbourhood size of the stimuli, number of neighbours (NN) was controlled across conditions (Mean NN: P+O+ 3.60; P+O– 3.70; P–O+ 3.82; P –O– 3.43). Constrained bigram and trigram frequencies of each prime verified there were no significant differences in orthographic frequency across prime conditions.

Twenty-four further stimulus pairs were created as fillers to prevent a strategy of making a decision before presentation of the second stimulus based on recognition of whether the prime was a pseudohomophone and promote comparison of prime and target. Fillers consisted of six primes from each of the four conditions paired with mismatching word stimuli.

Table 1 – Group performance on psychometric subtests.

Measure	Controls ($n=16$)		Dyslexics ($n=16$)		t
	Mean	SD	Mean	SD	
Age (years)	21.19	4.40	21.63	4.72	−0.27
DAST One-minute Reading	110.25	9.25	92.06	14.92	4.14**
DAST Nonsense Passage	93.94	4.19	88.69	6.34	2.76*
DAST Rapid Naming (s)	24.56	5.67	32.13	9.47	−2.74*
WAIS Digit Span	12.25	2.67	9.81	3.92	2.06*
WIAT Pseudoword Reading	105.63	6.51	98.44	12.32	2.06[a]
WRAT Reading	114.19	4.31	104.63	9.38	3.71**
WRAT Spelling	104.44	8.05	93.63	16.78	2.32*

Note. WAIS, WIAT and WRAT scores are age-scaled. *$p<.05$; **$p<.01$; [a]$p=.051$

4.3. *Procedure*

Participants made phonological decisions to pseudoword-word pairs presented visually in sequence. They decided whether the target word sounded the same as the prime. In a given trial participants looked at a fixation cross displayed for 1000 ms, followed by a prime presented in lower case and displayed for 200 ms. The target was separated from the prime by a variable inter-stimulus interval (ISI) of 200, 260, 320, 380, 440 or 500 ms, during which the screen was blank. For a given target, the ISI was constant across conditions and frequency of ISIs was controlled across the experiment. The word target was subsequently presented in upper case for a further 200 ms, and was followed by an inter-trial fixed interval of 3000 ms (see Fig. 7). Participants responded by pressing one of two designated keyboard keys (yes/no response). For the duration of the task, participants were seated comfortably in a dimly lit, sound-attenuated room in front of a projector screen. All stimuli were presented at eye-level at the centre of the screen, with stimulus strings subtending a maximum visual angle of 3.7° to ensure that the word stimulus was close to foveal vision. Stimuli were presented in black Arial font, in the centre of a white background and were presented pseudorandomly across four trials blocks, such that there was the same number of trials from each condition in each block, with rest breaks in between. Trials were presented and behavioural performance was recorded by E-Prime (Psychology Software Tools, Inc., Pittsburgh, USA). The testing session lasted approximately 15 min.

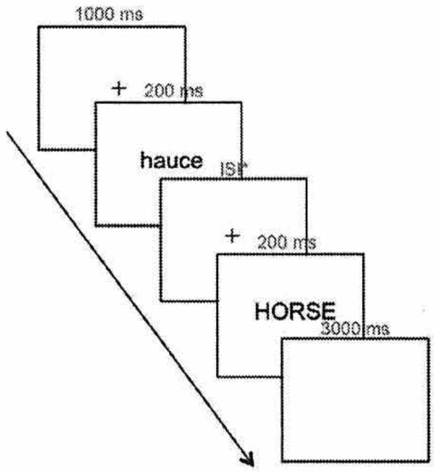

Fig. 7 – A single trial. Words were presented with each priming pseudoword condition, and critical trials were interspersed with non-priming fillers. *Variable ISI (controlled across prime conditions) of 200, 260, 320, 380, 440 or 500 ms.

4.4. *ERP processing*

The EEG was recorded with Synamps DC-amplifiers (NeuroScan, Sterling, VA, USA) from 36 Ag/AgCl electrodes, placed in an EasyCap (www.easycap.de) according to the 10–20 system. Bipolar recordings from electrodes set above and below the left eye recorded vertical eye movement. Electrode impedance was maintained below 5 kΩ. The online reference was the left mastoid and FPz served as the ground electrode. EEG activity was band-pass filtered on-line between 0.1 and 200 Hz and sampled at 1 kHz. The EEG was re-filtered off-line with a 30 Hz band-pass zero-phase shift low pass digital filter (48 dB/octave). Eye blinks were mathematically corrected using the algorithm provided by Scan 4.3 (Neuroscan, Inc.): A model eye-blink was computed from a minimum of 50 individual blinks, and, when the variance of the model at each recording channel was below 0.001 (which was the case in every participant), the amplitude of the model was subtracted from each channel proportionally to the overall size of the eye-blink at each recording site in the continuous EEG recording, which is more conservative than the method proposed by Gratton et al. (1983). Visual inspection of the EEG identified remaining artefacts to be manually rejected. The continuous EEG was sliced into epochs ranging from −100 to 1000 ms after the onset of the target word. Epochs with voltage exceeding ±75 μV were automatically rejected. Only corrected trials were included. There was a minimum of 30 valid epochs per condition in each participant (control group epochs: P+O+M=49.00, SD=7.88; P+O− M=44.19, SD=8.41; P−O+ M=42.63, SD=9.65; P−O− M=48.07, SD=9.55; dyslexic group epochs: P+O+ M=48.56, SD=6.79; P+O− M=42.31, SD=8.54; P−O+M=41.13, SD=8.75; P−O− M=47.44, SD=8.27). Baseline correction was performed in reference to pre-stimulus activity, and individual averages were digitally re-referenced to the average of the mastoid electrodes. Individual averages defined by the prime condition were computed and used to produce grand-mean averages for the dyslexic and control group. ERP data were collected simultaneously to behavioural data.

4.5. *ERP data analysis*

Main ERP components were identified based on their deflection, topography and latency. Time windows for analysis of each component were defined on the basis of the mean global field power produced by all electrodes taken together across the scalp. The same windows were used in all conditions and both groups: 85–115 ms for the P1; 150–180 ms for the N1; 150–220 ms for the P2; 250–320 for the N2; 260–360 ms for the P3; and 450–670 ms for the P600. Peak detection was time-locked to the electrode of maximal amplitude for each component: O2 for the P1; P8 for the N1; FCz for the P2 and N2, CPz for the P3 and P600. Similarly, mean amplitudes were measured at electrodes chosen based on their maximum sensitivity: O1, O2, P7 and P8 electrodes for the P1; O1, O2, P7 and P8 for the N1; F3, F4, Fz, FC3, FC4, FCz for the P2 and N2; C3, C4, Cz, CP3, CP4, CPz, for the P3 and P600. Mean amplitudes and peak latencies were subjected to 2 × 2 × 2 × electrode mixed analyses of variance (ANOVAs). Within-subject factors were phonological similarity (homophonic, non-homophonic) and orthographic similarity (orthographic neighbour, non-neighbour) and electrodes and a between subjects factor of group (control, dyslexic). Behavioural data were analysed with a three-way mixed ANOVA with within subjects factors of phonological similarity (homophonic, non-homophonic) and orthographic similarity (orthographic neighbour, non-neighbour), and a between subjects factor of group (control, dyslexic).

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Literate humans sound out words during silent reading

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Whether humans spontaneously sound out words in their mind during silent reading is a matter of debate. Some models of reading postulate that skilled readers access the meaning directly from print but others involve print-to-sound transcoding mechanisms. Here, we provide evidence that silent reading activates the sound form of words before accessing their meaning by comparing event-related potentials induced by highly expected words and their homophones. We found that expected words and words that sound the same but have a different orthography (homophones and pseudohomophones) reduce scalp activity to the same extent within 300 ms of presentation compared with unexpected words. This shows that phonological access during silent reading, which is critical for literacy acquisition, remains active in adulthood. *NeuroReport* 22:116–120 © 2011 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

Studies that have tested phonological effects during single word reading have shown brain activity modulations as early as 100 ms after stimulus onset [1–4], suggesting a fundamental role for phonology. However, whether phonological information is spontaneously retrieved when accessing semantic information while reading is open to debate [5–7]. To test whether the phonological form of written words is activated during silent reading, we measured the N2 and N400 peak amplitudes of event-related potentials (ERPs), which reflect the degree of phonological and semantic mismatch, respectively, between a word and the context in which it appears [8–11]. For example, in the spoken sentence 'an eagle is a bird of flare', the word 'flare' would elicit larger N2 and N400 compared with 'prey' as it is neither phonologically nor semantically expected in the sentence context [10]. As the N2 is sensitive to the phonological expectation about words, significant reduction in its amplitude for both an expected word and its homophone (HO) relative to an unexpected word in visually presented sentences would provide strong evidence that the sound form of words is retrieved during silent reading.

Most of the existing ERP studies investigating this question have not found convincing evidence for phonological involvement in accessing the meaning of written words. In the case of single word reading, one ERP study [11] testing phonological access in a semantic categorization task found no differences in the N400 between HOs of category exemplars (e.g. 'meet' for the category of food) compared with orthographic controls (e.g. 'melt'). In the context of behavioural data showing higher error rates in the HO condition (HOs were more likely to be accepted as correct category members than orthographic control items), the conclusion was that the phonological effects occur after semantic integration indexed by the N400. However, the possibility was raised that the increased processing demands of reading sentences for meaning might entail greater phonological involvement [11].

Earlier sentence reading studies have examined phonological activation by replacing semantically primed final words with unexpected words sharing initial phonemes [12], HOs [13,14] or pseudohomophones (PHs) (pseudowords homophonic to a real word) [15]. Some studies have found evidence for phonological effects in semantic integration indexed by the N400 [14,15], whereas other studies have not [12,13]. Furthermore, these studies have found only weak phonological reductions in the N2 range in an early stage and, moreover, concluded that the N2 modulations in reading are primarily related to orthographic violation [15]. However, these results have provided only limited insight with regard to spontaneous phonological activation in silent reading, because they have either (i) not used a controlled task (e.g. no behavioural monitoring in the case of Refs [12,14,15]), (ii) not used sentences with high cloze probability [13] and/or (iii) not controlled cloze probability across experimental conditions (i.e. they used different sentence contexts across conditions in [12,15]). Cloze probability is the numerical probability of a given word to be selected to complete a given sentence context (e.g. the cloze probability of 'prey' in the sentence starting 'An eagle is a bird of...' is close to 1).

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Indirect evidence for phonological activation in sentence reading comes from a study on misspellings [16], in which expectancy was manipulated by presenting low-cloze and high-cloze probability sentences containing a congruent word or its PH. In the N2 time range (N270), differences between words and PHs were found in the context of low-cloze sentences but not in that of high-cloze sentences. Although the aim of the study was to investigate the processing of misspellings, this result is compatible with phonological mediation in silent reading, as PHs, when highly constrained by sentence context, are phonologically expected. In the same study, words and PHs also reduced ERP amplitudes in the N400 range when presented in a high-cloze probability sentence [16], suggesting that phonological activation during silent reading may extend into the window of semantic integration [15,17].

Here, we tested whether participants who read silently for meaning would show phonological processing of stimuli that are orthographically and semantically inappropriate but phonologically expected, when reading highly constrained sentences. Our main question was whether HOs and PHs presented at the end of a highly constrained sentence would reduce the amplitude of the N2 peak relative to totally unexpected endings [10,18]. Our predictions were as follows: if retrieval of the phonological form of written words is spontaneous during silent reading, we should observe a reduced N2 peak in all conditions except for totally unexpected completions. In addition, retrieval of the phonological form of a HO or PH was expected to activate the semantic representation of the best completion (BC) and thus, similarly reduce the subsequent N400 [9,17].

Materials and methods

Participants

Fifteen undergraduate students participated in the partial fulfilment of a course requirement (11 women and 4 men, with a mean age of 19.3 years, range: 18–24 years) in our study, approved by the Bangor University's Ethics Committee. All had normal or corrected-to-normal vision and were native speakers of English.

Stimuli

To ensure that the 'best completion' stimuli were highly predictable from the preceding sentence context, a separate group of 37 participants completed a series of sentences that were missing the final word with their most likely ending (e.g. 'Rob looked at his watch to check the…' elicited the response 'time'). Sentences were included on the basis of their percentage predictability: each had a minimum of 0.80 cloze probability, with an average cloze probability of 0.84 for the final 'best completion' stimuli. There were four experimental conditions: BC (e.g. 'time'); HO of the BC (e.g. 'thyme'); PH of the BC (orthographically legal pseudowords homophonic to the BC, e.g. 'tyme'); and unrelated (UN, words unrelated to the sentence context, e.g. 'skull'). BC, HO and UN word lists were matched for lexical frequency (mean log = 1.13 ± 0.7), concreteness (mean = 465 ± 99), length (mean = 4.6 ± 1) and grammatical class [19]. The sentences ranged from five to 12 words in length.

Of the four stimulus conditions, three provided endings that were incongruent with the sentence whereas only one (BC) provided a congruent completion. To avoid spurious P300 effects prompted by unbalanced proportion between BC and other experimental conditions, we created a filler BC condition [20]. These fillers consisted of sentences with congruent endings but had no corresponding HO or PH equivalents and were not analysed. The complete stimulus set consisted of a total of 240 words: 40 words in each of the four critical experimental conditions (BC, HO, PH, UN) and 80 words in the filler BC condition.

Procedure

Participants were comfortably seated in a darkened, and acoustically shielded room. A high-resolution cathode ray tube monitor was centred approximately 100 cm from the participants' eyes. They were instructed to fixate at the centre of the screen and to minimize eye and body movements throughout the ERP recording. The participants were asked to indicate whether the final word was congruent or incongruent with the preceding sentence by pressing either the 'F' or 'J' keys (with the left and right index fingers, respectively). Response side was alternated between blocks and counterbalanced across participants. The 240 stimuli were divided into four blocks of 60 trials. In each trial, the sentence was presented one word at a time for 200 ms with an interstimulus interval of 300 ms. After the presentation of the final word, the participants had 2 s to respond. Each word subtended a maximum visual angle of 4 × 0.8°. Individual reaction times for correct responses were averaged as a function of the experimental condition. Incorrect responses and nonresponses were coded as errors.

Electroencephalography recording and analysis

Electroencephalography (EEG) data were recorded (1 kHz sampling rate; SynAmps2 amplifiers; Neuroscan Inc., El Paso, USA) from 32 Ag/AgCl electrodes in reference to Cz (impedance < 11 kΩ). The electrodes were placed in accordance with the International 10–20 System at the frontal (Fp1, Fp2, Fz, F3, F4, F7, F8), central (C3, C4), temporal (T7, T8), parietal (Pz, P3, P4, P7, P8) and occipital (O1, O2) sites, with additional electrodes in the anterior frontal (AFz), frontotemporal (FT9, FT10), frontocentral (FC1, FC2, FC5, FC6), centralparietal (CP1, CP2, CP5, CP6) and parietooccipital (PO9, PO10) locations. Electrodes above and below the left eye monitored eyeblink activity. EEG signal was filtered online between 0.1 and 100 Hz and was refiltered offline using a zero-phase shift using a 20 Hz cutoff low pass. Neuroscan software (Scan 4.2) was used to mathematically correct the eyeblinks. Epochs ranged from − 100 to 1000 ms after the final word onset. Baseline correction was made with reference to 100 ms prestimulus activity. At least 30 correct response epochs were obtained for each experimental condition (acceptance of BCs, rejections for the remainder) for each participant. Individual averages, which were digitally rereferenced to the global average reference, were averaged to produce the grand average ERPs. Mean amplitudes were measured at electrodes FC1, FC2 and Fz between 250 and 350 ms for the N2 and CP1, CP2 and Pz between 350 and 500 ms for the N400. For both the peaks, individual mean amplitudes and peak latencies for each condition were subjected to repeated measures analyses of variance with within-subject factors of condition (BC, HO, PH, UN) and electrodes (three electrodes).

Results

Behavioural data

Repeated measures analysis of variance indicated that experimental conditions significantly affected the reaction times [F(3,14) = 6.57, $P < 0.05$], with PH stimuli eliciting faster responses compared with other conditions (all $P < 0.05$; Fig. 1). Error rates also differed among the experimental conditions [F(3,14) = 12.25, $P < .01$; see Fig. 1]. Both BC and PH conditions yielded lower error rates than the HO and UN conditions (all $P < 0.05$). Differences between BC and PH on the one hand and between HO and UN on the other hand were nonsignificant (all $P > 0.1$).

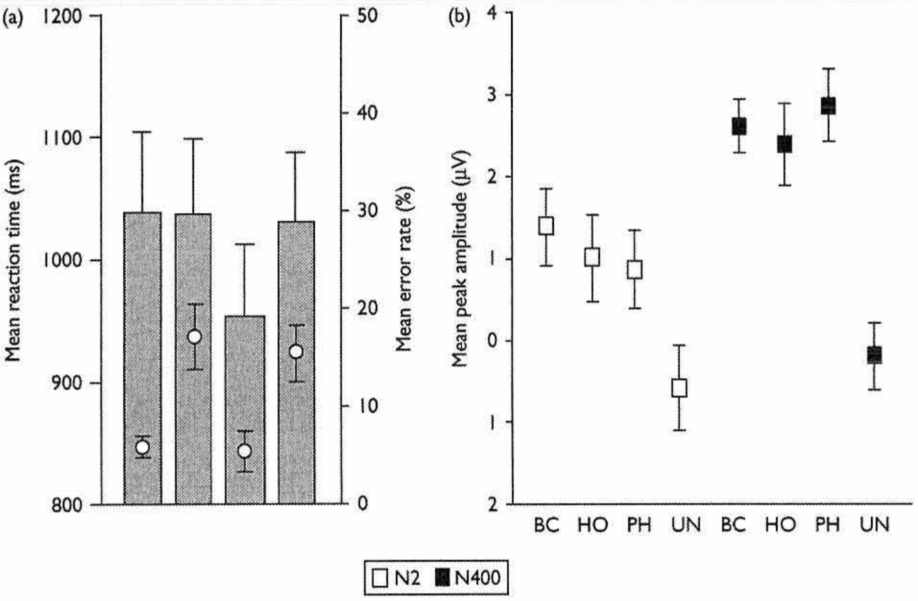
Event-related potential data

The P1 and N1 components elicited by words in the final position peaked at 115 and 223 ms, respectively, and were unaffected by experimental conditions either in amplitude or latency. The N2 peaked at 317 ms over the frontal area, and was maximal at Fz. The N400 was a broad negative wave maximal across centroparietal electrodes.

N2 peak latency was insensitive to experimental conditions ($P > 0.1$), but its mean amplitude was affected by experimental conditions [F(3,14) = 7.81, $P < 0.05$; Fig. 2]. Post-hoc *t*-tests indicated that the N2 elicited by the UN condition was larger compared with all other conditions: [BC–UN: $t(14) = 2.03$, $P < 0.05$; HO–UN: $t(14) = 2.82$, $P < 0.05$; PH–UN $t(14) = 2.70$, $P < 0.05$], whereas differences among BC, HO and PH considered in pairs were nonsignificant.

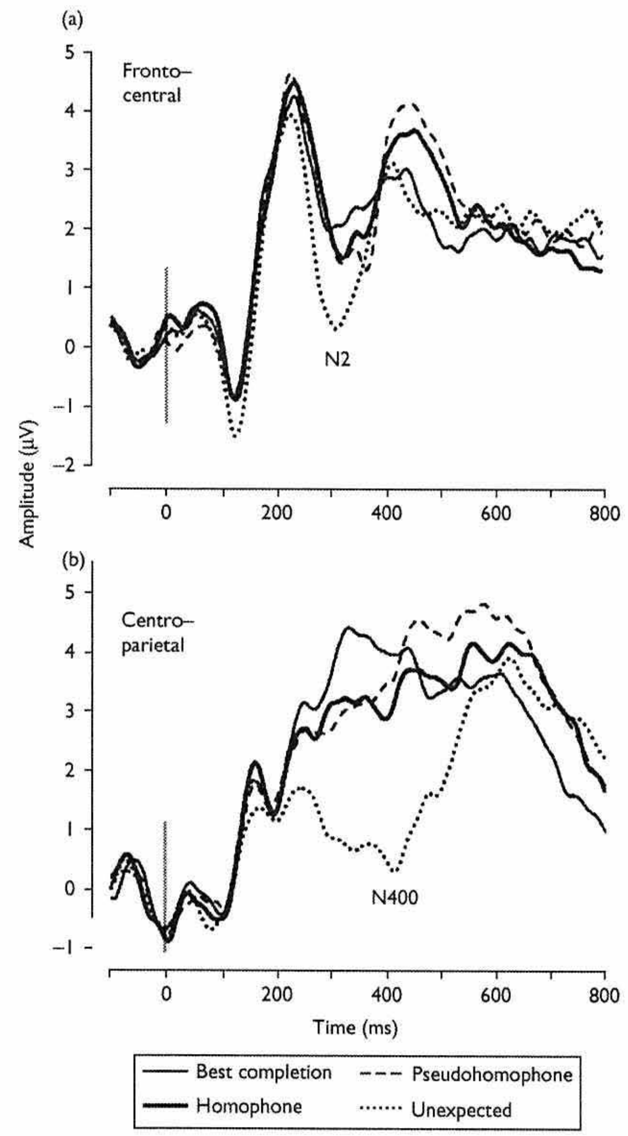
The N400 amplitude was modulated by experimental conditions, [$F(3,14) = 21.26$, $P < 0.05$]. Post-hoc comparisons showed that the N400 component was significantly more negative for the UN condition than in the other three experimental conditions [BC–UN $t(14) = 6.24$, $P < 0.05$; HO–UN $t(14) = 5.67$, $P < 0.05$; PH–UN

Fig. 1



(a) Reaction times for correct trials (bars) and error rates (circles) in the four experimental conditions. (b) Mean peak amplitude of the N2 and N400 in the four experimental conditions. BC, best completion; HO, homophone; PH, pseudohomophone; UN, unexpected completion. Error bars depict the standard error of the mean in all cases.

Fig. 2



Event-related potential waves over the (a) frontocentral region (linear derivation of electrodes FC1, FC2 and Fz) and (b) centroparietal region (linear derivation of electrodes CP1, CP2 and Pz) averaged across the 15 participants.

$t(14) = 8.57$, $P < 0.05$]. The BC, HO and PH conditions showed a substantially reduced wave and there were no differences among them ($P > 0.05$; Fig. 2). Owing to the absence of peak in the N400 range of BC, HO and PH, no latency analysis was carried out in the N400 range.

Discussion

This study investigated online phonological activation during silent reading and its implication in semantic integration mechanisms. We found that unexpected sentence completions prompted an N2 effect. As predicted, the N2 amplitude was significantly reduced for phonologically congruent completions (whether orthographically expected or not) compared with unexpected completions. Furthermore, a large amplitude N400 indexing violation of semantic expectancy was found only in the unexpected completion condition whereas the N400 elicited by phonologically congruent sentence completions (BC, HO, and PH) was substantially reduced and nondiscriminative. Thus, in a context in which orthographic and semantic expectations were maximal and despite the fact that phonological retrieval was detrimental to the task at hand, as HO and PH had to be judged as incorrect completions, participants systematically accessed the sound form of the printed word within 300 ms. Furthermore, the N400 reduction observed for all HO conditions indicates that phonological activation of the BC sound form triggered semantic access.

From a behavioural point of view, we found that orthography discriminated between the expected and homophonic completions. Error rates were higher in the HO condition than in other conditions. Moreover, participants were faster and more accurate in rejecting PHs than any other stimulus type. As both HO and PH conditions shared phonological representations with BCs, orthography is the only basis on which correct rejections could be made. Therefore, different performances in the two homophonic conditions were probably due to relative differences in orthographic familiarity [21]: PHs were orthographically unfamiliar, making it easier to reject them than HOs, which were real words.

It may be argued that amplitude reductions observed in the N2 and N400 ranges could have been prompted by orthographic rather than phonological similarity among BC, HO and PH conditions [22]. However, orthographic similarity is unlikely to account for the degree of attenuation observed here because (i) as HOs and PHs were correctly rejected and BC words were accepted, the N2 reduction found in former conditions should not have been as pronounced as that seen in the BC condition if this decision had been made based on orthography alone; (ii) nonhomophonic pseudowords usually elicit larger N400 amplitudes than PHs, even when they are matched for orthographic similarity with word targets [23] (orthographically driven effects have even been found as early as 150 ms [3]); and (iii) unexpected orthographic neighbours of highly expected words have been shown to elicit significantly larger N400 waves than expected sentence completions [24]. As in this study, HOs and PHs were less than 60% orthographically similar to BC words [HO mean similarity = 0.59 (based on normalized edit distance) [25], SD 0.18; PH normalized edit distance 0.55, SD 0.20] one would have expected larger N400 amplitudes if the effect had been driven by orthographic similarity.

Overall our results seem inconsistent with earlier studies showing larger N2 peaks to HOs [13,14] and PHs [15] compared with semantically congruent words. However, in our study, sentence cloze probability was manipulated so as to make the phonological priming effects particularly strong (see also ref. [16]), which we assume led to automatic phonological activation overriding the effects of orthographic expectation until after the window of semantic integration. We speculate that the earlier conflicting findings with regard to phonological integration indexed by the N2 may be accounted for by the absence of strong phonological expectations of the reader [12–15]. In this situation, phonological activation may be at a subthreshold level and vulnerable to interference from mismatch responses elicited by dissonant orthographic forms. This would result in the observed increased N2 modulations [12,13,15], indexing early conflicts between orthographic and phonological processing [15,18]. Such a conflict would presumably reduce phonological integration and subsequent semantic access triggered by the stimulus [11].

Conclusion

Despite being correctly rejected as inappropriate sentence completions, HOs and PHs seem to elicit N2s and N400s of similar amplitude to those elicited by predictable words. This result provides new evidence that while final meaning selection may be constrained by orthography, phonological information is accessed and mediates semantic access during sentence reading.

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Electrophysiological evidence for impaired attentional engagement with phonologically acceptable misspellings in developmental dyslexia

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Event-related potential (ERP) studies of word recognition have provided fundamental insights into the time-course and stages of visual and auditory word form processing in reading. Here, we used ERPs to track the time-course of phonological processing in dyslexic adults and matched controls. Participants engaged in semantic judgments of visually presented high-cloze probability sentences ending either with (a) their best completion word, (b) a homophone of the best completion, (c) a pseudohomophone of the best completion, or (d) an unrelated word, to examine the interplay of phonological and orthographic processing in reading and the stage(s) of processing affected in developmental dyslexia. Early ERP peaks (N1, P2, N2) were modulated in amplitude similarly in the two groups of participants. However, dyslexic readers failed to show the P3a modulation seen in control participants for unexpected homophones and pseudohomophones (i.e., sentence completions that are acceptable phonologically but are misspelt). Furthermore, P3a amplitudes significantly correlated with reaction times in each experimental condition. Our results showed no sign of a deficit in accessing phonological representations during reading, since sentence primes yielded phonological priming effects that did not differ between participant groups in the early phases of processing. On the other hand, we report new evidence for a deficient attentional engagement with orthographically unexpected but phonologically expected words in dyslexia, irrespective of task focus on orthography or phonology. In our view, this result is consistent with deficiency in reading occurring from the point at which attention is oriented to phonological analysis, which may underlie broader difficulties in sublexical decoding.

Keywords: developmental dyslexia, event-related potential, P3a, attention, orthographic processing, homophone, reading

INTRODUCTION

During the last decade, the reading difficulties experienced by individuals with developmental dyslexia have been consistently associated with a deficit in phonological processing (e.g., Snowling, 2000; Ramus, 2002). More specifically, weak phonological coding capacity would be responsible for weak phonological representations of words and, in turn, for difficulties in the learning of grapheme–phoneme correspondences necessary to decode unfamiliar words, for a deficit in constraining phonological analysis and segmentation, and, finally, for poor performance in phonological awareness tasks (Fowler, 1991; Manis et al., 1997; Swan and Goswami, 1997; Snowling, 2000; Vellutino et al., 2004).

However, evidence for weak phonological representations in developmental dyslexia is limited (see Ramus, 2002; Blomert et al., 2004; Ramus and Szenkovits, 2008) and largely derived from auditory tasks testing sensitivity to speech or acoustically modified stimuli within the context of tasks taxing working memory resources, and which usually require discrimination from a referent (see Ahissar et al., 2006; Banai and Ahissar, 2006, for a discussion). This has prompted alternative proposals of mechanisms that contribute to phonological processing impairments involving working memory during phonological access (Blomert et al., 2004; Ramus and Szenkovits, 2008; Menghini et al., 2011), attentional engagement with phonological information (Hari et al., 1999; Hari and Renvall, 2001; Facoetti et al., 2006, 2008, 2010; Ruffino et al., 2010), visuo-attentional processes engaged in orthographic analysis (e.g., Ans et al., 1998; Valdois et al., 2004; Bosse et al., 2007; Vidyasagar and Pammer, 2010) or perceptual filtering (Roach and Hogben, 2007, 2008; Geiger et al., 2008), or a combination of such more generic cognitive processes (e.g., Pennington and Bishop, 2009; Menghini et al., 2010, 2011).

Behavioral studies are limited in the extent to which they can provide information in support of or against the hypotheses presented above, not only with respect to the magnitude of the impairment but also with regard to the exact point in time when word recognition is affected. Event-related potentials (ERPs) allow us to plot the millisecond-by-millisecond time-course of visual word recognition processes (see Grainger and Holcomb, 2009) and provide a functional interpretation of deficient cognitive mechanisms based on existing knowledge of specific electrophysiological markers (Brandeis and Lehmann, 1986, 1994). We chose to use this technique to study the locus of the phonological deficit in dyslexia within a reading context. If reduced sensitivity to phonological information is the source of reading difficulties in dyslexia (as predicted by degraded phonological representations) then, from the moment that ERPs discriminate visual word stimuli such as pseudowords on the basis of their phonological properties, any differences between dyslexic and control readers should be manifest.

We know from ERP studies with normal, skilled readers that phonologically manipulated stimuli can reliably modulate the N2 peak, which occurs at least 100 ms before the N400 window. For instance, masked primes varied in phonological similarity to a target word elicit a graded amplification of N2 (N260: Grainger et al., 2006; Holcomb and Grainger, 2006). Furthermore, N2 amplitude has been shown to increase as a function of relative phonological and orthographic similarity of visually presented word rhyme pairs[1] (Kramer and Donchin, 1987). A modulation of the N2 elicited by phonological mismatch is also observed when the expected final word of a sentence is replaced with a phonologically dissimilar, unexpected stimulus. This effect has been shown using both auditory (also known as the phonological mismatch/mapping negativity, PMN; Connolly and Phillips, 1994; D'Arcy et al., 2004; Diaz and Swaab, 2007; Newman and Connolly, 2009) and visual (Connolly et al., 1995; Savill et al., 2011) presentation. Furthermore, orthographic stimuli that are phonologically similar or even identical to an expected stimulus can show N2 attenuation similar to the expected stimulus congruent with their phonological acceptability (e.g., Vissers et al., 2006; Briesemeister et al., 2009; Savill and Thierry, 2011; Savill et al., 2011).

Looking at earlier influences of phonological information embedded in words, studies with normal readers have also reported phonological effects in reading within the P2 range. For instance, rhyming visual word pairs have been shown to increase P2 amplitudes relative to non-rhyming pairs (Barnea and Breznitz, 1998; Kong et al., 2010). Other studies have shown effects of phonetic consistency of Chinese characters radicals read silently as early as 170 ms post-stimulus onset (Lee et al., 2007; Hsu et al., 2009). Given that phonetic consistency relates to the frequency of the phonological mapping to a character, Hsu et al. (2009) hypothesized that the P2 is sensitive to variations in the mapping between orthography and phonology. A similar conclusion was reached by Bles et al. (2007) in an ERP study examining the passive effects of word cohort size reduction in which participants simply monitored for change in letter color. The authors found that reduction in cohort size, which was achieved by letter-by-letter presentation, correlated with reduction in P2 amplitude. They proposed that the P2 is modulated by the inhibition of competing stimuli based on phonological or orthographic information. Consistent with this view, recent studies comparing pseudohomophones or homophones with words or pseudowords have also found modulations of the P2 peak (Meng et al., 2008; Zhang et al., 2009; Kong et al., 2010) with onset of difference found as early as 150 ms after stimulus onset (Sauseng et al., 2004; Braun et al., 2009). Braun et al. (2009), for example, found that pseudohomophones elicited greater P150 amplitudes as compared to orthographically similar pseudowords during a lexical decision task. They proposed that P2 (or, as they call it, P150) modulations in amplitude index the conflict between the unfamiliar orthographic representation of pseudohomophones and their familiar phonological representation, such that P2 amplitude is increased with increased competition. Interestingly, such interaction between phonological and orthographic information is delayed when the primes are not consciously perceived, in which case ERP modulations are found later, e.g., in or beyond the N250 range (Grainger et al., 2006; Ashby and Martin, 2008). Therefore, if phonological representations are impaired in dyslexia, it is reasonable to expect group differences in the P2–N2 range in relation to phonology–orthography interactions during reading.

However, most of the previous electrophysiological studies with dyslexic participants have shown differential effects between groups for phonological manipulation in visually presented words fairly late in the processing stream, i.e., from within the so-called N400 range. The N400 wave is a large negative deflection typically elicited in linguistic tasks involving violations of semantic expectation in sentence (e.g., Kutas and Hillyard, 1980, 1984; van Berkum et al., 1999; Hagoort et al., 2004) and single word priming contexts (Bentin et al., 1985, 1993), but is also elicited by other forms of expectancy violation in language, such as mismatching stimuli in rhyming tasks (Rugg, 1984; Rugg and Barrett, 1987). Studies reporting N400 differences between dyslexic and control readers with respect to phonological processing of visual word stimuli are confined to studies of rhyme judgment, in which dyslexic individuals typically show an attenuated N400 (Ackerman et al., 1994; McPherson et al., 1998; Rüsseler et al., 2007). Such observations have been taken as electrophysiological evidence of phonological processing difficulties in dyslexia (Rüsseler et al., 2007). N400 differences observed in rhyme judgment, however, can be influenced by anomalies in domain-general cognitive processes including working memory (e.g., Gunter et al., 2003), integration (Holcomb, 1993), inhibition (Gunter et al., 2003), and/or decision-making processes (Brown and Hagoort, 1993; Holcomb, 1993; Connolly and Phillips, 1994; Chwilla et al., 1995). This is particularly relevant, because rhyming judgment is a fairly complex, abstract task reliant on working memory for retrieval, maintenance, and segmentation of the phonologic representation of the first stimulus into onset and rime and comparison with the rime of the following target (Besner, 1987). This means that we ought to consider earlier modulations elicited by phonological and orthographic interactions in reading.

Recently, we investigated early phonological effects in dyslexic adults making homophony judgments on visual word stimuli (Savill and Thierry, 2011). By comparing responses to words primed by pseudowords orthogonally manipulated for orthographic and phonological similarity, we found that, like controls, dyslexic adults showed early phonological priming effects in the N2 and P3 ranges (attenuated N2 and increased P3). Main effects of phonological priming only showed differences between groups in the P600 range, a stage of stimulus re-evaluation. We did, however, find that the interactive effects of orthographic and phonological priming differed between groups for peaks spanning the P2, N2, and P3 ranges, following reduced orthographic priming effects in the N1 range in the dyslexic group. These results indicate that the processing of orthographic information and its later integration with

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[1] In this study, the N2 peak was largest to non-rhyming orthographically dissimilar word pairs "shirt-witch"; smallest to rhyming and orthographically similar pairs "match-patch," and of intermediate amplitude to non-rhyming, orthographically similar "catch-watch," and rhyming, orthographically dissimilar pairs "blare-stair."

phonological information is problematic in dyslexia, rather than sensitivity to phonological information *per se*; at least within the context of a demanding meta-linguistic homophony judgment task.

To determine whether processing differences between dyslexic and unimpaired readers are present from the onset of reading-related phonological analysis or whether differences emerge after phonological access has taken place in a more natural reading context, we decided to record ERP modulations elicited by phonological and orthographic priming during sentence reading. This study expands on a task that has previously been shown to elicit phonological modulations of the N2 in normal readers (Savill et al., 2011). To adapt the task for use with dyslexic participants, we increased the size of the stimulus set from Savill et al. (2011) and created high-cloze probability sentences (e.g., "Clare went on a diet to lose ___") ending either in (a) its expected best completion word ("weight"), (b) a word homophonic to the expected word ("wait"), (c) a pseudohomophone of the expected word ("wate"), or (d) an unexpected word ("string"). Since three of the four conditions were phonologically very close, and should have been primed by each sentence context phonologically, this enabled us to see how phonological representations were accessed from different, unexpected orthographic forms in dyslexic readers.

We were primarily interested to see whether dyslexic readers would show reduced early effects of phonological manipulations in the N2 range (i.e., less N2 attenuation, following phonologically reduced N2 amplitudes seen in Vissers et al., 2006; Grainger and Holcomb, 2009; Savill et al., 2011). We also anticipated that mismatching orthographic and phonological information (i.e., in the case of phonologically matched but orthographically incorrect homophones and pseudohomophones) would induce conflict during lexical access and increase P2 mean amplitude (Bles et al., 2007; Braun et al., 2009; Hsu et al., 2009) and we investigated whether such modulation would be different in dyslexic readers (we did not test this in Savill et al. (2011) due to the paper's focus on phonological main effects). Furthermore, since previous ERP studies of visual word processing in dyslexic participants have predominantly shown effects of phonological manipulations in the N400 range, we investigated whether group differences would also/alternatively appear at later, post-perceptual stages of processing.

In order to test automatic versus controlled phonological processing, we tested participants using two different tasks performed on the same stimuli: a semantic-judgment task we termed "ortho-semantic" focusing on orthography following Savill et al. (2011) ("is the final word the best way to complete the sentence?"); and a task we named "phono-semantic," which demanded focus on phonological form ("does the final word of the sentence sound like the best way to complete the sentence?"). We predicted that ERPs would provide evidence for a phonological deficit in reading in one of two ways:

(i) If the phonological deficit affecting reading in dyslexia has its source in degraded phonological representations and/or deficiency in extracting phonological information from written stimuli, dyslexic participants should show reduced sensitivity to phonological information and thus should display reduced phonological priming in response to homophones and pseudohomophones in both tasks. Therefore, we expected reduced N2 amplitude decreases for these conditions relative to the unrelated condition in dyslexic participants as compared to matched controls.

(ii) Alternatively, if we can find no evidence of group differences in early stimulus evaluation stages, but differences manifest later in processing (e.g., beyond 300 ms post-stimulus onset), this would indicate that the deficit in dyslexia is not apparent during decoding and/or perception phases, but related to more integrative, attention-regulated, stages of phonological analysis which involve working memory and re-evaluation mechanisms.

Finally, the use of two tasks enabled us to test the potential role of overt attention to phonology during reading. Indeed, if the processes at work are under the voluntary control of the participants, attending to orthography ("ortho-semantic" task), and phonology ("phono-semantic" task) should yield different patterns across tasks and, what is more, interact with participant group.

MATERIALS AND METHODS

PARTICIPANTS

Twelve adult participants with developmental dyslexia (six females, mean age 20.8 years) and 12 control adults (six females, mean age 22.9 years) participated in this study approved by the local Ethics committee of Bangor University. Participants were all students at Bangor University and had given informed consent to participate. All were right-handed according to the Edinburgh handedness inventory and native English speakers with normal or corrected-to-normal vision. Our dyslexic participants had a confirmed diagnosis of developmental dyslexia from an educational psychologist and were recruited through the university's Dyslexia Unit or through advertisement via the university's participant panel and were paid for participation. The dyslexic group consisted of high-functioning individuals who had compensated for their difficulties such that their reading level was within a normal range but at a level inconsistent with their academic ability. Performance on a series of subtests taken from the Dyslexia Adult Screening Test (DAST; Nicolson and Fawcett, 1998), Wide Range Achievement Test (WRAT-3; Jastak and Wilkinson, 1993), Wechsler Individual Achievement Test (WIAT-II; Wechsler, 2005), and Wechsler Adult Intelligence Scale (WAIS-III; Wechsler, 1997) showed that the dyslexic group performed significantly poorer than the control group across reading and spelling measures (**Table 1**).

STIMULI

To allow for the possibility of a greater loss of experimental trials from performance error due to testing dyslexic participants, we created additional stimuli to expand the stimulus set used by Savill et al. (2011). High-cloze sentences for which the best completion had an existing semantically unrelated homophone were created (e.g., "Clare went on a diet to lose ____": best completion is "weight"; homophone is "wait"). These were supplemented with filler high-cloze sentences for which the final word had a unique phonological form. All sentences were normed by 26 native English speakers who completed them with the most expected word. Sentences selected for the study had at least 92% terminal word agreement. Pseudohomophones of the target word were created to form the pseudohomophone con-

Table 1 | Group performance on psychometric subtests.

	Control group ($n = 12$)		Dyslexic group ($n = 12$)		t
	M	SD	*M*	SD	
Age (years)	22.92	6.13	20.75	1.29	1.20
Reading (WRAT; untimed[a])	115.58	6.10	102.83	11.34	3.43**
One minute reading (DAST)	117.25	11.99	96.17	15.68	3.70**
Pseudoword reading (WIAT[a])	114.67	5.55	90.17	14.62	5.43***
Nonsense passage (DAST)	95.58	3.87	82.67	9.46	4.38**
Spelling (WRAT[a])	108.42	5.71	96.33	5.60	5.23***
Rapid naming (DAST; s)	25.08	3.75	31.58	10.19	−2.07*
Digit span (WAIS[a])	11.75	2.34	9.08	2.35	2.78*

Raw scores are reported unless otherwise stated.
[a] *Standardized scores.*
$^*p < 0.05$. $^{**}p < 0.01$. $^{***}p < 0.001$.

dition (e.g., "wate") and a word semantically unrelated to the sentence stem was chosen for the unrelated condition (e.g., "string"). The final stimulus set consisted of 48 test sentences, shown once with their best completion, a homophone of the best completion, a pseudohomophone of the best completion, and an unrelated stimulus. A further two sets of 96 filler sentences were created: (a) a set of sentences ending with best completion words to be used in one of the tasks ("ortho-semantics") and (b) a set of sentences ending with unrelated homophones or pseudohomophones to be used in the other task ("phono-semantics"). The purpose of the fillers was to ensure equally probable yes or no responses in both tasks: In the ortho-semantic task a yes response was expected for best completions (48 items) and fillers (96 items) with homophones (48), pseudohomophones (48) and unrelated (48) requiring a no response; and for the phono-semantic task a yes response was expected for best completions (48), homophones (48), and pseudohomophones (48), with a no for unrelated (48), and filler items (96). Word lengths varied between 3 and 10 letters (terminal word $M = 4.9$, SD = 1.3) and terminal words did not significantly differ in length across conditions ($p > 0.2$). Kucera–Francis written frequency and concreteness of the sentence final words were controlled between best completion, homophone and unrelated conditions ($p > 0.1$). All pseudohomophones used were piloted in the 26 participants mentioned above to verify pronunciation was homophonic to the target word. Finally, the orthographic properties of the pseudohomophone stimuli did not differ from the other conditions in terms of constrained bigram and trigram counts and averaged orthographic neighbor frequency (verified by http://www.neuro.mcw.edu/mcword/, Medler and Binder, 2005) and were similar in orthographic overlap with best completion words as the homophones were (according to their normalized edit distance, see Lambert et al., 1999). A list of the stimuli used is given in the Appendix.

PROCEDURE

Participants were seated comfortably in a dimly lit, sound-attenuated room in front of a projector screen. They were instructed to fixate the center of the screen and perform one of two tasks: (a) in the "ortho-semantic" task, they were asked to press a designated key for final words which were expected according to the sentence context and another for any other ending; (b) in the "phono-semantic" task, they were asked to press a key for final words that sounded like the expected completion of sentences and another key for phonologically inadequate endings. Sentences were presented using EPrime (Psychology Software Tools, Inc., Pittsburgh, USA) at the center of the screen, at eye-level, one word at a time, subtending a maximum angle of 3.7°, in black Times New Roman font on a white background. Experimental trials were presented in pseudo-random order across five blocks such that filler and test trials were evenly distributed. Each test trial consisted of a fixation cross displayed for 200 ms, individual words in lower case displayed for 200 ms and separated by 300 ms inter-stimulus intervals featuring a fixation cross (**Figure 1**). After presentation of each final word the screen remained blank for a fixed period of 2000 ms to allow for participant response. A further 1000 ms separated trials. Task order and response sides were counterbalanced between participants.

The EEG data was recorded from 37 Ag/AgCl electrodes, placed in an elastic cap according to the extended 10–20 system, using Nuamps amplifiers (NeuroScan™, Sterling, USA). The online reference was the left mastoid and FPz served as the ground electrode. Electrodes positioned above and below the left eye recorded vertical eye movement. Electrode impedance was maintained below 5 kΩ. Recordings were band-pass filtered off-line between 0.1 and 30 Hz using a zero-phase shift digital filter. Eye blinks were mathematically corrected using the correction provided by Edit 4.3 (NeuroScan™, Sterling, USA). The continuous EEG was sliced into epochs ranging from −100 to 1000 ms after the onset of the target word. Epochs with voltage exceeding ±75 μV were automatically rejected. After baseline correction in reference to pre-stimulus activity, individual averages were re-referenced to the average of the mastoids. Individual averages were computed from correct trials in experimental condition (more than 35 epochs from each task for each case) and averaged together to produce grand-mean averages. Behavioral data were collected simultaneously to ERP data.

DATA ANALYSIS

Time windows for mean amplitude analyses were defined for the control group on the basis of mean global field power, expectations from previous experiments using similar stimuli (e.g., Connolly et al., 1995; Vissers et al., 2006; Thierry et al., 2008; Savill et al., 2011) and visual inspection of topographic distribution of ERP

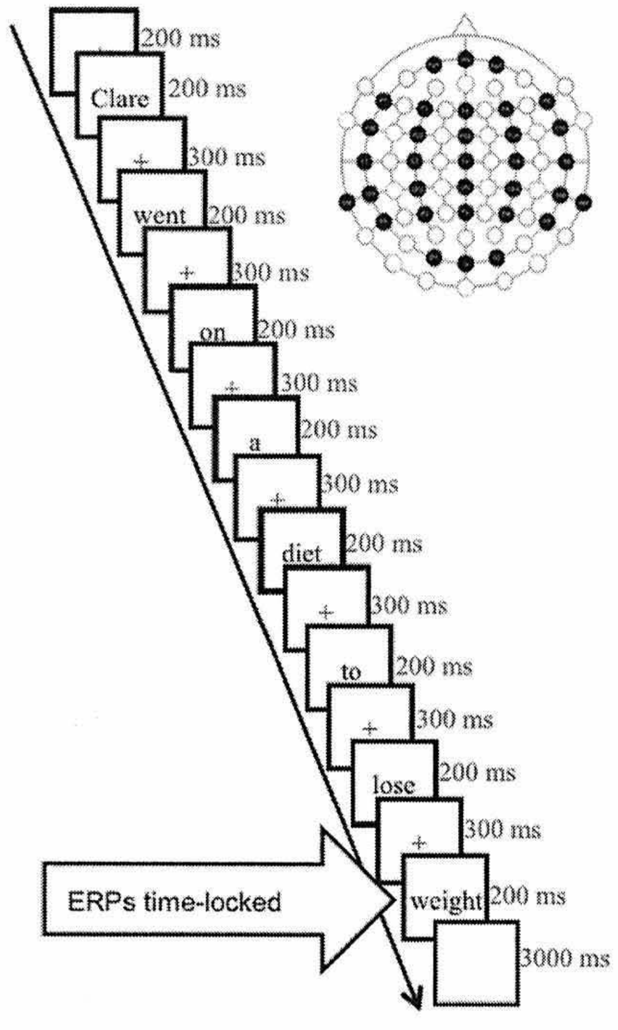

FIGURE 1 | Schematic of a single trial.

modulations (Luck, 2005). The expected P1/N1/P2/N2 peaks were observed, followed by a visible P3a peak in the control group only. Windows of analysis for the control group were 80–110 ms for the P1; 140–170 ms for the N1; 160–210 for the P2; 250–350 ms for the N2, 350–450 ms for the P3a; and 470–670 ms for the P600.

To determine appropriate time windows for mean amplitude analyses in the dyslexic group, automatic peak detection was performed on large temporal windows encompassing each peak to check for significant group differences in overall peak latency (70–110 ms for the P1; 130–180 ms for the N1; 160–230 ms for the P2; 250–370 ms for the N2, 340–470 ms for the P3a; and 470–700 ms or the P600). Peak detection was time-locked to the electrode of maximal amplitude for each observed peak: O2 for the P1; P7 for the N1; and FCz for the P2, N2, and P3a. As both the P2 peak and the P600 peak were found to peak significantly later in the dyslexic group, with a delay of approximately 16 and 26 ms respectively, the analysis windows were adjusted to 180–230 ms for P2 mean amplitudes and to 500–700 ms for P600 mean amplitudes in the dyslexic group. No other peaks showed a significant delay and so for all other peaks the same analysis window was used as for the control group.

Mean amplitudes were measured at electrodes selected *a priori* based on classical topography of main components and checked for maximal sensitivity based on visual inspection: O1, O2, P7, and P8 electrodes for the P1; O1, O2, P7, and P8 for the N1; FC3, FC4, FCz, and Cz for the P2, N2, and P3a peaks and Cz, CP3, CP4, CPz for the P600.

Mean ERP amplitudes and peak latencies were subjected to a mixed ANOVA with task ("ortho-semantic," "phono-semantic"), sentence condition (best completion, homophone, pseudohomophone, unrelated), and electrode as within-subject factors, and participant group (control, dyslexic) as between-subject factor. Error rates and reaction times (RTs) were also analyzed by means of a mixed ANOVA with task and condition as within-subject factors and participant group as between-subject factor. Greenhouse–Geisser corrections of degrees of freedom were applied where appropriate.

RESULTS

BEHAVIORAL DATA

Statistical analyses revealed a main effect of group on both accuracy, $F_{1,22} = 4.40$, $p = 0.05$, and RTs, $F_{1,22} = 13.79$, $p < 0.01$, such that dyslexic participants were overall less accurate and slower than matched controls (**Figure 2**). Sentence condition significantly influenced performance accuracy, $F_{3,66} = 17.34$, $p < 0.001$ and correct RT, $F_{3,66} = 14.07$, $p < 0.001$. Accuracy was significantly lower for homophone endings than any other condition. RTs, meanwhile, were significantly faster for pseudohomophone endings, and unrelated endings elicited significantly slower reaction times than best completions. There was also a near-significant group by condition interaction with respect to accuracy ($p = 0.08$), relating to poorer accuracy in the homophone condition in the dyslexic group compared to the other conditions. Task also interacted significantly with condition in terms of accuracy ($F_{3,66} = 6.09$, $p < 0.01$). *Post hoc* analyses showed that this interaction was driven by significantly poorer accuracy in the homophone condition in the "ortho-semantic" task, compared with no differences between conditions in the "phono-semantic" task. Task interacted significantly with condition also in terms of RT ($F_{3,66} = 5.35$, $p < 0.01$). *Post hoc* tests showed that pseudohomophones elicited significantly faster RTs compared to all other conditions in the "ortho-semantic" task, whereas in the "phono-semantic" task only the unrelated words elicited slower RTs than the other conditions. A trend for a task by group interaction on accuracy ($p = 0.08$) was driven by a trend in the dyslexic group to perform less accurately in the "ortho-semantic" task compared to the "phono-semantic" task ($p = 0.09$), whilst the control group showed no significant difference between tasks ($p = 0.69$).

EVENT-RELATED POTENTIAL RESULTS

No significant task effects were observed on ERP peak latencies or mean amplitudes, therefore valid EEG epochs for each trial of both tasks were averaged together to increase statistical power (accepted epochs $M = 83.20$, $SD = 11.42$; no significant differences between condition or group). All results reported below relate to the combined task averages.

No significant differences in P1 mean amplitude or latency were found between groups or conditions. The N1 tended to be smaller in the dyslexic group, as indicated by a group effect on N1 mean amplitudes ($F_{1,22} = 4.34$, $p < 0.05$; see **Figure 3**). No significant experimental modulations of the N1 were observed.

The P2 was significantly modulated by sentence condition ($F_{3,66} = 5.54$, $p < 0.01$). *Post hoc* tests showed that this effect was driven by the homophone and pseudohomophone conditions eliciting significantly larger responses compared to the unrelated condition (both $p < 0.01$). No significant group differences on mean amplitude were found (all $p > 0.50$). P2 peak latency was also significantly affected by sentence condition ($F_{3,66} = 5.50$, $p < 0.01$), such that the unrelated condition elicited shorter latencies relative to the other conditions (all $p < 0.05$). Analyses also showed a main effect of group ($F_{1,22} = 7.01$, $p < 0.05$) indicating significantly longer P2 latencies overall in the dyslexic group (control $M = 183$ ms; dyslexic $M = 199$ ms).

Sentence condition significantly modulated mean N2 amplitude ($F_{3,66} = 36.55$, $p < 0.001$; **Figure 4**) such that unrelated words elicited greater negativity in this range compared to all other sentence

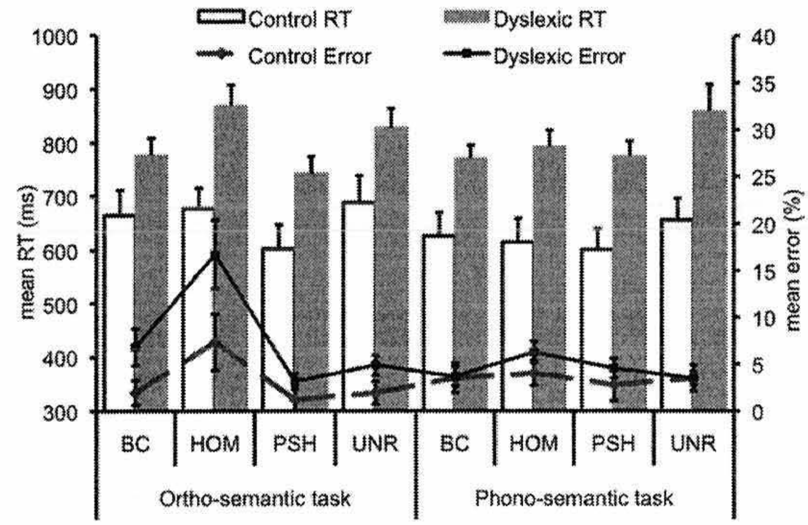

FIGURE 2 | Behavioral data for both tasks. Error bars represent 1 SE. BC, best completion; HOM, homophone; PSH, pseudohomophone; Unr, unrelated.

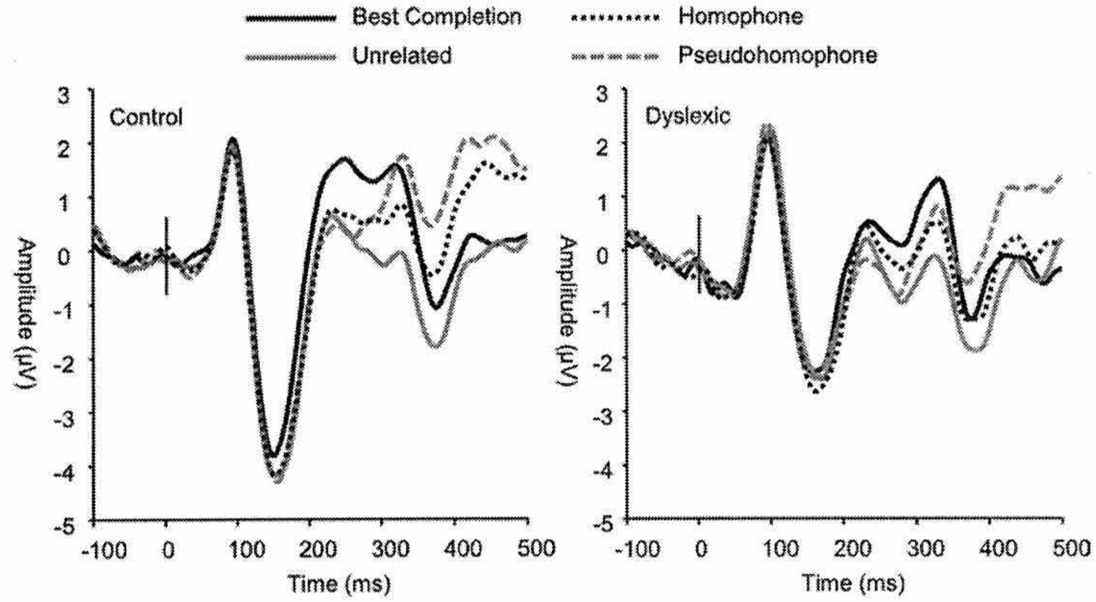

FIGURE 3 | Group effect on N1 amplitude. Linear derivation of O1, O2, P7, and P8 electrodes. Note negative amplitudes are plotted downward.

conditions (all $p < 0.001$). N2 latencies were also significantly modulated by sentence condition ($F_{3,66} = 3.21$, $p < 0.05$) due to the unrelated condition eliciting significantly shorter latencies than the homophone and pseudohomophone conditions ($p < 0.05$). No group differences were found in the N2 range (condition × group amplitude, $p = 0.77$; latency, $p = 0.30$).

The frontocentral P3 was significantly modulated by sentence condition ($F_{3,66} = 12.72$, $p < 0.001$). This effect related to significantly larger P3a amplitudes elicited in the homophone and pseudohomophone conditions relative to the best completion and unrelated conditions (each $p < 0.01$). The condition effect was qualified by a main effect of group on P3a amplitude, confirming that the P3a was significantly larger in the control group ($F_{1,22} = 15.11$, $p < 0.001$; **Figure 5**) and by a significant interaction of group and condition ($F_{3,66} = 3.19$, $p < 0.05$). Subsequent group-wise analyses showed that the control group showed a strong condition effect in the same direction as the observed overall condition effect ($F_{3,33} = 11.32$, $p < 0.001$), showing significant differentiation of pseudohomophone and homophone conditions from best completion and unrelated conditions (all $p < 0.01$), while the dyslexic group showed an effect driven only by smaller amplitudes to the unrelated condition compared to each other condition ($F_{3,33} = 4.51$, $p < 0.05$).

A trend for P3a peak latency differences induced by experimental condition was also found ($p = 0.06$), such that the best completion condition elicited significantly shorter latencies compared to the unrelated condition.

The P600 wave was also significantly modulated by sentence condition ($F_{3,66} = 8.03$, $p < 0.001$; see **Figure 6**) irrespective of group. Pairwise comparisons showed that this effect was due to significantly attenuated amplitudes for the best completion condition relative to each of the other conditions, respectively (all $p < 0.01$). Pairwise comparisons did not show significant differences in P600 amplitude between homophone, pseudohomophone, and unrelated conditions (all $p > 0.20$). P600 peak latency was also significantly affected by sentence condition ($F_{3,66} = 11.36$, $p < 0.001$), such that the homophone and pseudohomophone conditions elicited shorter latencies relative to the best completion and unrelated conditions (all $p < 0.01$). Analyses also showed a main effect of group on P600 latency ($F_{1,22} = 4.56$, $p < 0.05$) indicating significantly longer P600 latencies overall in the dyslexic group (control $M = 540$ ms; dyslexic $M = 576$ ms).

Bivariate correlations performed on mean amplitudes of ERP peaks for each experimental condition with their respective behavioral data are given in **Table 2**.

Table 2 | Significant correlations between individual mean amplitudes and behavioral data for each condition.

	N1	P2	N2	P3a	P600
BC accuracy					
HOM accuracy	–0.406*				
PSH accuracy					
UNR accuracy					
BC RT				–0.656**	
HOM RT			–0.414*	–0.595**	
PSH RT			–0.427*	–0.743**	
UNR RT				–0.532**	

*Values are Pearson r coefficients (n = 24). *p < 0.05; **p < 0.01 (two-tailed).*

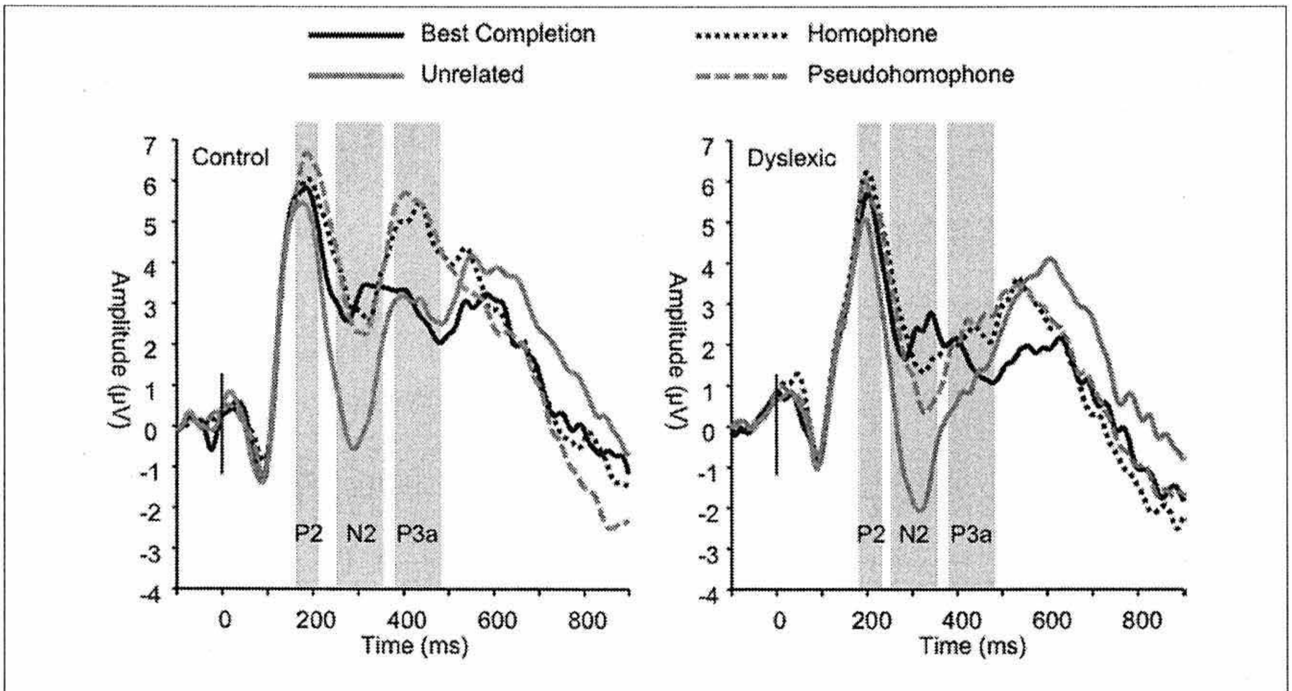

FIGURE 4 | Group grand averages showing P2, N2, and P3a peaks based on a linear derivation of FC3, FC4, FCz, and Cz electrodes. Time windows for mean amplitude analyses are marked by the gray bars.

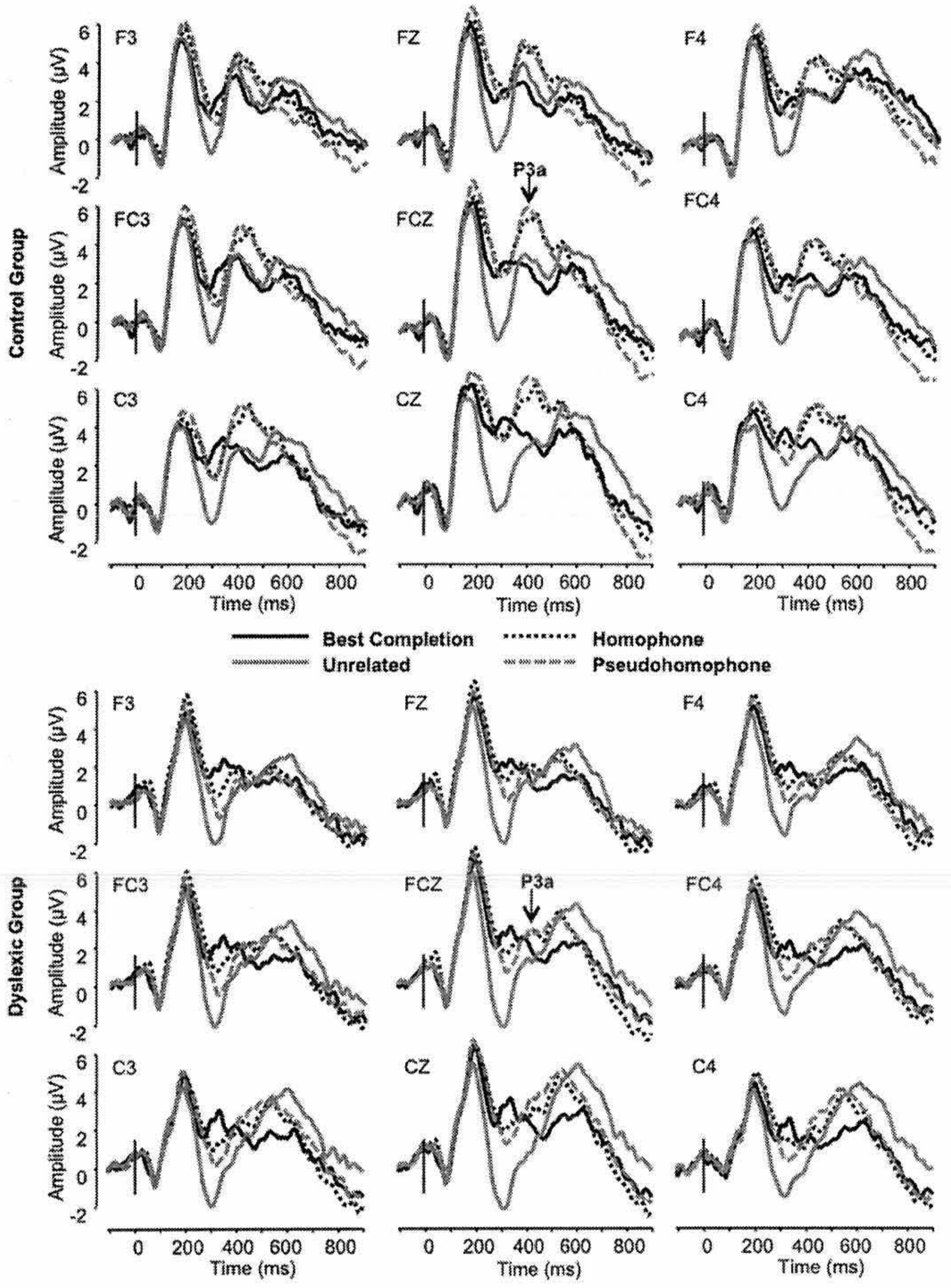

FIGURE 5 | Grand averages of frontocentral electrodes showing the diffuse group difference in P3a modulation.

DISCUSSION

This study aimed at detecting differences between individuals with developmental dyslexia and matched controls in orthographic/phonological integration mechanisms using ERPs.

We found early significant ERP modulations by orthographic and phonological priming in both the participant groups. However, despite poorer behavioral performance in the dyslexic group for the "ortho-semantic" and the "phono-semantic" variants of the task,

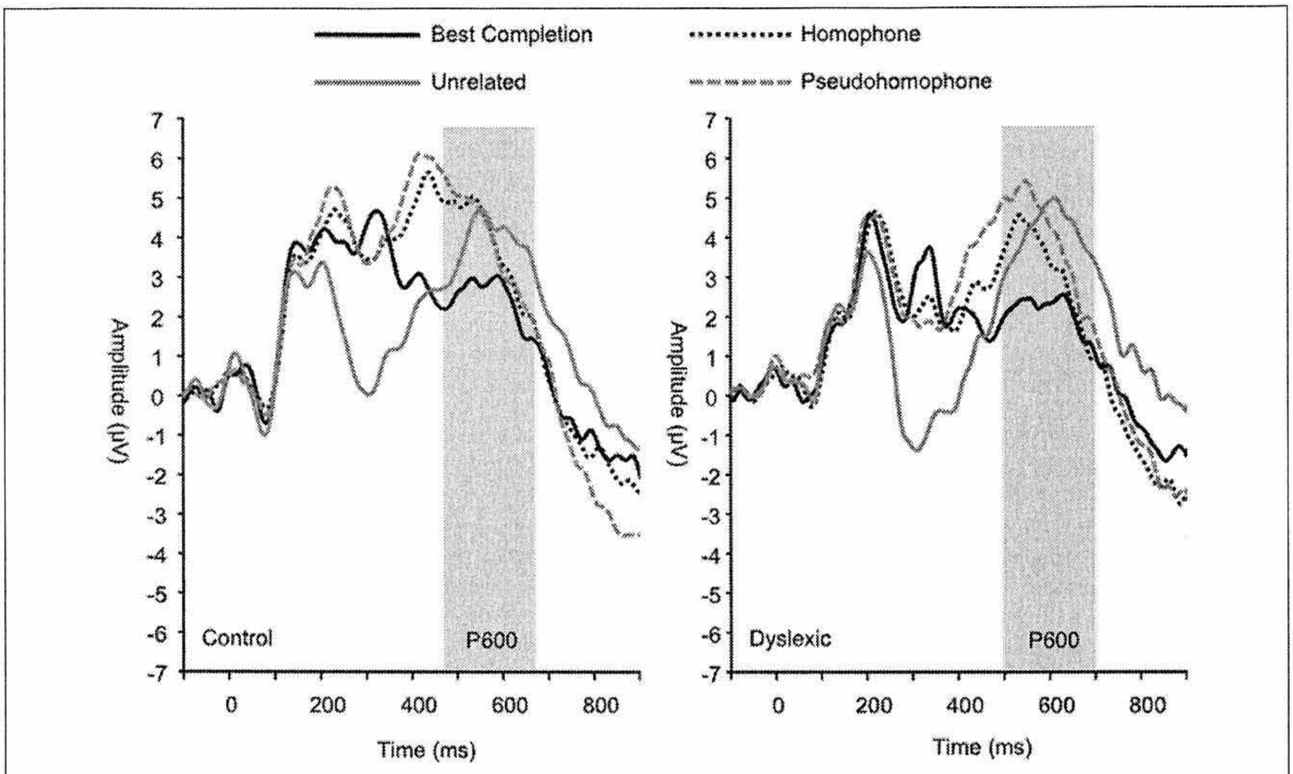

FIGURE 6 | Group grand averages showing the P600 peak, marked by the gray bar. Linear derivation of CP3, CP4, CPz, and Pz electrodes.

ERP analyses failed to show any significant group differences in experimental effects before the P3 range and no task-specific effects were found. N1 amplitude was generally smaller in the dyslexic group but no experimental effects within or between groups were observed. P2 and N2 amplitude were both significantly affected by the experimental manipulation but these effects did not interact with group. By contrast, the P2 peak was significantly delayed in the dyslexic group as compared to the control group, but again there was no group by condition interaction. Moreover, in the P3 range, pseudohomophone and homophone stimuli elicited a significant, albeit late, frontocentral P3a in control participants but failed to elicit a similar peak in this time window in the dyslexic group. The subsequent P600 wave peaked later in the dyslexic group but P600 amplitudes, which were increased to orthographically incorrect sentence completions, did not significantly differ between groups.

In this discussion we address the main result of our study, i.e., the differential P3a modulation in the two groups, first, and then we make observations regarding results in the N1, P2, N2, and P600 ranges.

P3a: DEFICIENT ORTHOGRAPHICALLY/PHONOLOGICALLY DRIVEN ORIENTATION OF ATTENTION IN DYSLEXIA?

We interpret the increase in P3a mean amplitude triggered by the homophone and pseudohomophone stimuli as a correlate of automatic attentional capture in the control group, because these stimuli had a "special" status: They were either the wrong completion which sounded like the correct completion in the "ortho-semantic" task or they were the correct completion but only in terms of phonology in the "phono-semantic" task. This special status prompted a P3a response that was not found for unambiguous targets or completely unrelated completions.

Critically, dyslexic participants failed to show this P3a modulation. The P3a is traditionally conceived as a response evoked over frontocentral areas of the scalp by the engagement of working memory following shifts in the orientation of attention (Squires et al., 1975; Donchin and Coles, 1988; Knight, 1997; Polich, 2007). It is classically elicited by deviant non-target stimuli in the context of an oddball paradigm (Courchesne et al., 1975; Knight, 1984; Katayama and Polich, 1996a,b; Spencer et al., 1999, 2001; Daffner et al., 2000; Simons et al., 2001; Debener et al., 2005; Sawaki and Katayama, 2006, 2007, 2008) and has been shown to be modulated by the degree of difficulty involved in discriminating distracters from targets (Cormerchero and Polich, 1998; Polich and Comerchero, 2003; Hagen et al., 2006). The P3a indexes automatic engagement of focal attention during stimulus evaluation (e.g., Katayama and Polich, 1998) for further processing of a stimulus as a potentially important signal (e.g., Daffner et al., 2000) and is thought to reflect context updating (Kok, 2001). In other words, our results suggest that normal readers automatically oriented their attention to these special, phonologically acceptable but orthographically unexpected stimuli, whereas dyslexic participants did not. This could stem from a visual–phonological integration failure or a general failure in orienting of attention to phonologically relevant material, possibly leading to deficient engagement of working memory, rather than a deficit in the perceptual decoding of orthographic and/or phonological information.

Previous studies have indeed reported reduced or absent P3a in participants with developmental dyslexia, using phonologically manipulated speech and tone oddball stimuli (Rüsseler et al., 2002; Fosker and Thierry, 2004; Hämäläinen et al., 2008). Fosker and Thierry (2004), for instance, found that the P3a elicited by phonological oddballs during an auditory lexical decision task in adult control participants was not found in the dyslexic group. However, when phonological oddballs were brought into the focus of attention, dyslexic participants produced P3b modulations comparable with controls (Fosker and Thierry, 2005). Rüsseler et al. (2002) have shown similar attentional modulations of dyslexic oddball effects on the P3 with tone stimuli. Anomalous frontal P3a-like modulations have also been shown in dyslexic adults engaged in tasks requiring shifts in spatial attention (Wijers et al., 2005). Overall, such results have led to the idea of impaired shifts and/or capacity for automatic attentional capture by phonological information rather than impaired phonological processing abilities.

This interpretation links with the literature derived from tasks with rapidly presented stimuli that propose disordered automatic orienting of attention (e.g., Facoetti et al., 2008) and sluggish attentional shifting in dyslexia (Hari and Renvall, 2001). Slow capture of attention has previously been observed in non-linguistic cued-detection and T2 detection in attentional blink tasks using visual and auditory stimuli in dyslexic children and adults (Brannan and Williams, 1987; Hari et al., 1999; Facoetti et al., 2003a,b, 2006, 2008, 2010; Buchholz and Aimola Davies, 2007; Lallier et al., 2010). Sluggish shifting of attention has also been reported in dyslexic individuals using auditory or visual stream segregation tasks (Helenius et al., 1999b; Petkov et al., 2005; Lallier et al., 2009). With respect to reading, sluggish attentional capture has been found to significantly predict non-word reading performance (Cestnick and Coltheart, 1999; Facoetti et al., 2006, 2010). Facoetti et al. (2008) hypothesized that a deficit in automatic attention could impact decoding due to deficient engagement and disengagement with each letter/grapheme. Such a deficit, along with the absence of the P3a in our dyslexic group, is unlikely to relate to a general deficit in automatic attention, as dyslexic participants have shown intact automatic orientation of attention in non-rapid tasks using nonverbal stimuli (Facoetti et al., 2008, 2010).

Although we did not test sluggish attentional shifting (since SOA was longer than 200 ms, e.g., Lallier et al., 2009), the present results are congruous with such interpretations derived from studies of visuospatial attention in decoding and whole word reading. In general terms, our data, which indicate a reduced tendency to react to, rather than detect, a mismatch between orthography and primed lexical phonological representations in dyslexia, are consistent with a deficit in engagement of attention with phonological information when it is not supported by expected orthographic mappings. In relation to visual attention hypotheses regarding developmental dyslexia, this could be due to a deficit in attentional engagement and disengagement with each letter/grapheme (Facoetti et al., 2008); and/or to under-specified orthographic representation in the lexicon of dyslexic individuals (Bosse et al., 2007; Prado et al., 2007; Lassus-Sangosse et al., 2008; Lallier et al., 2010). Alternatively, the absent P3a response in the dyslexic group could reflect a wider impairment in attentional filtering that could reduce their filtering of incorrect orthographic and/or relevant phonological stimuli. Roach and Hogben (2007, 2008) propose that such impairment would stem from a relative failure in uncertainty reduction in dyslexic individuals.

Importantly, the deviation in processing seems to be related to attentional capture rather than perceptual encoding or phonological access *per se*, since the dyslexic group studied here activated and accessed phonological lexical forms similarly to the control group (P2–N2 complex) as shown by the amplified response to homophones and pseudohomophones in the P2 range (see below, P2–N2 discussion). Furthermore, the significant correlations with RTs indicate that the attentional processes engaged in visual word analysis indexed by the P3a impact processing efficiency. How could this relate to reading difficulties more broadly? We suggest that a general weakness in engaging attention with orthographic–phonological correspondences could affect sensitivity to spelling and spelling errors, which in turn would impede the acquisition of accurate and stable lexical representations. Furthermore, our results are compatible with recent hypotheses of deficient working memory in relation to phonological analysis rather than perceptual encoding (e.g., Banai and Ahissar, 2006; Ramus and Szenkovits, 2008; Menghini et al., 2011).

A review of the neuroimaging literature in relation to P3a origins, orthographic–phonological mapping, and functional correlates of developmental dyslexia offers interesting insights into the neuroanatomical substrates likely to be involved in the process under study.

Firstly, patient and neuroimaging data have shown that temporoparietal cortex (TPJ) is fundamentally involved in P3 generation (both the P3a and P3b) with additional involvement from prefrontal areas in the case of the novelty P3a (Knight, 1984; Knight et al., 1989; Yamaguchi and Knight, 1991; Bledowski et al., 2004; Linden, 2005; Polich, 2007). The inferior parietal areas, in particular, have been implicated in attentional orienting based on stimulus relevance (Downar et al., 2001; Kiehl et al., 2001; Serences et al., 2005).

Secondly, left inferior parietal areas have been specifically implicated in the integration of orthographic and phonological information (Booth et al., 2002, 2004, 2007; Chen et al., 2002; Borowsky et al., 2006; Cao et al., 2006; Nakamura et al., 2006; Bitan et al., 2007; Graves et al., 2010; Newman and Joanisse, 2011) and more generally in sublexical decoding processes (e.g., Jobard et al., 2003; Levy et al., 2009; Graves et al., 2010), phonological judgments (Stoeckel et al., 2009; Hartwigsen et al., 2010), and verbal working memory involvement (see Ravizza et al., 2011). Note that inferior frontal areas have also been shown to be significantly activated during phonological tasks in which working memory load is high (e.g., Nixon et al., 2004; Strand et al., 2008; Thierry et al., 2003; Graves et al., 2010).

Thirdly, temporoparietal areas have consistently been shown to be underactivated in dyslexic readers (e.g., Hoeft et al., 2007; see Richlan et al., 2009 for a review) and inferior frontal areas frequently show abnormal activation (with greater activity associated with greater behavioral compensation; e.g., Hoeft et al., 2011 etc.). For instance, consistent with our interpretation, Cao et al. (2006, 2008) found reduced activations in left inferior parietal lobe of dyslexic children performing rhyme judgments on stimuli with conflicting orthographic and phonological information (e.g., pint-mint, jazz-has versus press-list, gate-hate), and reduced functional connectivity between left inferior parietal lobe and left inferior frontal and fusiform gyri.

This convergence of functional data regarding the TPJ and inferior frontal cortex in terms of (a) generation of the P3a, (b) phonological analysis in reading, and (c) loci of abnormal activation in dyslexia, provide empirical support for a functional link between attention, phonological processing in reading, and developmental dyslexia. Therefore, the P3a effects in the present study support the existence of a physiological relationship between attentional orienting mechanisms and phonological sublexical processing in reading; a relationship likely to be dysfunctional in developmental dyslexia.

N1: REDUCED ORTHOGRAPHIC SENSITIVITY IN DYSLEXIA?

Significant differences in visual word form processing between dyslexic and control readers in the P1–N1 range, thought to be letter-string specific, have previously been reported (Helenius et al., 1999a; Wimmer et al., 2002; Maurer et al., 2007; Taroyan and Nicolson, 2009; Savill and Thierry, 2011). In the present study, however, the only significant effect in the N1 range was an overall reduction in amplitude in the developmental dyslexic participants as compared to controls. This could be taken as a sign of reduced general sensitivity to orthographic stimuli (Maurer et al., 2005). However, the observation of smaller N1 overall may simply reflect greater latency variation in the dyslexic group yielding smaller average amplitudes (control N1 latency SD = 12.58; dyslexic latency SD = 15.04; see Picton et al., 2000). Alternatively, other random between–group differences unconnected to stimulus processing may have affected N1 amplitudes between groups. Overall, global N1 differences that are not qualified by an interaction with experimental conditions ought to be interpreted cautiously. Whilst reduced N1 amplitudes may index some form of reduced orthographic input in the dyslexic group that might contribute to the effects we observe downstream, such data alone can provide little supporting evidence of differential sensory integration mechanisms in developmental dyslexia and normal reading.

INTACT PHONOLOGICAL REPRESENTATIONS (P2 AND N2) BUT SLOW PROCESSING (P2 AND P600) IN DYSLEXIA?

Both participant groups showed similar amplification of the P2 in the homophone and pseudohomophone conditions relative to the unrelated condition, as well as similar attenuation of N2 mean amplitude in the homophone and pseudohomophone conditions relative to the unrelated condition, irrespective of task. This suggests that dyslexic readers' phonological representations of the anticipated word were well specified and that grapheme–phoneme conversion mechanisms allowed extraction and identification of the stimuli's phonological form not significantly different from that observed in control participants. This absence of differences between groups in the pattern of P2 and N2 mean amplitudes across experimental conditions suggests that a deficit in early sensitivity to phonological information may not be the main source of the persistent phonological deficit in reading, at least in the case of high-functioning dyslexic adults. Furthermore, a study similar to ours with Chinese dyslexic children using a sentence paradigm in which the second character of two-character Chinese words was replaced with homophonic or orthographically similar characters also failed to find group differences in P2 amplitude, but instead revealed P2 latency effects and later N400 modulations (Meng et al., 2007). The elicitation of earlier P2 latencies for homophonic replacements as compared to baseline in both groups suggests that early phonological extraction from orthography was intact in the dyslexic participants tested.

The P2 has been reported to be affected by stimulus salience in relation to task relevance (Potts and Tucker, 2001; Potts, 2004; Kieffaber and Herrick, 2005). In contrast to P3 modulations, it is not, however, thought to index orienting of attention (Potts, 2004). Thus, finding only group differences in the latency of the P2 suggests that the dyslexic group successfully identified the phonologically salient but semantically and orthographically incongruent homophones and pseudohomophones, albeit slower than controls. The significant P2 differentiation of the incorrect orthographic completions on the basis of phonological match (homophones and pseudohomophones versus unrelated conditions) discourages an alternative interpretation of the later P3a group difference being simply due to a general lack of orientation to orthographic form in the dyslexic group. Indeed, the later significant increases in P600 amplitude to incorrect orthographic completions relative to the best completion seen in both groups (in line with previous observations of P600 increases to misspellings in highly constrained sentences; Vissers et al., 2006) shows that the dyslexic group was sufficiently sensitive to orthographic form for incorrect forms to elicit stimulus re-evaluation. Furthermore, as homophones and pseudohomophones elicited the largest P2 amplitudes (rather than the best completion) in both groups, which is compatible with interpretations of frontal P2 amplitudes as sensitive to orthographic–phonological mapping and to competition between phonological and orthographic information, the absence of a later amplitude increase to the same stimuli within the P3a range in the dyslexic group suggests that the incorrect orthographic–phonological conflict was detected early but did not engage attention. In addition, ERP effects in the N2 range showed phonological integration in the dyslexic group (indexed by attenuated N2 amplitudes) comparable to both the normal readers in the present study and those tested in Savill et al. (2011). This also corroborates recent results in dyslexic readers (Savill and Thierry, 2011) and, on the basis of its occurrence immediately before the P3a window over the same electrodes, suggests that the emergence of dysfunctional phonological responses in reading coincides with the failure of attentional engagement.

The only group difference we observed prior to P3a amplitude effects was the finding that P2 latencies were longer overall for the dyslexic group. This P2 latency delay suggests that the initiation of phonological mapping may have been delayed, which, in turn, could account for the differences observed downstream in the P3a range. In the absence of a P3a peak in the dyslexic group, we cannot infer whether attentional engagement processes were progressively delayed, however the observation of P600 modulations involved in orthographic monitoring also peaked later in the dyslexic group suggesting that word recognition may be slowed down throughout the processing window. This finding is consistent with that of

Breznitz and colleagues, who found evidence for slower speed of processing during various forced-choice visual and auditory tasks, indexed by delayed P2 and P3 latencies in dyslexic readers (Breznitz and Meyler, 2003; Breznitz and Misra, 2003). These authors put forward the hypothesis of a temporal asynchrony between visual and auditory perceptual systems in dyslexia, which would affect word recognition because it requires synchronization of orthographic and phonological codes. Their and our data converge regarding the implication of slower engagement with orthographic and phonological code integration, in a context of intact perceptual analysis. However, our study differs in that it uses homophonic visual word stimuli and the consequent observation of a relative lack of attentional specificity in the context of orthographically inappropriate, but phonologically acceptable, stimuli. This contributes to the accumulating evidence supporting the key role of attentional processing in dyslexia and underlines the usefulness of techniques such as ERPs in the characterization of orthographic and phonological processing and, critically, the assessment of their interactions during reading.

CONCLUSION

In this study, we attempted to establish a link between the phonological deficit in dyslexia and visual word recognition using a reading task in a sentence context. The absence of a P3a modulation in dyslexic participants suggests that a failure to attend either to the correspondence between orthography and phonology, or to phonological relevance more generally, may be critical in the emergence of dyslexic symptoms, which may be exacerbated by slower initiation of ortho-phonological integration. By contrast, the absence of group differences in experimental effects in earlier time-windows immediately before the P3a peak (P2–N2 range) both suggests that early phonological extraction from orthographic stimuli may be intact and that dysfunction in sublexical analyses relating to phonological integration might not emerge until stages of attentional capture. However, one must be cautious before discarding earlier sensory integration mechanism deficits on the basis of null interactions. Future studies will further explore deficient orienting to orthographic forms and sensitivity to phonological information in relation to reading and the specificity of deficient orienting mechanisms in developmental dyslexia.

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APPENDIX

List of sentence stimuli.

Sentence stem	**BC**	**HOM**	**PSH**	**UNR**
Anti-war activists want world	peace	piece	peece	heavy
Emily combed Sylvia's beautiful	hair	hare	heyr	window
The moon shines at	night	knight	nyte	face
The dog was wagging its	tail	tale	tayl	yell
Baking bread involves kneading the	dough	doe	dow	unit
Instead of hands, cats have	paws	pause	porze	tap
There are 7 days in a	week	weak	weec	desk
Marie was not sure which dress to	wear	where	wair	register
The prisoner was locked in his	cell	sell	sel	germ
An eagle is a bird of	prey	pray	prai	flare
Pierre recommended a bottle of French red	wine	whine	wighn	boat
The jockey put the saddle on his	horse	hoarse	hauce	music
Pectorals and triceps are both types of	muscle	mussel	mussle	dawn
The gas man visited to read the	meter	metre	meater	prune
The little boy did as he was	told	tolled	toled	short
Clare went on a diet to lose	weight	wait	wate	string
The police quickly arrived at the murder	scene	seen	sene	ram
Groups work best if they work as a	team	teem	tiem	spice
The lecturer used a microphone so everyone could	hear	here	hier	point
Susan got some lozenges because her throat was	dore	soar	sawe	brute
Rob looked at his watch to check the	time	thyme	tyme	thwart
More troops were recruited to fight in the	war	wore	worr	mass
The bride's father proudly walked her down the	aisle	isle	ighl	fairy
The children were scared when they heard the lion	roar	raw	rore	cook
Umbrellas are used to stop getting wet from the	rain	rein	reyn	biscuit
At football today, Nick did not bother to pass the	ball	bawl	baul	dog
In front of the hotel is a beautiful sandy	beach	beech	beetch	train
They watched the car until it was out of	sight	site	syte	broke
The shop did not have the shoes in Anne's	size	sighs	seiz	act
Heather sang the song with her whole heart and	soul	sole	sowl	next
Gerard had over 100 vintage wines in his	cellar	eller	sella	ache
Kelly was annoyed at how much mess her kids had	made	maid	meyed	east
Pete took the lift to his office on the fifth	floor	flaw	flore	cost
The postal service in Britain is run by the Royal	mail	male	mayel	sting
Linda was 9 months pregnant, she was about to give	birth	berth	burth	plane
Rita tried to find the supermarket till with the shortest	queue	cue	quew	rapid
The defendant was relieved that the jury was on his	side	sighed	syed	pouch
The son inherits his father's possessions because he is the rightful	heir	air	ehr	frail
Andrew broke his leg and therefore was in a lot of	pain	pane	payn	mince
Jim put a belt on to keep his trousers around his	waist	waste	wayst	skull
Before walking up the garden path, Edmond had to open the	gate	gait	gayt	bone
When Lucy went to the seaside she took her bucket and	spade	spayed	spaid	garlic
The plumber came to fix the pipe that had sprung a	leak	leek	leec	blanket
They played eye-spy in the car to stop the children from getting	bored	board	borde	moral
If you are in debt, you may need to take out a	loan	lone	lown	open
She set her alarm clock to go off very early in the	morning	mourning	mawning	power
Sally put a lot of sugar in her coffee as she liked it really	sweet	auite	swete	urban
The length of time a king is on the throne is described as his	reign	rain	wrayn	outset