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Neurodynamics of selected language processes involved in word reading: An EEG study with French dyslexic adults

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ABSTRACT

This event-related potential (ERP) study aimed to examine at which point in the stream of four cognitive processes of word reading impairment occurs in dyslexic adults. Fourteen French native dyslexic speakers and eighteen matched controls performed a delayed phonological lexical decision task that consisted in deciding whether visual stimuli sounded like French words. Three hundred stimuli equally distributed among five experimental conditions (60 concrete French words, 60 pseudo-homophones, 60 pseudowords, 60 consonant and 60 symbol strings) were presented. Critically, two language processes involving phonological information, namely grapheme-to-phoneme conversion (N320) and memory retrieval of phonological information (Late Positive Complex) were impaired in dyslexics compared to controls. Moreover, lexical access (N400) was significantly modulated by six predictive variables assumed to be reliable markers of dyslexia. In contrast, and unexpectedly, the early processes of visual expertise for print (N170) appeared to operate in the same way in the two groups of participants. The locus of dyslexia is probably to be found primarily in some aspects of phonological processing during word reading. These findings support a clinical neurophysiology model postulating that at least two phonological processes during reading might be impaired in dyslexics, namely grapheme-to-phoneme conversion, and memory retrieval of phonological information.

1. Introduction

Reading is a complex cognitive skill that entails a cognitive processing stream involving several language processes, among which perceptual decoding of letters, grapheme-to-phoneme conversion, lexical access, and retrieval of phonological information from long-term memory. Although cognitively complex, reading skills are acquired without much difficulty by most children in their first language. However, those suffering from developmental dyslexia have problems learning to read, despite normal intelligence, adequate schooling and no neurological or sensory impairments (American Psychiatric Association, 2013). This reading disorder is characterized by lower accuracy and speed when reading in comparison with normal readers (Marchetti, Vaugoyeau, Colé, & Assaiante, 2022). It affects 5–10% of the school-age population (Peterson & Pennington, 2012).

The etiology of developmental dyslexia is still debated, and several hypotheses have been proposed (Stein, 2018). One of the most prevalent hypotheses is that of a phonological deficit. According to this hypothesis, dyslexics have difficulties in (1) recognizing and

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manipulating speech sounds (phonological awareness), (2) repeating pseudowords (verbal short-term and working memory), and (3) speedily naming lists of letters, digits, colors, or objects (Rapid Automatized Naming, RAN) (Snowling, 2001; Wagner & Torgesen, 1987). An alternative neurobiological hypothesis proposes “that the core difficulties in dyslexia reside in atypical neural oscillations” (Lallier, Molinaro, Lizarazu, Bourguignon, & Carreiras, 2017, p. 379). According to Lallier et al. (2017), this latter hypothesis is derived from theories postulating oscillatory neural activity as factors affecting the development of reading skills (Giraud & Ramus, 2013; Goswami, 2011).

There is an ongoing debate in the literature on whether phonological or visuo-attentional deficits are more prominent in dyslexia. The visual attention span (VAS) deficit hypothesis proposed by Valdois and her group (Bosse, Tainturier, & Valdois, 2007). “Posits that a subset of dyslexic individuals shows a multielement parallel processing deficit due to reduced visual attention capacity” (Valdois, 2022, p. 379). At the neurobiological level, a key role of the superior parietal lobules has been shown in this process as well as in the visuo-attentional deficits associated with developmental dyslexia (Peyrin et al., 2012). The debate centers on whether individuals with dyslexia exhibit a VAS deficit, involving difficulties in processing not only alphanumeric stimuli such as letters and numbers but also non-verbal symbols. The VAS theory posits that dyslexics should struggle in both letter and symbol-string tasks, providing strong support for visuo-attentional processing issues. On the contrary, difficulties in processing verbal characters such as letter strings but not symbols may support a phonological deficit in dyslexia. However, research findings are inconsistent. Some studies report worse symbol-string processing in dyslexics, supporting the VAS theory (Jones, Branigan, & Kelly, 2008; Lobier, Zoubrinetzky, & Valdois, 2012; Pammer, Lavis, Hansen, & Cornelissen, 2004; Zhao, Liu, Liu, & Huang, 2018), while others fail to find a deficit (Banfi et al., 2018; Cheng, Yao, Wang, & Zhao, 2021; Shovman & Ahissar, 2006; Yeari, Isser, & Schiff, 2017; Ziegler et al., 2010; for a review see Valdois, 2022). Another hypothesis associated to visual processing impairments in dyslexia is the magnocellular deficit hypothesis supporting an impairment in the magnocellular neurons of individuals with dyslexia (Livingstone, Rosen, Drislane, & Galaburda, 1991; Stein, 2019, 2022). According to this framework, visual impairments in dyslexia could lead to abnormal eye movements during reading (for a review see Premeti, Bucci, & Isel, 2022).

From an experimental point of view, testing the phonological hypothesis comes up against a major difficulty. Phonology is involved in the language processing system at different levels of linguistic analysis, such as phonological representation of linguistic units of different sizes (i.e., phoneme, syllable, word, sentence), or grapheme-to-phoneme conversion. Consequently, the search for the causes of developmental dyslexia is complicated, even if the disorder is confined to the phonological domain. Moreover, the issue of whether it is the nature of the phonological representations that is under-specified in dyslexics and/or the access to these representations remains an open question that is difficult to address experimentally (Ramus & Szenkovits, 2008). Unfortunately, experimental tasks designed for studying phonology involve not only pure phonological information, but also mental manipulations of speech sounds and even substantial short-term or working memory load. Moreover, these tasks are usually performed under time pressure. (Ramus & Ahissar, 2012; Ramus & Szenkovits, 2008).

The central aim of this study was to investigate which of the cognitive processes involved in reading are impaired in dyslexics. Our goal was to provide new neurophysiological evidence on different cognitive processes thought to be involved in reading with adult dyslexic native speakers of French using a delayed phonological lexical decision task. Given the speed of these language processes, we decided to use electroencephalography (EEG) to trace them with a high temporal resolution (millisecond range).

Since the 1980s, neuroimaging techniques and in particular EEG have made it possible to study online different language processes in healthy individuals (Kutas & Federmeier, 2011) but also in subjects suffering from language disorders such as developmental dyslexia (Premeti et al., 2022, for a review). Cognitive neuroscientists have identified specific electrical brain responses, i.e., event-related potentials (ERP), associated to various language processes. These ERP signatures have proven to be relevant indexes for modeling the functional architecture of the language processing system. From a modeling point of view, psycholinguists proposed dual-route models of reading based on reaction times. Among the most influential models, the Coltheart, Rastle, Perry, Langdon, and Ziegler (2001) model proposed two main distinct processes for reading after initial visual feature and orthographic processing. The direct or lexicosemantic route associates meaning directly with the visual form of words since word meaning has been stored in the mental lexicon, while the indirect or graphophonological route requires the association of graphemes to phonemes to access meaning. The reading of non-words, pseudowords, unknown words and low-frequency words is thought to be achieved through the indirect route. ERP data have challenged these models, enriching neurocognitive models of language processing (Friederici, 1995, 2002, 2011; Hagoort, 2005; Hasko, Groth, Bruder, Bartling, & Schulte-Körne, 2013; Molinaro, Barber, & Carreiras, 2011).

First and foremost, learning to read requires decoding letters at a pre-lexical processing stage. Previous ERP studies in normal readers suggested that the N170 (or visual N1) is a reliable marker of visual expertise for print (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Brem et al., 2006; Maurer, Brem, Bucher, & Brandeis, 2005a). The N170 is recorded over left-distributed occipitotemporal brain regions and peaks between 150 and 250 ms post-onset stimulus in skilled readers (Bentin et al., 1999; Brem et al., 2006; Maurer et al., 2005a; Maurer et al., 2007). A larger amplitude of the N170 for alphabetic stimuli than for strings of symbols has been reported in different languages in both adults (French: Bentin et al., 1999; Swiss-German: Brem et al., 2006) and children (German: Maurer, Brandeis, & McCandliss, 2005; Maurer et al., 2005a; Maurer, Brem, Bucher, & Brandeis, 2005b; Maurer et al., 2006) with normal reading ability. The N170 component has been linked to neural generators located in a particular region in the middle portion of the left fusiform gyrus known as the Visual Word Form Area (VWFA) (Cohen et al., 2000, 2002; Dehaene, 2010; McCandliss, Cohen, & Dehaene, 2003). This association has been observed in research that combines functional magnetic resonance imaging (fMRI) with ERPs (Brem et al., 2006), or uses ERPs source analysis (Brem et al., 2006, 2009; Maurer et al., 2005b). This area plays a crucial role in processing visual word forms and is notably activated when exposed to word-like stimuli (Cohen et al., 2000; McCandliss et al., 2003). Similarly, using intracranial EEG, Nobre, Allison, and McCarthy (1994) found at around 200 ms an ERP component unique for letter presentation in the posterior fusiform gyrus, unaffected by semantic priming or the lexicality effect, confirming the

reliability of the left-lateralized N170 ERP as a marker for visuo-orthographic processing. Moreover, it has been shown that children and adults with dyslexia exhibit a decreased activation of the VWFA (Maurer et al., 2007; McCandliss et al., 2003; Paulesu et al., 2001). In a recent review, Amora et al. (2022) reported that while most studies found a smaller N170 effect of visual expertise for print in different languages in dyslexics compared to control adults (e.g., Mahé, Bonnefond, & Doignon-Camus, 2013, 2012 in French), and children (e.g., Hasko et al., 2013 in German; Araújo, Bramão, Faisca, Petersson, & Reis, 2012 in Portuguese), a few studies failed to show any difference in the N170 effect between dyslexic and control adults (in Portugal: Araújo, Faisca, Bramão, Reis, & Petersson, 2015) and children (Maurer et al., 2011). This inter-study discrepancy could be explained by the severity of the reading deficit of the dyslexic participants included in the studies suggesting that the severity of reading and spelling impairments could impact orthographic processing in varying proportions (Mahé, Bonnefond, Gavens, Dufour, & Doignon-Camus, 2012; Maurer et al., 2011; Varga, Tóth, Amora, Czikora, & Csépe, 2021). It could also be explained by language transparency, since neurophysiological activations can be attributed to the consistency of grapheme-to-phoneme conversions of each language (Ziegler, Perry, Ma-Wyatt, Ladner, & Schulte-Körne, 2003, 2008). In addition, the rehabilitation received by a dyslexic should also improve sensitivity to print.

The next reading marker examined, the N320, is thought to signal the process of grapheme-to-phoneme conversion. It presents a peak at around 320 ms post-stimulus. It presents a bilateral distribution over the midtemporal gyrus, i.e., a cortical region. In normal readers, its amplitude has been found to be larger in response to phonologically pronounceable stimuli than non-pronounceable stimuli and especially in the left hemisphere in adults (Bentin et al., 1999; Simon, Bernard, Largy, Lalonde, & Rebaï, 2004, 2006), associated with phonological processing (Hagoort et al., 1999; Price et al., 1994). With respect to dyslexia, Araújo et al. (2015) compared the processing of phonologically legal (pseudowords) and phonologically illegal (non-words) stimuli in Portuguese expert readers. The authors reported a larger N320 component for phonologically legal than for phonologically illegal stimuli in the group of expert readers, but not in dyslexic readers. Moreover, comparing pseudowords and words in a spatiotemporal analysis, Mahé, Pont, Zesiger, and Laganaro (2018) found reduced N320 responses for both words and pseudowords in French dyslexic adults as compared to controls. Note however that this between-group difference was not reported by Araújo et al. (2012) in a study focusing on Portuguese children with and without dyslexia. In the same vein, neuroimaging studies have reported alterations within the structures underlying letter processing and grapheme-to-phoneme correspondences in dyslexic readers. A decreased activation in the left occipitotemporal areas associated with orthographic identification and integration has been reported in dyslexics (Blau et al., 2010; Kronbichler et al., 2006; Richlan et al., 2010; van der Mark et al., 2009; Wimmer et al., 2010). In addition, studies focused on dyslexia have reported an underactivation in the inferior parietal, superior temporal, middle and inferior temporal, inferior frontal gyrus and fusiform regions of the left hemisphere (for a meta-analysis, see Richlan, Kronbichler, & Wimmer, 2009). Underactivations have also been found in the left superior temporal gyrus (Blau, Atteveldt, Ekkebus, Goebel, & Blomert, 2009), as well as on the left supramarginal (Rumsey et al., 1997) and the left angular gyrus (Rumsey et al., 1997; Shaywitz et al., 1998). Analogous results in children have reported an underactivation of the middle portion of the middle temporal gyrus (Maurer, 2011), of the left posterior superior sulcus (Maurer et al., 2011) and on the left temporoparietal areas including the posterior part of the superior temporal, angular and supramarginal gyri (Simos et al., 2000). The underactivation of regions that are associated to phonological processing and more precisely to grapheme-to-phoneme conversion and letter to sound integration (Van Atteveldt, Formisano, Goebel, & Blomert, 2004) may indicate deficiencies in the automatic application of the grapheme-to-phoneme conversion rules. According to Blomert (2011), neuroimaging studies show that although individuals with dyslexia acquire associations between letters and speech sounds, this mechanism of conversion does not seem to be fully automated. Finally, some fMRI studies have reported an altered connectivity between the inferior parietal lobule and the visual word form area in dyslexia (Di Pietro et al., 2023).

At the lexical level, a well-known ERP component studied in different languages and different populations, i.e. the N400, is associated to lexical-semantic integration processes (Kutas & Hillyard, 1980). It peaks between 300 and 500 ms over centroparietal regions. The N400 exhibits an increase in amplitude for semantically unrelated information when compared to semantically related content or when information violates expectations (Isel, Hahne, Maess, & Friederici, 2007; Kutas & Federmeier, 2011; Kutas & Hillyard, 1980). In addition, Van Petten and Kutas (1990) highlighted another functional role of the N400, namely access to the lexicon. The lexical N400 effect is reflected by a larger N400 amplitude in response to low lexical frequency word processing compared to high lexical frequency word processing (for a review, see Kutas & Federmeier, 2011). Moreover, it has also been shown in adults that the N400 was larger for pseudowords than for words; this lexicality effect is consistent between languages (German: Braun et al., 2006; Briesemeister et al., 2009; Hutzler et al., 2004; Spanish: Carreiras, Vergara, & Barber, 2005). Regarding dyslexia, several studies reported a significantly reduced N400 amplitude in dyslexic adults compared to controls in both a visual word recognition task in English with words varying with respect to word frequency (Johannes, Mangun, Kussmaul, & Münte, 1995) and a discrete object-naming task in Portuguese (Araújo, Faisca, Reis, Marques, & Petersson, 2016). With respect to latency, fewer studies have reported latency differences in dyslexics with respect to normal readers. Rüsseler, Becker, Johannes, and Münte (2007) found that the N400 peaked around 92 ms earlier in normal German readers than in dyslexics, and that the plateau of the waveform lasted around 32 ms longer in the dyslexics than in the controls.

Finally, regarding later phonological processing, we will now introduce the last of the ERP components studied in the processing chain addressed in this study, namely the Late Positive Component (LPC; also known as P600 (Savill & Thierry, 2011);). The LPC is assumed to reflect the process of retrieving phonological information from memory. It occurs between 500 and 900 ms after stimulus presentation over centro-parietal regions (Hasko et al., 2013). The LPC might be associated to word recognition memory, as evidenced by its higher amplitudes in response to correctly recognized old words compared to new words (Rugg & Curran, 2007). In a study on German dyslexic and control children, Hasko et al. (2013) showed that the LPC over the left centro-parietal electrodes was larger for familiar words and pseudohomophones than for pseudowords, but in controls only. This result was taken as evidence that the easier it is to retrieve phonological information from memory (word, pseudohomophone), the greater the amplitude of the LPC should be.

Consistently with this possible functional role of the LPC, both [Rüsseler, Probst, Johannes, and Münte \(2003\)](#) in German and [Rasamimanana, Barbaroux, Colé, and Besson \(2020\)](#) in French reported significantly reduced amplitudes of LPC in dyslexics compared to controls using either an old/new task (i.e., deciding whether a word had already been presented or not) or a matching task with previously learned associations between images and monosyllabic words. The authors suggested that their results could be taken as evidence that dyslexics have difficulties in retrieving phonological information from long-term memory compared to control readers. Interestingly, [Savill and Thierry \(2011\)](#) using a phonological priming paradigm with a phonological judgement task also reported a smaller amplitude of LPC in dyslexics compared to controls over a cluster of centroparietal electrodes without specific lateralization to the left or right hemisphere.

1.1. This study

The aim of this study was to further examine which language processes assumed to be involved during word reading, namely visual expertise for print, grapheme-to-phoneme conversion, word recognition and retrieval of phonological information in long-term memory, may be impaired in developmental dyslexia. The strength of our approach was to examine the neurodynamics of four different reading processing stages using the same experimental design in the same 32 participants who saw 300 stimuli of different kinds. Participants performed a delayed phonological lexical decision task in which they had to decide whether each visually presented string sounded like a French word. We specifically chose this task because it requires readers to perform a lexical search among the phonological representations stored in their mental lexicon (for a discussion of a lexical unit, see [Levelt, 1989](#)). In order to study the role of phonological and orthographic information in reading, we compared stimuli involving either both phonological and orthographic representations (word), one of them, namely phonological representation (pseudohomophone), or none (pseudoword and consonant). Moreover, we added a symbol condition which, compared to the other conditions, allowed us to study the sensitivity to visual expertise for print. Consequently, we manipulated the type of stimulus involving different levels of sublexical and lexical orthographic and phonological processing, i.e., 60 concrete French words (e.g., *chaise*, 'chair'), 60 pseudohomophones (i.e., **chèse*), 60 pseudowords (i.e., **chuse*), 60 consonant strings (i.e., **nbvrzc*), and 60 symbols (i.e., *§ÇYD&*). Based on previous studies, we selected different ERP markers known to be potentially associated with the different language processes under investigation. Among them, the N170 (visual expertise for print), the N320 (phonological processing and grapheme-to-phoneme conversion), the N400 (lexical access), and the LPC (late retrieval of phonological information in long-term memory). The uniqueness of our study lies in the investigation of a pipeline of language processes involved in reading through suitable ERP markers, all within a single task. Moreover, we studied these processes in adults, specifically in highly educated students, a population that has been less explored in dyslexia research. In doing so, our study sheds new light on the functioning of reading processes in adults by setting aside developmental factors typically involved in developmental studies. The examination of various ERP markers allowed us to trace online with a high temporal resolution which processing steps are impaired in dyslexia. This approach enables us to clarify the roots of dyslexia which can be found on a continuum ranging from early visual processing to phonological information retrieval from long-term memory. Examination of these points will contribute to a more unified and complete understanding of how the reading mechanism works in dyslexia.

1.2. Predictions

Firstly, with respect to orthographic processing, we hypothesized that if visual expertise for print is disturbed in developmental dyslexia, we should observe a reduced N170 effect (the N170 in response to the stimuli containing non alphabetic characters, i.e., symbols) subtracted from the N170 in response to the stimuli containing alphabetic characters (i.e., words, pseudohomophones, pseudowords, consonant strings) in the dyslexic group compared to the control one. Additionally, a more focused analysis should lead to predicting a difference between consonants and symbols but only in controls. This should be due to a reduced sensitivity to print in dyslexics.

Moreover, if grapheme-to-phoneme conversion is dysfunctional in dyslexics, then we expect lower N320 amplitudes in dyslexics than in controls. We also expected to highlight this inter-group difference by comparing pronounceable (pseudowords) to unpronounceable stimuli (consonant strings).

At the lexical level, based on the hypothesis that dyslexics have an impaired lexical access, a reduced lexicality N400 effect (words against pseudowords) should be expected in dyslexics compared to controls.

Finally, under the hypothesis that retrieval of linguistic information from long-term memory is disrupted in developmental dyslexia, smaller LPC effects in dyslexics than in controls when comparing words and pseudohomophones against pseudowords (no phonological representation) should be observed.

2. Methods

2.1. Participants

Fourteen adults with developmental dyslexia (6 males; mean age = 21.2 ± 0.6 years) and eighteen control adults (5 males; mean age = 21.1 ± 0.5 years) took part in this study. All were native French speakers with normal or corrected-to-normal vision (more than 8/10 in each eye according to Parinaud's optometric scale; [Parinaud, 1888](#)) and presented no neurological or cognitive problems. They were all right-handed as assessed by the Humphrey Laterality Questionnaire ([Hécaen & Ajuriaguerra, 1963](#)). Dyslexics and controls were matched in age, biological gender and educational level. All dyslexic participants had been diagnosed during childhood (mean

age of diagnosis = 7.5 ± 2.1 years) and had completed several years of remediation training with a speech therapist (mean = 8.4 ± 3.5 years). All participants were students at Nanterre University and other higher educational institutions in Paris, France. They were recruited through announcements from the university, specifically by the “Disabilities and Accessibility Service,” as well as official recruitment sites for participants in experiments.

2.2. Screening tests

Prior to the ERP experiment, all participants performed a battery of standardized tests in order to assess their reading skills, phonological awareness, visuo-attentional skills and non-verbal intelligence. Reading skills were evaluated with the French reading test *L'Alouette* (Lefavrais, 1965), which determines a reading age as a function of both reading time and number of errors. The ECLA 16+ Battery Test (Gola-Asmussen, Lequette, Pouget, Rouyer, & Zorman, 2011) was employed to measure several reading abilities (Text reading (*Pollueur*), regular and irregular word reading and pseudoword reading, phonological skills (initial phoneme deletion, spoonerisms, non-word repetition), and rapid letter naming). Visuo-attentional skills were evaluated with a five-consonant global report task (Bosse et al., 2007). Nonverbal intelligence was evaluated by the Matrices and the similarities subtests of the Wechsler Adult Intelligence Scale IV (WAIS-IV) (Wechsler, 2009). As can be seen in Table 1, dyslexic and non-dyslexic readers performed differently in most of these tests. All dyslexic participants were below the efficiency threshold score proposed by (Cavalli et al., 2018).

The study was approved by the local ethics committee of the Institutional Human Experimentation Committee of Lille University in France (DYS-EEG-EM N° 2020-441-S87) and was performed in accordance with the principles of the Declaration of Helsinki. Written consent was obtained from all participants after they had been informed of the experimental procedure. All participants were paid 15 euros per hour for their participation. The whole procedure lasted approximately 2 h.

2.3. Linguistic materials

A total of 300 stimuli equally distributed in 5 conditions were selected: (1) Sixty words (W) (e.g., *chaise*^{chair}) were chosen in the French database *Lexique 3* (New, Pallier, Ferrand, & Matos, 2001). All the words were monosyllabic concrete nouns of five to six letters with a high frequency of occurrence per million (45.0–592.2, $M = 148.1$, $SD = 110.9$). Most of the stimuli have a frequency of above 100 per million. Moreover, both orthographic ($M = 4.8$, $SD = 3.8$) and phonological ($M = 10.9$, $SD = 6.6$) neighbors, number of homographs ($M = 1.4$, $SD = 0.6$) and homophones ($M = 3.5$, $SD = 1.9$) were also controlled in order to select the final sample of 60 words (for detailed word features, see Table 2); (2) Sixty Pseudohomophones (PH) that are not lexicalized in French but are pronounced in the same way as French words. These stimuli have a phonological representation in the French lexicon but not an orthographic one (**chèse*^{same pronunciation as “chaise” (chair)}). These pseudohomophones were created from the 60 French words used in the Word condition of this study by replacing one phoneme with another one, or by adding or eliminating a double consonant or a silent letter (Farioli, Grainger, & Ferrand, 2011); (3) Sixty pseudowords (PW) i.e., stimuli that are phonotactically and orthotactically legal in French but

Table 1
Assessment of reading and other cognitive functions of participants.

	Control readers	Dyslexic readers	Group difference
Age (years)	21.1 ± 0.5	21.2 ± 0.6	$t(31) = -0.133$, ns
No-meaning text reading (words correctly read/minute)	143.8 ± 5.9	101.7 ± 4.3	$t(31) = 5.444$, p***
No-meaning text reading (Reading efficiency Score, CTL)	430.7 ± 17.7	304.9 ± 13.5	$t(31) = 5.444$, p***
Text reading (words correctly read/minute)	204.9 ± 5.8	148.1 ± 7.8	$t(31) = 5.983$, p***
Regular word reading (score/20)	19.3 ± 0.2	18.7 ± 0.3	$t(31) = 1.908$, mg
Regular word reading (time in seconds)	11.0 ± 0.6	19.9 ± 1.9	$t(31) = -4.901$, p***
Irregular word reading (score/20)	18.8 ± 0.4	17.6 ± 0.5	$t(31) = 1.997$, mg
Irregular word reading (time in seconds)	10.6 ± 0.6	18.1 ± 1.7	$t(31) = -4.499$, p***
Pseudoword reading (score/20)	18.6 ± 0.3	17.0 ± 0.6	$t(31) = 2.572$, p*
Pseudoword reading (time in seconds)	16.2 ± 1.4	33.2 ± 2.5	$t(31) = -6.346$, p***
Initial phoneme deletion (score/10)	8.9 ± 0.3	7.9 ± 0.7	$t(31) = 1.473$, ns
Initial phoneme deletion (time in seconds)	38.8 ± 2.8	50.3 ± 2.4	$t(31) = -2.992$, p**
Spoonerisms (score/20)	18.7 ± 0.3	14.1 ± 1.2	$t(31) = 4.016$, p***
Spoonerisms (time in seconds)	89.2 ± 8.5	216.4 ± 31.5	$t(31) = -4.351$, p***
Non-word repetition (score/20)	19.0 ± 0.1	18.6 ± 0.3	$t(31) = 1.252$, ns
Non-word repetition (time in seconds)	68.8 ± 2.2	78.6 ± 3.2	$t(31) = -2.620$, p*
Rapid automatized naming (RAN) letter (score/50)	49.6 ± 0.1	47.7 ± 1.7	$t(31) = 1.277$, ns
Rapid automatized naming (RAN) letter (time in seconds)	16.1 ± 0.7	22.4 ± 1.5	$t(31) = -4.032$, p***
Visuoattentional span (score/100)	93.1 ± 1.4	75.9 ± 4.2	$t(31) = 4.266$, p***
Similarities subtest WAIS IV (standard note)	10.8 ± 0.5	10.1 ± 0.6	$t(31) = 0.872$, ns
Matrices subtest WAIS IV (standard note)	10.5 ± 0.6	10.1 ± 0.3	$t(31) = 0.509$, ns

Mean value (\pm standard error of mean) for the different tests run for the two groups of participants (control readers, dyslexic readers).

not significant (ns) = $p > 0.10$; marginal (mg) = $0.05 < p < 0.10$; $0.01 < p < 0.05$; $0.001 < p < 0.01$; $p < 0.001$. The formula to calculate the reading efficiency score on the Alouette no-meaning reading test is: “CTL: $A \times 180/RT$ ”, where “A” represents the number of words correctly read (including self-corrections, with a maximum value of 265), and “RT” refers to the reading time taken to read the text (with a 3-min time limit or a maximum value of 180 s). In the abbreviation CTL, the letter “C” stands for the count of words accurately read, while “TL” represents the reading time or the amount of time taken to read the text (Cavalli et al., 2018).

Table 2

Means (\pm standard deviations) for the words' characteristics. Information taken from the French database *Lexique 3* (New et al., 2001).

Characteristics	Mean (\pm SD)
Lexical frequency	148.1 \pm 110.9
Number of homographs	1.4 \pm 0.6
Number of homophones	3.5 \pm 1.9
Number of orthographic neighbors	4.8 \pm 3.8
Number of phonological neighbors	10.9 \pm 6.6

that are not lexicalized. PW were created from the word condition by changing one grapheme of the word in initial, median, or final position of the word such that the resulting string does not exist in French, e.g., **chuse*); (4) Sixty *consonant strings* (CS) which are sequences with no syllables. They are orthographically illegal and phonologically unpronounceable strings such as **nbvrzc*. Consonant strings were matched for their shape with words so that each ascender letter was matched to an ascender letter and each descender letter to a descender letter; (5) Sixty *symbol strings* (SS; non-alphabetic stimuli; § $\text{\textcircled{C}}\text{\textcircled{D}}\text{\textcircled{E}}$). Symbol strings were matched for the number of characters with high frequency words. We used 12 symbols as in a previous ERP study by Mahé et al. (2012). Words, pseudohomophones and pseudowords were matched on number of syllables, letter and bigram frequency (based on the Lexique-Infra 1.11 database; Gimenes, Perret, & New, 2020; $p > 0.05$ for all comparisons). French is considered as a language of low transparency; it is highly inconsistent from phonology to spelling, and less consistent from spelling to phonology (Ziegler, Jacobs, & Stone, 1996). All the words used in the experiment are complex from a spelling point of view as they are composed of bigrams, but this factor was kept constant for all stimuli in our study. In addition, words and pseudowords were also matched on number of letters ($p > 0.05$). It was not possible to match Pseudohomophones with Words and Pseudohomophones on number of letters since the creation of the Pseudohomophones was partly based on adding or eliminating a letter from the corresponding Words (see also Farioli et al., 2011). A list of the stimuli used is given in the Appendix.

2.4. Experimental design

Stimuli were presented in “Arial Narrow” font, with 47-point lower case letters. The 300 stimuli were distributed in 5 blocks of 60 stimuli each (12 stimuli from each of the 5 categories). In each block, the stimuli were pseudorandomized according to the following constraints: (1) no more than two stimuli of the same category were presented in succession, and (2) no more than three stimuli requiring the same response YES or NO followed one another. Words and their corresponding pseudohomophones were not presented within the same block.

Before starting the experiment, participants carried out a practice block of 12 trials that were not presented in the experiment trials. During the training session, feedback was given to the participants to ensure that they understood the task. Participants were tested individually in a soundproof room during continuous EEG. The experiment lasted around 30–40 min for each participant.

Participants performed a delayed phonological lexical decision task (Bergmann & Wimmer, 2008; Hasko et al., 2013; Kronbichler et al., 2007; van der Mark et al., 2009) in which they had to decide as accurately as possible whether each visually presented stimulus sounded like a French word, by pressing a YES (for the “word” and “pseudohomophone” conditions) or NO (for the “pseudoword”, “consonant string” and “symbol string” conditions) computer key. We chose the offline version of the phonological lexical decision task in order to avoid motor artifacts on the critical ERP. This task was designed with a delay of 1300 ms post-stimulus offset to reduce the impact of task-dependent decision-making and verification procedures on the EEG signal. All stimuli were presented in the center of the screen, at eye-level, approximately 90 cm away from the participants and ranged from 2.0 to 2.5° of visual angle. The Matlab software (version 9.10.0.1684407, R2021a), and the Psychtoolbox extensions (version 3.0.16) (Brainard, 1997; Kleiner et al., 2007;

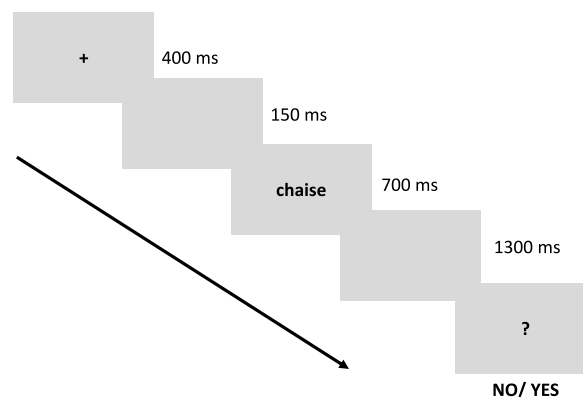


Fig. 1. The time course of a trial.

Pelli, 1997) were used to present the stimuli and to record participants' responses.

The time course of a trial is presented in Fig. 1. Each trial started with a black fixation cross flashing in the center of a gray screen for 400 ms. The fixation cross was followed by a gray screen for 150 ms, replaced by the stimulus for 700 ms. Then, a second gray screen appeared for 1300 ms, followed by the question mark screen which remained until the participant pressed the response button. After the participant's response, the next trial was presented. After each block there was a short pause.

2.5. ERP recording and analysis

Continuous electroencephalogram (EEG) was recorded from 64-channel electrodes using the BioSemi Active-two system (BioSemi, Amsterdam, Netherlands). Sixty-four electrodes mounted in an elastic cap were placed according to the international 10–20 system. Six external flat electrodes were positioned: 2 over the right and left mastoids, 2 above and below the right eye to record eye blinks, and 2 next to the right and left eye to monitor eye movements. Two additional electrodes (CMS/DRL) were used as an online reference (Schutter, Leitner, Kenemans, & Honk, 2006).

Data were sampled at 512 Hz with an online 0.5–100 Hz frequency bandpass filter. Electrode offsets were kept below 50 mV. Further ERP processing was done offline. The EEG data were analyzed using the EEGLAB toolbox (v2021.1) (Delorme & Makeig, 2004). First, EEG data were filtered with a 0.05–45 Hz bandpass filter. Bad channels were removed using the Clean Rawdata function. Next, an independent component analysis (ICA) decomposition (extended infomax algorithm; Lee, Girolami, & Sejnowski, 1999) was run followed by an automatic identification and rejection of independent components with artifacts using ICLabel (Pion-Tonachini, Kreutz-Delgado, & Makeig, 2019), specifically targeting artifacts caused by eye blinks and saccadic eye movements.

Then, an interpolation (spherical) of missing channels was done and EEG data were re-referenced to an average reference.

Next, the continuous EEG was segmented into epochs from 150 ms pre-stimulus until 1000 ms post-stimulus onset, with 150 ms of each epoch corresponding to a pre-stimulus baseline, using the ERPLAB Toolbox v8.30 (Lopez-Calderon & Luck, 2014). Only trials with correct responses to the delayed phonological lexical decision task and with no artifacts were kept for further statistical analyses. A two-way ANOVA including Condition (5 levels) \times Group (2 levels) showed that there was no difference in the number of trials available for analysis between Conditions and Group ($p > 0.05$). Then, the ERP data were baseline-corrected to the mean amplitude of the 150 ms pre-stimulus interval. Finally, in each experimental condition, the segmented ERP data were averaged over trials and over participants (i.e., grand average; weighted average based on number of trials). Data with more than 20 out of 60 trials per condition after artifact rejection were kept for further analyses. With respect to the behavioral data, two participants were excluded: one due to an accuracy score of 0% for the pseudohomophone condition, and another because of a score below 2 SD (20%) from the mean accuracy of the dyslexic group on the pseudoword condition. Concerning ERP data, one participant was excluded due to a number of items below 20 (out of 60; 33%) across experimental conditions.

2.6. Data analysis

For the behavioral data, Student *t*-tests were run on the assessment of reading and other cognitive functions of the two groups of participants. Moreover, a repeated measures two-way ANOVA with Condition (5 levels: word, pseudohomophone, pseudoword, consonant string, symbol string) as within-subjects factor and Group (2 levels: dyslexic, control) as between-subjects factor was conducted on accuracy (percentage of errors) as the dependent variable.

For the neurophysiological data, the four different ERP components, i.e., N170, N320, N400 and LPC were statistically analyzed in 4 time windows (TW) which were first selected based on previous studies and then adjusted by visual inspection of the grand averages recorded in this study: For the N170: 150–270 ms (Mahé et al., 2012); for the N320: 310–380 ms (Araújo et al., 2015; Simon et al., 2004); for the N400: 400–500 ms (Hasko et al., 2013), and for the LPC: 600–800 ms (Hasko et al., 2013). For each ERP component, repeated-measures ANOVAs were conducted with Condition (5 levels: word, pseudohomophone, pseudoword, consonant string, symbol string) as within-subjects factor and Group (2 levels: dyslexic, control) as between-subjects factor on each of the dependent variables, i.e., amplitude, peak latency, and area under the curve. Planned comparisons were used to test the a priori hypotheses whenever possible. Otherwise, post-hoc pairwise comparisons using a modified Holm procedure were run. Significance was considered when the *p*-value was below 0.05.

According to the literature (N170: Mahé et al., 2012; N320: Simon et al., 2004; Araújo et al., 2015; Bentin et al., 1999; N400: Hasko et al., 2013; LPC: Savill & Thierry, 2011) and after visual inspection, we selected the following cluster of electrodes for each ERP component: for the analysis of the N170, we focused on the P7 and P8 electrode sites over left and right occipitotemporal regions; for the N320 component we examined the T7 and T8 electrodes over left and right temporoparietal regions; for the N400 we chose the central cluster comprising Cz, CPz and Pz; finally, for the LPC component we selected a centro-parietal cluster of electrodes including CPz, CP1, CP2, Cz, C1, and C2. For each component, mean amplitude and peak latency were calculated. As no clear peak could be observed for the LPC, we analyzed the area under the curve.

Finally, to verify the reliability of the analysis, we further ran different linear mixed effects models (LME, Baayen, 2008). These models will be detailed later for each ERP component. We always started with the simple model including Condition as fixed factor and subject as random factor.

3. Results

3.1. Assessment of reading and other cognitive functions

Table 1 present a summary of the results of the different tests. The Student t-test showed that performances in several tests were significantly worse in dyslexics compared to controls: Alouette Test (words correctly read per minute) ($p < 0.001$), Alouette Test (reading efficiency score) ($p < 0.001$), Pseudoword reading time ($p < 0.001$), Initial phoneme deletion (time) ($p < 0.01$), Initial phoneme deletion (time) ($p < 0.01$), Spoonerisms (score) ($p < 0.001$), Spoonerisms (time) ($p < 0.001$), Rapid automatized naming of letters (time) ($p < 0.01$), Non word repetition (time) ($p < 0.01$) and Visuo-attentional span test (score) ($p < 0.001$).

In contrast, the two groups were matched on age ($p > 0.10$), and on the Similarity and Matrix WAIS IV test ($p > 0.10$ and $p > 0.10$, respectively). Moreover, neither the score of Initial phoneme deletion, the score of Rapid automatized naming of letters, nor the score of non-word repetition reached the significance level when comparing the dyslexic and control groups ($p > 0.10$).

3.2. Behavioral results

Fig. 2 displays mean accuracy for the five experimental conditions.

There was a main effect of Condition [$F(4,120) = 11.01$, $MSE = 146.38$, $p = 0.001$, $\eta_p^2 = 0.268$]. Post-hoc analyses revealed that responses were less accurate for pseudowords (89.9 ± 13.8) compared to words ($98.9 \pm 1.7\%$), consonants ($98.5 \pm 3.9\%$) and symbols ($99.7 \pm 0.8\%$) ($p_{\text{holm}} < 0.001$, respectively). In addition, responses for pseudohomophones ($94.6 \pm 3.8\%$) were less accurate than for symbols ($99.7 \pm 0.8\%$) ($p_{\text{holm}} < 0.05$). Given that in our design 120 trials implicated the YES response and 180 trials the NO response, we ran additional t-tests on the control group concerning the percentage of incorrect responses, in order to exclude the possibility that the unequal number of YES and NO responses might generate a bias in participants' responses. The percentage of error for words and pseudohomophones was 2.9% while it was 1.4% for pseudowords, consonant strings, and symbol strings. A paired samples t-test on the control group showed that there was no significant difference in the percentage between YES and NO conditions ($p > 0.05$).

The ANOVA also revealed a main effect of Group [$F(1,30) = 10.48$, $MSE = 45.18$, $p = 0.003$, $\eta_p^2 = 0.259$], reflecting a lower accuracy in dyslexics ($94.5 \pm 6.7\%$) than in controls ($98 \pm 2.4\%$). Lastly, a Condition by Group interaction was found [$F(4,120) = 5.22$, $MSE = 146.38$, $p = 0.019$, $\eta_p^2 = 0.148$]. Post-hoc analyses showed that the pseudoword condition compared to all the other conditions was associated with significantly lower accuracy (compared to word: $p_{\text{holm}} < 0.001$, pseudohomophone: $p_{\text{holm}} = 0.004$, consonant: $p_{\text{holm}} < 0.001$, symbol: $p_{\text{holm}} < 0.001$) in dyslexics but not in controls.

3.3. Electrophysiological results

Table 3 presents a summary of the statistics of the four ERP components under investigation in this study and Table 4 a summary of

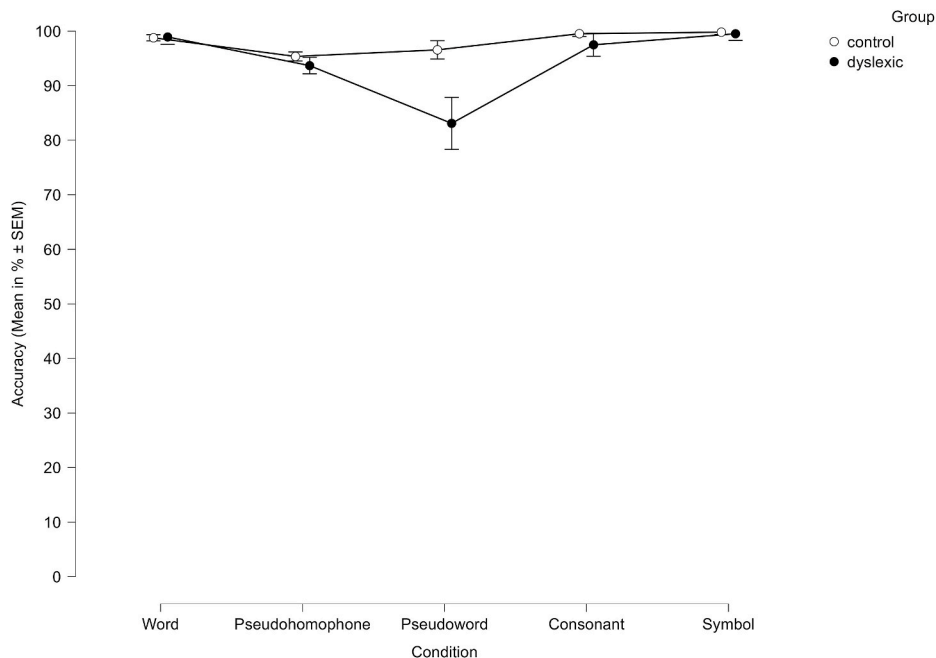


Fig. 2. Mean accuracy (in percentage) for the five conditions (words, pseudohomophones, pseudowords, consonant strings, symbol strings) and the two groups of participants (control, dyslexic). Error bars represent standard error of the mean.

Table 3

Summary of the ERP results found for the four ERP components examined (N170, N320, N400, LPC) for mean amplitude, peak latency and area according to the repeated measures ANOVA with a 5-level Condition and the Planned comparisons.

ERP	ERP characteristics	Main effect or Interaction	Significant result	Planned comparisons	<i>p</i> for the main effect	<i>p</i> for the interaction
N170	Mean Amplitude	Interaction	Condition x Electrode	Aplabetic stimuli- Symbols		P7 P8 <i>p</i> ** mg
N320	Mean Amplitude	Main Effect	Group	Pseudoword- Consonant	<i>p</i> *	
N400	Mean Amplitude	Main Effect	Condition	Word- Pseudoword	<i>p</i> *	
LPC	Area	Interaction	Condition x Group	Word- Pseudohomophone		Control <i>p</i> *** Dyslexic ns

ns: $p > 0.10$.

mg: $0.05 < p < 0.10$.

$0.001 < *p < 0.05$.

$0.001 < **p < 0.01$.

$p^{***} < 0.001$.

Table 4

Summary of the averaged amplitudes (or area under the curve for LPC) with standard deviation for each ERP, each of the 5 conditions (W: words, PH: pseudohomophones, PW: pseudowords, CS: consonant strings, SS: symbol strings), each electrode (when applicable) for the control (A) and the dyslexic (B) group.

A)											
Control											
	W		PH		PW		CS		SS		
N170	P7	P8	P7	P8	P7	P8	P7	P8	P7	P8	
	-3.2 (±3)	-1.9 (±1.9)	-3.6 (±2.8)	-1.9 (±2.5)	-3.2 (±2.6)	-2.1 (±2.6)	-3.5 (±3.2)	-2.7 (±2.6)	-2.6 (±3.4)	-3.1 (±3.1)	
N320	T7	T8	T7	T8	T7	T8	T7	T8	T7	T8	
	-1.5 (±3.4)	-1 (±2.3)	-2.5 (±5.7)	-0.2 (±1.8)	-2.6 (±6.1)	-0.3 (±1.9)	-2 (±3.5)	-1.7 (±2.9)	-1.8 (±2)	-2 (±2.8)	
	Cluster: Cz, CPz, Pz										
N400	1.8 (±1.6)		1.7 (±2.3)		0.9 (±1.6)		1.6 (±1.5)		2 (±1.9)		
	Cluster: CPz, CP1, CP2, Cz, C1, C2										
LPC	0.3 (±0.3)		0.6 (±0.6)		0.4 (±0.4)		0.4 (±0.4)		0.4 (±0.3)		
B)											
Dyslexic											
	W		PH		PW		CS		SS		
N170	P7	P8	P7	P8	P7	P8	P7	P8	P7	P8	
	-2.7 (±2.8)	-1.6 (±1.9)	-3.1 (±2.9)	-1.8 (±2.1)	-2.3 (±3.2)	-1.6 (±2.2)	-2.5 (±3.1)	-2.2 (±2.4)	-1.9 (±3.1)	-1.8 (±2.6)	
N320	T7	T8	T7	T8	T7	T8	T7	T8	T7	T8	
	-0.4 (±1.6)	-0.3 (±2)	-0.5 (±1.6)	-0.4 (±2.2)	-0.5 (±1.8)	-0.5 (±2.3)	-1.1 (±1.5)	-0.2 (±2.4)	-1.3 (±2.6)	-0.3 (±2.9)	
	Cluster: Cz, CPz, Pz										
N400	1.1 (±1.9)		0.6 (±1.8)		0.6 (±1.5)		0.8 (±1.4)		1.8 (±2.7)		
	Cluster: CPz, CP1, CP2, Cz, C1, C2										
LPC	0.3 (±0.2)		0.3 (±0.2)		0.3 (±0.2)		0.3 (±0.2)		0.4 (±0.2)		

the averaged amplitudes (or area under the curve when applicable) for each ERP component. In order to verify the inter-subject variability, we tested the hypothesis of equality of variances using Levene’s test for each ear component and each condition. No significant result was found ($p_{Levene's} > 0.05$), indicating the homogeneity of variance sample population.

First, we conducted a series of ANOVAs on the five levels of the factor Condition. Then, we ran additional ANOVAs by focusing only on the two relevant levels corresponding to each ERP component under investigation.

3.3.1. N170 (time window: 150–270 ms)

3.3.1.1. Mean amplitude

3.3.1.1.1. ANOVA with a 5-level condition. Neither the main effect of Condition [$F(4,120) = 1.03, MSE = 2.83, p = 0.380$] nor of Group [$F < 1$] were significant. The ANOVA revealed a significant Condition by Electrode interaction [$F(4,120) = 5.51, MSE = 1.90, p = 0.003, \eta_p^2 = 0.155$]. Planned comparisons indicated that the N170 was larger for all alphabetic stimuli plotted together than for

symbols, and that this effect was only significant at the P7 electrode ($d_{p7} = -0.7 \mu\text{V}$) ($t(31) = 2.84, p = 0.005$). No other main effect or interaction reached the significance level. In addition, a post hoc analysis was conducted, revealing that the N170 amplitude was more negative for pseudohomophones ($-3.38 \mu\text{V}, \pm 2.87$) than for symbols ($-2.30 \mu\text{V}, \pm 3.28$) at the P7 electrode ($p_{\text{holm}} = 0.038$). No interaction (Condition by Group, Condition by Electrode by Group) reached the significance level [$F_s < 1$], (see Figs. 3a, 3b and 3c).

3.3.1.1.2. Linear mixed models. In the first model, we included Condition (consonant, symbol) and Electrode (P7, P8) as fixed factors and Subject as random factor. This model showed a significant Condition by Electrode interaction [$F(1,55) = 4.331, p = 0.042$]. Further Student t-tests indicated that the N170 was only significant on P7 [$t(31) = -2.88, p = 0.007$].

In a second model, we kept the same fixed factors and the same random factor as in the previous model, but this time we added, in a bottom-up fashion, the various dimensions derived from the tests conducted on participants to assess their reading performance (for a summary of these tests, see Table 1) as well of some of their cognitive functions' abilities. These dimensions were considered here as potential predictor variables of dyslexia. The results showed that by adding one by one the different "dyslexia predictors", we found that only the score on the Spoonerisms test (i.e., measures of phonological awareness by examining participant skills in converting the initial phonemes of two words and by creating two non-existing words) explained a significant part of the Condition by Electrode interaction [$F(1,48) = 4.640, p = 0.036$].

3.3.1.2. Peak latency

3.3.1.2.1. ANOVA with a 5-level condition. The ANOVA revealed no significant main effect (Condition: [$F(4,120) = 1.93, p = 0.110$]; Group: [$F < 1$] or interaction ([Condition by Group: [$F(4,120) = 1.57, p = 0.187$]; Condition by Group by Electrode: [$F < 1$]; Condition by Electrode: [$F(4,120) = 2.005, p = 0.098$]).

In summary for the N170, a significant Condition by Electrode interaction was found indicating a larger amplitude in consonants compared to symbols but only on the P7 electrode.

3.3.2. N320 (time window: 310–380 ms)

3.3.2.1. Mean amplitude

3.3.2.1.1. ANOVA with a 5-level condition. The ANOVA failed to show a significant effect of Condition [$F < 1$]. In contrast, a significant main effect of Group was found [$F(1,30) = 4.62, \text{MSE} = 30.82, p = 0.040, \eta_p^2 = 0.133$], indicating that in average the amplitudes were more negative for the control group ($-1.6 \mu\text{V}, \pm 3.2$) than for the dyslexic one ($-0.2 \mu\text{V}, \pm 2.1$), as graphically represented in Fig. 4a. The difference in the mean between the two groups was $-0.7 \mu\text{V}$. No other main effect or interaction was found (Condition by Group: [$F < 1$]; Group by Electrode: [$F < 1$]; Condition by Electrode: [$F(4,120) = 1.21, p = 0.31, \text{MSE} = 5.62$]; Condition by Group by Electrode: [$F(4,120) = 2.53, p = 0.079, \text{MSE} = 5.62$], see Fig. 4b).

3.3.2.1.2. Linear mixed models. With respect to the amplitude of the N320, no linear mixed model showed a significant effect.

3.3.2.2. Peak latency

3.3.2.2.1. ANOVA with a 5-level condition. The ANOVA revealed no main effect (Condition: [$F < 1$]; Group: [$F(1,30) = 2.67, \text{MSE} = 522.55, p = 0.113$]) or interaction (Condition by Group: [$F(4,120) = 1.16, \text{MSE} = 535.58, p = 0.328$]; Condition Electrode: [$F < 1$]; Condition by Electrode by Group [$F < 1$]).

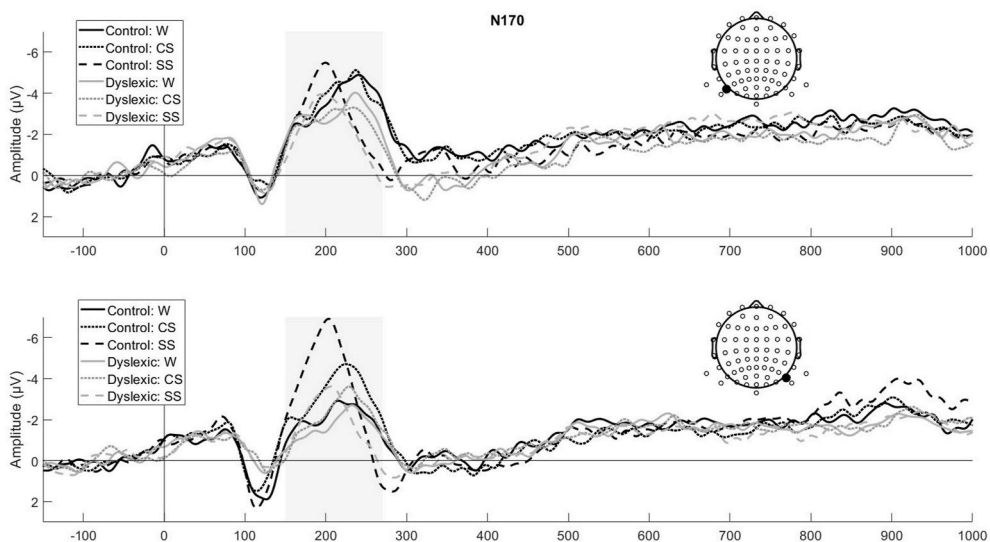


Fig. 3a. Illustration of the N170 amplitude for word (W), consonant (CS) and symbol strings (SS) over the P7 (up) and P8 (down) electrodes for both control and dyslexic readers. The time window selected for the N170 is highlighted in gray (150–270 ms). Negativity is depicted upwards.

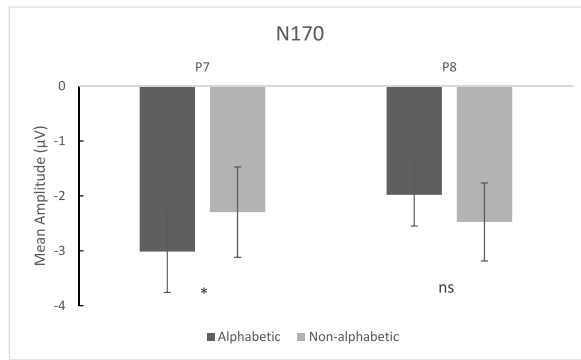


Fig. 3b. The mean amplitude of the N170 for the alphabetic stimuli (word, pseudohomophone, pseudoword, consonant string, symbol string) plotted together and for the non-alphabetic stimuli (symbol string) across dyslexic and control participants. The planned comparison (contrast) separately run on P7 and P8 revealed that the N170 was larger for all alphabetic stimuli than for symbols, but only at the P7 electrode.

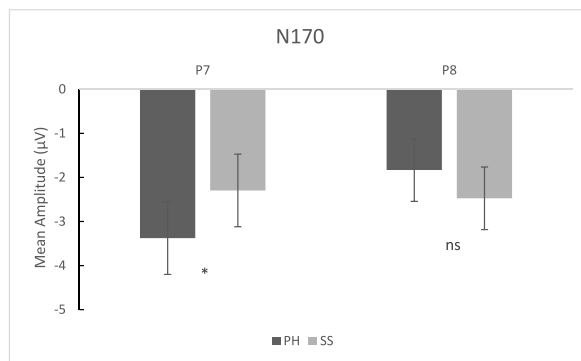


Fig. 3c. Mean amplitude of the N170 for the pseudohomophone (PH) and for the symbol condition (Post-hoc comparison) averaged across dyslexic and control participants. Post-hoc analyses revealed that the N170 amplitude was more negative for pseudohomophones as compared to symbols only at the P7 electrode.

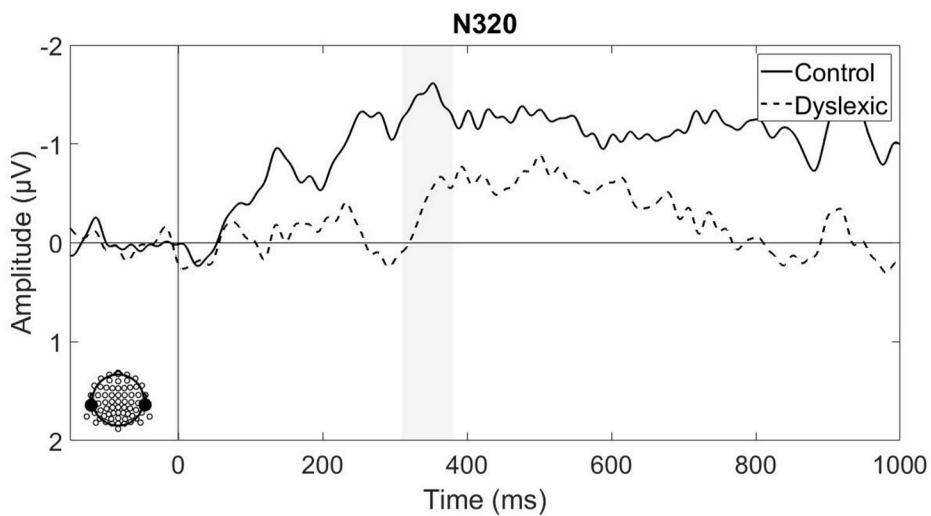


Fig. 4a. The group effect on the N320 component over temporoparietal (T7 and T8) electrodes in control and dyslexic readers.

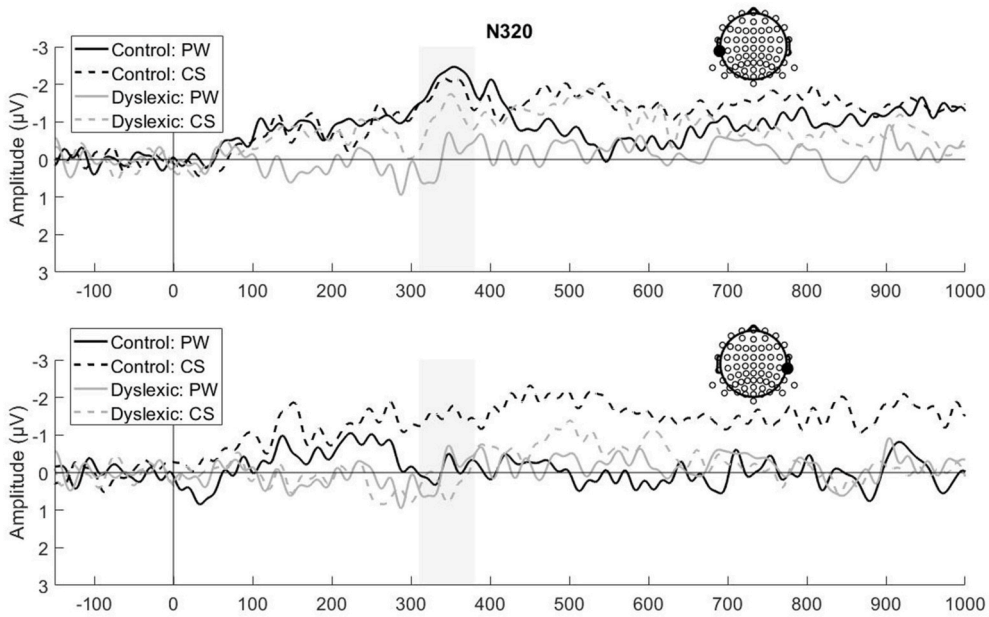


Fig. 4b. Illustration of the N320 amplitude for pseudowords and consonant strings over the T7 (up) and T8 (down) electrodes for both control and dyslexic readers. The time window selected for the N320 is highlighted in gray (310–380ms). Negativity is depicted upwards.

To sum up, when all conditions were examined together, results indicated a significant group effect with larger N320 amplitudes for controls as compared to dyslexic participants.

3.3.3. N400 (time window: 400–500 ms)

3.3.3.1. Mean amplitude

3.3.3.1.1. ANOVA with a 5-level condition. Fig. 5 displays the N400 in both the word and pseudoword conditions. There was a main effect of Condition [$F(4,120) = 3.24, MSE = 7.56, p = 0.027, \eta_p^2 = 0.097$]. Planned comparisons indicated that the N400 was significantly larger for pseudowords than for words [$t(31) = |2.0|, p < 0.05$]. No other main effect (Group: [$F(1,30) = 1.55, MSE =$

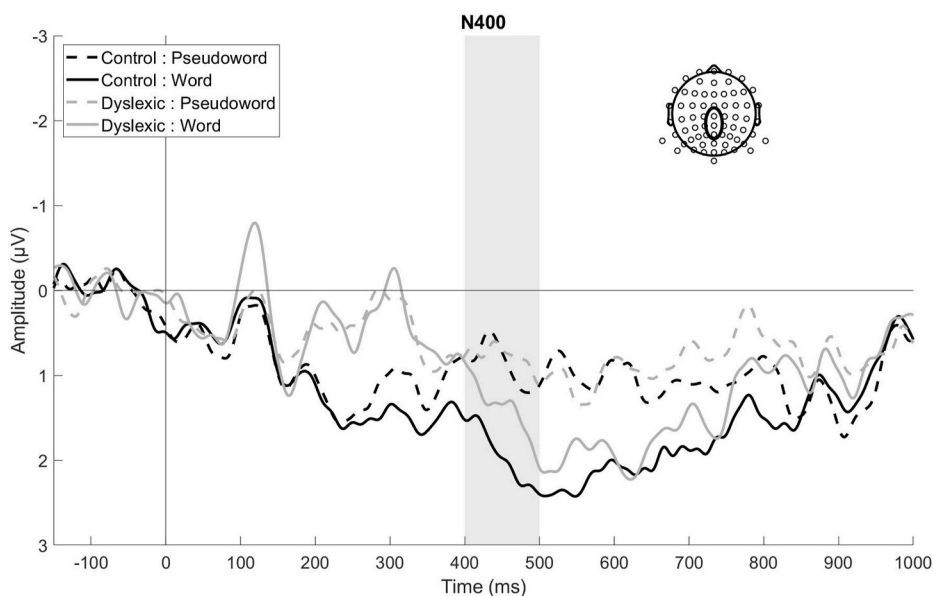


Fig. 5. Illustration of the N400 amplitude for words and pseudowords across centro-parietal electrodes (cluster of electrodes: Cz, Pz, CPz) for both control and dyslexic readers. The time window selected for the N400 is highlighted in gray (400–500ms). Negativity is depicted upwards.

10.53, $p = 0.22$) or interaction (Condition by Group: [$F < 1$]) was significant.

3.3.3.1.2. Linear mixed models. In our initial model with Condition (2 levels: word, pseudoword) as fixed factor and subject as random factor, we found a significant effect of Condition [$F(1,30) = 5.062, p = 0.032$]. Further, paired samples t-tests showed that the pseudoword condition was more negative as compared to the word condition [$t(31) = 2.360, p = 0.025$]. The effect size, measured by Cohen's d , was 0.417.

In a second model, we retained Condition as fixed factor and Subject as a random factor, and we added as random effects in a bottom-up fashion, the various dimensions derived from tests conducted on participants to assess their reading performance (for a summary of these tests, see Table 1) as well as the dimensional values of the tests on the cognitive functions. We found that the following random effects added one by one significantly modulated the Condition effect: Meaningless text (*Alouette*) [$F(1,28) = 5.676, p = 0.024$]; Meaningful text (*Pollueur*) [$F(1,28) = 6.228, p = 0.019$]; Regular word reading [$F(1,26) = 6.262, p = 0.019$]; Pseudoword reading [$F(1,8) = 6.696, p = 0.031$]; Initial phoneme deletion [$F(1,9) = 6.135, p = 0.036$]; Spoonerisms [$F(1,8) = 5.584, p = 0.045$].

Test focusing on the evaluation of reading skills such as text and word reading and word and pseudoword reading changed the condition effect more significantly than tests focusing more on the assessment of phonological awareness.

3.3.3.2. Peak latency

3.3.3.2.1. ANOVA with a 5-level condition. No significant main effect of Condition or Group or interaction between them was found [$F_s < 1$].

In summary, results showed a significant Condition effect with larger amplitudes for pseudowords as compared to words independently of group (N400 effect). Critically, six predictive variables related to reading skill performances and to phonological awareness significantly modulated this Condition effect.

3.3.4. LPC (time window: 600–800 ms)

3.3.4.1. Area under the curve

3.3.4.1.1. ANOVA with a 5-level condition. A repeated-measures ANOVA only revealed a significant Condition by Group interaction [$F(4,120) = 2.58, MSE = 0.050, p = 0.041, \eta_p^2 = 0.079$]. Planned comparisons revealed that the area under the curve was significantly larger for pseudohomophones than for words in controls ($t(31) = 3.8, p < 0.001$) but not in dyslexics ($p > 0.10$). Furthermore, post-hoc comparisons showed that pseudohomophones and pseudowords differed significantly in the control group ($p_{\text{holm}} < 0.05$ only (see Figs. 6 and 7)).

3.3.4.1.2. Linear mixed models (area under the curve). In the first model where Condition was set as fixed factor and Subject as a random factor, the main effect of Condition was significant [$F(1,31) = 4.618, p = 0.040$].

In the second model, we kept the same model to which we added in a bottom-up fashion, the various dimensions derived from tests conducted on participants to assess their reading performance (for a summary of these tests, see Table 1) as well as the dimensional values of the tests on the cognitive functions. The results showed that only the score on regular word reading and the score during pseudoword reading kept the effect of Condition significant (respectively: [$F(1,31) = 4.618, p = 0.040$]; [$F(1,31) = 4.618, p = 0.040$]).

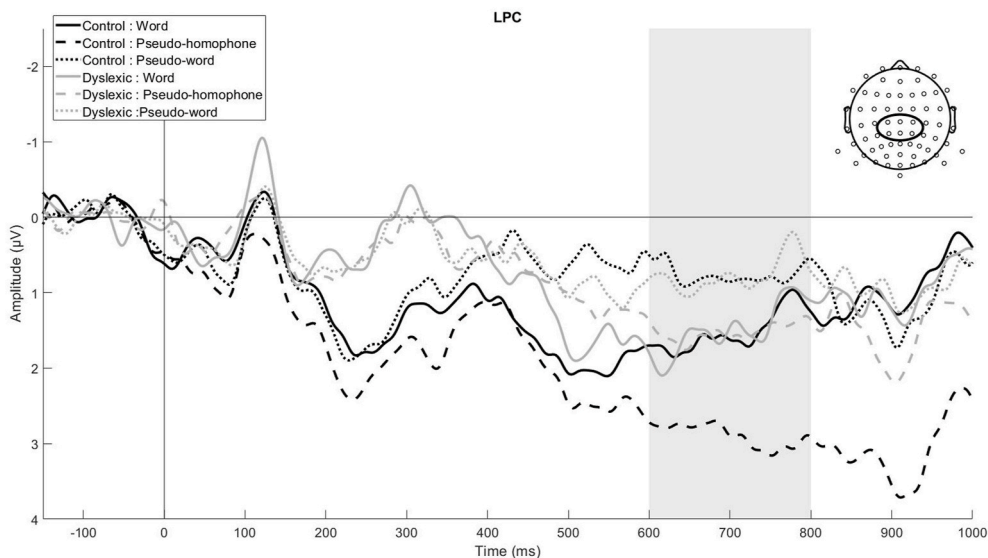


Fig. 6. Illustration of the LPC component for words, pseudohomophones and pseudowords across centro-parietal electrodes (cluster of electrodes: CPz, CP1, CP2, Cz, C1, C2) for both control and dyslexic readers and the mean area under the curve. The time window selected for the LPC is highlighted in gray (600–800ms). Negativity is depicted upwards.

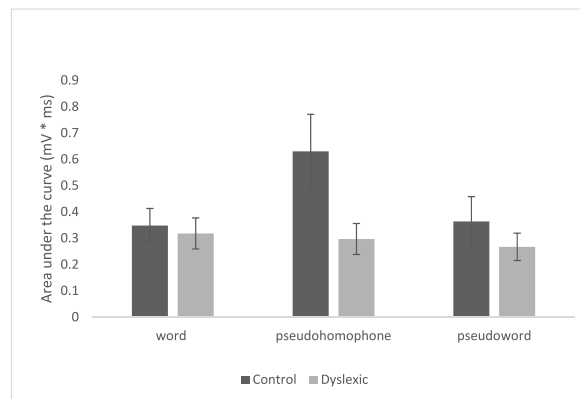


Fig. 7. Area under the curves for the dyslexic and control groups in the three experimental conditions: word, pseudohomophone, pseudoword. Error bars represent standard error of the mean.

To sum up for the LPC, a significant Condition by Group interaction indicated larger areas under the curve for pseudohomophones than for words, but only in the control group. In addition, a significant effect of Condition that emerged on the Linear Mixed Models with larger areas under the curve for pseudohomophones as compared to words remained significant when the scores on regular word reading and pseudoword reading were added as random factors to the Linear Mixed Model.

4. Discussion

The aim of this study was to investigate at which point, in the stream of four cognitive processes of word reading, impairment may occur in dyslexic adults. We focused on (1) visual expertise for print, (2) grapheme-to-phoneme conversion, (3) word recognition, and (4) retrieval of phonological information from long-term memory. To trace the time course of these four cognitive processes, we used electroencephalography (EEG) because of its high temporal resolution. The strength of our methodological approach was to examine online the neurodynamics of several reading processing stages by means of the same experimental design with the same 32 participants who saw a sample of 300 stimuli varying along a continuum from lexicalized (concrete French words) to non-lexicalized (symbols) stimuli.

Behaviorally, as expected, and in accordance with previous studies (Mahé et al., 2012; Silva et al., 2022), dyslexic participants were less accurate than control readers, especially when reading pseudowords. This finding lends support to the hypothesis that dyslexics have difficulties in reading pseudowords, which burden the grapheme-to-phoneme conversion due to the lack of both orthographic and phonological representations of such stimuli (Bergmann & Wimmer, 2008).

At the neurophysiological level, ANOVAs showed that the two language processes responsible for processing phonological information, namely grapheme-to-phoneme conversion (N320) and the retrieval of phonological information from memory (Late Positive Complex, LPC), were impaired in dyslexics compared to controls.

Under the hypothesis that the N320 reflects grapheme-to-phoneme conversion during reading (Bentin et al., 1999; Simon et al., 2004), the observation in our study that the amplitude of the N320 was significantly smaller for dyslexics ($-0.2 \mu\text{V}$) than for controls ($-1.6 \mu\text{V}$; effect size: $1.4 \mu\text{V}$) constitutes strong evidence that dyslexics probably encounter difficulties at this stage of processing. Note that between-group differences were observed independently of condition as initially expected, but this finding is consistent with studies reporting reduced N320 amplitudes in French dyslexics during a word and non-word reading aloud task (Mahé et al., 2018) as well as in Portuguese adults during a reading task (Araújo et al., 2015). However, these results should be interpreted with caution because of an absence of significant effect of both Condition and Condition by Group interaction. Further research using more complex stimuli from different points of view (length, syllabic structure, morphological characteristics) could better highlight a difference between pronounceable and unpronounceable stimuli for the investigation of the grapheme-to-phoneme mechanism.

Finally, at a later stage of phonological information retrieval from long-term memory as is likely to be the case in the processing of pseudohomophones, dyslexics again seem to have difficulties. For the LPC, we showed that the area under the curve was larger for pseudohomophones than for words and the pseudoword condition but only in controls. This result, which is in accordance with our initial prediction concerning LPC, suggests that the activation of the phonological representations from long-term memory involved by pseudohomophones differed qualitatively in dyslexics compared to controls. In the same vein, Silva et al. (2022) also showed lower LPC amplitudes over centroparietal electrodes in dyslexics in comparison with controls. Taken together, these findings support the idea that the mechanism of retrieving linguistic information from long-term memory functions poorly in developmental dyslexia, in line with our hypothesis. Two points should be considered when discussing our data. First, the phonological lexical decision task used here requires maintaining the visually presented stimuli in working memory before the participants give their answer. Although we cannot totally exclude a possible role played by working memory due to the delay between the stimulus disappearance and the participant's response, this role is probably reduced as the amount of information held in working memory was relatively small (5–6 letters per stimulus). Second, behavioral results show that the dyslexic and the control group differed on visuo-attentional span. This pattern

echoes the VAS deficit and could point toward a mixed deficit in the dyslexic group. Although none of our conditions allowed us to explore specifically this dimension, future EEG studies should consider this aspect.

In contrast, and unexpectedly, both the early processes of visual expertise for print (N170) and the process of lexical access (N400) appeared to work in the same way in the two groups of participants, at least when dyslexia was statistically analyzed as a categorical variable rather than as a dimensional one.

Although we found, in accordance with studies reporting the N170 as a neurophysiological marker for print expertise (Bentin et al., 1999; Silva et al., 2022), a larger left-lateralized (P7 electrode) N170 amplitude in response to alphabetic stimuli (words, pseudo-homophones, pseudowords, consonants) than to symbols, critically, we failed to report a Condition by Group interaction. This absence of interaction suggests that the sensitivity to alphabetic stimuli was similar in both dyslexics and controls. Even if on the P8 electrode the N170 descriptive statistics suggest a peak-to-peak difference between consonants and symbols in the expert readers but not in dyslexic readers, this effect in expert readers was not supported by inferential statistics run on mean amplitude. Consequently, we interpret this absence of impairment at the early stage of visual expertise for print in our sample of dyslexics as being one of the possible consequences of successful language training by speech and language therapists. It should be remembered here that we tested students with a high educational level and good reading experience. Notably, neuroimaging studies have shown that remediation plays a significant role in enhancing language processing difficulties and improving reading performance, as demonstrated in children (Temple et al., 2003) and adults (Eden et al., 2004) with dyslexia, who presented increased activity in left hemisphere reading networks. Note, however, that this increased activity was found on temporoparietal areas. No difference was observed between dyslexic and control participants in the N170 in a study with French university students during a lexical decision task (Cheviet, Bonnefond, Bertrand, Maumy-Bertrand, & Doignon-Camus, 2022). In the context of university dyslexic readers, an interesting observation aligns with the proposed hypothesis of a spatiotemporal reorganization within the reading network in adults with dyslexia (Cavalli et al., 2017). According to these authors, dyslexic participants exhibited an earlier activation of the frontal network associated with morphological and semantic characteristics of words compared to the control group. This suggests a higher reliance on semantic information included in morphemes, in order to compensate their reading challenges. Our results also support the development of such mechanisms in order to compensate their reading difficulties, at least in higher education students with dyslexia.

Unexpectedly, the dyslexics we tested in this study did not show any difficulties with lexical access as suggested by the absence of a significant group difference for the canonical N400 amplitude comparison between words and pseudowords (Braun, Hutzler, Ziegler, Dambacher, & Jacobs, 2009). In other words, the classical N400 effect (i.e., larger N400 in the pseudoword condition than in the word condition) was comparable in size between the dyslexics and the controls. Note that other studies also failed to show an N400 amplitude difference in dyslexic adults with respect to normal readers (Rüsseler et al., 2003; Silva, Ueki, Oliveira, Boggio, & Macedo, 2016). To account for this absence of inter-group difference at the lexical level, we can only speculate that the dyslexic students we tested might have sufficiently trained their process of lexical access to compensate the lexical difficulties that are often observed in dyslexic children.

However, although the ANOVA failed to show different N400 effects (pseudoword *minus* word) between dyslexics and controls, further analyses using linear mixed models (LMM) revealed that this effect was significantly modulated by six predictive variables assumed to be good markers of dyslexia, namely meaningless text (*Alouette*), regular word reading, pseudoword reading, initial phoneme deletion, and spoonerisms. It should be noted that among these 6 indicators of dyslexia, it is those which assess reading skills such as text and word reading and word and pseudoword reading that explained the greatest part of variance in the effect; in contrast, predictors related to phonological awareness modulated the N400 effect less.

These contrasting results between ANOVAs and LMM for the N400 suggest that when dyslexia is considered as a categorical variable (dyslexics, controls), the variation in reading performances between individuals in each group, particularly among dyslexics, attenuates the influence that the Group factor can have on the N400 effect. In other words, in the dyslexic group, we can hypothesize that some individuals may have scores close to those of the controls with the lowest reading performances, which could explain the absence of interaction between Condition and Group in our ANOVAs.

On the other hand, when we considered in the LMM dyslexia as a dimensional variable expressed through different predictive variables assumed to be good predictors of dyslexia, then we saw significant modulation of lexical access abilities according to the scores obtained on each predictor, even though the words used were short, concrete and frequent. Thus, our study shows the limitations of the categorical approach for studying certain phenomena such as dyslexia. In contrast, the dimensional approach provides a finer granularity of analysis and enables inter-individual variations to be captured within a larger sample size.

We now attempt to discuss how a dual-route architecture (see Coltheart et al., 2001) could account for our EEG data. The initial marker we investigated, the N170, may be linked to lexical and orthographic processing as outlined in the dual-route model of reading. This is evident from distinctions observed between alphabetic and non-alphabetic stimuli. Importantly, this mechanism appears to be preserved in dyslexic participants. Notably, this processing mechanism remains observable in dyslexic participants, with the absence of differences attributed to dyslexics' remediation and the use of short stimuli derived from high-frequency words. Furthermore, based on the hypothesis that the greater or lesser ease of using the direct lexical route should be reflected by variations in the lexical N400 effect size (i.e., $N400_{\text{pseudoword}} - N400_{\text{word}}$), smaller N400 effects should be observed in dyslexics compared with controls because of their difficulties in accessing the lexical properties of words. Interestingly, this prediction was only partially confirmed in our EEG data as we failed to report a significant Condition by Group interaction in the ANOVA, suggesting that processing of words and pseudowords was similar in both groups. In contrast, Linear Mixed Model (LMM) analyses showed that six predictive variables assumed to be robust markers of dyslexia significantly explained the variation of the N400 effect size. The latter result suggests that word recognition may be less automatic in dyslexics, even if they are higher education students and the words to be read were short, morphologically simple and highly frequent.

Regarding the non-direct route, our data indicate that dyslexics had more difficulties with grapheme-to-phoneme conversion as suggested by the N320, i.e., a neurophysiological marker thought to signal this conversion, whose amplitude was significantly smaller in dyslexics than in controls. Unfortunately, the current neurophysiological data do not allow us to conclude whether dyslexics make greater use of the indirect route to compensate for the lesser effectiveness of the direct route. The only thing we can say is that the conversion mechanism of the dyslexics in our sample seems to be less effective. Lastly, the reduced Late Positive Component (LPC) effect observed in the dyslexic group, particularly between stimuli requiring a decomposition to access the phonological properties of the stimuli (pseudohomophones) and stimuli whose phonological properties are activated through the direct route (words), due to the reduced LPC amplitude in response to pseudohomophones in the dyslexic group only, lead us to surmise that direct access to phonological representations may be impaired in dyslexia.

Future studies should propose appropriate experimental designs to examine the transition from one route to the other, as well as the precise characteristics of the words that lead dyslexic readers to use the indirect route to compensate for a lack of efficiency in the direct one. To do this, it would be appropriate to systematically manipulate various psycholinguistic factors such as those mentioned above.

It is important to note that in some reading tests, dyslexics and controls did not significantly differ. For example, the reading ability scores for reading isolated regular and irregular words was similarly performed in both groups. However, while the dyslexics' scores did not significantly differ from those of controls, they remained significantly different with respect to reading time, which was longer in average for dyslexics than for controls (see Table 1). One possible explanation could be a trade-off effect: to achieve the same performances as controls, dyslexics may favor accuracy over speed. Further investigation is necessary. Further studies are needed especially to investigate the role of lexical frequency and phonological neighborhood on the lexical abilities of dyslexics during word reading.

Finally, none of the correlations between the behavioral data and the neurophysiological data reached the significance level. This unexpected result can probably be explained by the fact that our sample of dyslexics was too small. Further studies with larger sample sizes ($N = 30$) will provide new answers. However, we must keep in mind that it is difficult to constitute a large homogeneous cohort of individuals with language disorders. An additional plausible explanation for the absence of significant correlations could be the fact that our participants with dyslexia had undergone several years of remediation. Despite still qualifying as dyslexic, as evidenced by their poorer performance compared to controls in various tests evaluating reading skills, phonological awareness, and visuo-attentional skills, it is possible that they have compensated certain reading difficulties, such as visual expertise for print and lexical access, as demonstrated by comparable results on the N170 and the N400 components when compared to controls. However, our study demonstrated significant differences between groups in terms of phonological processes, as evidenced by the smaller N320 and LPC in dyslexics compared to controls. This suggests impairments in grapheme-to-phoneme conversion and in the retrieval of phonological information from long-term memory. Consequently, the dyslexic participants tested in our sample exhibit difficulties typically associated with dyslexia, particularly during phonological processing. Taken together, our data suggest that phonological processes are less easily trained than letter decoding and lexical access processes.

5. Conclusions

This ERP study aimed to explore at which moment, in the time course of four cognitive processes of word reading, impairment may occur in dyslexic adult native speakers of French. Tracing the processes from visual expertise for print to retrieval of phonological information from long-term memory, we showed that the locus of developmental dyslexia is probably to be found primarily in different aspects of the phonological processing during word reading. Indeed, while ERP markers thought to signal some features of phonology were significantly modulated in dyslexics compared to controls, suggesting a phonological dysfunction, visual expertise for print (N170) appeared to be qualitatively and quantitatively similar in both dyslexics and controls. Our data also indicated that lexical access as indexed by the N400 was significantly modulated by six predictive variables of dyslexia. Taken together, our findings encourage a cautious attitude before systematically concluding that dyslexics have learning difficulties in visual expertise for print, at least in adults. Our data show that highly educated adult dyslexics do not have such difficulties, perhaps because of the effective training they received in childhood and the language experience they have with reading in higher education, even if they probably use compensatory reading strategies as attested by longer reading times than in controls. These findings lend support to a clinical neurophysiology model postulating that at least two phonological processes during reading might be impaired in dyslexics, namely the grapheme-to-phoneme conversion (N320), and the memory retrieval of phonological information (LPC). However, the cascading effect between the 4 cognitive processes of word reading investigated in this study remains an open question to be studied in the future. Further studies should also examine the different language processes involved in reading by using a more ecological reading situation, namely sentences. This may make it possible to understand the role of linguistic predictions in the reading process deficiencies observed in the developmental dyslexia population.

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Statement on generative AI technology

The authors did not use generative AI technologies for the preparation of this work.

CRedit authorship contribution statement

Aikaterini Premeti: Writing – review & editing, Writing – original draft, Visualization, Validation, Formal analysis, Data curation. **Maria Pia Bucci:** Writing – review & editing, Validation, Data curation. **Karin Heidlmayr:** Writing – review & editing, Validation, Data curation. **Pierre Vigner:** Writing – review & editing, Visualization, Validation, Data curation. **Frédéric Isel:** Writing – review & editing, Validation, Supervision, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

Declarations of interest: none.

Data availability

Data will be made available on request.

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Appendix. Stimuli used in the phonological lexical decision task

Word	Pseudo-homophone	Pseudo-word	Consonant String	Symbol String
arbre	harbre	albre	cnlxs	þ*¥Ø?
bande	bende	bante	kcvhn	þ§?¥£
boîte	boitte	boïpe	hcrle	!¥§*
caisse	caice	cusse	nbvrzc	þ-?£‡Ø
carte	karte	curte	ncvts	Ø‡¥?
chaîne	chainne	chaïlle	ckvnwc	-??D
chaise	chèse	chuse	clvcwx	þ£‡Ø-?
chien	chiaïn	pien	mkrcz	D?¥?
classe	clace	clusse	rfnzzc	‡?þ*¥Ø
cœur	kœur	tœur	xcvzm	þ??¥D
corde	quorde	corge	snclv	§Ø£-
coude	quoude	coufe	xzstr	þ£‡Ø-
crâne	krâne	crâge	nszxm	Øþ£-
cuisse	cuice	cuinne	czvxs	?Dþ*¥
doigt	doight	duigt	kcrql	§?¥D‡
fille	phille	nille	lrttz	þ-?£Ø
flamme	phlamme	flumme	dtswzc	‡DØ?*
fleur	phleur	cleur	ltcvz	¥*£‡
fleuve	phleuve	fleune	htncvz	DØ£?‡
frère	fraire	frare	tvns	!Øþ£-
gorge	gorje	girge	qzwcj	§£-Ø!
goutte	goute	goube	qcvhzh	-‡¥?Dþ
gueule	gueulle	gueute	pvmvtn	§Ø?‡*D
herbe	erbe	herfe	kcwcd	þ?£§
jambe	geambe	lambe	gwnhv	*¥£!
lampe	lempe	limpe	tsngc	*§Ø?
lettre	lètre	luttre	trltnz	¥?¥?Dþ
lèvre	laivre	lècre	dxzsr	!£?Ø
ligne	lygne	lagne	trqzc	-!D??
neige	neije	noge	xsrpv	£þ??-
nuage	nuaje	vuage	rscqv	Ø*£?þ
nuque	nuke	naque	xsgczv	D!£§‡
ombre	hombre	omtre	cndvx	ØD?‡*
oncle	honcle	ontle	nzxf	£*¥!?
ongle	hongle	onple	vnrtw	‡?§-£
ordre	hordre	ardre	mzter	?¥-§D

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Word	Pseudo-homophone	Pseudo-word	Consonant String	Symbol String
phrase	frase	phruse	qkvczv	¥-§p?D
pièce	piaice	rièce	jnvr	?§bØD
pierre	piaire	pioerre	grcmnv	¥?pD-Ø
plage	plaje	clage	qbcjv	ØDp-Ø
plume	plumme	chume	gcnnv	p‡-*
pomme	pome	vomme	jcnzv	D¥-§‡
prêtre	praitre	pritre	gcnlvs	¥-Ø?p
prince	praince	trince	qvrnxz	¥‡§Ø*£
règle	raigle	rèpe	nwjtv	-D‡£
route	rhoute	ruite	wnxhv	p-†‡
sable	çable	souble	znhtc	¥D?*
sœur	seur	nœur	zncvx	£-pD*
table	thable	tuible	kcctc	?Ø§‡¥
tante	thante	xante	tcvtc	?‡Ø¥§
terre	tairre	tève	fcnnv	¥Ø?p§
titre	tytre	fitre	frhvc	‡?Ø*
toile	thoile	toine	fcrtv	?§‡¥Ø
train	trein	prain	hscxv	‡‡D¥-
troupe	troupe	froupe	fvnrqc	??p?¥
ventre	vantre	pentre	wcmfvs	-D£§‡
verre	vairre	vurre	txrlv	p¥?£§
veste	vaiste	neste	zcvbn	p¥Ø?*
viande	viende	vianfe	cvcmtc	§‡D-¥
vitre	vytre	bitre	xvlnc	£¥§*

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