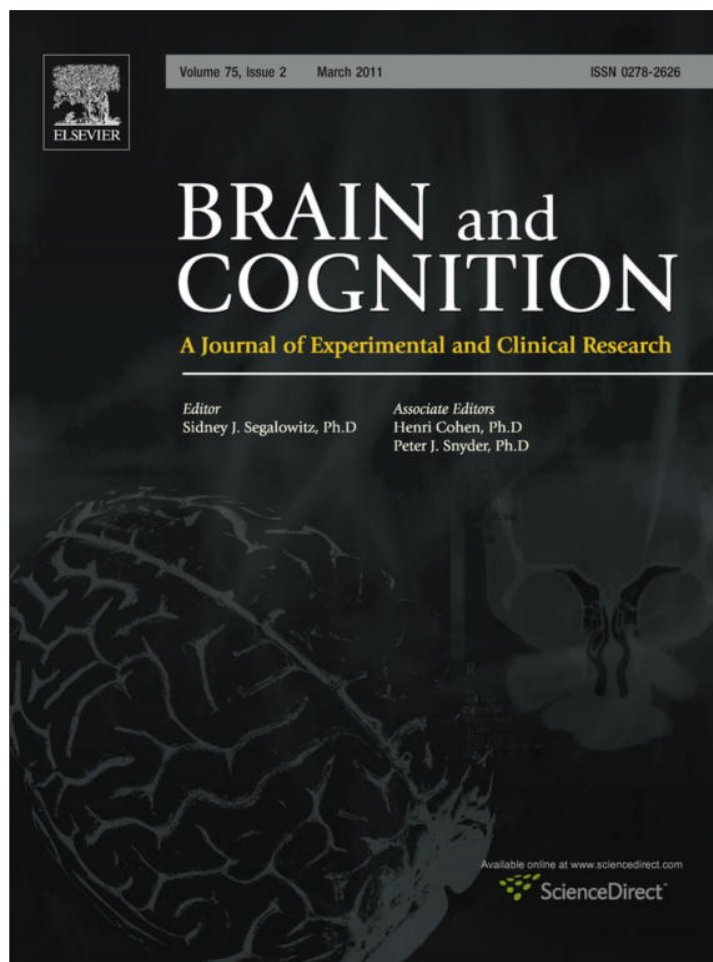


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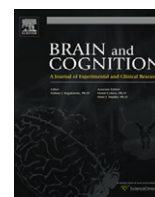
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Behavioral performances in participants with phonological dyslexia and different patterns on the N170 component

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ABSTRACT

Adults with phonological dyslexia and controls performed a lexical decision task while ERPs were recorded in the occipitotemporal pathway. Based on N170 durations, two subgroups were formed: *dysl1* showing longer N170 durations and *dysl2* showing normal N170 durations. While the *dysl1* subgroup had poorer accuracy for infrequent words and pseudo-words, the *dysl2* group responded more slowly than controls to pseudo-words. N170 amplitudes were larger in the left hemisphere for controls irrespective of items. In the *dysl1* subgroup, N170 amplitudes were larger in the left hemisphere than the right for words but not for pseudo-words, a sign of hemispheric compensation, while in the *dysl2* subgroup signs of bilateralization were observed. Moreover, in the *dysl1* subgroup, P100 amplitudes were smaller than controls. These results indicate different behavioral profiles of dyslexics with different patterns of P100 and N170 components. The ERP changes may be due to different behavioral strategies employed by each subgroup, logographic in *dysl2* and phonological in *dysl1*.

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1. Introduction

Developmental dyslexia is defined as a difficulty in learning to read in children with normal intelligence and motivation levels, in the absence of sensory or sociocultural anomalies (Seymour, 1990; Shaywitz, 1998; see Habib (2000), for a review). Lyon, Shaywitz, and Shaywitz (2003) emphasize that the main abnormality of dyslexics is in the phonological component. Dyslexic subtypes have been described, such as surface dyslexia, considered as a deficit in the lexical pathway of the Dual Route Cascaded (DRC) model (Coltheart, Rastle, Perry, Ziegler, & Langdon, 2001), leading to difficulties in reading irregular words but not regular words or non-words (Castles & Coltheart, 1993; Manis, Seidenberg, Doi, McBride-Chang, & Petersen, 1996; Samuelsson, 2000), orthographic representations (Castles, Datta, Gayan, & Olson, 1999; Stanovich, Siegel, & Gottardo, 1997), judgments in correct spelling, reading comprehension (Samuelsson, 2000), and in visual implicit memory (Samuelsson, Bogges, & Karlsson, 2000).

In contrast, phonological dyslexia, one of its most common types (Georgiewa et al., 2002; Liberman, Shankweiler, & Liberman, 1989; Ramus et al., 2003; Snowling, 1991, 2000) with high levels of spec-

ificity and robustness (Morris et al., 1998), is defined as impaired reading of pseudo-words and infrequent words with relative sparing of real and common words. Participants with phonological dyslexia committed more errors than those with surface dyslexia in phonological treatment requiring position analysis, while the reverse was found in a spelling task requiring orthographic treatment (Manis et al., 1996). Behavioral anomalies in phonological dyslexia include weak phonological awareness and short-term verbal memory, delayed access to the mental lexicon (Paulesu et al., 1996; Snowling, 2000), and slower reading of pseudo-words, evident in transparent languages such as Italian and those with inconsistent grapheme-phoneme conversions, but perhaps more severe in opaque ones (Landerl, Wimmer, & Frith, 1997; Lindgren, De Renzi, & Richman, 1985; Paulesu et al., 2001). Seymour (1997) considers phonological dyslexia as an alphabetic disorder marked by deficient orthographic structure. Other explanations include delayed information processing speed (Breznitz & Meyler, 2003; Tallal & Gaab, 2006), more specifically in rapid auditory processing (Benasich & Tallal, 1996, 2002), a deficit in the magnocellular pathway (Livingstone, Rosen, Drislane, & Galaburda, 1991; Stein, 2001), or impaired attention (Facoetti, Ruffino, Peru, Paganoni, & Chelazzi, 2008; Lum, Conti-Ramsden, & Lindell, 2007). The underlying factors may include disturbed interhemispheric communication (Badzakova-Trajkov, Hamm, & Waldie, 2005) or developmental changes in

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cerebral organization (Shaywitz et al., 2002; Temple et al., 2003; Wijers, Been, & Romkes, 2005).

Nevertheless, Ziegler et al. (2008) reported that the difference between surface dyslexia (impaired lexical pathway) and phonological dyslexia (impaired non-lexical pathway) is not so clearcut as defined by the DRC model of Coltheart et al. (2001), by finding lexical and non-lexical deficits in both, more in line with a multifactorial disorder (Pennington, 2006). Other authors suggest that all dyslexics are at the low end of the normal range in phonological skills (Manis et al., 1999), in a continuum of reading skills relative to control readers (Manis et al., 1996).

Within the population of phonological dyslexics, certain subgroups have been described. Friedman (1995) observed six cases with acquired phonological dyslexia, three with a specific disturbance in connections between spelling and phonology and three with a more generalized phonological impairment. In a meta-analysis, Tree (2008) reported four subtypes, the two described by Friedman (1995) comprising respectively 13% and 18.5% of cases, a third representing a mixed type (8%), but the majority (60.5%) with a selective impairment in reading non-words, due to impaired grapheme-phoneme conversion (Coltheart et al., 2001). These results concern acquired as opposed to developmental dyslexia. Techniques using functional magnetic resonance imaging (fMRI) reveal hypoactivation in left temporoparietal regions of developmental phonological dyslexics, together with hyperactivation in homologous regions on the opposite hemisphere during pseudo-word rhyming (Simos et al., 2000). Relative to control readers, hypoactivation was also found in left inferior frontal gyrus and more posterior regions, which was corrected by phonological intervention (Shaywitz et al., 2004). Temple et al. (2003) demonstrated more important right-sided activation after phonological training in the same type of dyslexics, indicating bilateral representation as a compensatory response during reading. Shaywitz et al. (2003) compared persistent as opposed to compensated dyslexics. In a pseudoword rhyming task, all dyslexics demonstrated underactivated left superior temporal and occipitotemporal regions relative to controls. But compensated dyslexics had higher activation in anterior regions than controls and persistent dyslexics, indicating a compensatory mechanism. Only persistent dyslexics presented a functional connectivity between left occipitotemporal regions and right prefrontal areas, involved in working memory and memory retrieval. The authors suggested that both dyslexic subgroups did not rely on the same reading strategies.

We examined event-related potentials (ERPs) during a lexical decision task (discriminations between words and pseudo-words) in participants with phonological dyslexia relative to four theories of dysfunction: selective attention (Buchholz & Davies, 2007; Facchetti, Lorusso, Paganoni, Umiltà, & Mascetti, 2003; Lum et al., 2007), deficits in orthographic processing (Seymour, 1997), differences in developing cerebral organization (Shaywitz et al., 2002; Temple et al., 2003; Wijers et al., 2005), and delayed information processing speed (Breznitz & Meyler, 2003; Stringer & Stanovich, 2000; Tallal & Gaab, 2006). We first examined the P100 component reflecting physical characteristics of stimuli, sensitive to selective attention for spatial (Hillyard, Teder-Sälejärvi, & Münte, 1998) and non-spatial (Taylor, 2002) material, probably at the level of extrastriate cortex (Clark & Hillyard, 1996; Smith, Cacioppo, Larsen, & Chartrand, 2003). In spatial attention tasks, Heinze et al. (1994) and Mangun, Hopfinger, Kussmaul, Fletcher, and Heinze (1997), found higher P100 amplitudes covarying with higher blood flow in the contralateral fusiform gyrus of the attended hemifield, indicative of a P1 attention effect. Likewise, Caharel et al. (2007) found a delayed and reduced P1 component in schizophrenics liable to deficits in selective attention. An attention deficit in dyslexia may be exhibited in the form of reduced P100 amplitudes relative

to controls. Dyslexic symptoms considered as an orthographic deficit may cause alterations in the N170 component, based on findings of larger intracranial N200 amplitudes in left fusiform gyrus of epileptics reading orthographic material relative to faces irrespective of pronounceability (Nobre, Allison, & McCarthy, 1994). Moreover, Bentin, Mouchetant-Rostaing, Giard, Echallier, and Pernier (1999) reported larger N170 amplitudes in left posterior hemisphere for letter combinations and larger amplitudes in right hemisphere for non-letter symbols, leading one to consider this component as a marker of orthographic encoding (Rossion, Joyce, Cottrell, & Tarr, 2003; Simon, Bernard, Largy, Lalonde, & Rebaï, 2004; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). A third possible explanation of dyslexia concerns bilateral as opposed to unilateral treatment found in controls (Shaywitz et al., 2002; Temple et al., 2003), assessed by ERP amplitudes in right relative to left hemisphere, reflecting the number of recruited neurons (Ponton, Eggermont, Kwong, & Don, 2000). A fourth possible explanation posits slowed information processing speed in dyslexic participants relative to controls (Breznitz & Meyler, 2003), examined by ERP peak latencies and reaction times (RTs).

Wimmer, Hutzler, and Wiener (2002) observed in children with poor reading skills lower N1 amplitudes at left frontal and right central sites, reflecting an “early deficit in the activation of phonological codes in response to letter strings”. According to Bentin et al. (1999), pronounceable stimuli in a rhyme decision task may be represented by the N320 component, larger in left (T3 electrode) than in right (T4 electrode) hemisphere. Simon et al. (2004) recorded the left-sided N320 only for pseudo-words and consonant chains during passive reading, with a possible generator in mid-temporal gyrus, associated with phonological treatment (Hagoort et al., 1999; Price et al., 1994). A phonological deficit may be assessed by accuracy rates and RTs for pseudo-words, and N320 component, dependent on grapheme-phoneme conversion (Coltheart et al., 2001).

Other ERPs linked with dyslexia include the Mismatch Negativity (MMN) for auditory stimuli (Bonte, Poelmans, & Blomert, 2007; Bradlow et al., 1999; Schulte-Körne, Deimel, Bartling, & Remschmidt, 2001) and the fronto-central P3a as an index of phoneme awareness (Fosker & Thierry, 2004). Dyslexic and control readers differed in an implicit but not an explicit auditory oddball paradigm for the centroparietal P3b, emphasizing the importance of attentional resources (Fosker & Thierry, 2004, 2005). Unlike controls, dyslexic participants showed a bilateral P300 in the Continuous Performance Test of attention (Taroyan, Nicolson, & Fawcett, 2007). Moreover, Georgiewa et al. (2002) observed larger P300 amplitudes in dyslexics at a left frontal site during silent reading of words and pseudo-words, perhaps as a compensatory response, which may also be involved in reduced contingent negative variation (CNV) waves for anticipatory activation and an enhanced N220 for letter string processing during the detection of non-words (Bergmann, Hutzler, Klimesch, & Wimmer, 2005). We focused on occipitotemporal P100, N170, and N320 wavelengths, as no previous experimenters to our knowledge used analyses of these three components in the context of a single study.

2. Materials and methods

2.1. Participants

Twenty-nine controls (18 women and 11 men, mean age = 22.3 years, SD = 2.1) and 23 dyslexics (15 women and 8 men, mean age = 23.8 years, SD = 7.9) participated in the study after informed consent was obtained, all right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), with French as their maternal tongue and normal or corrected-to-normal visual acuity. These

were 1–7-year students at the University of Rouen with no history of neuropsychiatric symptoms. Dyslexic participants with phonological troubles were recruited from the Preventive Medicine Service, diagnosed during childhood by a certified orthophonist according to the International Statistical Classification of Diseases and Related Health Problems for developmental disorders and standardized tests, in remedial training for a period between 4 and 8 years. Dyslexic participants were evaluated with the “Alouette” reading test (Lefavrais, 1965) and the BELEC (“Batterie d’évaluation du langage écrit et de ses troubles”, Mousty, Leybaert, Alegria, Content, & Morais, 1994), comprising reading of regular, irregular, long, short, frequent, and non-frequent words, reading and repeating pseudo-words, and copying. Controls considered themselves as good readers. Based on N170 durations (Table 1), calculated in each subject for each electrode and in each condition by taking two intersection points relative to baseline (see below), two dyslexic subgroups were distinguished, dysl1 ($n = 12$) with a much longer duration than dysl2 ($n = 11$).

2.2. Participant characteristics

To examine oral reading skills, the “Alouette” test was used (Lefavrais, 1965). Since this test has been standardized only in children, raw data are presented in Table 2. Due to variations in heterogeneity of variances, non-parametric Mann–Whitney U-tests were used (Table 3), performances being lower as expected in both dyslexic subgroups vs. controls for reading time, word/min, and errors ($p < 0.006$), each subgroup not differing from each other. In addition, all participants underwent the d2 attention test (Brickenkamp, 1998), where they had to cross out among four letters (b, d, p, or q) the “d” only with two lines either above or below it under 20 s per line. The first measure corresponds to the number of letters treated independently of correctness (TN), the second to the number of correct responses (TN-E), and the third to the number of correct responses minus confusion errors (concentration performance, CP). The participants also underwent the Standard Progressive Matrices (PM38) (Raven, Court, & Raven, 1995), measuring non-verbal reasoning and cognitive flexibility, highly correlated with the general intelligence factor (Raven, Court, & Raven, 1977). These two tests were used to evaluate cognitive abilities beside reading, to exclude those with a wider range of cognitive deficits. No difference was found between controls and each dyslexic subgroup in both tests (U-tests, $p > 0.05$, Table 3).

2.3. Stimuli

Two-syllable words and pronounceable pseudo-words composed of 5–7 letters were presented. Commonly used words with regular spelling were selected from the “Lexique 3.01” database (New, Pallier, Brysbaert, & Ferrand, 2004), controlled for ortho-

graphic and phonological neighborhood at two levels of word frequency. The list was presented in capital letters in pseudorandom order, comprising 50 frequent words, 50 infrequent words, and 50 pseudo-words in black Courier type on a grey background with normal luminance at a visual angle of 2° .

2.4. Tasks and procedure

The participants were comfortably seated in a darkened, silent room in front of a computer screen and performed a lexical decision task by clicking on one of two buttons on the computer mouse, the left one when seeing a word and the right one when seeing a word that does not exist in the French language. In a first session, the number of correct responses and RTs were measured, followed by a session comprising behavior and ERPs (Fig. 1). To avoid repetition and learning effects, a minimal delay of 3 days intervened between the sessions, so that the accuracy rate was the equivalent in both phases. In the behavioral session, participants were asked to respond as rapidly and accurately as possible. Each stimulus was presented for 1 s, with an interstimuli interval varying between 900 and 1100 ms, when a fixation point appeared to maintain attention. In the behavior + ERP session, the same method was used, except participants answered after a beep signal 1 s after visual stimulus onset to prevent movement-related artifacts on electroencephalographic (EEG) activity. A block of 20 items was presented, with pauses in between as needed. A training session comprising a few test trials was given prior to the first session.

2.5. ERP recordings

EEG activity was recorded from 32 surface electrodes: FP1, F7, F3, T7, C3, TP7, CP3, P7, P3, PO7, PO3, O1, XO1, FP2, F8, F4, T8, C4, TP8, CP4, P8, P4, PO8, PO4, O2, XO2, Fz, Cz, CPz, Pz, POz and Oz, distributed according to the 10–10 classification system with a reference electrode in an antero-fronto-central position (AFz). The EEG was amplified, digitalized at a rate of 256 Hz, filtered (band-pass 0.1–100 Hz), sampled (1 point per 3.92 ms), and stored on an IBM-compatible computer with Deltamed™ software (Paris, France). Electrode impedance was kept below 5 K Ω .

2.6. Data analyses

A common average reference was recalculated off-line (Bertrand, Perrin, & Pernier, 1985) with a multi-electrode reference composed of F7, F3, C3, T7, CP3, TP7, P3, P7, F8, F4, C4, T8, CP4, TP8, P4, P8, Fz, Cz, CPz, and Pz. Only trials with correct responses were included in averaging. Approximately 5% of the trials were rejected because of ocular movements or artifacts ($>100 \mu\text{V}$ at FP1 and FP2 electrodes). In the final phase, the data were digitally low-pass filtered with a 48 Hz cut-off.

Data were analyzed with Statistica™ software (Statsoft, France, 1998). Correct responses and RTs were evaluated by ANOVA with item (frequent words/infrequent words/pseudo-words) as the within-subject factor, and group (dyslexic1/dyslexic2/controls) as the between-subject factor. For ERPs, a three-way ANOVA was conducted with item, hemisphere (left/right), and electrode (O/PO/P) as within-subject factors and group as the between-subject factor. We focused on P100 and N170 components, defined after examining grand average topographies respectively as the maximal positive deflection between 60 and 170 ms and the maximal negative deflection between 100 and 240 ms at occipitotemporal sites. We also focused on occipitotemporal electrodes: O1, PO7 and P7 for the left hemisphere, and O2, PO8 and P8 for the right, based on their sensitivity to orthographic pre-semantic words (Bentin et al., 1999; Simon et al., 2004). ERPs were analyzed for peak amplitudes and latencies for the two components

Table 1

Electrophysiological and behavioral differences between groups. The table shows longer N170 duration and lower accuracy rate for dysl1, the dysl2 showing longer reaction times and shorter N170 duration.

	N170 duration on left hemisphere (ms)	N170 duration on right hemisphere (ms)	Accuracy rate (%)	Reaction time (ms)
Controls mean	102.32	92.42	98.10	745.81
SD	11.15	7.76	0.49	36.19
Dysl 1 mean	140.18	129.02	86.55	897.35
SD	12.19	10.89	4.54	88.57
Dysl 2 mean	83.21	80.96	93.78	1023.25
SD	11.39	11.65	1.31	79.91

Table 2
Reading, attentional, and non-verbal performances for controls and dyslexics (mean ± SD). Raw data are presented for the reading test, and standard values for d2 attention (mean = 100) and Raven (mean = 50) tests. (TN = treated items; TN-E = correct responses, CP = correct responses minus confusions).

Alouette reading test				
	Age (years)	Reading time (min)	Number of words per minute	Number of errors
Controls (n = 29)	22.3 ± 2.1	1.51 ± 0.28	145.41 ± 22.53	3.83 ± 3.13
Dyslexics (n = 23)	23.8 ± 7.9	2.21 ± 0.41	107.96 ± 24.53	12.17 ± 5.66
Dysl1 (n = 12)	27.2 ± 10.5	2.35 ± 0.42	100.5 ± 27.11	10.67 ± 7.15
Dysl2 (n = 11)	24.1 ± 8.4	2.06 ± 0.34	116.1 ± 19.39	13.82 ± 2.93

d2 attention test			
	TN	TN-E	CP
Controls	103.93 ± 8.17	104.69 ± 8.29	105.45 ± 8.62
Dyslexics	102.13 ± 8.65	101.17 ± 8.61	101.96 ± 8.29
Dysl1	101.67 ± 8.06	100.5 ± 9.17	101.08 ± 9.69
Dysl2	102.64 ± 9.62	101.91 ± 8.44	102.91 ± 6.79

Raven matrices	
Controls	61.72 ± 22.89
Dyslexics	60 ± 23.41
Dysl1	59.58 ± 23.50
Dysl2	60.46 ± 24.44

Table 3
Non-parametric comparisons in the form of p-values with Mann–Whitney U-test for each subgroup in the following tests: Raven Progressive Matrices, d2, Alouette reading. Blackened numbers are significant, only on the reading measures. TN = treated items; TN-E = correct responses; CP = correct responses minus confusions.

Tests measures	Mann–Whitney U-test			
	Controls vs. dyslexics	Controls vs. dyslexics 1	Controls vs. dyslexics 2	Dyslexics 1 vs. dyslexics 2
Raven matrices	0.796	0.819	0.880	0.689
TN (d2)	0.555	0.390	0.952	0.538
TN-E (d2)	0.289	0.197	0.705	0.538
CP (d2)	0.207	0.112	0.694	0.406
Reading time (alouette)	0.000	0.000	0.001	0.091
Words per minute (alouette)	0.000	0.000	0.006	0.132
Number of errors (alouette)	0.000	0.001	0.000	0.110

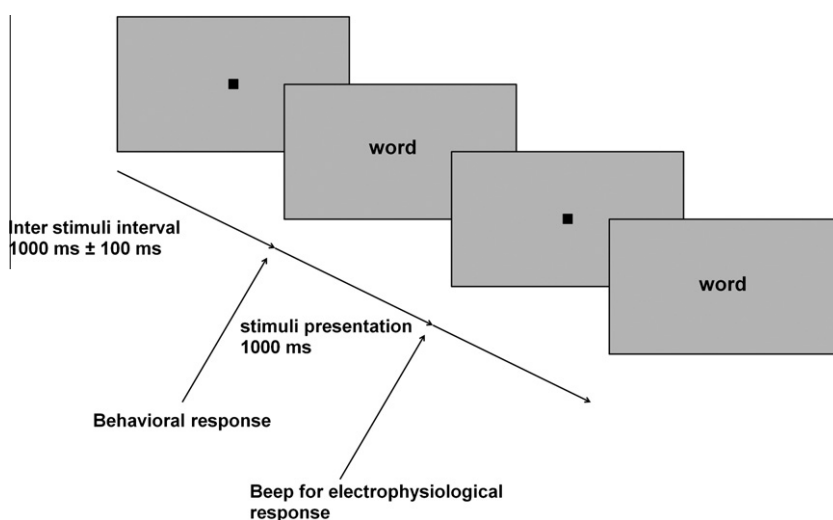


Fig. 1. Schema of stimulus presentation. In the behavioral session, responding was immediate, while in the behavioral + ERP session, responding occurred following a beep sound 1 s after stimulus presentation, the following stimulus only appearing after the subject had responded.

as well as N170 duration (Fig. 2): the first intersection is defined by crossing of the N170 in its descending phase relative to baseline and the second by crossing of the N170 in its ascending phase relative to baseline, adjusted for each subject. Greenhouse–Geisser corrections were applied with adjusted degrees of freedom corresponding to the epsilon (ϵ) value (Keselman &

Rogan, 1980), with post hoc Tukey HSD comparisons when main effects or interactions reached the required level of significance at $p < 0.05$. Regression analyses was conducted on N170 duration in each hemisphere, task accuracy, and reading skills (reading time, errors, and words per minute) for dyslexic and control participants.

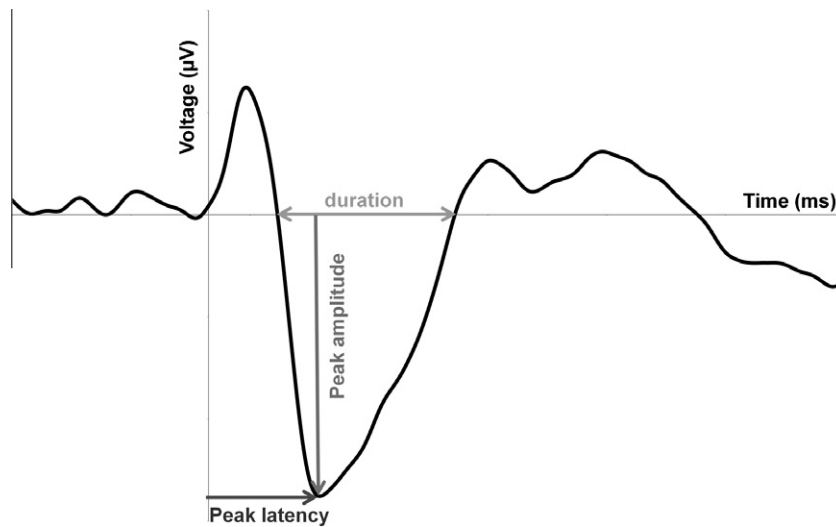


Fig. 2. Presentation of ERP characteristics: peak amplitudes, peak latencies, and duration.

3. Results

3.1. ERPs

3.1.1. Subgrouping dyslexic participants

Inspection of ERPs revealed two distinct dyslexic subgroups: dysl2, who, like controls, exhibited a N170 but no N320 and dysl1 with the two waves almost fused together, rendering the analysis of N320 amplitudes and latencies irrelevant. We thereby analyzed three groups for N170 amplitude, latency, and duration.

3.1.2. N170 duration, peak amplitude, and peak latency

3.1.2.1. N170 duration. As expected from visual inspection, a group effect occurred for N170 duration ($F(2, 49) = 6.80$; $p = 0.002$), due to higher values in the dysl1 subgroup relative both to controls (HSD Tukey $p = 0.004$) and the dysl2 subgroup ($p = 0.001$) (Fig. 3), the latter two not differing from each other ($p > 0.05$).

The group \times item \times hemisphere interaction was significant for N170 duration ($F(4, 98) = 3.52$; $\epsilon = 0.89$; $p = 0.01$) (Fig. 4). Restrictive analysis on the group factor revealed that the hemisphere \times item interaction is significant for dysl1 ($F(2, 22) = 4.83$; $\epsilon = 0.92$; $p = 0.003$) and dysl2 ($F(2, 20) = 5.64$; $\epsilon = 0.77$; $p = 0.02$), but not for controls ($F(2, 56) = 0.08$; $\epsilon = 0.91$; $p = 0.92$). For the dysl1 subgroup, N170 duration was longer in the left hemisphere than the right for words (frequent: $p = 0.0002$, infrequent: $p = 0.03$), not pseudo-words ($p = 0.96$). In addition, N170 duration was shorter in the right hemisphere for frequent than for infrequent words ($p = 0.02$), and the latter shorter than pseudo-words ($p = 0.01$). For the dysl2 subgroup, N170 duration was longer in the left hemisphere than the right for frequent words ($p = 0.006$), not infrequent ones ($p = 0.11$), or pseudo-words ($p = 0.75$). Moreover, frequent words generated longer durations than infrequent ones ($p = 0.0005$) or pseudo-words ($p = 0.005$) in the left hemisphere but not the right.

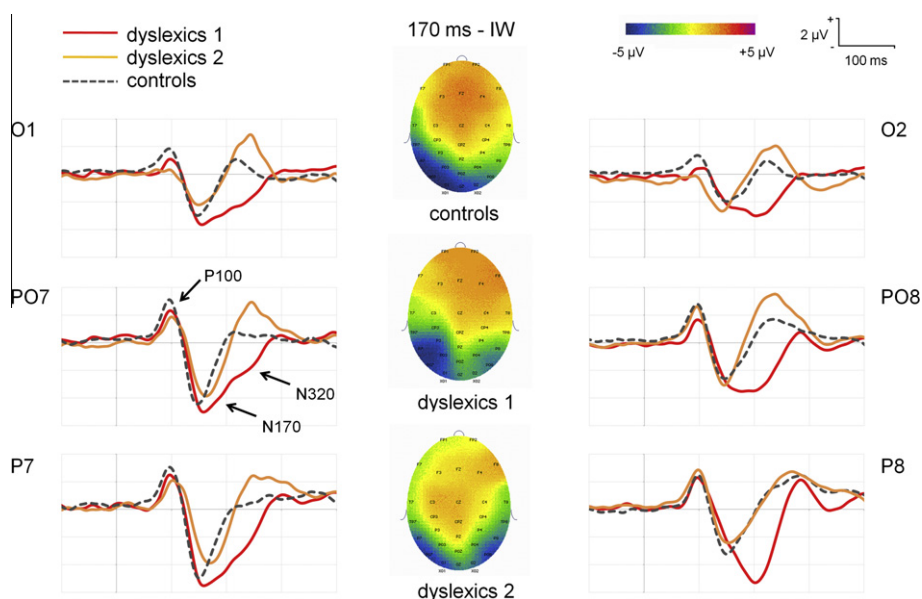


Fig. 3. Electrophysiological tracings of the N170 component for normal, dysl1, and dysl2 readers at O1, O2, PO7, PO8, P7, and P8 electrodes and mappings approximately 170 ms post-stimulus during readings of infrequent words (IW). We see the distinction between dyslexic subgroups on N170 duration, longer for dysl1, plus N170 lateralization is left-side dominant for controls and dysl1 and bilateralized for dysl2 in reading infrequent words.

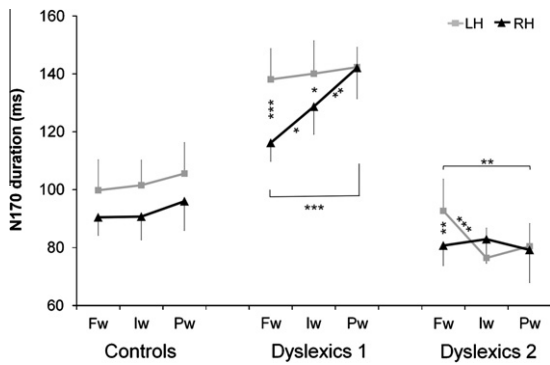


Fig. 4. Group \times item \times hemisphere interaction for N170 duration. In dysl1 subjects, the left hemisphere was dominant only for words. In dysl2 subjects, the left hemisphere was dominant only for frequent words. fw = frequent words; iw = infrequent words; pw = pseudo-words. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.1.2.2. *N170 peak amplitude and latency.* A group \times item \times hemisphere interaction was found for N170 peak amplitudes ($F(4, 98) = 2.78$; $\epsilon = 0.99$; $p = 0.03$, Fig. 5). Restrictive analysis on the group factor revealed that the hemisphere \times item interaction is significant only in controls ($F(2, 56) = 3.13$; $\epsilon = 0.99$; $p = 0.05$), only nearing significance in dysl1 ($F(2, 22) = 3.35$; $\epsilon = 0.96$; $p = 0.057$), and is non-significant in dysl2 ($F(2, 20) = 0.08$; 0.87 ; $p = 0.90$), the latter showing bilateral effects (Fig. 5). Post hoc analyses revealed that in control and dysl1 participants, N170 amplitudes were higher in the left hemisphere than the right irrespective of items (HSD Tukey $p < 0.001$). In controls, pseudo-words tended to cause larger amplitudes than frequent words on the left side, of borderline significance ($p = 0.059$). Unlike controls, left N170 amplitudes of dysl1 participants were larger for frequent words than pseudo-words ($p = 0.02$).

3.1.3. *P100 peak amplitude and latency*

Analyses of P100 amplitudes show a group effect ($F(2, 49) = 3.7332$; $p = 0.03$) caused by lower amplitudes in dysl1 than controls (Tukey $p = 0.03$; Fig. 6), dysl2 not differing either from dysl1 ($p = 0.68$) or from controls ($p = 0.29$). On the contrary, no effect was found on P100 latencies and no item or hemisphere effects were found on P100 amplitudes and latencies.

3.2. Behavioral performances

There was a group effect ($F(2, 49) = 6.62$; $p = 0.0028$), as the dysl1 subgroup was less accurate than controls (HSD Tukey $p = 0.002$) and the dysl2 subgroup (HSD Tukey $p = 0.03$) in the lexical decision task, the latter two not differing from each other (HSD Tukey $p = 0.34$). The group \times item interaction ($F(4, 85) = 5.14$;

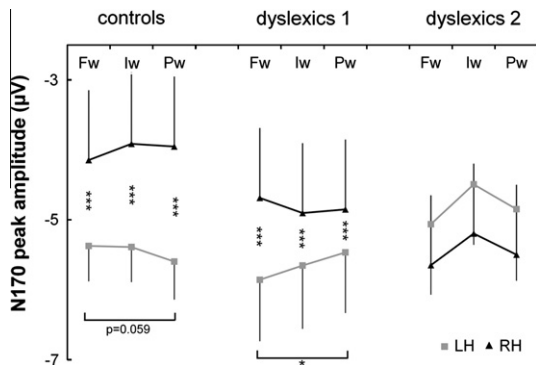


Fig. 5. N170 peak amplitudes were larger in the left hemisphere than on the right for all items in controls and the dysl1 subgroup. fw = frequent words; iw = infrequent words; pw = pseudo-words. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

$\epsilon = 0.87$; $p = 0.002$) is due to lower accuracy for infrequent words and pseudo-words ($p < 0.05$, Tukey HSD) in the dysl1 but not the dysl2 subgroup ($p > 0.05$, Tukey HSD) relative to controls (Fig. 7). As expected in phonological dyslexia, there was no intergroup difference for frequent words.

Group ($F(2, 49) = 5.83$; $p = 0.005$) and group \times item interaction ($F(2, 58) = 6.93$; $\epsilon = 0.59$; $p = 0.001$) terms were significant in regard to RTs, with only the dysl2 subgroup responding more slowly than controls ($p = 0.002$), dysl1 showing only a tendency ($p = 0.07$). Although participants in all groups responded more quickly for frequent than infrequent words and for infrequent words than pseudo-words, RTs for the latter were higher than controls only in the dysl2 subgroup ($p = 0.01$, Fig. 8).

As shown in Tables 2 and 3, the groups did not differ in Raven and d2 attention tasks. These negative results contrast with reading scores, both slower and less accurate.

3.3. Link between performances and ERPs

A correlation analysis was undertaken between N170 duration, accuracy, and reading skills (Fig. 9 and Table 4). Only N170 duration in the right hemisphere ($r = -0.28$) or both hemispheres ($r = -0.27$) was inversely correlated with words/min. Weak correlations for the other variables may be due to small sample sizes.

4. Discussion

Two dyslexic subgroups were distinguished on the basis of lexical decisions and N170 durations. Although the subgroups had equally inferior reading skills relative to those of controls, only the dysl1 subgroup was marked by longer N170 durations and lower accuracy in reading infrequent words and pseudo-words,

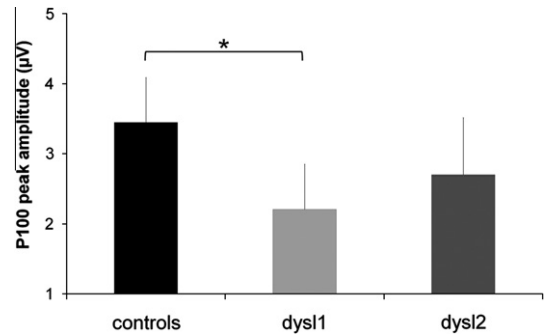


Fig. 6. P100 peak amplitudes were smaller for the dysl1 subgroup relative to controls. * $p < 0.05$.

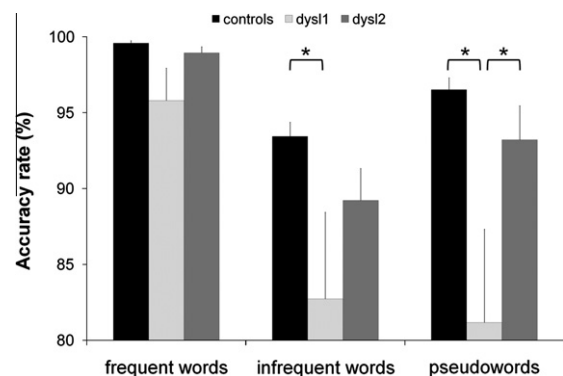


Fig. 7. Lower accuracy rates in the lexical decision task for infrequent words and pseudo-words in the dysl1 but not in the dysl2 subgroup relative to controls.

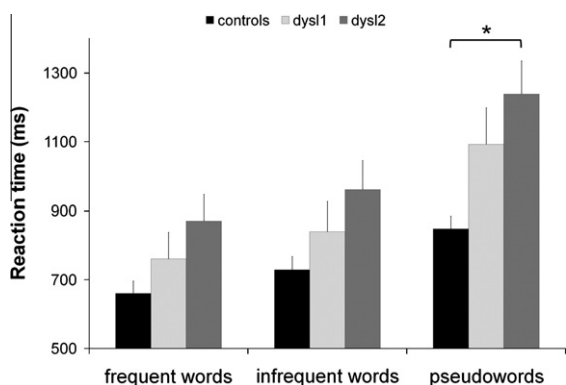


Fig. 8. RTs for pseudo-words in the lexical decision task were higher than normal only in the dysl2 subgroup.

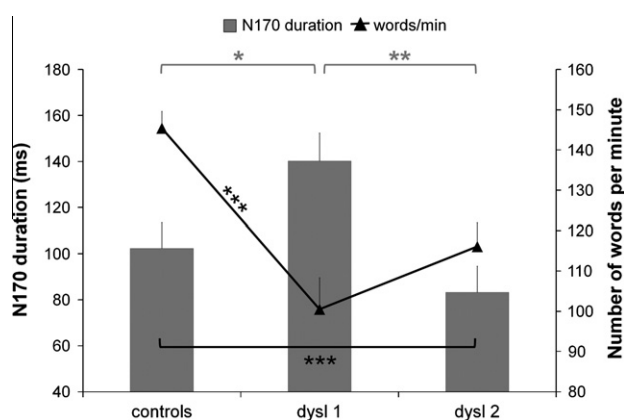


Fig. 9. N170 duration in the left hemisphere relative to words correctly read. Longer N170 duration was correlated with lower number of words. Significance in grey concerns durations, significance in black reflects words per min. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

the hallmark of phonological dyslexia (Ramus, 2003). The dysl2 subgroup was characterized by slower responses than controls in reading pseudo-words, indicating a difficulty in phonological mediation (Fosker & Thierry, 2005; Ramus, 2004; Ramus et al., 2003; Seymour, 1997; Siok, Jin, Fletcher, & Tan, 2003). It is uncertain whether behavioral differences are due to dyslexia as such or to compensatory strategies promoting either accuracy or speed. In a fMRI study, Shaywitz et al. (2003) distinguished accurate but non-fluent readers with hypoactivation in left parietotemporal and occipitotemporal cortex from inaccurate non-fluent readers with normal activation of these regions, presumably because of a

memory-based strategy, rather than the use of analytic word identification. Our dysl1 subgroup may be similar to the former, exhibiting a more analytic strategy than the dysl2 subgroup. However, other studies (Bosse & Valdois, 2003, paragraph 25; Bosse, Tainturier, & Valdois, 2007) are concordant with the existence of subgroups differing on the basis of dysfunction itself, in particular children reading pseudo-words poorly due to phonological or visuo-attentional deficits.

We examine four possible explanations of phonological dyslexia, namely deficits in selective attention, or in orthographic and phonological processing, bilateral representation of language, and slowed information processing speed.

4.1. Selective attention

Facoetti and Molteni (2001) and Facoetti et al. (2003) underline the role of selective attention in phonological dyslexia. As an index of attention, we examined the P100 component (Clark & Hillyard, 1996; Di Russo & Spinelli, 1999; Hillyard et al., 1998). In support of its role, we found that, irrespective of items, the dysl1 subgroup had lower P100 peak amplitudes in occipitotemporal regions, a sign of limited attentional resources (Buchholz & Davies, 2007; Facoetti & Molteni, 2001), associated with difficulties in extracting the physical characteristics of visual stimuli (Hillyard et al., 1998; Rebai, Bernard, Lannou, & Jouen, 1998). Some authors report sluggish automatic capture of both hemifields in dyslexia (Hari, Renvall, & Tanskanen, 2001), others a difficulty in orienting (Facoetti, Paganoni, Turatto, Marzola, & Mascetti, 2000; Facoetti, Turatto, Lorusso, & Mascetti, 2001) or focusing (Facoetti, Paganoni, & Lorusso, 2000; Facoetti et al., 2000; Rayner, Murphy, Henderson, & Pollatsek, 1989) attention. Selective spatial attention is an important factor in reading efficiency and visual search performance (Casco, Tressoldi, & Dellantonio, 1998; Iles, Walsh, & Richardson, 2000).

Fewer attentional resources or impairments in early processing of verbal stimuli by dysl1 participants may underlie deficits in encoding (Thompson et al., 2005) and subsequent grapheme-phoneme conversions (Facoetti et al., 2003). Attentional deficits may lead to increased N170 durations in dysl1, a sign of difficulties in orthographic and phonological processing (Bentin et al., 1999; Simon et al., 2004), or interference with rapid processing of the form of words, preventing effective use of logographic information (Habib, 2000). Nevertheless, neither dyslexic subgroup differed from controls in the d2 selective attention test based on letter cancelling, a less complex task than lexical decision. It remains to be seen whether more difficult tests discriminate between the groups, for example, by using letter strings instead of letters.

Unlike the visual verbal decision task for which our participants had a specific deficit, P100 amplitudes were unchanged in those executing a moving dot task (Schulte-Körne, Bartling, Deimel, & Remschmidt, 2004) or an auditory lexical decision task with pho-

Table 4

Correlations between N170 duration (mean; LH: mean of O1–P07–P7 electrodes, RH: mean of O2–P08–P8 electrodes), accuracy rate, and raw scores in the Alouette reading test (reading time, number of errors and words per minute).

	N170 dur	N170 dur (LH)	N170 dur (RH)	Accuracy rate	Reading time	Errors	Words (min)
N170 duration		.94**	.90**	-.09	.25 ^a	.19	-.27*
N170 duration (LH)			.74***	-.08	.22	.15	-.24
N170 duration (RH)				-.17	.23	.14	-.28*
Accuracy rate					-.31*	.01	.27 ^a
Reading time						.65***	-.94**
Number of errors							-.66***
Words (min)							

^a .08 > $p > .05$.
* $p < .05$.
** $p < .01$.
*** $p < 0.001$.

nological priming (Bonte & Blomert, 2004). In the latter study, the P100 was recorded in different brain regions (Fz, FCz, and Cz electrodes) than our own. It would be interesting to test attentional resources of dyslexic participants in a non-linguistic context to determine to what extent this tendency may be generalized.

4.2. Orthographic and phonological processing

There is evidence that the N170 component reflects orthographic processing (Bentin et al., 1999; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Rossion et al., 2003; Simon et al., 2004), on which other components such as the N230 are grafted during visual word form searching in the mental lexicon (Simon et al., 2004), together with the N320, a possible index of grapheme-phoneme conversion (Bentin et al., 1999; Simon et al., 2004). Since the N320 was absent in dysl2 and controls, we analyzed the N170 associated with pre-lexical orthographic processing (Simon et al., 2004), followed by other components of the DRC model (Coltheart & Rastle, 1994; Coltheart et al., 2001), unless a logographic strategy is used (Simon, Petit, Bernard, & Rebai, 2007, global vs. local processing, paragraph 1), which appears to have been the case for control and dysl2 readers. Logographia corresponds to rapid processing of the global perception of a word, mostly relevant for frequent words (Frith, 1985; Simon et al., 2007, global vs. local processing, paragraph 1). Lexical searches follow to enable word recognition, but less frequent words may lead to additional processing of a phonological nature.

In controls, the N170 component was larger in the left hemisphere than the right irrespective of items, concordant with verbal dominance in our right-handed persons, true for over 96% of the population (Pujol, Deus, Losilla, & Capdevila, 1999; Rasmussen & Milner, 1977). Furthermore, in the left hemisphere, pseudo-words generated larger amplitudes than frequent words. This result may be interpreted as an augmentation in orthographic and phonological processing, logographic processing being insufficient for this type of material. In contrast, dysl2 participants exhibited a pattern of longer N170 durations for frequent words than pseudo-words in the left hemisphere, indicating logographic and visual processing, rather than decoding and phonological processing. In further contrast, dysl1 readers showed item sensitivity in the right hemisphere, minimal for frequent words and maximal for pseudo-words. This result might be due to deficient grapheme-phoneme conversion in the left hemisphere. Though some authors report left minineglect due to right hemisphere anomalies in dyslexia (Hari et al., 2001; Lorusso, Facoetti, Toraldo, & Molteni, 2005), our data suggest a left hemisphere deficit (Shaywitz et al., 2004). Item sensitivity in the right hemisphere was not observed in controls and probably the result of a compensatory response, the N320 being larger in the left hemisphere for pronounceable items (Simon et al., 2004). Another result of interest is the inverse correlation existing between N170 duration and reading proficiency as determined by our reading test. Since the dysl1 subgroup had longer N170 durations and lower accuracy relative to controls, this result, together with presence of the N320, indicates suboptimal phonological processing.

4.3. Compensatory bilateralization

While most readers are lateralized in the left hemisphere (Bentin et al., 1999; Rossion et al., 2003; Simon et al., 2004), compensatory hyperactivation on the right may occur in phonological dyslexia (Habib, 2003; Pugh et al., 2001; Simos et al., 2000, 2002; Temple et al., 2003; see Lyytinen et al. (2005), for a review), as a response to anomalies in left posterior regions while reading (Brunswick, McCrory, Price, Frith, & Frith, 1999; Paulesu et al., 2001; Shaywitz et al., 2002; Temple et al., 2003). In controls, the N170 was larger in left than right hemisphere. Dyslexic individuals

seem to exhibit two distinct types of hemispheric change. The dysl1 subgroup displayed right-sided amplification of N170 durations relative to controls in a manner proportional to item difficulty. These participants appeared to treat words predominantly in the left hemisphere but pseudo-words bilaterally, possibly via grapheme-phoneme conversion. Lavidor, Johnston, and Snowling (2006) reported a right-hemisphere shift of an orthographic-based strategy to compensate for the phonological deficit. On the contrary, dysl2 participants did not exhibit left-sided dominance for orthographic processing, as N170 amplitude was bilaterally distributed. In addition, they displayed no hemispheric difference in N170 duration, indicating bilateral representation of orthographic or logographic processing. The word form seems therefore predominant in these participants, showing augmented right-hemisphere treatment based on visuospatial processing and visual form memory (Campbell & Butterworth, 1985), with bilateral representations of language, as seen in normal-reading children (Bakker, 1979; Spironelli & Angrilli, 2009). Right hemisphere involvement is also shown by delayed RTs as a result of interhemispheric communication (Marzi, Bisiacchi, & Nicoletti, 1991).

4.4. Delayed information processing speed

Breznitz and Meyler (2003) showed retarded P2 and P3 components and RTs in phonological dyslexia on visual and auditory linguistic and non-linguistic tasks, concordant with a generalized slowing of information processing speed. Other authors document slower conduction speed in the magnocellular visual system of dyslexic participants (Livingstone et al., 1991; Stoet, Markey, & López, 2007). However, Breznitz and Misra (2003) found retarded RTs and P3 but not P2 in auditory phonological and visual orthographic tasks.

In our study, there was no group difference in ERP latencies. However, the dysl2 subgroup responded more slowly than controls, particularly to pseudo-words, RTs for the dysl1 subgroup showing a tendency in that direction. Tallal and Piercy (1974), in a phonemic task, showed that children with developmental aphasia distinguished less well auditory cues, a sign of delayed encoding, as in children with reading disabilities (Breier et al., 2001). Thus, retarded RTs to pseudo-words may be due to slowed phonological processing.

As mentioned in the previous section, slowed RTs in the dysl2 subgroup may be due to retarded interhemispheric exchanges, similar to reports by Von Plessen et al. (2002) and Henderson, Barca, and Ellis (2007). There appears to have been a speed-accuracy trade-off, in that the dysl1 subgroup was less accurate for infrequent words and pseudo-words while the dysl2 subgroup was slower for pseudo-words. The question arises as to whether ERP changes are due to dyslexia as such or the use of different strategies employed by the participants as a result of behavioral intervention, of a logographic nature in dysl2 and of a phonological nature in dysl1 participants. Different orthophonic treatments may favor the use of one method of reading over others. Conversely, the subgroups may represent separate entities potentially identifiable by genetic factors. Subgroup differences in ERPs may enrich our understanding of phonological dyslexia above definitions based strictly on reading pseudo-words.

5. Conclusion

Participants with phonological dyslexia were distinguishable by different patterns on P100 and N170 components. The reduction of P100 amplitudes in dysl1 participants is concordant with an attentional deficit. Their longer N170 durations may be due to slower grapheme-phoneme conversions, perhaps due to reading with

right-hemisphere lateralization for phonological material. In contrast, dys12 participants showed bilateralization of orthographic material with an N170 relatively similar between hemispheres and normal durations. This pattern seems to demonstrate access to a visuospatial (logographic) strategy. It remains to be determined whether the subgroup distinction holds for other tasks and whether biological factors or behavioral remediation is responsible. Our results show reduced attentional resources, poorer left-hemisphere treatment during reading, a different type of cerebral organization (either cause or consequence of dyslexia), and retarded information processing speed as underlying causes of dyslexia.

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