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Phonological deficits in dyslexia impede lexical processing of spoken words: Linking behavioural and MEG data

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ABSTRACT

Phonological difficulties have been identified as a core deficit in developmental dyslexia, yet everyday speech comprehension, which relies on phonological processing, is seemingly unaffected. This raises the question as to how dyslexic readers process spoken words to achieve normal word comprehension. Here we establish a link between neural correlates of lexical and sublexical processing in auditory words and behaviourally measured phonological deficits using magnetoencephalography (MEG). Spatiotemporally resolved cortical responses to phonological and lexico-semantic information were computed with the event-related regression technique (Hauk et al., 2009) and correlated with dyslexic and non-dyslexic subjects' phonological skills. We found that phonological deficits reduced cortical responses to both phonological and lexico-semantic information (phonological neighbours and word frequency). Individuals with lower phonological skills – independent of dyslexia diagnosis – showed weaker neural responses to phonological neighbourhood information in both hemispheres 200–500 ms after word onset and reduced sensitivity to written and spoken word frequency between 200 and 650 ms. Dyslexic readers showed weaker responses to written word frequency in particular compared to the control group, pointing towards an additional effect of print exposure on auditory word processing. Source space analysis localised phonological and lexico-semantic effect peaks to the left superior temporal gyrus, a key area that has been related to core deficits in dyslexia across a range of neuroimaging studies. The results provide comprehensive evidence that phonological deficits impact both sublexical and lexical stages of spoken word processing and that these deficits cannot be fully compensated through neural re-organization of lexical-distributional information at the single word level. Theoretical and practical implications for typical readers, dyslexic readers, and readers with developmental language disorder are discussed.

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1. Introduction

Developmental dyslexia is a neurological reading disorder that persists into adulthood despite normal intelligence and is commonly associated with a phonological processing deficit, leading to poor performance on tests that tap into phonological awareness and letter-sound decoding (Aaron, 1987; Litt & Nation, 2014; Peterson & Pennington, 2015; Romani et al., 2008; Saksida et al., 2016). Dyslexia affects the reading development of 7–10 % of the population (Ramus et al., 2013). However, despite their poor performance on phonological language tasks, dyslexic readers' acquisition and comprehension of speech is largely unaffected (Griffiths & Snowling, 2001). This raises the question as to how exactly dyslexic readers with phonological deficits process spoken words to achieve normal word comprehension.

Several hypotheses have been suggested to explain struggling readers' phonological processing difficulties. The Phonological Representation Hypothesis of Dyslexia (Hatcher & Snowling, 2002) postulates that people with developmental dyslexia have either poorly specified phonological representations (Swan & Goswami, 1997a; 1997b; Vellutino, 2004) or problems with accessing these representations accurately (Boets et al., 2013; Ramus & Szenkovits, 2008). More recently, it has been proposed that phonological deficits originate from inefficient perceptual sampling of the speech signal due to reduced cortical entrainment to the speech envelope (Goswami, 2011; Goswami et al., 2014; Lallier et al., 2017; Lizarazu et al., 2015, 2021; Molinaro et al., 2016). However, currently neither framework specifies whether and how phonological-prosodic processing difficulties affect the processing of lexico-semantic information in speech and what neural resources this involves.

The current paper addresses this gap by investigating the link between phonological skills and cortical responses to phonological sublexical, phonological lexical, and lexico-semantic information during auditory word processing. To better understand the neural underpinnings of these effects, MEG recordings from dyslexic and non-dyslexic readers were analysed with a linear regression approach for the first time. This method allowed us to capture both temporal and spatial cortical response dynamics with high sensitivity to continuous linguistic variables (phonological neighbourhood and word frequency), representing phonological and lexico-semantic processing. While poor phonological skills might not always constitute a language impairment, they could affect lexical analysis for typical readers, too, and as such provide important information on the relationship between low-level processing and the formation of higher-level linguistic skills. Below we discuss previous research on the neuro-cognitive processing of phonological and lexical information among typical and dyslexic readers, outlining gaps in this research.

1.1. *Phonological processing in typical and dyslexic populations*

Phonological processing difficulties in dyslexia were first attested with behavioural tasks that tap into phonological knowledge, an important predecessor of the development of phonemic awareness and fluent reading. Phonological knowledge is a broad term that refers to different types of internalised information derived from the phonological structure of words.[1] Dyslexic readers perform worse on tasks that tap into phonological knowledge such as pseudoword reading and repetition (Griffiths & Snowling, 2001; Rack et al., 1992; Snowling, 1981), phonemic segmentation (Bradley & Bryant, 1978; Muter et al., 1998; Wimmer, 1996), syllable (stress) detection (Goswami, Mead, et al., 2013), and general rhythmic tasks (Goswami, Huss, et al., 2013). Dyslexic readers also show slower statistical learning of the phonological regularities embedded in the auditory stream (Zhang et al., 2021). Despite the clear evidence of phonological deficits at the behavioural level, spatial-temporal information of cortical responses is needed to trace the neurobiological basis of these deficits.

Although the neural underpinnings of phonological deficits are still poorly understood, EEG data indicate that atypical phonological processing can be traced at the neurobiological level. Dyslexic children show atypical waveforms around the N400 component in response to phonological priming (Jednoróg et al., 2010) and during picture-word matching when phonological mismatches are presented, leading to greater negativity and later peaks compared to controls (Desroches et al., 2013). Importantly, atypical networks for phonological processing seem to persist into adulthood. A reduced left-hemisphere bias in dyslexic adults has been found, as shown by weaker entrainment to 30 Hz acoustic modulations in left auditory cortex (Lehongre et al., 2011). Similarly, dyslexic readers show reduced cortical entrainment to the prosodic components of speech that carry phonological information at lower frequencies (<10 Hz; Di Liberto et al., 2018; Lizarazu et al., 2015; Molinaro et al., 2016). Together these studies point at persistent cortical differences of phonological processing between control and dyslexic individuals that stem from auditory speech sampling deficits at multiple levels of granularity (fine phonemic and coarser prosodic features).

However, it is unclear whether these differences in auditory and phonological processing occur only at early sublexical stages or throughout the whole time-course of lexical access. Understanding the time-course of phonological processing in dyslexia better could improve targeted remediation of auditory training, which often fails to produce significant improvements (Van Herck et al., 2022). Phonological neighbourhood is a psycholinguistic measure that could help to disentangle the time-course of phonological difficulties as it taps into both sublexical and whole-word phonological stages (Strauß et al., 2022). Typically, two words constitute neighbours when their phonological structure is identical except for one phoneme (e.g. *cat/can*), which can be substituted, added, or deleted (i.e. they have a Levenshtein distance of one; Vitevitch & Luce, 2016). Effects of phonological neighbourhood on word recognition have been found as early as 150 ms post stimulus onset in healthy adult

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[1] Here we refer to phonological knowledge as the awareness of language-specific phoneme inventories, phonological contrasts, allophonic distributions, syllabic structures, prosodic information, and phonotactic rules and frequencies.

populations (Miozzo et al., 2015). At these early, sublexical word processing stages, high neighbourhood density (i.e. many phonological neighbours surrounding a given word) has a facilitative effect on phoneme processing since words in dense neighbourhoods typically consist of frequent phonotactic patterns. A second effect of neighbourhood density has been observed at later stages, when the full form of a word starts to become available to the listener (i.e. from around 300–400 ms; Dufour et al., 2013; Winsler et al., 2018), with some differences between languages. In English, for example, adults recognize words with many phonological neighbours more slowly than words with few neighbours (Dufour et al., 2013; Luce & Pisoni, 1998; Vitevitch & Luce, 1998, 1999, 2016), whereas in Spanish words with many neighbours are processed faster (Vitevitch & Rodríguez, 2005). This cross-linguistic discrepancy has not yet been fully resolved, but several factors have been identified as possible contributors, including word length (Spanish words tend to be longer than English words), the locus where phonological neighbours overlap (due to the high number of inflections in Spanish, many phonological neighbours are generated through phonological edits at the word offset, while onsets overlap), and phonotactic differences since neighbourhood frequency can be positively correlated with phonotactic probability (Vitevitch, 2002, 2012; Vitevitch & Luce, 1998, 1999, 2016; Vitevitch & Rodríguez, 2005). Crucially, in both English and Spanish, learning the phonological patterns of words that enable formation of phonological neighbourhoods impacts lexical access of spoken words.

Interestingly, phonological neighbourhood information seems to play an important role in dyslexic readers' auditory processing despite their phonological deficits. Thomson et al. (2005) showed that children with dyslexia are affected similarly by phonological neighbourhood density as children without dyslexia in a serial recall task, i.e. they better recall targets that reside in dense neighbourhoods. These findings seem surprising since dyslexic readers' phonological deficits would suggest imprecise phonological (neighbour) representations. This raises the question whether whole-word phonological representations are affected less in dyslexia than sublexical phonological representations. Detailed spatial-temporal information is needed to answer this question and better understand what linguistic knowledge and neural resources dyslexic readers engage when processing phonological neighbourhood information. This is the first aim of the current study.

1.2. *Lexico-semantic processing in typical and dyslexic populations*

Given the phonological deficits outlined above, it remains an important topic of debate how dyslexic listeners achieve normal word acquisition and comprehension. One strategy could be the use of lexico-semantic instead of phonological information. Word frequency is a well-studied psycholinguistic effect which reflects word processing at the lexical level and is often used as a proxy for lexico-semantic activation (Fairs et al., 2021; Strauß et al., 2022). High frequency words are processed faster and elicit lower evoked cortical response amplitudes (Sereno et al., 2020), most likely because frequent encounters lead to more efficient synaptic connections for a given word within the lexical network (Hauk & Pulvermüller, 2004). Consequently, less activation is needed to retrieve frequent words.[2] Since high word frequency reduces system demands, neural re-organisation of cortical responses to word frequency information at the lexical level might serve as a possible compensation mechanism for weak phonological sampling because lexico-semantic processing relies less on the analysis of fine phonemic detail and more on the development of whole-word memory traces via repetitive exposure (Bidelman et al., 2021; Hauk & Pulvermüller, 2004; Klimovich-Gray et al., 2023; Schwarz et al., 2022). For instance, only low-frequency words, but not high-frequency words, benefit from high phonotactic probability (Strauß et al., 2022), suggesting that words with high frequency rely less on phoneme-by-phoneme processing.

Some behavioural evidence indeed suggests that high word frequency acts as a compensatory effect for difficulty in retrieving phonological word representations. Spanish children and adults with phonological dyslexia read long and low frequency words more slowly than typical readers (Davies et al., 2007; Suárez-Coalla & Cuetos, 2012), indicating problems with rapidly decoding long phonological sequences when frequency of exposure cannot be used for compensation, e.g. due to poor home literacy experiences (Jiménez et al., 2009; Rivero-Contreras et al., 2021). However, the evidence is mixed as to whether dyslexic readers benefit from a high frequency base to the same extent as typical readers (Lázaro et al., 2013; Suárez-Coalla et al., 2017). Furthermore, recent evidence suggests that access to lexical-level information could be impeded in dyslexic readers. Using eye-tracking, Araújo et al. (2020) found that phonological neighbourhood and word frequency affect dyslexic readers at later processing stages than typical readers as indicated by longer offset eye-speech lags. This questions whether any word frequency compensation can take place at the single word level since imprecise phonological access could impede access to lexical-level information, thereby countervailing any potential higher-level compensation.

Neurobiological evidence on word frequency effects shows that infrequent words elicit higher evoked responses than frequent words around 400 ms post visual presentation for both dyslexic and typical adult readers (Johannes et al., 1995; Rüsseler et al., 2003). However, Johannes et al. (1995) report that the N400 amplitude difference between high and low frequency words is more pronounced in dyslexic adults, and Rüsseler et al. (2003) show that evoked responses to low-frequency words are more positive for non-dyslexic than dyslexic adults in this time-window. This points towards subtle differences between dyslexic and non-dyslexic adults' processing of visual word frequency around 400 ms after word

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[2] Reduced system demands for high-frequency words are captured by a number of theoretical frameworks, proposing that high-frequency words have higher base-level resting-states (McClelland & Elman, 1986), lower activation thresholds (Marslen-Wilson, 1990), are more strongly connected on various linguistic levels (Dahan et al., 2001), or have a higher a-priori probability of being encountered (Norris & McQueen, 2008).

onset. In order to trace potentially earlier word frequency differences, more sensitive analysis tools are required.

Due to the limited evidence, the nature and cause of cortical processing differences at the lexical level remain an important topic of investigation. Dyslexic children and adults not only have phonological processing difficulties, but typically also read less than good readers (Hamilton, 2013; Huettig et al., 2018). Both reduced reading exposure and phonological deficits could be the cause of previously observed cortical differences and delayed lexico-semantic access. However, to the best of our knowledge, neural evidence on word frequency effects in dyslexia (as a proxy for lexico-semantic processing) exclusively comes from visual presentation paradigms (Araújo et al., 2020; Dürrwächter et al., 2010; Heim et al., 2013; Johannes et al., 1995; Lázaro et al., 2013; Paul et al., 2006; Rivero-Contreras et al., 2021; Rüsseler et al., 2003). The spoken word paradigm of the present study can help to reveal whether phonological deficits are linked to atypical word frequency effects since auditory processing is influenced less by print exposure. Therefore, the second aim of this study is to examine whether phonological deficits affect sensitivity to written and spoken word frequency information as a proxy for lexico-semantic processing in spoken words.

1.3. *The present study*

Despite the fact that dyslexia has been classified primarily as a phonological auditory deficit (Lallier et al., 2017), more is known about the neurobiological markers of dyslexia in visual word processing. While it is clear that the majority of people with developmental dyslexia struggle with the processing of sublexical phonological information, it remains unclear how imprecise phonological representations affect word processing at the lexical level. Equally, there is no clear understanding of how phonological processing differences affect variability in downstream lexical activation of neurotypical readers. In the current study we address this gap and examine how a phonological deficit affects sensitivity to phonological sublexical, phonological lexical, and lexico-semantic information in the auditory modality.

We employed a naturalistic paradigm, passive listening to auditorily presented words, and recorded magnetoencephalographic responses (MEG) from 14 Spanish native speakers with a diagnosis of dyslexia and 14 speakers without reading difficulties. Phonological neighbourhood size was used as a proxy for phonological encoding, and written and spoken word frequencies (token) as estimates for lexico-semantic encoding (Duchon et al., 2013). We chose to include both written and spoken frequency to further dissociate what drives processing differences at the lexical level, print exposure or phonological deficits. Written word frequency effects are more strongly influenced by print exposure than spoken frequency effects. If print exposure alone causes cortical differences in word frequency processing, no detrimental effect of phonological deficits on spoken word frequency should emerge.

The MEG data were analysed with a trial-level regression approach because regression-based analyses are more suited for continuous variables such as phonological neighbourhood and word frequency than factorial designs (Cohen, 1983; Hauk et al., 2006). Event-related regression coefficients (ERRCs) were calculated for phonological neighbourhood (number of phonological neighbours) and the two measures of whole-word frequency. The regression estimates for phonological neighbours and word frequency measures were then correlated with participants' behavioural phonological test scores. In addition, ERRCs were source localised within selected ROIs using beamforming to reveal the cortical sources of the observed effects.

2. Methods and materials

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study procedures or analysis plans was preregistered prior to the research being conducted.

2.1. *Participants*

All participants were monolingual native speakers of Spanish, right-handed, had normal or corrected-to-normal vision, and reported no hearing impairments. Fourteen typical readers ($f = 7$, mean age $= 23.1$, age range: 12.8–44.9) were matched with 14 dyslexic readers ($f = 8$, mean age $= 26.9$, age range: 12.8–44.8) in age ($t\ (26) = -.82$, $p = .421$). This sample size resulted in ca. 1680 observations per group, which has been recommended for linear regression modelling (Brysbaert & Stevens, 2018). All dyslexic readers reported reading and/or writing difficulties and had a formal diagnosis of dyslexia. Skilled readers reported no reading/spelling problems and did not have a dyslexia diagnosis. Written consent was obtained from all participants (or their legal guardian if below 18 years old). The study was approved by the BCBL ethics board and all participants were reimbursed for their time.

2.2. *Behavioural data*

A full list of the administered tests are reported in Lizarazu et al. (2015). Here we report the behavioural tests used in the main analysis.

2.2.1. *Intelligence quotient*

Participants aged 12–14 were administered the Wechsler Intelligence Scale for Children-Revised battery (WISC-R; Wechsler, 2001), and participants over 14 were administered the Wechsler Adult Intelligence Scale battery (WAIS; Wechsler, 2008) to measure general intelligence.

2.2.2. *Reading*

Reading skills were assessed with the word and pseudoword reading lists of the PROLEC-R battery (Cuetos et al., 2009). Rate-correct scores were calculated from accuracy (x out of 40) and total reading time (in seconds; cf. Liesefeld et al., 2015; Woltz & Was, 2006):

$$(\mathrm{Accuracy}\ /\ \mathrm{Time}) * 100$$

2.2.3. Phonological awareness

Participants were administered the phonological awareness test PECO (Ramos & Gordillo, 2007). It assesses phonological skills in Spanish at the syllable and phoneme level and includes syllable and phoneme identification (selection of the picture that contains given syllable/phoneme, 10 items), syllable and phoneme addition (combination of syllables/addition of a single phoneme to form words, 10 items), and syllable and phoneme omission (object naming while omitting a given syllable/phoneme, 10 items). Total number of correct answers are scored N out of 30.

2.2.4. Phonological Composite Score

A Phonological Composite Score was calculated from PECO scores and pseudoword reading scores to derive a robust measure of phonological skills, using the formula

$$\frac{z\,(PECO) + z\,(Pseudoword\,((Accuracy\,/\,Time)\,{*}100))}{2}$$

2.3. Functional data (MEG recordings)

2.3.1. Stimuli and procedure

Words and pseudowords were recorded by a male native Spanish speaker and digitised at 44.1 kHz using a digital recorder (Marantz PMD670). Audio files (*.wav) were segmented using Praat (Boersma & Weenink, 2022). During the MEG recording, words were presented auditorily to the participants at 75 decibel (dB) sound pressure level (SPL). Each trial showed a fixation cross for 300 ms, which remained on the screen while the spoken stimulus was played. Participants had maximally 600 ms to respond.

Targets consisted of Spanish words and pseudowords, presented in random order. Each target was presented twice. Participants were instructed to press a button if the target word was an animal. Accuracy on the task was high for both control (M = 98 %, SD = 3 %, range: 88–100 %) and dyslexic participants (M = 98 %, SD = 2 %, range: 93–99 %), indicating sufficient attention to the stimuli. For our analysis we selected only the first presentation of real words (N = 120; cf. supplementary materials). The properties of these stimuli are summarised below.

2.3.2. Stimuli properties

Stimuli were 4–12 phonemes long (M = 6.72, SD = 1.96), had a mean duration of 649 ms (SD = 145, range: 330–997 ms), and had their phonological uniqueness point after the end of the word except for two items (*buey, saltamontes*). Three measures were used to derive predictors for the regression analysis.

(1) Number of Phonological Neighbours for each target (M = 8.81, SD = 11.42, range: 0–58) was taken from the Subtitle corpus provided by the EsPal database (Duchon et al., 2013). This measure refers to the number of phonological neighbours that can be derived for a given word (e.g. *cat*) by changing a single phoneme through substitution (*can*), addition (*cats*), or deletion (*at*).

(2) Written Word Frequency (token frequency per million words) was derived from the written corpus of the EsPal database (M = 84.61, SD = 100.00, range: .22–606.37). Frequency per million words is a standardised measure that is independent of corpus size. It is calculated by dividing the number of times the word appears in the corpus by the total number of words in the corpus multiplied by one million.

(3) Spoken Word Frequency (token frequency per million words) was taken from the EsPal Subtitle corpus (M = 56.17, SD = 87.71, range: .15–649.76).

The correlation matrix (Spearman) of Phonological Neighbours, Written Frequency, Spoken Frequency, Mean (M) Biphone Frequency (position specific), Word-Initial (1st) Biphone Frequency, and Number of Phonemes is presented in Fig. 1 (all derived from the EsPal Subtitle corpus except Written Frequency which was derived from the written EsPal corpus). Spoken Frequency and Written Frequency were correlated ($r = .71$, $p < .001$), indicating that the two types of frequency measures are comparable. Note that Phonological Neighbourhood was moderately correlated with Spoken Frequency ($r = .32$, $p < .001$), but not Written Frequency ($r = .09$, $p = .306$), allowing us to interpret these predictors independent of one another. All three predictors (Phonological Neighbours, Written Frequency, Spoken Frequency) were z-scored for the regression analysis.

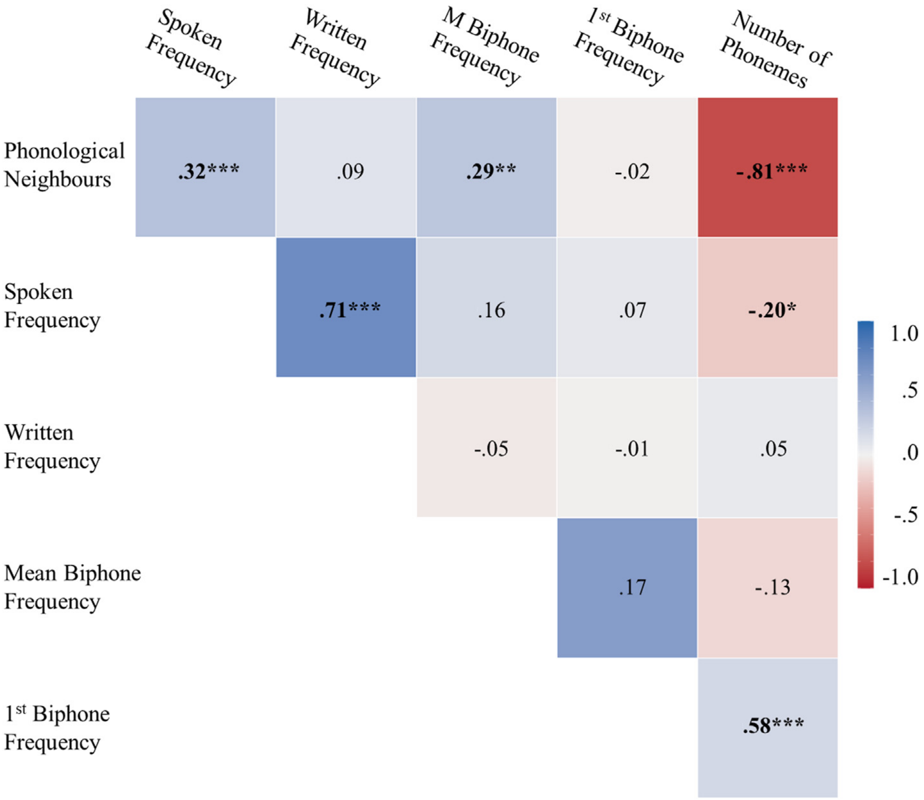
The correlation matrix also shows that Phonological Neighbours are not correlated with the Word-Initial Biphone Frequency ($r = -.02$, $p = .823$) and are only moderately correlated with Mean Biphone Frequency ($r = .29$, $p = .001$). Independence of Phonological Neighbourhood from phonotactic properties, especially at the word onset, is important since phonotactic probability can influence the strength and directionality of phonological neighbourhood effects (Vitevitch & Luce, 1998, 1999).

Pseudowords were of a similar length to real words (4–10 phonemes long, 2–4 syllables), and consisted of phonotactically legal combinations (e.g., *acupo*). Participants did not respond to pseudowords (passive listening).

2.3.3. MEG data acquisition and preprocessing

MEG data was acquired in a magnetically shielded room with a whole-scalp system (Elekta Neuromag, Helsinki, Finland) and the bandpass filter set to .01–330 Hz, 1 kHz sampling rate. Subjects' head positions were continuously monitored with four Head Position Indicator (HPI) coils. Coil position was digitised relative to the anatomical fiducials - nasion, left and right preauricular points - with a 3D digitizer (Fastrak Polhemus, Colchester, VA, USA). Eye movements were monitored with two pairs of electrodes in a bipolar montage placed on the external chanti of each eye (horizontal electrooculography (EOG)) and above and below the right eye (vertical EOG). Electrocardiogram (ECG) was monitored using two electrodes, placed on the right side of the participants' abdomen and below the left clavicle.

To remove external magnetic noise from the MEG recordings, data were preprocessed off-line using the Signal Space Separation (SSS) method (Taulu & Kajola, 2005) implemented in Maxfilter 2.1 (Elekta Neuromag). MEG data were also corrected for head movements, and bad channel time courses were reconstructed using interpolation algorithms implemented in the software. Subsequent data analysis was



	Spoken Frequency	Written Frequency	M Biphone Frequency	1st Biphone Frequency	Number of Phonemes
Phonological Neighbours	**.32*** **	.09	**.29** **	-.02	**-.81*** **
Spoken Frequency		**.71*** **	.16	.07	**-.20* **
Written Frequency			-.05	-.01	.05
Mean Biphone Frequency				.17	-.13
1st Biphone Frequency					**.58*** **

Fig. 1 – Correlation matrix (Spearman) between predictor variables and selected word form variables. *p < .05; **p < .01; ***p <. 001.

done using the open source MNE Python platform (Gramfort et al., 2013). Data was band-pass filtered between .1 and 40 Hz with a zero-phase FIR filter. Blink and heart beat artefacts were removed with the automated independent component (ICA) analysis implemented in MNE Python. ICA components were identified based on high correlation value with the EOG and ECG electrodes. MEG data were then divided into epochs of .8 sec length, from .1 sec before to .7 sec after word onset. Epochs were rejected if maximum–minimum amplitudes exceeded 4000e-15 fT in magnetometers and 4000e-13 fT/cm in gradiometers. The average percentage of epochs retained was 91 % (SD = 10 %) for control subjects and 95 % (SD = 4 %) for dyslexic participants.

2.3.4. *Event-related regression coefficient (ERRC) analysis*

Event-related regression coefficient (ERRC) analysis was first performed at the sensor level, and later effect estimates were projected to the brain using source reconstruction methods. Single-predictor regression analyses of the MEG data were conducted using MNE Python (version .24.dev0; Gramfort et al., 2013). For each participant, three separate single-predictor regressions were fitted to the epochs at each sensor and each time point (Hauk et al., 2006, 2009; Miozzo et al., 2015) to extract the effects of Phonological Neighbours, Written Word Frequency (token), and Spoken Word Frequency (token) respectively (Duchon et al., 2013). We decided against a multiple regression analysis since Spoken and Written Word Frequency as well as Phonological Neighbours and Spoken Word Frequency were correlated (Fig. 1), thus leading to multicollinearity. However, an additional multiple-regression model with Phonological Neighbours and Spoken Word Frequency is reported in the footnotes so as to ensure that the Phonological Neighbour response is independent of word frequency influences.

In the linear-regression equation $y = Xb$, y is the response at one MEG sensor at a given latency across trials, X is the predictor of interest (i.e. number of Phonological Neighbours/ Word Frequency), and b is the estimated slope that reflects the relationship between the predictor and the observed data, i.e. the event-related regression coefficient (ERRC). The resulting ERRCs (‘beta values’) of Phonological Neighbours, Written Word Frequency, and Spoken Word Frequency represent the effect that these linguistic metrics have on the cortical sensor-space responses during spoken word processing. Since all predictor variables were z-scored, the regression coefficients reflect “signal change in microvolts per standard deviation of the predictor variable” (Hauk et al., 2006, p. 1388).

The goal of the current analysis was to test whether the magnitude of the cortical response to Phonological Neighbours and Word Frequency was modulated by a person's phonological abilities and dyslexia diagnosis. To derive an estimate of the response magnitude, we computed the root mean square (RMS) of ERRC values from pairs of gradiometers and averaged the resulting values across the frontal, temporal, and parietal sensors, where effects for the corresponding regressors had been observed in previous work (Dufour et al., 2013). These values were then subjected to the secondary statistical analysis (see section *Statistical Analysis*).

Additionally, the unprocessed ERRCs from all time samples of fronto-temporal sensors were subjected to source estimation (using MATLAB, 2016).

2.4. *Source reconstruction of ERRCs*

Subjects took part in structural MRI scanning in a single session at the BCBL in Donostia-San Sebastian, Spain. A 3.0 T S MagnetomTrio Tim scanner (Siemens AG, Erlangen, Germany) was used, and a high-resolution T1-weighted (wT1) scan was acquired with a 3D ultra-fast gradient echo (MPRAGE) pulse sequence. A 32-channel head coil was used with the following acquisition parameters: FOV 5 256; 160 contiguous axial slices; voxel resolution 1 mm 3 1 mm 3 1 mm; TR 5 2300 ms, TE 5 2.97 ms, flip angle 5 98.

The wT1 images and the digitised head shapes were co-registered to the MEG coordinate system using anatomical landmarks via an iterative closest point (ICP) algorithm (Besl & McKay, 1992). wT1 images were segmented using the SPM8 toolbox (Wellcome Department of Cognition Neurology, London, UK) embedded in Fieldtrip (Oostenveld et al., 2011) to extract brain, skull, and scalp. A single-shell semi-realistic head model constructed from the participant's segmented wT1 images was used to estimate the forward model and leadfield matrix (Nolte, 2003). To account for inter-individual variability in brain structure, aligned grids in individual headspaces were created using the atlas-based Montreal Neurological Institute (MNI). The source model was defined on a regular 3D grid in MNI space. Individual grids were volumetrically morphed to the MNI template grid using a nonlinear transformation (1 cm resolution). A grid with 2982 fixed grid points inside the brain was obtained per participant.

The linearly constrained minimum variance (LCMV) beamformer was used to estimate the activity at each grid point in the brain volume (Van Veen et al., 1997). Instead of the sensor signals as an input to the source analysis, we used raw sensor-level ERRCs from all sensors (before applying rms), following the established procedure by Hauk and colleagues (Hauk et al., 2006, 2009; Miozzo et al., 2015). With this method, the localised ERRCs are comparable to evoked responses, but instead of averaging the response within a condition, the response represents a weighted average of all trials.

The covariance matrix (CM) of the LCMV beamformer was calculated from the sensor-level ERRCs. The subject-specific leadfields and CMs were used to estimate the inverse spatial filters (beamformers) for all the grid points. A lambda regularisation parameter for the common filter estimation was specified as 5 %, to reduce sensitivity to noise and increase consistency of the spatial maps across individuals. Source trials were estimated using the already computed spatial filter and regularisation parameter.

Further analysis was limited to pre-selected 14 regions of interest (ROIs) from the AAL MNI atlas provided by Fieldtrip. These region are commonly associated with language processing tasks (e.g. Fontaneau et al., 2015; Strauβ et al., 2022; Winsler et al., 2018): Inferior frontal gyrus, opercular part; Superior frontal gyrus; Inferior frontal gyrus, triangular part; Heschl's gyrus; Middle temporal gyrus; Temporal pole; Superior temporal gyrus (all left/right). To extract the dominant signal reflecting the main pattern of variation of all the grid points in the same ROI we used Singular-Value Decomposition (SVD) and considered the first singular vector. This method enables identification of the main direction of all the dipoles of a ROI while discarding the contribution of the outlier dipoles. Resulting source amplitudes were then normalised by applying the root mean square and group-averaged within the same time-windows, consistent with the procedure of the sensor space analysis.

2.5. *Statistical analysis*

2.5.1. *Behavioural measures of phonological skills*

Paired t-tests were used to assess group differences on the behavioural tests. In addition, three measures of phonological skills (Pseudoword Reading, Phonological Awareness (PECO), Phonological Composite Score) were compared to one another with Bayesian modelling (R package brms, version 2.18.0; Bürkner, 2017) to assess which best predicts reading group (dyslexic/non-dyslexic).

2.5.2. *Event related regression coefficients in selected time-windows*

Regression estimates (ERRCs) were root-mean-squared and averaged within time-windows of interest motivated by previous EEG research on neighbourhood and frequency effects in auditory word processing of neurotypical adults. Dufour et al. (2013) found effects of neighbourhood density on two ERP components, the Phonological Mismatch/Mapping Negativity (PMN) and the N400. The PMN (or N280) is a fronto-central component around 250–350 ms associated with spoken word processing and has been detected in tasks where the initial phoneme of an acoustically presented word is incongruent with the expected one (Newman & Connolly, 2009). The component therefore has been interpreted as pre-lexical phonological mapping. In the same time window, Dufour et al. (2013) found that electrophysiological responses to words with dense neighbourhoods exhibit lower amplitudes than words with few phonological neighbours. In addition, Dufour et al. (2013) found that words with many neighbours elicit greater negativities at the N400 (a centro-parietal component, which is also associated with semantic processing, e.g. Kutas & Federmeier, 2000). The findings align with later replications such as Winsler et al.'s (2018) EEG megastudy of spoken word recognition, who report similar effects of phonological neighbourhood. Words with denser phonological neighbourhoods exhibited greater negativities from 200 to 300 ms and greater positivity from 300 to 400 ms. Taken together, these studies show that phonological information affects early, sublexical stages of word access as well as the later word-selection stage.

With respect to word frequency, effects on auditory lexical decision have been found as early as 100–200 ms post-stimulus onset (Winsler et al., 2018), though typically word frequency effects in auditory processing reliably start later than this. Dufour et al. (2013), for example, found two effects of frequency on auditory word recognition, both eliciting lower ERP amplitudes for high frequency words compared to low frequency words: First, an effect on the P350 component emerged, starting around 350 ms post stimulus onset. The P350 is therefore thought to reflect lexical identification (Friedrich et al., 2004). Secondly, a late N400 effect was observed, starting from stimulus offset until ca. 80 ms post-stimulus, which is thought to reflect lexical selection/retrieval after the full word has become available to the listener.

Based on these previous findings and visual inspection of the data, Phonological Neighbourhood estimates were computed for the time-windows 90–110 ms, 200–330 ms, 330–400 ms, and 400–500 ms, and Written and Spoken Word Frequency estimates were calculated for the time windows 200–330 ms, 330–400 ms, 400–500 ms, and 500–650 ms.

2.5.3. *Correlation of MEG responses and phonological scores*

Statistical analyses were conducted using the software R (version 2021.9.2.382; RStudio Team, 2021). The averaged ERRCs of Phonological Neighbourhood, Written Word Frequency, and Spoken Word Frequency within each time window of interest were modelled with (1) participants' continuous Phonological Composite Scores, (2) Group, based on dyslexia diagnosis (control *vs* dyslexic), (3) Hemisphere (left/right), and respective two-way interactions between all three predictors. In order to avoid overfitting, the models were optimised in a stepwise backwards procedure by removing predictors that did not significantly contribute to model fit as indicated by AIC scores. The categorical predictors Group and Hemisphere were sum-contrast coded. P-values were corrected for multiple comparisons (fdr) within each variable of interest (i.e. Phonological Neighbours, Written Frequency, and Spoken Frequency).

3. Results

3.1. *Behavioural results*

Table 1 summarises the behavioural assessment for skilled readers (control group) and for those diagnosed with dyslexia (dyslexic group).

3.1.1. *Intelligence quotient*

Dyslexic and control subjects were matched on IQ and had normal intelligence as indicated by the WISC-R and WAIS tests (t (20) = 1.22, p = .238; IQ range: 100–130).

3.1.2. *Real word reading*

Main effects of accuracy and speed were found in the real word reading test, with dyslexics making significantly more errors (t (14) = 4.67, p < .001) and reading significantly more slowly (t (16) = −4.35, p < .001). Dyslexics' lower performance on real word reading was also reflected in the accuracy-time combined real word reading score (Acc/Time * 100; t (25) = 5.31, p < .001).

3.1.3. *Pseudoword reading*

Dyslexic readers also performed worse than controls on the pseudoword reading test, as reflected by lower accuracy (t (16) = 6.31, p < .001), slower reading (t (16) = −4.45, p < .001), and a lower score on the combined pseudoword reading score (Acc/Time * 100; t (25) = 7.17, p < .001).

3.1.4. *Phonological awareness*

Although some dyslexic participants scored highly on phonological awareness (PECO), on average, they made more phonological errors than controls (t (26) = 2.24, p = .034).

3.1.5. *Phonological Composite Score*

The pseudoword reading score and the phonological awareness score were combined into a Phonological Composite Score (PCS), which indicated that dyslexic participants had lower phonological skills (t (26) = 6.53, p < .001).

3.1.6. *Assessment of phonological measures*

Pseudoword Reading Score, Phonological Awareness Score (PECO), and combined Phonological Composite Score (all z-scored) were compared as behavioural phonological measures for predicting dyslexia diagnosis versus control participants using Bayesian modelling (R package brms, version 2.18.0;

Table 1 – Group characteristics and behavioural scores. Group differences are calculated from paired t-tests. Phonological Composite Score is derived from the Pseudoword Score and Phonological Awareness Score. *p < .05; **p < .001.

	Control Group N = 14, f = 7			*Dyslexic Group* N = 14, f = 8			Group Difference
	Mean	SD	Min-Max	Mean	SD	Min-Max	t-value
Group Characteristics							
IQ	120.8	8.6	100.0–130.0	117.4	5.6	108.0–127.0	1.22
Age (in years)	23.1	11.9	12.8–44.9	26.9	12.4	12.8–44.9	−.82
Behavioural Tests							
Real word reading							
Accuracy (/40)	39.9	0.4	39.0–40.0	37.9	1.6	35.0–40.0	4.67**
Speed (in s)	24.1	4.5	19.0–33.0	40.0	12.9	23.0–66.0	−4.35**
Real word Score	170.1	29.0	121.2–205.3	104.7	35.7	53.0–169.6	5.31**
Pseudoword reading							
Accuracy (/40)	38.8	1.1	37.0–40.0	33.1	3.2	28.0–40.0	6.31**
Speed (in s)	40.6	5.9	29.0–49.0	62.0	16.9	46.0–110.0	−4.45**
Pseudoword Score	97.6	16.3	75.5–134.5	56.6	13.9	25.5–83.3	7.17**
Phonological Awareness (/30)	22.1	8.0	14.0–30.0	15.0	8.8	7.0–30.0	2.24*
Combined Score							
Phonological Composite Score	0.6	0.5	−.1-1.8	−0.6	0.5	−1.1-0.4	6.53**

Table 2 – Comparison of phonological measures predicting dyslexia diagnosis. N = 28; brm (Group ~ Combined, data = data, family = bernoulli (link = "logit")).

	Pseudoword Reading		Phonological Awareness		Phonological Composite Score (PCS)	
	Post. mean	95 % CI	Post. mean	95 % CI	Post. mean	95 % CI
Intercept	−.45	−2.64; 1.52	.03	−.83; .88	.39	−.97; 1.96
Predictor	**−10.58**	**−22.83; -3.83**	**−.93**	**−1.90; -.09**	**−5.81**	**−10.47; -2.55**

Bürkner, 2017). Table 2 shows the three models based on uninformative priors. Phonological Awareness was the worst predictor (smallest effect estimate) for dyslexia diagnosis versus control. Although the model using the Pseudoword Reading Score yielded the largest effect estimate, it also showed larger credible intervals than the model using the Phonological Composite Score. More importantly, using phonological awareness or pseudoword reading alone as a measure would be problematic for several reasons. Some dyslexic readers score at ceiling on isolated tests, especially phonological awareness, most likely because they received more specific training on related tasks to improve their reading in the past, and as such phonological awareness scores did not align well with dyslexia diagnosis as shown by our analysis. Pseudoword Reading, on the other hand, while a sufficient predictor of dyslexia diagnosis in our sample, would be insufficient as a phonological measure as it also taps into reading exposure. The Phonological Composite Score was therefore used in all subsequent analyses.

3.2. *Sensor results*

Sensor results are presented in pre-selected time-windows for the effects of Phonological Composite Score (PCS), Hemisphere (left *vs* right), and Group (Control *vs* Dyslexic) on the MEG-based regression coefficients for Phonological Neighbours, Written Word Frequency, and Spoken Word Frequency. Fig. 2 presents the correlations between PCS and the regression coefficients averaged by Group. Here we present only significant effects ($p < .05$) after correcting for multiple comparisons. Full model summaries can be found in the associated repository. Topographic plots of the ERRCs can be found in the supplementary materials.

3.2.1. *Phonological neighbourhood*

Better phonological skills (i.e. higher Phonological Composite Scores; PCS) led to stronger neural responses to Phonological Neighbourhood from 200 to 330 ms ($b = 6.24e\text{-}14$, $t = 3.23$, $p = .008$), from 330 to 400 ms ($b = 8.64e\text{-}14$, $t = 3.79$, $p = .003$),

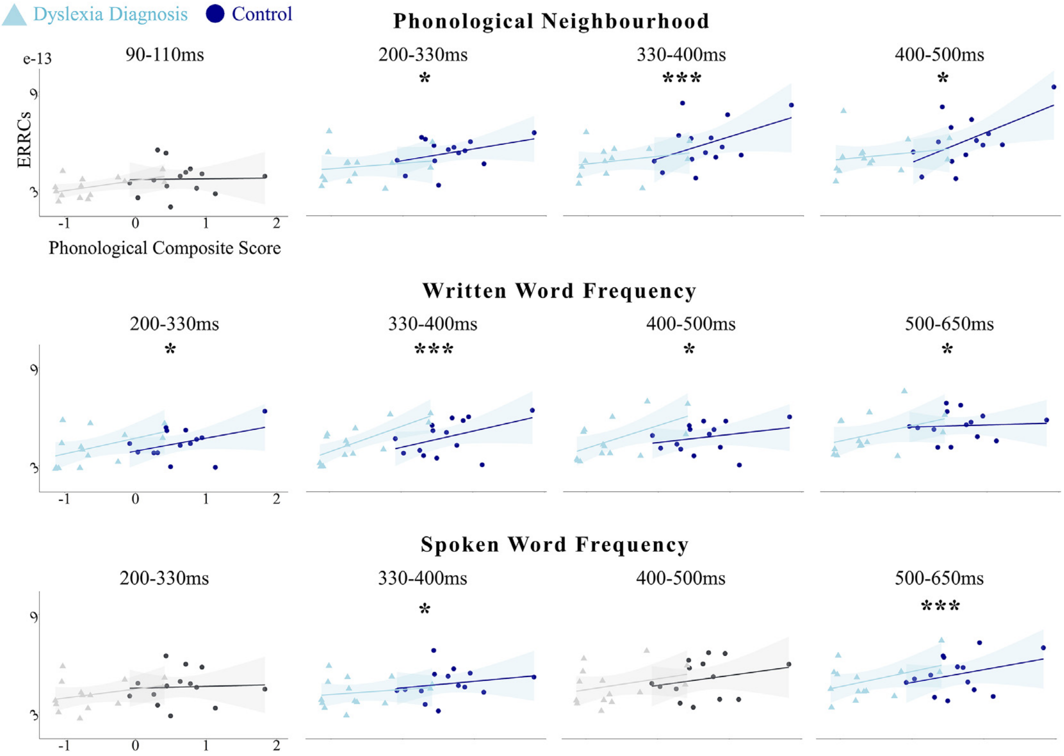


Fig. 2 – Correlations between Phonological Composite Score (PCS) and Event-Related Regression Coefficients (ERRCs) averaged by Group (Dyslexic/Control). Note: the group interactions were not significant. Significant time-windows (fdr corrected) are presented in blue and marked by an asterisk. The time-windows with the strongest PCS effect are marked with three asterisks. Same scales are applied throughout.

and from 400 to 500 ms post spoken word onset (b = 1.16e-13, t = 2.92, p = .005). No other effects (Group, Hemisphere) were significant.

To confirm that the Phonological Neighbour effects were separate from Spoken Word Frequency (which were moderately correlated, r = .32, p < .001), we conducted a supplementary analysis where both variables were entered into a multiple regression simultaneously. Resulting ERRCs were subjected to the same secondary analysis. The main effects mirrored the original results.[3] Full details on this analysis can be found in the supplementary files.

3.2.2. *Written word frequency*

PCS also significantly increased neural responses to Written Word Frequency in the time-windows 200–330 ms (b = 8.81e-14, t = 3.21, p = .007), 330–400 ms (b = 1.29e-13, t = 4.73, p < .001), 400–500 ms (b = 9.39e-14, t = 3.18, p = .002), and 500–650 ms post spoken word onset (b = 4.79e-14, t = 2.42, p = .034).

In addition, an effect of Group (Control/Dyslexic) was found between 330 and 400 ms (b = −6.52e-14, t = −3.03, p = .004) and between 400 and 500 ms (b = −5.18e-14, t = −2.22, p = .046), with Dyslexic readers showing weaker responses to Written Frequency than typical readers. No significant Hemisphere effect was found.

3.2.3. *Spoken word frequency*

PCS had a significant effect on neural responses to Spoken Frequency from 330 to 400 ms (b = 4.01e-14, t = 2.32, p = .048) and from 500 to 650 ms (b = 5.48e-14, t = 2.47, p = .048) post spoken word onset. No other effects were significant.

3.3. *Source space results*

The time-windows from the sensor analysis were subjected to source estimation in 14 regions of interest. Table 3 shows source localised activity of Phonological Neighbourhood, Written Frequency, and Spoken Frequency averaged across all subjects (and results by group can be found in the supplementary materials). The peaks of the effects (betas) in those time-windows that were significant in the sensor analysis were in the left superior temporal gyrus (STG; Phonological Neighbourhood: 200–330 ms: 2.39; 330–440 ms: 2.37; 400–500 ms: 2.49; Written Word Frequency: 200–330 ms: 2.14; 330–400 ms: 2.11; 400–500 ms: 2.12; 500–650 ms: 2.14; Spoken Word Frequency: 330–400 ms: 2.01; 500–650 ms: 2.01. Fig. 3 shows the beta estimates averaged across all subjects and mean activity in the left STG by group. In addition, the left inferior frontal gyrus (IFG, triangular part) was activated in a sustained manner during the early

Table 3 – Source localised regression estimates of Phonological Neighbours, Written Word Frequency, and Spoken Word Frequency in 14 ROIs. Effect peaks are presented in bold font.

Hemis.	Region		Phonological Neighbours			Written Word Frequency				Spoken Word Frequency			
		90–110	200–330	330–400	400–500	200–330	330–400	400–500	500–650	200–330	330–400	400–500	500–650
Left	IFG, opercular part	1.38	1.39	1.34	1.34	1.20	1.25	1.22	1.24	1.26	1.20	1.15	1.21
	Superior frontal gyrus	1.30	1.46	1.24	1.31	1.31	1.22	1.34	1.23	1.17	1.15	1.28	1.20
	IFG, triangular part	**2.24**	2.24	2.18	2.13	1.80	1.87	1.86	1.94	2.03	1.80	1.74	1.83
	Heschl's gyrus	1.09	1.34	1.29	1.39	1.13	1.19	1.11	1.13	1.13	1.16	1.07	1.07
	Middle temporal gyrus	1.87	2.25	2.09	2.20	1.94	1.90	2.09	2.01	2.00	1.97	1.86	1.86
	Temporal pole	1.81	1.92	2.08	1.95	1.70	1.60	1.68	1.65	1.54	1.75	1.70	1.61
	Superior temporal gyrus	2.11	**2.39**	**2.37**	**2.49**	**2.14**	**2.11**	**2.12**	**2.14**	**2.12**	**2.01**	**2.10**	**2.01**
Right	IFG, opercular part	1.37	1.60	1.59	1.58	1.39	1.38	1.32	1.35	1.33	1.26	1.38	1.33
	Superior frontal gyrus	1.34	1.29	1.29	1.30	1.12	1.24	1.11	1.17	1.14	1.06	1.09	1.17
	IFG, triangular part	1.44	1.54	1.66	1.50	1.37	1.49	1.37	1.45	1.36	1.27	1.46	1.36
	Heschl's gyrus	1.05	1.28	1.31	1.31	1.21	1.06	1.19	1.03	1.00	1.11	1.18	1.20
	Middle temporal gyrus	1.59	1.68	1.74	1.61	1.43	1.41	1.48	1.49	1.52	1.30	1.45	1.60
	Temporal pole	1.83	1.87	1.86	1.93	1.58	1.59	1.61	1.66	1.61	1.57	1.54	1.68
	Superior temporal gyrus	1.94	2.04	2.13	2.06	1.76	1.69	1.86	1.62	1.63	1.60	1.80	1.87

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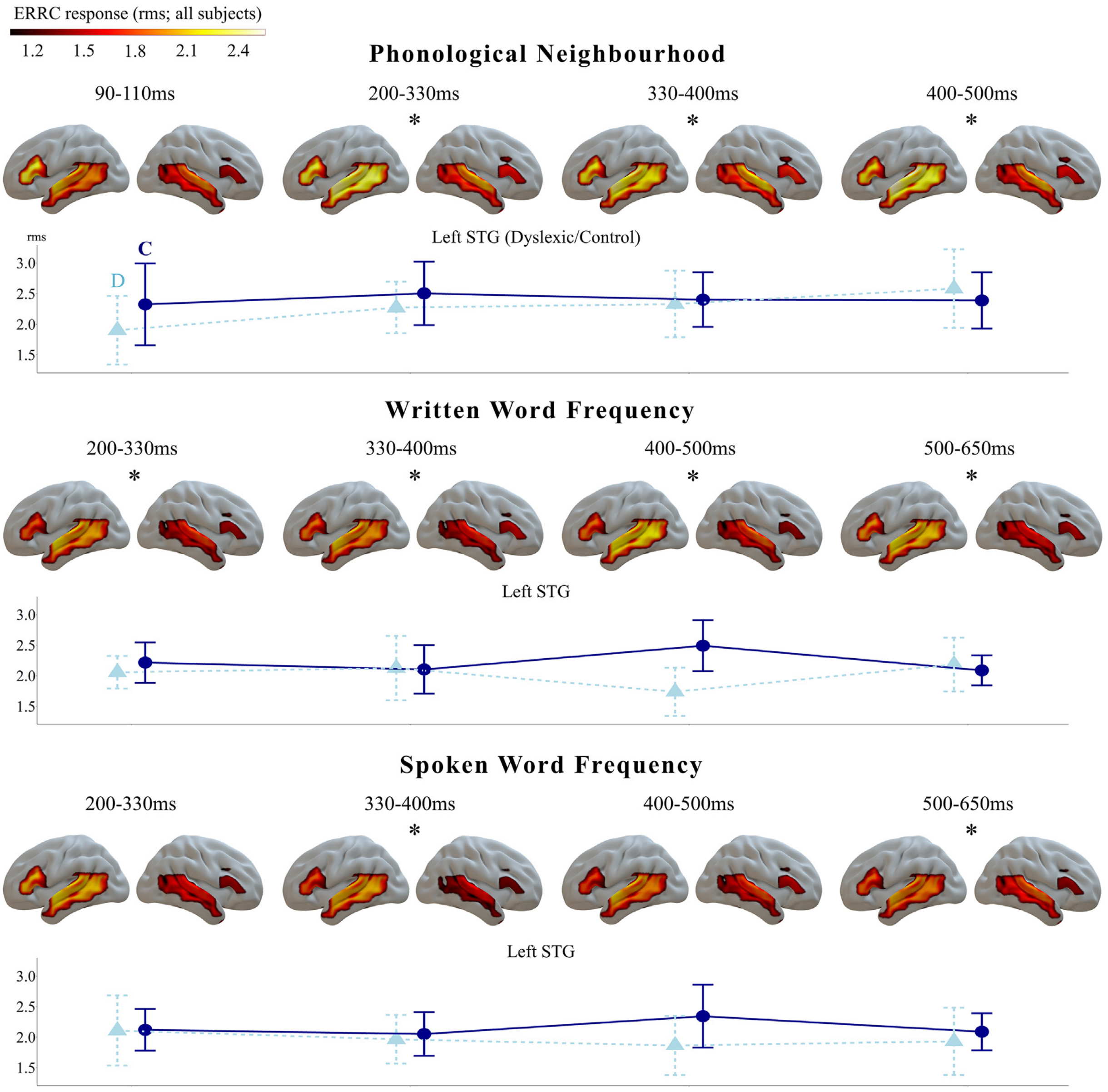
[3] The results showed that better phonological skills led to stronger neural responses to Phonological Neighbourhood from 200 to 330 ms (b = 5.93e-14, t = 2.97, p = .018), from 330 to 400 ms (b = 8.68e-14, t = 3.67, p = .004), and from 400 to 500 ms post spoken word onset (b = 1.08e-13, t = 2.62, p = .031). In addition, the earliest 90–110 ms time-window also showed a significant effect of PCS (b = 3.96e-14, t = 2.32, p = .048) after accounting for spoken word frequency in this way (which in the single-predictor regression was marginal, with the associated p = .054).


Phonological Neighbourhood

Written Word Frequency

Spoken Word Frequency

Fig. 3 – Event-Related Regression Coefficients (ERRCs) are root mean squared (rms), averaged over all subjects, and source localised in 14 ROIs. Time-windows that were significant in the sensor analysis are marked by an asterisk. Dot plots show the mean activity and standard error averaged by Group (Dyslexic/Control) in the peak ROI, the left superior temporal gyrus (STG). Same scales are applied throughout.

stages of phonological neighbour processing, peaking 90–110 ms after word onset.

4. Discussion

4.1. *Summary of findings*

Phonological deficits are a common indicator of developmental dyslexia (Griffiths & Snowling, 2001; Litt & Nation, 2014; Ramus et al., 2013; Romani et al., 2008; Saksida et al., 2016). Despite this, dyslexia is typically only diagnosed after the onset of reading tuition when such deficits severely impact reading progress. Many phonological processes (i.e. those pertaining to phrasal and lexical prosody and phonetic/phonological features), however, are rooted in the auditory language system and as such precede reading acquisition and the establishment of phoneme-to-letter mappings. Despite the critical role of phonological processes for efficient spoken language processing, it is unclear what other processes of spoken word analysis are directly impacted by phonological deficits. Uncovering such effects can benefit pre-readers, early readers, and adults with dyslexia by targeting remediation protocols towards affected phonological and non-phonological processing pathways. Importantly, the results suggest that they could also benefit other struggling readers with and without a clear neuro-cognitive impairment by supporting the pervasive impact of phonological skills throughout early tuition.

In the current study we examined how phonological deficits affect the neural dynamics of linguistic information processing during spoken word recognition. We focused on two key processes of spoken word analysis, phonological and lexico-semantic processing. (1) Phonological processing was assessed as the ability to analyse the phonological neighbourhood of words, where neighbourhood information is thought to impact both initial sublexical and later whole-word phonological stages of word recognition. (2) Lexico-semantic processing was assessed as listeners' sensitivity to the spoken and written frequency of words. The ERRC method (Hauk et al., 2006) was applied to MEG data of dyslexic readers for the first time to derive regression estimates of listeners' cortical responses to phonological neighbourhood and word frequency (written and spoken). The regression estimates were then correlated with participants' behavioural phonological skills and source localised using beamforming.

The results showed that phonological deficits impede processing of phonological neighbourhood information and word frequency as early as 200 ms after word onset. Regardless of dyslexia diagnosis, better phonological skills led to enhanced processing of phonological and lexico-semantic information, highlighting the importance of phonological skills across the neurodiverse spectrum, especially in left temporal language areas. Neural responses to written word frequency (compared to spoken word frequency) was particularly diminished in dyslexia, suggesting that exposure to printed words plays an additional role in spoken word processing. The findings suggest that neural re-organisation of lexical-distributional information at the single word level is not a compensation strategy for weaker phonology. Importantly, phonological training could benefit word processing at multiple linguistic levels and processing stages for readers with and without language impairments. The findings and their implications are discussed in detail below.

4.2. *Reduced sensitivity to phonological neighbourhood in dyslexia*

Although phonological neighbourhood played an important role in dyslexic readers' auditory processing – in line with findings of neighbourhood processing by dyslexic children (Thomson et al., 2005) – we found clear evidence that phonological deficits lead to behavioural and neural spoken word processing differences. On average, non-dyslexic readers had better phonological skills than dyslexic readers as indicated by behavioural test scores, and better phonological skills led to stronger neighbourhood encoding, especially in the left hemisphere. It is important to interpret these neighbourhood effects within the context of the language presented since it has been shown that phonological neighbourhoods produce different effects in different languages (Vitevitch & Luce, 2016). Here, stimuli were presented in Spanish. In Spanish, words with many phonological neighbours are processed faster, i.e. many phonological neighbours benefit lexical access (Vitevitch & Rodríguez, 2005), arguably so because of amplified activation of the phonological network. This means increased sensitivity to an increasing number of phonological neighbours reflects a processing advantage. The finding that dyslexic listeners, and generally listeners scoring low on phonological tasks, are less sensitive to phonological neighbours therefore likely reflects a processing disadvantage.

With respect to the time-course of phonological neighbourhood processing, an effect of phonological skills on the cortical response to phonological neighbours was found as early as 200 ms after word onset (Fig. 2). This suggests that phonological deficits impede phonological neighbourhood effects earlier than previously attested in the dyslexia literature,[4] which found effects of atypical phonological processing around 400 ms after word onset (Desroches et al., 2013; Jednoróg et al., 2010). In line with these earlier findings, in our data a secondary neighbourhood effect emerged at the point in time when the full word-form becomes available to the listener. Together, these early and late neighbourhood effects indicate that worse phonological processing affects both the sublexical stage of word access (200–330 ms) as well as the later word-selection stage (330–500 ms), both of which are also critical processing stages impacted by phonological neighbourhood information in neurotypical adults (Dufour et al., 2013; Strauß et al., 2022; Winsler et al., 2018). This suggests that dyslexic readers have phonological difficulties at multiple stages of the auditory word recognition process, namely pre-lexical and lexical phonological mapping, at least during single word processing.

An important matter of the ongoing debate is whether phonological deficits cause reading difficulties, or whether reduced reading skill inhibits the acquisition of phonological knowledge. Previous research shows that the ability to detect and manipulate phonemes (phonemic awareness) improves with learning to read (Morais et al., 1986), and that illiterate adults perform worse on tasks that tap into phonological awareness compared to literate people (Huettig & Mishra, 2014). This suggests that the relationship between phonological awareness and reading is bidirectional. Dyslexia thus may lead to lower phonological awareness due to the condition's inherent reading difficulties. However, it is important to point out that the phonological deficit in dyslexia encompasses more phonological skills than phonemic awareness alone. We defined phonological skills as the awareness of language-specific phoneme inventories, phonological contrasts, allophonic distributions, syllabic structures, prosodic information, and phonotactic rules and frequencies. This is reflected in broader phonological deficits such as difficulty in retrieving words, phonological short term memory, recalling abstract information, and articulating "phonologically challenging material such as tongue-twisters" (Share, 2021). Importantly, it has been shown that some of these phonological skills precede reading instruction and that they predict individual differences in later reading acquisition (Bradley & Bryant, 1983). Moreover, low phonological awareness even persists in successfully compensated dyslexic readers (Frith, 1997).

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[4] Note that this early effect of phonological neighbourhood in the present study cannot be attributed to the phonotactic frequency of the word onset since word-initial biphone frequency was not correlated with phonological neighbourhood ($r = -.02$; Fig. 1).

Nevertheless, given the reciprocal relationship between phonological skills and reading (e.g., Castles & Coltheart, 2004; Wagner et al., 1994), we cannot rule out that (part of) the phonological deficit observed here stems from reduced exposure/experience to reading in people with dyslexia. In future work, reading-age matched groups will be required to support the potential causal role of phonological deficits in the manifestations of dyslexia.

Regardless of the causal directionality of phonological deficits, reading difficulties, and dyslexia, the present findings suggest that phonological processing difficulties occur within different phonological domains below and at the word-level. This observations ties in with the temporal-perceptual sampling hypothesis of dyslexia (Goswami, 2011; Goswami et al., 2014; Lallier et al., 2017; Lizarazu et al., 2015, 2021; Molinaro et al., 2016), which suggests that phonological deficits originate from atypical neural entrainment of oscillations (rhythmic changes in neural excitability) to salient speech cues, i.e. rapid changes (rise-times) of the speech amplitude (Goswami et al., 2014; Lallier et al., 2017). Synchronisation of oscillations to speech cues is especially important for the correct identification of words and phonological segments in the speech stream (Gross et al., 2013). However, dyslexic listeners show imprecise entrainment to speech cues pertaining to various levels of the prosodic-phonological hierarchy at the rate of phrases (Molinaro et al., 2016), syllables (Lizarazu et al., 2015), phonemes (Di Liberto et al., 2018; Lizarazu et al., 2015), and, as has been shown recently, speech edges (large amplitude transients in the speech envelope after a period of low power; Lizarazu et al., 2021). The findings that phonological deficits affect sentence-level speech processing at multiple levels of analysis are compatible with our findings at the single word level, where phonological difficulties emerged in different time-windows that correspond to distinct hierarchical levels, i.e. at the sublexical and at the whole-word level. While more research is needed to consolidate speech sampling deficits with phoneme-level deficits, the evidence, together with the findings discussed in this paper, suggest an underlying phonological impairment that cannot be explained by the acquisition of literacy alone. Phonological deficits at higher-level linguistic structures (e.g. sentence and word prosody, whole-word phonology) seem to be linked to sublexical processing deficits (e.g. phonemic processing, Di Liberto et al., 2018), thus affecting phonological access during both continuous and single-word speech processing.

A link between atypical oscillations in speech processing and disrupted phonological processing is further supported by our localisation of the phonological neighbourhood effect in the present study, which peaked in the left hemisphere STG (Fig. 3), an area close to the auditory cortex. D'Mello and Gabrieli (2018) have argued that stronger activity in left temporo-parietal areas emerges as a function of learning to read and of the development of phonological awareness in typical readers (Turkeltaub et al., 2003), and concurrently these areas have been suggested as a possible locus for divergent cerebral structure and functioning in dyslexia, leading to linguistic difficulties (Eden & Zeffiro, 1998; Vellutino, 2004). This theory receives support from a range of evidence that shows atypical activation of the left superior temporal cortex in dyslexia (Breier et al., 2003; Corina et al., 2001; Georgiewa et al., 1999; Temple et al., 2001). With respect to the MEG-based evidence, Lizarazu et al. (2021) showed that dyslexic readers have imprecise entrainment to speech edges driven by group differences in left temporal regions, and Lehongre et al. (2011) located a deficit in auditory steady state response to 30 Hz noise in dyslexics to the left prefrontal and the superior temporal cortices. These effects could be linked to genetically-caused microstructural differences, where abnormal connectivity to and from temporal language areas has been found (Giraud & Ramus, 2012). Importantly, some evidence suggests that phonological training can enhance activity in the left STG and improve dyslexic children's reading skills (Simos et al., 2002). This aligns with our results and suggests an important role of the left STG (and connections with left IFG, cf. Boets et al., 2013) for those auditory and linguistic operations that dyslexic readers struggle with, such as phonological parsing in the present study. In addition, the pars triangularis of the left IFG was activated in a sustained manner from the earliest stages of phonological neighbour processing (as early as 90–110 ms after word onset), highlighting the combinatorial function of this area during the retrieval of lexical-phonological information and its connection to temporal areas (Rivas-Fernández et al., 2021).

4.3. *Effects of phonological deficits on lexico-semantic processing*

The present study provides novel neural-level evidence that readers with weak phonological skills also show reduced responses to non-phonological, lexical information. Crucially, neural differences of written and spoken word frequency effects were found between dyslexic and non-dyslexic readers in the auditory modality for the first time, building on atypical neural responses to word frequency in the visual modality (Johannes et al., 1995; Lázaro et al., 2013; Paul et al., 2006; Rüsseler et al., 2003). Lower phonological skills led to weaker written and spoken word frequency effects between 200 and 650 ms (Fig. 2). This suggests that auditory lexical-level processing is impeded for individuals with dyslexia and for those with weaker phonological skills overall. Moreover, like the phonological neighbourhood effect, both word frequency effects peaked in the left STG (Fig. 3). The shared locus of the phonological neighbourhood and word frequency effects could be one important factor for the close connection between phonological deficits and reduced cortical sensitivity to word frequency.

A close connection between phonological and lexical processing is also supported by the partially overlapping time-course of the effects of phonological neighbours and word frequency. Previously, neural correlates of phonological neighbourhood processing during picture-naming were reported as early as 150 ms after word onset by Miozzo et al. (2015) who also reported semantic-related features being co-activated in the same time-window, thus showing that phonological word form (sublexical) and lexical (semantic) information are processed in parallel by the language-activated cortical areas. This is further in line with psycholinguistic models proposing parallel processing of phonological sub-lexical information and lexical competition

(Kuperman et al., 2009; Marslen-Wilson, 1987). Our findings seem consistent with these models and highlight the parallel - or at least closely temporally overlapping - nature of phonological and lexical information processing, where frequency effects also begin to emerge before full word access has been achieved (i.e. at sublexical stages).

We also tested the hypothesis that word frequency could act as a compensatory effect for difficulty in retrieving phonological word representations since high word frequency reduces system demands (Hauk & Pulvermüller, 2004). This was not confirmed by our data. The lack of compensation effects in the present study stands in contrast to recent findings from reading, which show semantic compensation in visual single word processing (van der Kleij et al., 2019). This difference between visual and auditory results suggests that if top-down compensation takes place in auditory processing, it likely does so with respect to broader contextual-semantic effects at the sentence level (Klimovich-Gray et al., 2023; Nation & Snowling, 1998).

Taken together, the results show that poor phonological skills impede access to word frequency information, suggesting a downstream effect of phonological deficits on lexico-semantic processing in the auditory modality. However, this has not yet been addressed in current theories of developmental dyslexia, which do not specify whether and how phonological processing difficulties affect the processing of lexical information in speech (e.g. Goswami, 2011; Hatcher & Snowling, 2002). Moreover, the effect of phonological skills on written word frequency was stronger and more consistent than its effect on spoken word frequency. An effect of group (dyslexia diagnosis) on written frequency processing provides additional evidence that differences between dyslexic and non-dyslexic listeners are more pronounced for written than for spoken word frequency. These findings could point towards an additional effect of reduced print exposure on the written word frequency response, exacerbating the differences between readers with good versus poor phonological skills (Chateau & Jared, 2000). However, this needs to be interpreted with caution given the correlation between written and spoken frequency measures ($r = .71$) and the lack of a print exposure measure in the behavioural data.

4.4. *Wider implications for neurodevelopmental language disorders*

The findings of the present study show that phonological skills impact listeners' word processing at multiple levels of granularity and that this relationship holds across the whole sample tested, but especially for dyslexic readers with poor phonological skills. Other groups with particular phonological struggles could thus be affected in this way, too, such as individuals with Developmental Language Disorder (DLD, formerly known as Specific Language Impairment/SLI; Marshall et al., 2011; Nithart et al., 2009). DLD is characterised by difficulties in acquiring language, leading to multiple linguistic deficits, including verbal, grammatical, and syntactic deficits (Ramus et al., 2013). Like developmental dyslexia, the condition occurs despite normal intelligence and adequate learning opportunities (Leonard, 1998). Like many readers with dyslexia, many people affected by DLD have difficulty with phonological tasks such as repeating pseudowords, which suggests that they also have underlying deficits in phonological processing, word recognition, and verbal short-term memory (Gallon et al., 2007; Gathercole & Baddeley, 1990; Van der Lely & Howard, 1993; Montgomery, 1995; Snowling et al., 2000). Importantly, a number of children with DLD also have difficulties learning to read, with estimates ranging between 35 and 70 % (Bishop & Adams, 1990; McArthur et al., 2000; Snowling et al., 2000). These reading difficulties have been linked to phonological deficits, i.e. deficits relating to those skills that we have defined as ‘phonological skills’ (e.g. Joffe, 1998; Leitão et al., 1997; Nathan et al., 2004; Snowling et al., 2000). Macchi et al. (2014), for example, observed that children with both DLD and phonological deficits performed poorly in pseudoword reading compared to reading level-matched control children. In line with this finding, longitudinal studies show that phonological deficits in children with DLD at age six have a detrimental effect on reading acquisition, and, after controlling for the effect of phonological deficits, neither speech perception nor production predicts literacy skills (Nathan et al., 2004). This suggests that although phonological deficits may not be the sole source of reading difficulties in DLD, a lack of phonological skills among a significant subgroup of this disorder has a negative impact on their reading acquisition as it does in dyslexia. A similar relationship between phonological deficits, lexical analysis, and reading acquisition as suggested in the present work could thus affect a number of people with DLD, too. Careful assessment of individuals with DLD in terms of their phonological and reading deficits in future work is required to further investigate this potential link and unravel whether all of those individuals with both DLD and phonological processing deficits have reading difficulties (Bishop & Snowling, 2004).

In addition to phonological deficits, further language abilities such as grammatical and syntactic deficits are typically impaired in DLD, and it has been argued that dyslexia and DLD should be treated as related, but distinct conditions (Catts et al., 2005). This raises the question whether phonological deficits can explain grammatical and syntactic deficits in DLD, or whether an additional impairment is causing these symptoms (Ramus et al., 2013). One possibility is that phonological knowledge acts as a mediator between auditory sampling and higher-level language functions (Tallal, 2003). This theory is compatible with our findings that poor phonology is associated with weaker lexical-level encoding, and raises the question whether this detrimental bottom-up effect of poor phonological skills on lexical-level processing (and potentially higher morpho-syntactic levels) might be particularly exacerbated in DLD, perhaps because individuals with DLD do not have the same compensation abilities at the sentential level as has been found for dyslexic readers (Klimovich-Gray et al., 2023). In turn, impeded development of higher-level processing skills may stifle top-down support for phonological difficulties, creating a vicious circle. Uncovering the origins, prevalence, and effects of phonological deficits on language development, and their overlap among different neurodevelopmental conditions, is therefore crucial for our theoretical understanding of language disorders and remediation plans (Messaoud-Galusi & Marshall, 2010; Ramus et al., 2013; Van der Lely & Marshall, 2010).

Phonological training, while particularly important for those struggling to read and process speech, is likely to also benefit typical readers given that phonological skills and neural responses varied between listeners in a continuous fashion in the present study. This finding is in line with the current view that reading disorders, as well as many other neurodevelopmental conditions, are dimensional/gradient rather than categorical (Snowling et al., 2020). This could explain some of the discrepancies in the dyslexia literature since traditional group-level analyses cannot reflect these fine-grained individual differences. Going forward, continuous analysis approaches of behavioural and neuroimaging data promise to be a productive way to expand our current understanding of language disorders and other neurodevelopmental conditions. Moreover, future research should address phonological deficits in DLD and their impact on higher-level linguistic processes and compare these effects to dyslexic and neurotypical populations.

In summary, the results reported here indicate that top-down compensation through lexical-level word frequency is limited and much more effective when strong phonological skills have been developed. This suggests that – at least at the single word level – weaker phonological skills cannot be compensated with enhanced lexico-semantic engagement, despite the fact that lexico-semantic effects such as word frequency in general reduce system demands (Hauk & Pulvermüller, 2004). Remediation strategies which strengthen bottom-up processing may thus be even more important for dyslexia than previously assumed because phonological training seems to benefit word processing at multiple linguistic levels and processing stages beyond phoneme representations.

5. Conclusion

In the present study we showed that the processing of spoken words is critical to our understanding of dyslexia. The results support the view that phonological deficits are a core deficit in dyslexia and add to current theories by showing that these deficits affect auditory word processing at both pre-lexical and lexical levels. Importantly, the results demonstrate that better phonological skills (as indicated by behavioural phonological test scores) can be traced back to stronger neural encoding of phonological neighbourhood and lexical-level word frequency regardless of reading disorder. This suggests that better phonological skills can boost word processing via non-phonological pathways for both dyslexic and non-dyslexic readers. Therefore, effective phonological training could also benefit the lexico-semantic processing pathway of struggling readers with and without dyslexia, as well as readers with other developmental language conditions (such as DLD). Further studies with both age- and reading-level matched controls are needed to test this hypothesis and explore the developmental trajectory of our findings across the neurodiverse spectrum. Future work should also address how effects of phonological neighbourhood and word frequency play out while listening to phrases or sentences to further investigate the link with atypical oscillations found in connected speech.

Open practices section

The study in this article earned Open Data and Open Materials badge for transparent practices.

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Ethics

The study was performed in accordance with the Ethics of the World Medical Association (Declaration of Helsinki).

Data availability

The data and analysis protocols presented in this study can be found on the Open Science Framework (OSF), “Spoken Word Processing in Dyslexia”, https://doi.org/10.17605/OSF.IO/FEPDU.

CRediT author statement

Julia Schwarz: Conceptualization, Methodology, Software, Formal analysis, Writing - Original Draft, Visualization, Funding acquisition; **Anastasia Klimovich-Gray**: Conceptualization, Methodology, Software, Formal analysis, Writing - Review & Editing, Supervision; **Mikel Lizarazu**: Methodology, Software, Writing - Review & Editing; **Marie Lallier**: Investigation/Data Collection, Validation, Writing - Review & Editing.

Declaration of competing interest

The authors have no competing interests to declare.

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Supplementary data

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