

Neural correlates of statistical learning in developmental dyslexia: An electroencephalography study

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ABSTRACT

The human brain extracts statistical regularities from the surrounding environment in a process called statistical learning. Behavioural evidence suggests that developmental dyslexia affects statistical learning. However, surprisingly few studies have assessed how developmental dyslexia affects the neural processing underlying this type of learning. We used electroencephalography to explore the neural correlates of an important aspect of statistical learning – sensitivity to transitional probabilities – in individuals with developmental dyslexia. Adults diagnosed with developmental dyslexia ($n = 17$) and controls ($n = 19$) were exposed to a continuous stream of sound triplets. Every so often, a triplet ending had a low transitional probability given the triplet's first two sounds ("statistical deviants"). Furthermore, every so often a triplet ending was presented from a deviant location ("acoustic deviants"). We examined mismatch negativity elicited by statistical deviants (sMMN), and MMN elicited by location deviants (i.e., acoustic changes). Acoustic deviants elicited a MMN which was larger in the control group than in the developmental dyslexia group. Statistical deviants elicited a small, yet significant, sMMN in the control group, but not in the developmental dyslexia group. However, the difference between the groups was not significant. Our findings indicate that the neural mechanisms underlying pre-attentive acoustic change detection and implicit statistical auditory learning are both affected in developmental dyslexia.

1. Introduction

The brain is capable of detecting statistical regularities in sequential information through a process called statistical learning (Saffran, Aslin, & Newport, 1996). This type of learning involves implicit and innate mechanisms that allow the brain to identify repeated patterns using the transitional probability of sequential information such as speech. For example, research has shown that infants as young as 8 months old (Saffran et al. 1996) and even neonates (Teinonen, Fellman, Näätänen, Alku, & Huotilainen, 2009) can learn the transitional probabilities of a syllable stream, which enables them to detect word boundaries and extract individual words from natural speech.

Developmental dyslexia is a condition that impedes reading and

spelling abilities. Most traditional studies characterised problems in phonological processing as the core deficit in developmental dyslexia (Snowling, 2000; Ramus et al., 2003; Vellutino, Fletcher, Snowling, & Scanlon, 2004), although not all children with developmental dyslexia show phonological processing deficits (Lachmann & Bergström, 2023; Lachmann, Bergström, Huber, & Nuerk, 2022; Lachmann & van Leeuwen, 2008; Morris et al., 1998; It has also been reported that most individuals with developmental dyslexia show difficulties in non-linguistic tasks, including perceptual processing (Ahissar, Protopapas, Reid, & Merzenich, 2000; Christmann, Lachmann, & Steinbrink, 2015; Giraud & Ramus, 2013; McAnally & Stein, 1996; Sperling, Lu, Manis, & Seidenberg, 2005), and tasks of implicit statistical learning (Arciuli & Simpson, 2012; Du & Kelly, 2013; Evans, Saffran, & Robe-Torres, 2009; Howard,

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Howard, Japikse, & Eden, 2006; Menghini, Hagberg, Caltagirone, Petrosini, & Vicari, 2006; Vicari et al. 2005). Additionally, phonological difficulties may be considered an outcome of a broad perceptual or statistical learning deficit (e.g. Banai & Ahissar, 2018). In line with this, several studies suggest that auditory statistical learning is impaired in children, adolescents, and adults with dyslexia (Gabay, Thiessen, & Holt, 2015; Dobó et al., 2021; Kahta et al., 2019; Vandermosten, Wouters, Ghesquière, & Golestani, 2019), but the results are mixed (van Witteloostuijn, Boersma, Wijnen & Rispens, 2019).

Despite behavioural evidence on statistical learning deficits in developmental dyslexia, the underlying neural mechanisms of these deficits remain unclear. The present study aimed to investigate the neural correlates of statistical learning in individuals with developmental dyslexia using electroencephalography (EEG). Such studies are critical since EEG signals are susceptible to statistical regularities and may reveal group differences even when behavioural measures do not indicate learning effects (Koelsch, Busch, Jentschke, & Rohrmeier, 2016).

Statistical learning is reflected in several components of the event-related potentials (ERPs). When the brain encodes the transitional probabilities of stimulus sequences, it predicts stimuli with high transitional probability, which is associated with reduced ERP response to these predicted stimuli compared with unpredicted stimuli. Statistical learning effects can thus manifest as differences in ERP amplitudes for expected versus unexpected stimuli (for a review, see Daikoku, 2018). Statistical learning is reflected in both early ERP components, such as the auditory brainstem response (ABR; Skoe, Krizman, Spitzer, & Kraus, 2015), P50 (Daikoku, Yatomi, & Yumoto, 2017; Paraskevopoulos, Kuchenbuch, Herholz, & Pantev, 2012), N100 (Sanders, Newport, & Neville, 2002), and MMN (Koelsch et al., 2016; Moldwin, Schwartz, & Sussman, 2017), and in later ERP components, such as P200 (Balaguer et al., 2007; Cunillera, Toro, Sebastián-Gallés, & Rodríguez-Fornells, 2006) and N400 (François, Chobert, Besson, & Schön, 2013).

The MMN is typically measured with an oddball protocol. In such experiments, a series of standard stimuli are interspersed with acoustic deviants ("oddballs"; e.g., sounds differing in pitch, timbre or location; Christmann, Lachmann, & Berti, 2014; Garrido et al. 2008; Rinne, Anttila, & Winkler, 2001; Sussman, Winkler, & Schröger, 2003; Winkler & Czigler, 2012). The MMN is the electrophysiological response to such deviants. For example, if most sounds are presented from the right side, a location change (a sound presented on the left side) elicits a location MMN. The main generators of the MMN have been localised in the auditory cortex (Garrido et al., 2008). Because developmental dyslexia is related to sensory processing dysfunctions, including those of the auditory cortex (Clark et al., 2014; Goswami, 2014; for a review, see Gu & Bi, 2020; Gertsovski & Ahissar, 2022), the MMN has been used to investigate the neural basis of this disorder (Kujala et al. 2000). Reduced MMN amplitude in children (Lachmann, Berti, Kujala, & Schröger, 2005; for an overview, see Bishop, 2007) and young adults (Schulte-Körne, Deimel, Bartling, & Remschmidt, 2001) with developmental dyslexia reflects poor performance in syllable and tone discrimination and impaired tuning to native language speech representations (Bruder et al. 2011). The MMN has, therefore, been suggested as a neurophysiological endophenotype for developmental dyslexia (Neuhoff et al., 2012). However, one study also suggests that only certain aspects of auditory processing may be affected (Kujala, Lovio, Lepistö, Laasonen, & Näätänen, 2006): while the pitch MMN was shown to be impaired in that study, the location MMN was enhanced. Hence, MMN differences between individuals with dyslexia and normal controls might depend on the type of deviant (pitch or location).

Statistical learning can also be reflected in MMN potentials (François, Cunillera, García, Laine, & Rodríguez-Fornells, 2017; Koelsch et al., 2016; Moldwin et al., 2017). Tsogli, Jentschke, Daikoku, and Koelsch (2019) presented sequences of tone triplets that could contain "acoustic deviants" (stimuli from an irregular location) and "statistical deviants" (triplet endings that occurred with a low transitional probability given

the two preceding triplet items). The statistical deviants and acoustic deviants elicited prominent mismatch ERPs approximately 150–250 ms after stimulus onset. The mismatch response elicited by statistical deviants was referred to as *statistical MMN* (sMMN; Koelsch et al., 2016), in contrast to the MMN elicited by acoustic (location change) deviants.

Importantly, although both sMMN and location MMN are elicited by low-probability sounds, they rely on different learning dynamics and processing systems: The location change can be detected on a moment-to-moment basis, such as a series of stimuli coming from the right side being interrupted by a stimulus from the left side. Hence, a few standard events are already sufficient for the auditory sensory memory to generate the location MMN. By contrast, the elicitation of an sMMN requires an extended learning period to encode the statistical regularities underlying the arrangement of sound sequences. Despite lots of neuroscientific evidence that central auditory processing (as reflected in the MMN for acoustic deviants) is affected in developmental dyslexia (Kujala et al., 2000; Lachmann et al., 2005; for an overview, see Bishop, 2007; Schulte-Körne et al., 2001), no previous study examined the sMMN for statistical deviants.

Therefore, in this study, we aimed to substantiate the evidence for central auditory processing deficits in dyslexia by utilizing the location MMN, while also forging new ground in the field of dyslexia research by investigating statistical learning using the sMMN. That is, the current study investigated both the sMMN and location MMN to understand how developmental dyslexia (in adults) affects the processing of acoustic, compared with statistical, deviants. Assuming that developmental dyslexia adversely affects the prediction of sensory stimuli in the auditory cortex (Jaffe-Dax, Kimel, & Ahissar, 2018; Lieder et al. 2019; Gertsovski & Ahissar, 2022), we hypothesised that statistical deviants and acoustic deviants would elicit weaker mismatch responses (i.e., both a weaker sMMN and a weaker location MMN) in individuals with developmental dyslexia than in controls. Confirmation of this hypothesis would provide evidence that developmental dyslexia is associated with generally reduced predictive processes of sounds, with regards to both processing of acoustic deviants, which requires auditory sensory memory operations, and of statistical deviants, which requires a longer period (usually at least several minutes) for the statistical learning of the local transition probabilities.

2. Materials and methods

2.1. Participants

A power analysis (Cohen, 1988) with a standard level of .05 and a statistical power of .8, revealed a minimum of 16 participants to detect a large effect size of .9. Previous studies (Tsogli, Jentschke, Daikoku, & Koelsch, 2019; Tsogli, Jentschke, & Koelsch, 2022) using an identical statistical learning paradigm and similar dependent measures also included 21 participants and detected large effect sizes. Individuals were recruited through a database of the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. Participants included in the analyses reported a diagnosis of developmental dyslexia in childhood.

Twenty-one adults diagnosed with developmental dyslexia in childhood (11 females, mean age = 26 years, SD = 5.3) and 20 age- and gender-matched control participants without a diagnosis of developmental dyslexia (14 females, mean age = 26 years, SD = 3.1) were screened for eligibility to participate in this study. Three of the individuals with developmental dyslexia were excluded because their diagnosis in childhood was not based on diagnostic testing. Furthermore, we excluded one individual from the developmental dyslexia group and one from the control group because both performed in the nonverbal intelligence test (Standard Progressive Matrices; Raven & Court, 1998) with an IQ score < 70 (two SD below the normal range). After these exclusions, our study sample included 17 adults with developmental dyslexia (12 females, mean age = 23.8 years, SD = 4.2)

and 19 control participants (13 females, mean age = 25.6 years, SD = 3.3) (see Table 1 for details) who met the following inclusion criteria: German as the native language, right-handedness (Edinburgh Inventory; Oldfield, 1971), no history of neurological or audiological disorders, no diagnosis of general or specific language impairment, no mental retardation, and no formal musical training for more than 5 years (beyond regular school lessons).

The study protocol was approved by the Ethics Committee of the Max-Planck-Institute (approval number: 2018/352). All participants were informed of the purpose of the study and the procedures in place to ensure their safety and the confidentiality of their personal data. All the participants provided written informed consent to participate in this study.

2.1.1. Evaluation of spelling and reading skills

Spelling skills were assessed with the German “Rechtschreibtest” (Ibrahimović & Bulheller, 2013). In this test, participants were asked to fill in the missing words of a text, mainly composed of irregular German words, that a skilled and German native-speaking experimenter read aloud. Silent text reading speed and reading comprehension skills were assessed with the “Lesegeschwindigkeits- und Verständnistest für die Klassen 5–12” (LVGT 5–12; Schneider, Schlagmüller, & Ennemoser, 2017). In this test, participants were asked to read as much of a continuous text as possible within 4 min and to select certain text passages which of three given words best fits the context of meaning.

2.1.2. Stimuli

2.1.2.1. Sounds. We used the same stimuli and sequences as in a previous study (Tsogli et al., 2019). Each sound consisted of a Shepard tone (Shepard, 1964), combined with the sound produced by one of six different percussion instruments (i.e., a surdo, a tambourine, agogô bells, a hi-hat, castanets, or a woodblock). We obtained the percussive sounds from the Philharmonia Orchestra website (http://www.philharmonia.co.uk/explore/sound_samples). We used six distinct Shepard tones based on six frequencies (i.e., F₃ [174.61 Hz], G₃ [196.00 Hz], A₃ [220.00 Hz], B₃ [246.94 Hz], C₄ [277.18 Hz], and D₄ [311.13 Hz]), each tone resulting from the superposition of nine sinusoidal components spaced an octave apart. The specific combinations of Shepard tones and percussive sounds were counterbalanced across participants. Examples of sounds are provided in Appendix A.

Another set of six sound combinations was created for a practice phase at the start of each experiment. These sounds were similar to those used in the main experiment but differed in terms of the frequencies providing bases for Shepard tones (i.e., E₃ [164.81 Hz], F₃ [184.99 Hz], G₃ [207.65 Hz], A₃ [233.08 Hz], C₄ [261.62 Hz], and D₄ [293.66 Hz])

Table 1

Demographic and diagnostic data (raw scores) of the control and developmental dyslexia groups.

	Control	Dyslexia	<i>t</i> (34)	<i>p</i>	Cohen's <i>d</i>
N (females)	19 (13)	17 (12)			
Age	25.6 (± 3.3)	23.8 (± 4.2)	1.41	0.167	0.472
Intelligence	28.0 (± 3.7)	27.0 (± 3.9)	0.79	0.436	0.263
Spelling	70.8 (± 4.1)	46.5 (± 9.6)	9.71	< 0.001	3.373
Text reading					
Reading	48.5 (± 10.6)	32.5 (± 8.9)	4.91	< 0.001	1.637
Comprehension					
Reading Speed	1190.7 (± 232.8)	803.94 (± 202.4)	5.29	< 0.001	1.766
(number of read words)					

Note. Averages are reported as mean ± standard deviation. The intelligence scores and spelling and reading test scores are raw scores.

and the percussive sounds used (i.e., the sounds of a woodblock, a tambourine, agogô bells, castanets, a hi-hat, and a bass drum). An additional target Shepard tone based on C₄ (554.37 Hz), which did not have an accompanying percussive sound, was used for a cover task and a passive listening component of the experimental procedure (see Experimental Procedure). All sound stimuli had a tone duration of 220 ms, including rising and falling periods of 10 ms and 20 ms, respectively, a constant loudness, and a sampling frequency of 44,100 Hz with 16-bit resolution.

2.1.2.2. Triplet sequences. The stimuli described above, hereafter referred to as sounds A to F, were combined into sound triplets. Each 220 ms sound was followed by an 80 ms pause, such that the total duration of each triplet was 900 ms. There were no additional pauses between triplets. That is, the triplet sequence was perceived as a continuous stream of tones. As shown in Fig. 1, sounds A and B and sounds C and D were paired to create two distinct two-sound sequences (i.e., AB and CD) that served as the first two sounds of each triplet, hereafter referred to as *triplet roots*. Sounds E and F could be used as the last sound of a triplet, hereafter referred to as *triplet endings*. Combining the two roots and two triplet endings yielded four possible triplets (i.e., ABE, ABF, CDE, and CDF). The assignment of different sounds as triplet roots or endings was counterbalanced across participants to ensure that any possible acoustical differences between sounds would be cancelled out across participants and not bias the neural responses of interest.

Exposition Sequences. The sequence of sounds used during the exposition phase comprised a total of 2400 sound triplets, divided into six blocks (each with 400 sound triplets, and a duration of about 6 min). The triplets were presented in a pseudo-randomised order with no two sequentially adjacent triplets being identical. Each of the two roots had an equal probability of occurring in a given triplet regardless of the ending sound of the previous triplet.

Each sound stimulus was presented from a speaker to either the participant's right or left side. These speakers were positioned at 60° angles in the azimuthal plane. For each participant, one side was pseudo-randomly selected as the standard side for stimuli presentation, and the other was the deviant side. The lateralisation of the stimuli was balanced across blocks and counterbalanced between participants, and whether the location was “standard” or “deviant” was considered in the data analyses. For the triplet root sounds (i.e., sounds A, B, C, and D), 95% of the stimuli were presented from the standard side and the remaining 5% from the deviant side. For the triplet endings (i.e., sounds E and F), 80% of the stimuli were presented from the standard side and the remaining 20% from the deviant side. The triplet's endings presented from the deviant side are henceforth referred to as “acoustic deviants”.

To generate statistical deviants, we set distinct probabilities for a transition (namely, transitional probability) from a given root to a given ending within a triplet. The sensitivity to transitional probability is one of the important aspects of statistical learning mechanisms (Perruchet & Pacton, 2006; Saffran et al. 1996). The transitional probability for a given triplet ending was either 90% or 10%, (Fig. 1a). Low-probability triplet endings (i.e., the low probability for the root-to-ending transition) are henceforth referred to as “statistical deviants”. Each statistical deviant was followed by at least 3 triplets that were not statistically deviant. “Standard triplets” did not contain acoustic deviants, nor statistical deviants (these standard triplets accounted for 72% of all triplets). The remaining 28% of triplets were deviant triplets: The first two stimuli of these deviant triplets, i.e. the triplet “root”, were presented from the standard location, and the last tone of the deviant triplets was either (i) a statistical deviant only (8% of all triplets), (ii) an acoustic deviant only (18% of all triplets), or (iii) it was a combined deviant, i.e. both a statistical and an acoustic deviant (2% of all triplets, these events were excluded from the data analysis, and only employed to prevent participants from predicting that any acoustic deviant would not be a

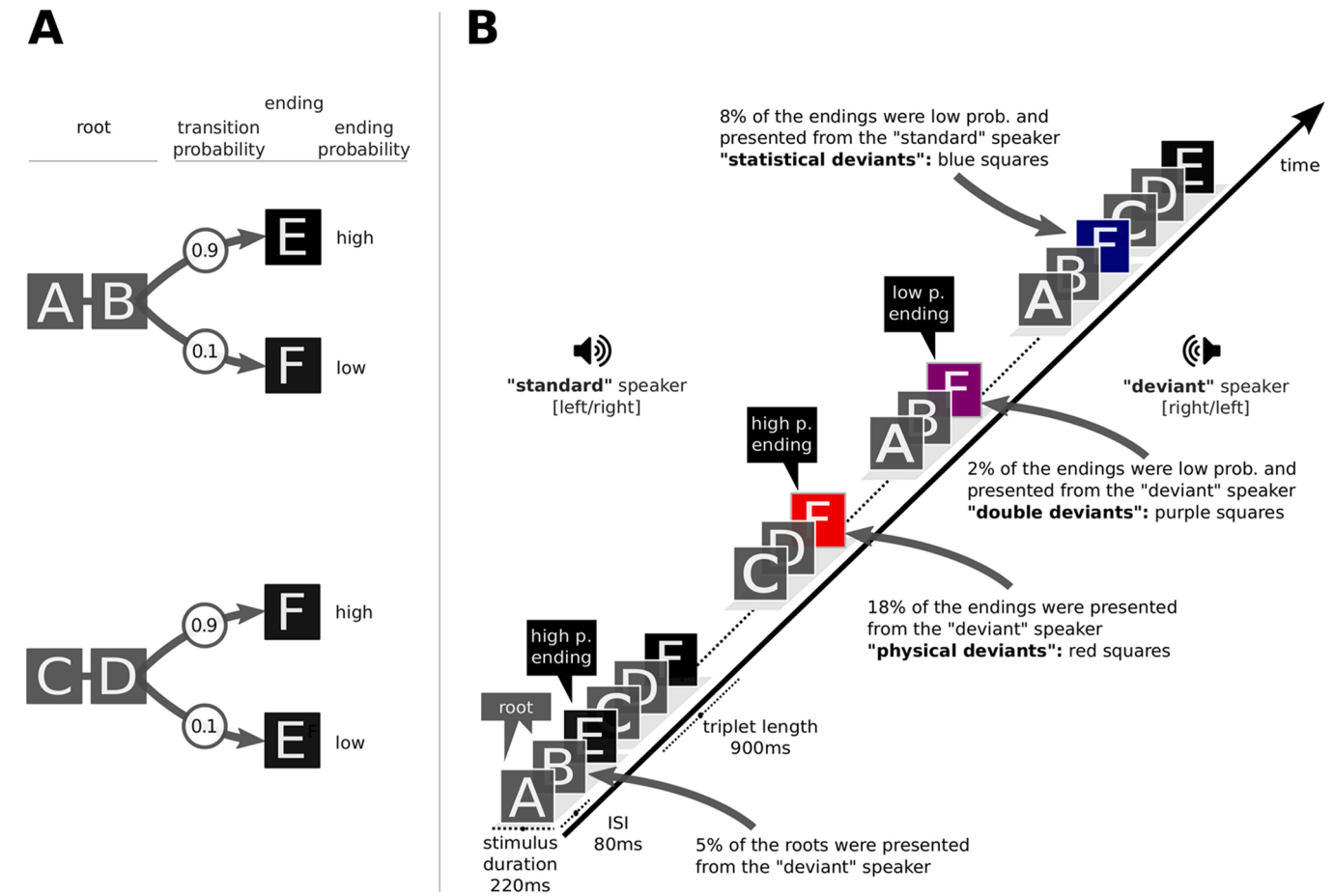


Fig. 1. Triplets and stream in this study. (A) Four types of triplets were generated from six different sounds (designated with letters from A to F) produced by pairing a Shepard tone with various percussive sounds. Each triplet consisted of a root containing two conserved sounds (AB or CD) and a triplet ending with a high (90%) or a low (10%) transitional probability, given the triplet's root. Each triplet root had a 50% probability of occurring regardless of the ending sound of the previous triplet. (B) Examples of a possible triplet sequence including standard triplets (triplet endings in black boxes), triplets with a statistically deviant ending (triplet endings in blue boxes) or an acoustic deviant ending (triplet ending in red box), and a triplet with a doubly deviant ending (i.e., statistically deviant and acoustic deviant; triplet ending in the purple box). Reprinted, with permission, from Tsogli et al. (2019). Abbreviations: ISI = inter-stimulus interval; p. & prob. = probability.

statistical deviant). The probabilities of the four different triplet types are summarized in Table 2.

Behavioural Testing Sequences. Each behavioural testing phase of the experiment consisted of twelve trials, with each trial involving a pair of triplets separated by a 335-ms pause. The triplets in each pair had the same root but different endings with low vs. high transition probabilities, respectively (i.e., statistical deviant vs. no deviant). The order in which the statistically deviant and standard triplets were played was counterbalanced across trials. Varying the order in which the same-root triplets within a pair were played created four sequentially distinct pairings (i.e., ABE to ABF, ABF to ABE, CDE to CDF, and CDF to CDE). Each sequentially distinct pairing was played three times during each behavioural testing phase, and consecutively played pairings had alternating triplet roots (i.e., each AB pairing was followed by a CD

pairing that was in turn followed by an AB pairing). During behavioural testing phases, all triplets were played from both speakers, i.e., the task focused on statistical sequence regularity, wherein location was not a factor.

2.1.3. Experimental design

The participants completed a multi-stage experiment with six blocks while undergoing EEG monitoring (see 'Collection and Analysis of EEG Data') inside an electromagnetically shielded chamber. Immediately before the experiment, the participants were provided with instructions concerning the procedures for the experiment's different phases (see below). To ensure that only implicit learning could occur, the instructions did not include any description of the possible location or statistical deviance of the triplets. The participants then completed a 1-min practice session in which they were asked to press a key as soon as possible after hearing a target sound (i.e., C#5 [554.37 Hz]). If necessary, each participant repeated the practice session until they had correctly pressed the key after 80% of the target sound presentations.

Each of the six blocks included an exposition phase comprising the passive listening of the sequence of 400 triplets and a subsequent behavioural testing phase in which the participants performed actions based on a triplet sequence. During the exposition phase, participants were instructed to react to the high-pitched tones (cover tasks, 67% of all tones) while they were exposed to the sequence (see Exposition Sequences). At the same time, they watched a silent movie (nature or

Table 2

The 2 × 2 types of triplet endings based on location and statistical constraints.

		Transition probability	
		High (90%)	Low (10%)
Sound Location	Standard (80%)	Standards (72%)	Statistical deviants (8%)
	Deviant (20%)	Acoustic deviant (18%)	Double deviant (2%)

Extended data

wildlife documentaries) on a monitor in front of them. While the cover task was not particularly demanding (e.g., in terms of attentional resources), it minimised the possibility of the participants intentionally focusing their attention on statistical properties. We included the target sounds (cover task) only to have an additional control to prevent participant disengagement and distraction.

During the behavioural testing phase, the participants listened to paired statistically deviant and standard triplets (see Behavioural Testing Sequences). After each pair of triplets, a participant was asked to choose which triplet in the pair sounded more familiar and to rate their confidence in a given answer on a scale ranging from 1 (no certainty) to 5 (certainty).

2.1.4. Acquisition and analysis of EEG data

We obtained 64-channel EEG data (Brain Amp, Brain Products, Munich, Germany) through cap-mounted electrodes placed over the participants' scalps in accordance with the extended international 10–20 system. The left mastoid electrode was used as the reference electrode, and the neck electrode was used as the ground electrode. The electrodes were clustered into six regions of interest: a left frontal region (F7, F5, F3, FT7, FC5, and FC3), a middle frontal region (F1, FZ, F2, FC1, FCZ, and FC2), a right frontal region (F8, F6, F4, FT8, FC6, and FC4), a central left region (T7, C5, C3, TP7, CP5, and CP3), a central middle region (C1, Cz, C2, and CPZ), and a central right region (T8, C6, C4, TP8, CP6, and CP4). Horizontal and vertical electrooculograms were recorded bipolarly through electrodes placed at the outer canthi of the eyes and above and below the right eye. Electrode impedance was kept < 5 k Ω . Signals were recorded with a 0.25–1,000-Hz band pass filter and a 500-Hz sampling rate.

EEG data were analysed in EEGLAB 13 (Delorme & Makeig, 2004) in MATLAB R2018b (The MathWorks, Natick, Massachusetts). Continuous raw data files were re-referenced to the algebraic mean of the left and right mastoid electrodes and filtered with a 0.5-Hz high-pass filter and a 30-Hz low-pass filter implemented with finite impulse response designs and Blackman windows of 550 points and 2750 points, respectively. Channels with excessive noise were identified through visual inspection and interpolated when necessary. The mean number of interpolated channels per participant was 0.22. Independent component analysis was used for the linear decomposition of continuous data to remove the contributions of artefacts affecting scalp sensors (e.g., slow drifts, eye blinks or movement, and muscle artefacts). Epochs were removed from further analyses if the amplitude changes exceeded $\pm 45 \mu\text{V}$ in any channels, including the electrooculogram (less than 10% of the trials). The epochs of target stimuli ("cover task") were removed from the analysis. The average and range of epoch number of standards were 1672 (range: 1384–1724) in the control group and 1687 (range: 1641–1727) in the dyslexia group. The average epoch number of statistical deviants was 192 (range: 144–200) in the control group and 194 (range: 179–200) in the dyslexia group. The average epoch number of acoustic deviants was 425 (range: 328–441) in the control group and 427 (range: 400–443) in the dyslexia group.

Student's *t*-test showed that there were no significant differences between groups $t(37) = 0.69, p = .5$. Selective response averaging was conducted separately for standard triplets without both statistical and acoustic deviants, triplets with an acoustic deviant (but not with a statistical deviant), triplets with a statistical deviant (but not an acoustic deviant), and triplets with both an acoustic deviant and a statistical deviant (see 'Exposition Sequences').

Averages were computed using a 100 ms pre-stimulus baseline. We directly addressed the hypothesis of the present study, focusing on the average MMN amplitudes measured within a 150–250 ms time window. In addition, we also detected an obvious positive component approximately 100–140 ms after the onset of the stimuli, henceforth referred to as P120. This ERP appears to be a P1-like component in terms of polarity and the fact that it is temporally followed by the N1 and the MMN. Because this effect was not hypothesised, we investigated the average

amplitudes within a 100–140 ms time window in an exploratory manner.

2.1.5. Statistical analysis

2.1.5.1. Between-group comparisons of participant characteristics. Statistical analyses were conducted using jamovi version 1.2 (Jamovi Project, 2020). We used Bonferroni-corrected *t*-tests (dividing 0.05 by the number of tests) when comparing demographic characteristics and scores on tests of intelligence, spelling skills, and reading abilities between participants with developmental dyslexia and the control group.

2.1.5.2. Analyses of exposition phase data. We used separate ANOVA models to analyse the effects of stimulus deviance on P120 and MMN effect amplitudes during the exposition phase. One ANOVA model featured the within-participant factor of *Sound location* (i.e., location standard triplet endings or acoustic deviant triplet endings), and the other featured the within-participant factor of *Transitional probability* (i.e., sequence standard triplet endings or statistically deviant triplet endings). In total, we used 4 ANOVAs, 1 for the analysis of the location MMN, 1 for the analysis of the statistical MMN, 1 for the analysis of the P120 elicited by acoustic (location-change) deviants and 1 for the analysis of the P120 elicited by the statistical deviants. Each of these ANOVAs included the between-participants factor of group (i.e., participants with developmental dyslexia vs. the control group) and three further within-participants factors: (i) anterior-posterior scalp distribution, i.e. differences between ERP responses in frontal vs. central areas of the brain; (ii) lateralization, i.e. differences between ERP responses in left, medial, and right areas of the brain and (iii) blocks, i.e. differences between ERP responses elicited in the 3 experimental blocks into which the entire experimental session was divided (instead of the actual six blocks).

The posterior region was not included because of low amplitude sizes. To increase the signal-to-noise ratio, the ANOVA models included three blocks, rather than the actual six, by merging the data from pairs of blocks.

We selected $p < .05$ as our threshold for statistical significance and used a false discovery rate method for the post hoc testing of significant effects. To determine whether the spelling and reading scores correlated with the P120 and MMN effect amplitudes, we calculated Pearson correlation coefficients.

2.1.5.3. Analyses of behavioural testing phase data. We used a two-tailed *t*-test to determine whether the frequency of correct answers during behavioural testing exceeded chance levels (i.e., >0.5). We also used ANOVA models to compare participants with developmental dyslexia and the control group in terms of response accuracies and reaction times (RT) and included experimental blocks as a within-subject factor in these analyses. As in our analyses of exposition phase data, we assumed three blocks, the first, second, and third blocks, instead of the actual six blocks of the experiment, to obtain a higher signal-to-noise ratio. We selected $p < .05$ as our threshold for statistical significance and used Bonferroni correction for the post-hoc testing of significant effects. We conducted Pearson correlation analysis to determine whether response accuracy rates correlated with confidence ratings and literacy test scores.

3. Results

3.1. Participant characteristics

Relative to the control group, the developmental dyslexia group had lower average scores for spelling abilities, reading comprehension, and reading speed (Table 1), confirming the diagnosis of developmental dyslexia given in childhood. However, the two groups were comparable

in terms of age and intelligence (age: $t(34) = 1.41, p = .167$; IQ: $t(34) = 0.50, p = .620$).

3.1.1. EEG results

3.1.1.1. P120 and MMN responses to acoustic (location-change) deviance. In this analysis, only standards and deviants presented on high-probability triplet endings were included to examine whether developmental dyslexia affects ERP responses to acoustic deviants (see Appendix B for mean P120 and location MMN amplitudes in each condition).

Acoustic deviants elicited a P120 followed by a location MMN, which was maximal at anterior frontal electrodes (Fig. 2a–b). An ANOVA for the P120 indicated a significant interaction between sound location (standard, deviant) and group: $F(1, 34) = 5.52, p = .025, \eta^2 p = .14$. Posthoc analysis showed that acoustic deviants elicited a larger P120 response compared with that by location standards in the control group but not in the developmental dyslexia group.

Likewise, an ANOVA of the location MMN indicated a significant interaction between sound location (standard, deviant) and group: $F(1, 34) = 5.16, p = .03, \eta^2 p = .13$ (see Appendix C for complete results). Posthoc analyses indicated (i) that both the control group and developmental dyslexia group showed a significant location MMN ($p < .001$), and (ii) that the acoustic deviants elicited a larger MMN in the control group than the developmental dyslexia group ($p = .014$). Analysing ERP responses separately in each group further showed that acoustic deviants elicited a significant location MMN in both the dyslexia group and the control group ($p < .001$; Fig. 2c). Higher spelling scores correlated

with larger acoustic deviance-induced P120 effects ($r = .37, p = .03$ see Appendix C). No other correlations between literacy test scores and EEG responses were observed.

3.1.1.2. P120 and MMN responses to statistical deviance. Next, we examined whether developmental dyslexia affects ERP responses to statistical deviants, i.e. to triplet endings with high vs. low transitional probability (only triplet endings without location change were included in this analysis). In both groups, statistical deviants elicited a larger P120 than standards. The effects of statistical learning on P120 amplitudes were prominent at medial electrodes (Fig. 3b–c). An ANOVA detected a significant interaction between *Transitional Probability* and *Lateralisation* ($F[2,68] = 4.15, p = .020, \eta^2 p = .11$). Post-hoc tests revealed that the P120 responses to statistical deviants were greater than those to the standards at medial electrodes ($p = .009$); however, no such effects were apparent in the left ($p = .23$), nor the right region ($p = .53$). The ANOVA did not indicate a significant interaction between *Transitional Probability* and *Group* ($F[1,34] = 0.88, p = .36, \eta^2 p = .025$).

In the control group (but not in the developmental dyslexia group), the P120 was followed by an, which was maximal over anterior frontal electrodes (Fig. 3a–b; see Appendix B for mean amplitudes of P120 and sMMN in each condition). These observations were reflected in an ANOVA indicating a significant interaction between *Transitional probability* (high vs. low probability), *Scalp area* (frontal vs. central), and *Group*: $F(1, 34) = 5.50, p = .025, \eta^2 p = .14$ (for complete results, see the Appendix D). Post-hoc tests revealed that the sMMN response at frontal electrodes was significant in the control group ($p = .032$) but not in the

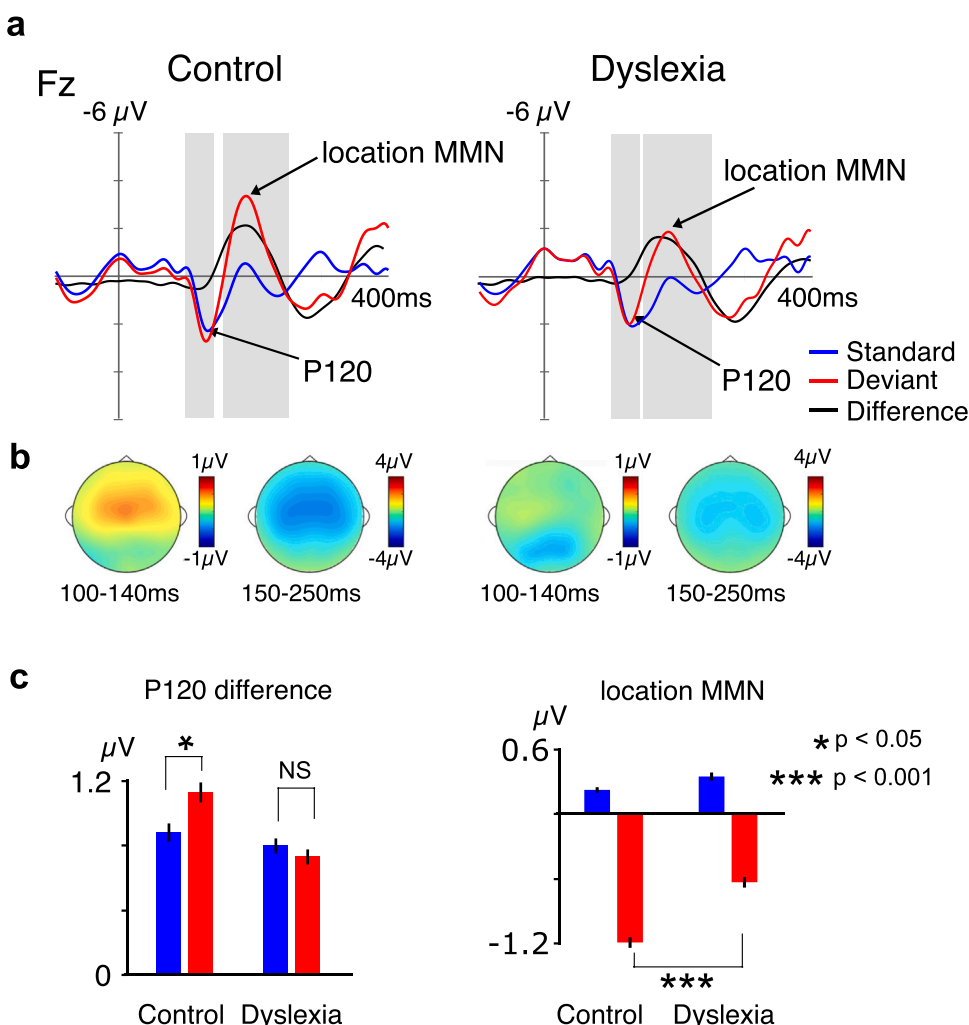


Fig. 2. Location MMN results. (a) Mean ERP responses to triplet endings as recorded from the FZ electrode. Grey areas indicate the time windows used for quantifying the P120 (~100–140 ms) and the location MMN (150–250 ms) components. Averaged ERP responses to standards (blue) and acoustic deviants (red), as well as differences between them (black), are shown separately for each group. Only triplet endings were included in this analysis (see Methods). (b) Isopotential maps showing the scalp distributions of differences between the ERPs evoked by acoustic (location) deviants and standards, separately for the P120 and the location MMN, and separately for each group (the two left maps show results of the control group, and the two right maps show results of the group with developmental dyslexia). (c) The left image shows that acoustic deviants (red bars) elicited larger P120 amplitudes than standards (blue bars) in the control group, but this was not the case in the developmental dyslexia group. The right image shows that both groups showed significant location MMNs. Further, the location MMN was larger in the control group than in the developmental dyslexia group. Bars show mean amplitudes for a fronto-central region of interest (average of F1, FZ, F2, FC1, FCZ, FC2, C1, C2, and CPZ), and error bars indicate standard errors of the mean. Abbreviations: ERP = event-related potential, location MMN = location mismatch negativity.

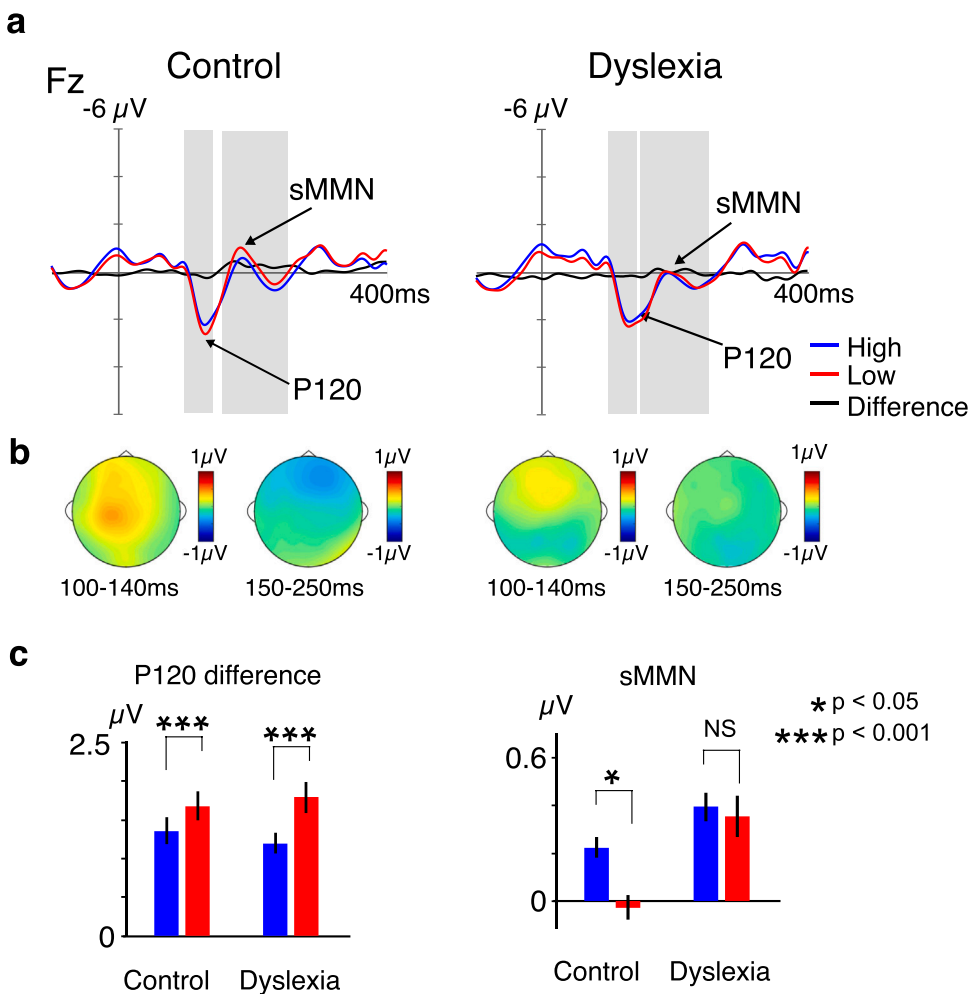


Fig. 3. Statistical MMN results. (a) Mean ERP responses to triplet endings as recorded from the Fz electrode. Grey areas indicate the time windows used for quantifying the P120 (100–140 ms) and the statistical MMN (150–250 ms) components. Averaged ERP responses to standards (blue) and statistical deviants (red), as well as differences between them (black), are shown separately for each group. Only triplet endings were included in this analysis (see Methods). (b) Isopotential maps showing the scalp distributions of differences between ERPs evoked by statistical deviants and standards, separately for the P120 and the statistical MMN, and separately for each group (the two left maps show results of the control group, and the two right maps show results of the group with developmental dyslexia). (c) The left image shows that statistical deviants (red bars) elicited larger P120 amplitudes than standards (blue bars) in both groups. The right image shows that a significant statistical MMN was elicited in the control group, but not in the developmental dyslexia group. Bars show mean amplitudes for a fronto-central region of interest (average of F1, FZ, F2, FC1, FCZ, FC2, C1, Cz, C2, and CPZ), and error bars indicate standard errors of the mean. Abbreviations: ERP = event-related potential, location MMN = location mismatch negativity.

developmental dyslexia group ($p = .74$; Fig. 3c). At central electrodes, the sMMN was not significant in either of the groups. These results reflect that the sMMN had a frontal scalp distribution.

We now turn to the learning effects across the experimental blocks. The effects of statistical learning on P120 amplitudes gradually increased as the experiment progressed to later blocks, as reflected by a significant interaction between transitional Probability, Lateralisation, and Experimental blocks ($F[4136] = 2.78$, $p = .029$, $\eta^2 p = .08$). Post hoc tests revealed that statistical deviants elicited a significant P120 during the third block ($p < .001$), but not in the first ($p = .15$) nor the second blocks ($p = .85$). Analogous analyses for the sMMN did not yield any significant results (see Appendix D).

3.1.2. Behavioural results

Regarding the cover task, the participants discovered 94.3% ($SD = .02$) of the high-pitched tones during the exposition phase, indicating that the participants paid attention to the acoustical stimuli and that this task was relatively easy to perform.

Regarding the statistical learning task, after each block during the exposition phase, the participants listened to one standard triplet and one deviant triplet in each of the twelve trials. Following such a triplet pair presentation, participants chose which triplet sounded more familiar to them, and rated their confidence in a given answer on a scale ranging from 1 ("very uncertain") to 5 ("very certain"). To evaluate the behavioural performance, we used a two-tailed t -test to determine whether the frequency of correct answers exceeded chance levels (see Appendix B for the original data). Further, we used ANOVAs to compare response accuracies, RTs, and confidence ratings between individuals

with developmental dyslexia and controls. ANOVAs were computed with *group* (developmental dyslexia vs. control) as a between-subjects factor, and *Experiment block* as a within-subjects factor.

An ANOVA revealed no effects on response accuracies and confidence ratings (all p 's $> .05$ Fig. 4, and see Appendix E). There were no interactions with the factor *Group*. That is, the frequency of correct answers in the control group was not significantly higher than in the dyslexic group. However, response accuracy tended to be higher in the control group than in the dyslexic group (Fig. 4, right). As for the reaction time, a significant main effect of the experimental block was indicated ($F[2,68] = 7.92$, $p < .001$, $\eta^2 p = .189$). Post-hoc tests revealed that the reaction time in the second and last blocks was significantly faster than that in the first block (2nd: $p = .006$; 3rd: $p < .001$). No other effect was found in the ANOVA of behavioural results.

To determine whether response accuracy rates correlated with confidence ratings in a given answer, we also conducted a Pearson correlation analysis. Response accuracies did not correlate with confidence ratings, neither in the control ($r = -0.18$, $p = .19$) nor in the developmental dyslexia group ($r = -0.05$, $p = .70$). Similarly, response accuracies did not correlate with reading or spelling scores. In summary, the behavioural performance in the control group, but these trends were statistically not significant.

4. Discussion

In this study, we investigated ERP responses to a continuous stream of sound triplets, in which some triplet endings were acoustic deviants

Correctness ratios

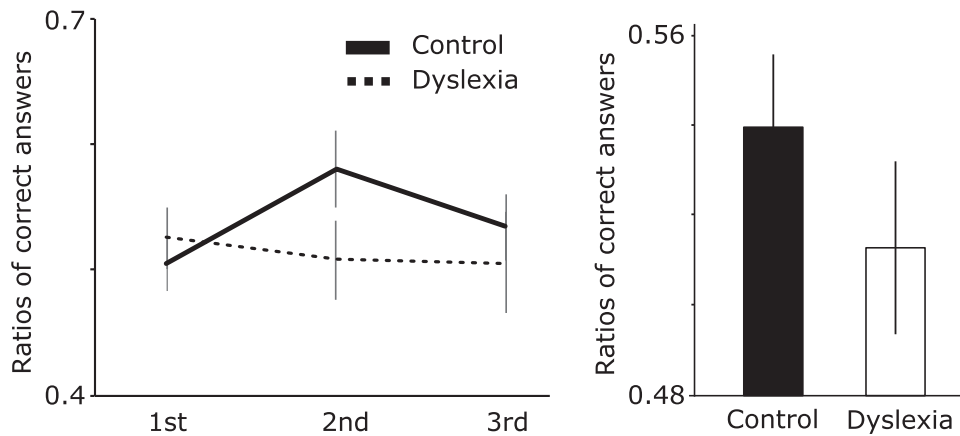
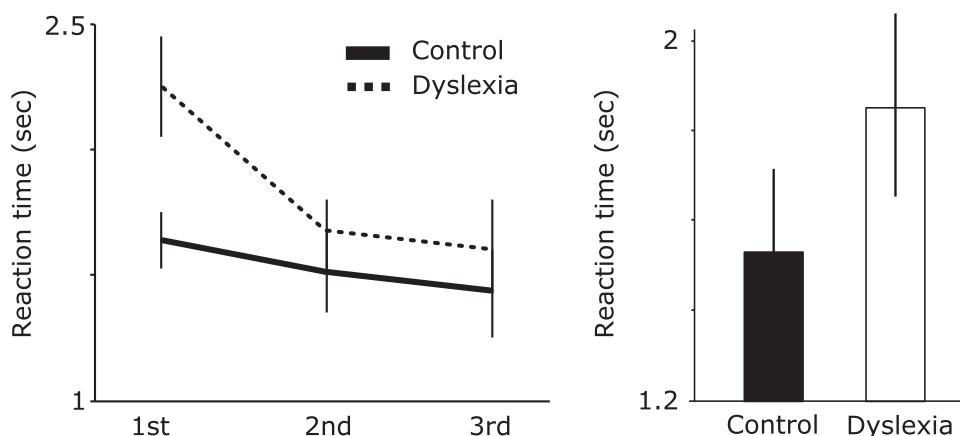


Fig. 4. Behavioural testing results across experimental blocks. Each behavioural testing phase consisted of twelve trials, and in each of these trials, the participants were presented either first with a standard triplet and then with a statistically deviant triplet or vice versa. Following the presentation of such a triplet pair, participants had to choose which of the two triplets sounded more familiar to them (two-alternative forced choice). For the computation of the behavioural data, we divided the entire experimental session into three blocks (instead of the actual six blocks, to obtain a higher signal-to-noise ratio). The top panel shows correctness ratios, and the bottom panels show reaction times. The images on the left show the results in each of the first, second, and third blocks, separately for each group. The images on the right show the averages of the entire experimental session, separately for each group. Correctness ratios tended to be higher, and reaction times lower, in the control group, but these trends were statistically not significant. Error bars indicate standard errors of the mean.

Reaction time



(location-change) or statistical deviants. Our findings showed that the acoustic deviants elicited a large location MMN, with a smaller amplitude observed in participants with developmental dyslexia compared with controls, which supports previous evidence of a smaller MMN in individuals with developmental dyslexia (Gu & Bi, 2020; Lachmann et al., 2005; Neuhoﬀ et al., 2012). Furthermore, we observed a significant sMMN and a behavioural effect of statistical learning in control participants, but not in individuals with developmental dyslexia, despite no significant difference between groups in a direct comparison. This result suggests that individuals with developmental dyslexia may have a reduced learning of sequential statistical structure, which supports previous studies indicating that auditory statistical learning may be impaired in developmental dyslexia (Gabay et al., 2015; Dobó, Lukics, Szóllósi, Németh, & Lukács, 2021; Kahta et al., 2019; Vandermosten et al., 2019), although the findings have been inconsistent (van Wittenloostuijn et al., 2019).

Previous studies have suggested that individuals with developmental dyslexia exhibit a domain-general statistical learning impairment. For example, they show weaker domain-general statistical learning across various sensory domains (Hung, Frost, & Pugh, 2018) such as auditory (Arciuli & Conway, 2018; Dobó et al., 2021; Gabay et al., 2015; Kahta & Schiff, 2019; Vandermosten et al., 2019) and visual stimuli (Sigurdardottir et al. 2017) as well as speech and non-speech information (Plakas, van Zuijen, van Leeuwen, Thomson, & van der Leij, 2013). Our findings support this domain-general account because we observed weaker location MMN responses (detecting acoustic deviance due to a location

change) and no sMMN responses (detecting statistical deviance) in individuals with developmental dyslexia compared to controls. As we used non-speech auditory stimuli, the weaker location MMN and sMMN responses observed in individuals with developmental dyslexia are not limited to speech. Thus, our results are consistent with the presence of an underlying impairment in predictive processing in individuals with developmental dyslexia, resulting in the impairment of processing prediction errors across several cognitive domains, including basic auditory processing, statistical learning, and speech and non-speech information.

It is still unclear whether the predictive processing impairments observed in dyslexia stem from predictions of content (first-order predictions) or context (second-order predictions, also known as the precision of first-order prediction errors). Dyslexia may lead to a less effective precision-weighted attentional selection, resulting in reduced modulation of bottom-up prediction-error processing compared to controls. Researchers have proposed that controls are more efficient and noise-tolerant with repeated targets due to improved stimulus-specific predictions, while dyslexics struggle with the gradual build-up of predictions around repeated stimuli, reducing the attentional load (Ahissar, 2007). It has been suggested that repetition suppression arises from adaptive changes in predictions about the content and precision of sensory inputs, resulting in minimized prediction error (Aukstulewicz & Friston, 2016). Moreover, it has been postulated that hampered precision-weighted attentional selection modulates repetition suppression (Friston, 2018). Thus, future studies could investigate the processing of first- and second-order predictions separately in individuals

with developmental dyslexia, with the hypothesis that the latter, but not the former, is impaired in dyslexia.

The location MMN reflects auditory sensory memory operations (Bendixen, Prinz, Horváth, Trujillo-Barreto, & Schröger, 2008; Sussman & Winkler, 2001). Specifically, it measures the brain's ability to establish a memory representation of standard auditory events after just a few presentations (such that location changes generate a location MMN). This allows for the detection of location changes in auditory stimuli. In contrast, the sMMN requires longer periods of learning to establish representations of the sequential statistical structure, which involves knowledge of transitional probabilities (Koelsch et al., 2016; Tsogli et al., 2019). The sMMN is thus a measure of the brain's ability to detect statistical deviants based on the underlying transitional probability structure of the auditory stimuli.

In our experiment, we found that the sMMN was most prominent at anterior frontal electrodes (as illustrated in Fig. 3b). In contrast, the location MMN effect was more broadly distributed across central and frontal areas (as depicted in Fig. 2b). These findings suggest that the neural sources of the sMMN responses are, at least in part, distinct from those of the location MMN, indicating that these responses may reflect different neural operations. Notably, a recent fMRI study on the sMMN has also supported this idea (Tsogli, Skouras, & Koelsch, 2022).

We observed a reduced location MMN in individuals with developmental dyslexia compared with controls. Consistent with our findings, a previous study using task discrimination of sound locations produced with interaural phase differences of 500 Hz sinusoidal 500 ms sounds also found impaired localization performance in dyslexic groups compared to control groups (Amitay et al., 2002). However, contrasting results were reported in another study which found a diminished pitch MMN but an enhanced location MMN in developmental dyslexia only when the stimulus sequences were presented with 50 ms sounds but not with the 100 ms sounds (Kujala et al., 2006). These findings suggest that the stimulus parameters may influence the location MMN in individuals with dyslexia, such as stimulus duration and spectral richness. The reasons for these partly contradictory results remain to be determined.

Both the location MMN and sMMN were preceded by P120 responses. Participants with developmental dyslexia exhibited no significant difference in P120 responses between acoustic deviants and standards compared to controls. The P120 observed in our study appears to be a P1-like component, both in terms of polarity and the fact that it is followed by the N1 and the MMN. As this effect was not hypothesised, it will not be discussed further. However, it is worth noting that previous studies have reported the atypicality in the P1 component in sound processing in dyslexia (Stefanics et al., 2011).

Regarding behavioural results, correct answers were higher than chance levels in the control group. However, there was no significant difference between the control and dyslexic groups in terms of learning effects (Fig. 4 and Appendix E) and the learning effects were weak in both groups. Future studies might use experimental paradigms with stronger statistical learning effects to reveal potential behavioural differences between controls and individuals with developmental dyslexia.

One possible limitation of our study is that the observed increase in the P120 amplitude for statistical deviants across blocks may be attributed to attentional, rather than learning effects since participants performed a behavioural test at the end of each block. Thus, it is possible that participants paid more attention to the tone sequences in the later blocks because they anticipated the test. Another limitation is that the cover task, which requires participants to focus on the stimuli, may have influenced the implicit process of stimulus learning by directing attention towards the stimulus itself. However, participants were only instructed to focus on detecting a specific acoustic property, very high-pitched target-tones, rather than the statistical transition properties of all sounds. The cover task thus minimized the possibility of the participants intentionally focusing their attention on the statistical properties. A third limitation is the relatively small sample size, which could have hampered the statistical power of our results. While we expected a large

effect size based on a power analysis of previous studies on the sMMN (Tsogli et al., 2019; Tsogli et al., 2022), our final sample size was small. We calculated a minimum sample size of 16 based on a within-subject effect rather than a between-subject effect (i.e., group comparison). Nevertheless, we observed a significant group interaction in the location MMN, but the effect size was rather small. Future studies with larger sample sizes and different experimental paradigms (see also below) could identify even more differences between individuals with developmental dyslexia and controls. Finally, a fourth limitation is the relatively small sMMN amplitude observed in controls. Future studies could use experimental paradigms with statistically deviant triplets that are easier to learn and detect, leading to larger sMMN amplitudes. For example, instead of a continuous stream of triplets, triplets could be segmented by physical pauses.

5. Conclusions

Our findings are consistent with evidence showing that statistical learning and the underlying neural correlates may be impaired in individuals with developmental dyslexia, as revealed by an absent sMMN in our study. The observation that the location MMN was also impaired in individuals with developmental dyslexia suggests that their learning of regularities is impaired even when relatively short intervals are sufficient for detecting regularities. Our findings might point to a more general underlying impairment in predictive processing in individuals with developmental dyslexia, leading to the impairment of processing prediction errors across several cognitive domains such as basic auditory processing and statistical learning. These insights may have implications for applications related to the detection and treatment of dyslexia.

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Declaration of Competing Interest

The authors declare no competing financial interests.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.biopsycho.2023.108592](https://doi.org/10.1016/j.biopsycho.2023.108592).

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