



## The role of reading experience in atypical cortical tracking of speech and speech-in-noise in dyslexia



Florian Destoky<sup>a,\*</sup>, Julie Bertels<sup>a,b</sup>, Maxime Niesen<sup>a,c</sup>, Vincent Wens<sup>a,d</sup>, Marc Vander Ghinst<sup>a,c</sup>, Antonin Rovai<sup>a,d</sup>, Nicola Trotta<sup>a,d</sup>, Marie Lallier<sup>e</sup>, Xavier De Tiège<sup>a,d</sup>, Mathieu Bourguignon<sup>a,e,f</sup>

<sup>a</sup> Laboratoire de Neuroanatomie et Neuroimagerie translationnelles, UNI-ULB Neuroscience Institute, Université libre de Bruxelles (ULB), 808 Leenik Street, Brussels 1070, Belgium

<sup>b</sup> Consciousness, Cognition and Computation Group, UNI-ULB Neuroscience Institute, Université libre de Bruxelles (ULB), Brussels, Belgium

<sup>c</sup> Service d'ORL et de Chirurgie Cervico-Faciale, ULB-Hôpital Erasme, Université libre de Bruxelles (ULB), Brussels 1070, Belgium

<sup>d</sup> Department of Functional Neuroimaging, Service of Nuclear Medicine, CUB Hôpital Erasme, Université Libre de Bruxelles (ULB), Brussels, Belgium

<sup>e</sup> BCBL, Basque Center on Cognition, Brain and Language, San Sebastian 20009, Spain

<sup>f</sup> Laboratory of Neurophysiology and Movement Biomechanics, UNI-ULB Neuroscience Institute, Université Libre de Bruxelles (ULB), Brussels, Belgium

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### ABSTRACT

Dyslexia is a frequent developmental disorder in which reading acquisition is delayed and that is usually associated with difficulties understanding speech in noise. At the neuronal level, children with dyslexia were reported to display abnormal cortical tracking of speech (CTS) at phrasal rate. Here, we aimed to determine if abnormal tracking relates to reduced reading experience, and if it is modulated by the severity of dyslexia or the presence of acoustic noise.

We included 26 school-age children with dyslexia, 26 age-matched controls and 26 reading-level matched controls. All were native French speakers. Children's brain activity was recorded with magnetoencephalography while they listened to continuous speech in noiseless and multiple noise conditions. CTS values were compared between groups, conditions and hemispheres, and also within groups, between children with mild and severe dyslexia.

Syllabic CTS was significantly reduced in the right superior temporal gyrus in children with dyslexia compared with controls matched for age but not for reading level. Severe dyslexia was characterized by lower rapid automatized naming (RAN) abilities compared with mild dyslexia, and phrasal CTS lateralized to the right hemisphere in children with mild dyslexia and all control groups but not in children with severe dyslexia. Finally, an alteration in phrasal CTS was uncovered in children with dyslexia compared with age-matched controls in babble noise conditions but not in other less challenging listening conditions (non-speech noise or noiseless conditions); no such effect was seen in comparison with reading-level matched controls.

Overall, our results confirmed the finding of altered neuronal basis of speech perception in noiseless and babble noise conditions in dyslexia compared with age-matched peers. However, the absence of alteration in comparison with reading-level matched controls demonstrates that such alterations are associated with reduced reading level, suggesting they are merely driven by reduced reading experience rather than a cause of dyslexia. Finally, our result of altered hemispheric lateralization of phrasal CTS in relation with altered RAN abilities in severe dyslexia is in line with a temporal sampling deficit of speech at phrasal rate in dyslexia.

### 1. Introduction

Dyslexia is a developmental disorder in which reading acquisition is specifically delayed despite normal intelligence, peripheral vision and audition, appropriate schooling, and the absence of psychiatric disorders (Lyon et al., 2003). In most children, dyslexia would stem from a deficit in phonological awareness (Goswami, 2015; Saksida et al.,

2016). Phonological awareness refers to the ability to identify and use the elementary sound units of spoken language (i.e., phonological information) to process oral and written language (Wagner and Torgesen, 1987). Accordingly, to better understand the neural underpinnings of dyslexia, many studies have sought and found traces of altered neural activity in tasks involving phonological awareness (Bonte et al., 2007; Hämäläinen et al., 2015; Leppänen et al., 2012; Paz-Alonso et al., 2018). However, some interventional studies did not find any specific benefit for children at high risk of dyslexia of training phonological awareness (Krashen, 1999; Olson et al., 1997; Pape-Neumann et al., 2015). This negative outcome has led some researchers to suggest that phonological

\* Corresponding author.

E-mail address: [florian.destoky@ulb.be](mailto:florian.destoky@ulb.be) (F. Destoky).

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awareness may correlate with upcoming reading abilities but would not determine them (Catts and Adlof, 2011).

According to the temporal sampling framework for developmental dyslexia (Goswami, 2011), abnormal temporal sampling of speech by auditory cortical oscillations would cause a deficit in both reading acquisition and phonological awareness. A tangible manifestation of the abnormal sampling would be an abnormal alignment of cortical oscillations to the different linguistic structures of speech, which can be derived from electrophysiological recordings. Indeed, when listening to connected speech, human auditory cortical activity tracks the fluctuations of speech temporal envelope at frequencies matching the occurrence rate of words/phrases/sentences (below 2 Hz; the phrasal rate hereafter) and syllables (2–8 Hz; the syllabic rate hereafter) (Ahissar et al., 2001; Bourguignon et al., 2013; Destoky et al., 2019; Gross et al., 2013; Luo and Poeppel, 2007; Meyer et al., 2017; Meyer and Gumbert, 2018; Molinaro et al., 2016; Vander Ghinst et al., 2019). Such cortical tracking of speech (CTS) is thought to be essential for speech comprehension (Ahissar et al., 2001; Ding et al., 2016; Luo and Poeppel, 2007; Meyer et al., 2017; Peelle et al., 2013; Riecke et al., 2018; Vanthornhout et al., 2018). CTS would subserve the segmentation or parsing of incoming speech for further speech recognition (Ahissar et al., 2001; Ding et al., 2016; Ding and Simon, 2014; Gross et al., 2013; Meyer et al., 2017). In line with the temporal sampling deficit hypothesis, CTS at low frequencies was found to be altered in dyslexia (Di Liberto et al., 2018; Molinaro et al., 2016; Power et al., 2016). Indeed, compared with typical readers of the same age, children with dyslexia show reduced phrasal CTS in both the right auditory cortex and the left inferior frontal gyrus, and reduced feedforward coupling between these two brain areas (Molinaro et al., 2016).

However, a recent replication study did not find any CTS alteration in dyslexia (Lizarazu et al., 2021). There are several reasons that may explain the discrepancy with the aforementioned studies. The degree of CTS alteration in dyslexia may indeed depend on (i) the language, (ii) the difficulty of the listening task, and (iii) the severity of the reading deficit present in the selected sample of dyslexic readers. Concerning the language, altered CTS was found in English and Spanish dyslexic child readers (Di Liberto et al., 2018; Molinaro et al., 2016; Power et al., 2016), but not in French (Lizarazu et al., 2021). However, in French, the lexical stress is totally predictable as it always falls on the last syllable. In contrast, lexical stress in Spanish and English changes depending on the word itself and is used to differentiate between words made of the exact same sequence of phonemes. The perfect predictability of lexical stress in French leads to a “stress deafness” in native French speakers (Dupoux et al., 1997). Because of this “stress deafness” in French, the atypical right-hemisphere neural oscillatory sampling for the low frequencies seen in English and Spanish dyslexic readers might be less severe in French dyslexic readers (Lallier et al., 2017). Concerning the difficulty of the listening task, all studies assessing CTS in dyslexia were conducted in noiseless conditions. Yet, the speech perception deficit in dyslexia is exacerbated in adverse listening conditions (Lachmann and Weis, 2018; Ziegler et al., 2009). This speech in noise (SiN) perception deficit is not due to poor spectrotemporal, low-level auditory resolution but rather to inaccurate speech representation (Lachmann and Weis, 2018), especially when the background noise is composed of speech (Calcutt et al., 2015; Lachmann and Weis, 2018; Ziegler et al., 2009). Hence, the CTS alteration in dyslexia should be most salient in SiN conditions, even for French speakers. Finally, concerning the severity of the reading deficit of the included children with dyslexia, the phonological deficit is more commonly seen in severe than mild dyslexia (Saksida et al., 2016). Also along this line, reading abilities correlate with some aspects of CTS in noisy conditions (Destoky et al., 2020). Yet, none of the previous studies assessing CTS in dyslexia (Di Liberto et al., 2018; Lizarazu et al., 2021; Molinaro et al., 2016; Power et al., 2016) considered the possibility that CTS is altered only in the most severe form of dyslexia. Also, two of the four

studies reporting a CTS deficit in dyslexia (Di Liberto et al., 2018; Leong and Goswami, 2014; Molinaro et al., 2016; Power et al., 2016) did not include a control group matched for reading level (Leong and Goswami, 2014; Molinaro et al., 2016). However, it is well established that reading acquisition itself influences cognitive and cerebral functions (Carreiras et al., 2009; Goswami, 2015). One way to attempt to control the effect of reading experience, and get novel insights into the causal link between CTS deficit and dyslexia, is to compare children with dyslexia with controls matched for the reading level in addition to the classical comparison with age-matched controls.

This study therefore aimed at determining if and how altered CTS is associated with dyslexia. As most innovative aspects, we (i) included comparison with both controls matched for age and younger controls matched for the reading level, (ii) assessed the impact of the severity of the reading deficit on uncovered CTS alterations, and (iii) included challenging listening conditions to exacerbate potential CTS alterations in native French readers. This design was selected to get insight into the three following research questions: (i) Is CTS altered in French speaking children with dyslexia, and if so, is this alteration associated with reduced reading experience or with dyslexia itself? (ii) Is such alteration dependent on the severity of dyslexia? And (iii) is CTS alteration in dyslexia more salient in challenging noisy conditions, possibly depending on the severity of the reading deficit?

## 2. Methods

This study focuses on non-overlapping aspects of the data previously documented in Destoky et al. (2020). That former study examined the link between neural markers of brain ability to deal with SiN and reading abilities. The results in Destoky et al. (2020) were focused on a contrast between CTS in noise vs. noiseless conditions, thereby disregarding potential effects in noiseless conditions. Moreover, comparisons between children with and without dyslexia were focused on effects highlighted in typical readers, with the risk of overlooking alterations specific to dyslexia. The present study focuses on uncontrasted CTS values to characterize possible alterations in CTS in noiseless condition, and determine if such alterations are affected by noise or severity of the reading deficit.

### 2.1. Participants

Seventy-eight children enrolled in elementary school were included in this study: 26 children with a formal diagnosis of dyslexia (*Dys*; mean  $\pm$  SD age,  $10.2 \pm 1.1$  years; 17 females), 26 typical readers matched for age (*Ctrl-Age*;  $10.0 \pm 1.0$  years; 13 females), and 26 younger children matched for reading level (*Ctrl-Read*;  $7.8 \pm 0.6$ ; 11 females). Sample size was selected to be slightly above that in previous studies reporting significant differences in CTS between individuals with dyslexia and controls (Di Liberto et al., 2018; Lizarazu et al., 2021; Molinaro et al., 2016; Power et al., 2016). Children with dyslexia had received a diagnosis of dyslexia, which implies that they had (at the time of diagnosis) at least 2 years of delay in reading acquisition that could not be explained by low IQ or social or sensory disorders. We included only children without attention deficit, without psychiatric or neurological disorder, and with normal peripheral hearing. Each participant came to the lab once for an assessment of their reading abilities, related cognitive abilities and peripheral audition, and once for a structural and functional brain assessment. Both assessments were performed on the same day for most of the participants, and less than two weeks apart otherwise. A previous study of our group has already reported on this sample, and on the outcome of the comprehensive neuropsychological evaluation they underwent (Destoky et al., 2020).

Table 1 presents the scores on which participants were matched: age, IQ, socioeconomic status, and reading abilities, the latter being assessed by reading speed on lists of regular words, irregular words and pseu-

**Table 1**

Mean and standard deviation of behavioral scores in each reading group of 26 children and comparisons (*t*-tests) between groups. The number of degrees of freedom was 50 for all comparisons except for those involving auditory attention (TAP) scores (49 for dyslexic readers vs. age-matched controls; 38 for dyslexic readers vs. reading-level-matched controls) and socioeconomic status for which some data were missing (49 for dyslexic readers vs. age-matched controls; 47 for dyslexic readers vs. reading-level-matched controls). IQ, intelligence quotient; SD, standard deviation. RAN, rapid automatized naming.

	Dyslexic readers		Age-matched control		Reading-level-matched control		Dyslexic readers compared with controls			
	Mean	SD	Mean	SD	Mean	SD	age <i>p</i>	<i>t</i>	reading level <i>p</i>	<i>t</i>
Chronological age	10.2	1.08	9.97	1.01	7.76	0.60	0.36	0.93	<0.0001	10.3
non-verbal iq	111	11	114	10	112	9	0.30	-1.04	0.784	-0.28
socioeconomic status	6.12	2.44	6.96	1.45	6.96	2.47	0.14	-1.50	0.17	-1.40
Text (Alouette) reading accuracy	89.0	5.7	96.2	2.1	89.0	6.46	<0.0001	-6.07	0.988	0.01
Text (Alouette) reading speed	141	61	292	91	138	64	<0.0001	-7.04	0.867	0.17
Irregular words reading [words/s]	0.54	0.33	1.16	0.44	0.40	0.35	<0.0001	-5.82	0.15	1.47
Regular words reading [words/s]	0.73	0.41	1.35	0.41	0.61	0.35	<0.0001	-5.51	0.29	1.06
Pseudo-words reading [words/s]	0.42	0.24	0.78	0.30	0.39	0.21	<0.0001	-4.88	0.61	0.50
Phoneme suppression	7.92	2.15	9.04	1.75	8.42	1.27	0.046	-2.05	0.31	-1.02
Phoneme fusion	7.73	1.59	9.31	0.97	8.92	1.16	<0.0001	-4.32	0.003	-3.08
Forward digit span	5.08	0.84	5.8	0.69	5.15	0.78	0.001	-3.41	0.73	-0.34
Backward digit span	3.69	0.79	4.5	1.33	3.38	0.75	0.011	-2.66	0.156	1.44
RAN time (s)	24.38	7.84	20.11	3.02	30.6	7.51	0.013	2.59	0.005	-2.91
TAP mean response time (ms)	627	99	613	75.4	667	93.4	0.59	0.53	0.07	-1.86
TAP SD response time (ms)	140	45	129	30.3	171	46.7	0.33	0.98	0.02	-2.36
TAP correct responses	15.58	0.58	15.7	0.68	15.3	1.07	0.42	-0.81	0.11	1.65
TAP false responses	2.15	2.26	0.84	1.28	1.21	0.97	0.014	2.54	0.89	0.13

dowords (ODEDYS-2 (Jacquier-Roux et al., 2002)), and by reading speed and accuracy on a connected text (Alouette-R test (Lefavrais, 2005)) Table 1. shows that all groups had similar IQ and socioeconomic status, that dyslexic readers compared with age-matched controls had about the same age and lower reading scores, and that dyslexic readers compared with reading-level-matched controls were older and had similar reading scores. A previous analysis of the reading scores also revealed that our dyslexic readers had a rather homogenous reading profile, characterized by similar reading difficulties in the two reading routes (Destoky et al., 2020). Compared to normative data for the Alouette-R test (Lefavrais, 2005), 62% of the *Dys* showed a deficit (score below the percentile 10) in reading speed and only 38% showed a deficit in reading accuracy, highlighting the effectiveness of the remediation that took place in the time between diagnosis and inclusion in the study. These figures were much lower in *Ctrl-Age* (speed, 3.8%; accuracy, 0%) and *Ctrl-Read* (speed, 7.7%; accuracy, 19%), as expected of control groups.

Table 1 also presents the results for other behavioral scores. Phonological awareness was assessed with the initial phoneme suppression and initial phoneme fusion tasks of the ODEDYS-2 (Jacquier-Roux et al., 2002). Rapid automatized naming (RAN) abilities were assessed with the RAN task of the ODEDYS-2 (Jacquier-Roux et al., 2002). RAN is thought to correlate with—and predict upcoming—reading abilities because it evaluates, among other things, the serial processing, the oral production (Georgiou et al., 2013) and lexical access (Georgiou et al., 2018) which are profoundly involved in reading abilities. Verbal short term memory and working memory were assessed with the forward and backward digit repetition tasks of the ODEDYS-2 (Jacquier-Roux et al., 2002). Finally, auditory attentional abilities were assessed with the TAP auditory attentional subtest (Zimmermann and Fimm, 2002).

All children were native French speakers, reported being right-handed, had normal hearing according to pure-tone audiometry (normal hearing thresholds between 0 and 25 dB HL for 250, 500, 1000, 2000, 4000, and 8000 Hz) and normal SiN perception as revealed by a SiN test (Lafon 30) from a French language central auditory battery (Demanez et al., 2003).

This study was approved by the local ethics committee (Comité d’Ethique Hospitalo-Facultaire Erasme-ULB, 021/406, Brussels, Belgium; approval number: P2017/081) and conducted according to the principles expressed in the Declaration of Helsinki. Participants were recruited mainly from local schools through flier advertisements or from

social networks. Participants and their legal representatives signed a written informed consent before participation. Participants were compensated with a gift card worth 50 euros.

## 2.2. Reading subgroups

As a preliminary step to test our working hypothesis that CTS is modulated by the severity of the reading deficit in dyslexia, we partitioned the *Dys* group into two subgroups maximally differing on their reading abilities. To do so, the 5 reading scores (see Table 1) were first corrected for age, time spent at school and IQ as done in our previous study (Destoky et al., 2020), and further standardized. We then used the k-means clustering algorithm implemented in MATLAB to identify 2 subgroups. Since all the reading scores in one subgroup were higher than those in the second subgroup, we refer to them as the mild (*Dys-Mild*;  $n = 16$ ; 11 females; mean  $\pm$  SD age,  $10.4 \pm 1.0$  years) and severe subgroups (*Dys-Severe*;  $n = 10$ ; 6 females;  $10.0 \pm 1.2$  years).

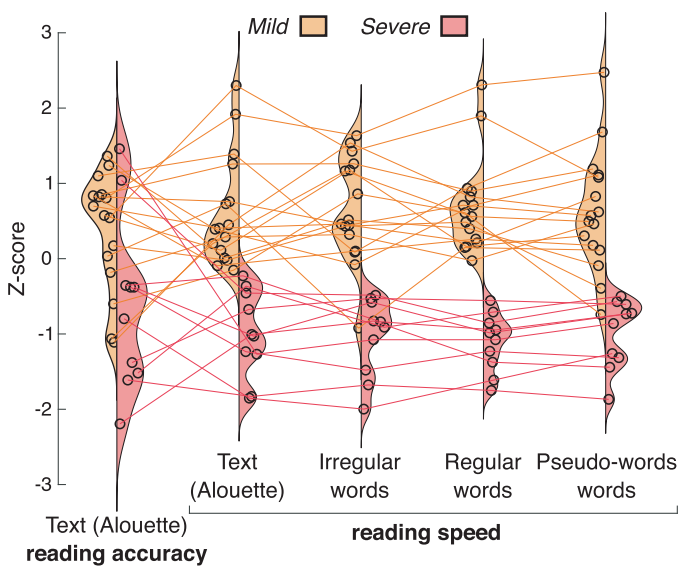
Fig. 1 presents the dispersion of the reading scores within and across subgroups. Although the subgroups were not so well separated on the reading accuracy score, they were overall clearly separated on the reading speed scores. Only two individual values from different children of the *Dys-Mild* subgroup (one for irregular word reading speed and one pseudoword reading speed) fell below the maximum score of the *Dys-Severe* subgroup. The two concerned *Dys-Mild* children had their 3 other reading speed scores in the bulk of the distribution for *Dys-Mild*. Overall, these observations made on reading scores indicate that children in the *Dys-Severe* subgroup suffered from limited reading speed (but not necessarily accuracy) compared with those in the *Dys-Mild* subgroup. This view is also supported by the comparison of the Alouette-R test scores with normative data: a deficit in reading speed (score below percentile 10) was seen in a substantially larger proportion of *Dys-Severe* (90%) than *Dys-Mild* (44%), while a deficit in reading accuracy was seen in a more comparable proportions of *Dys-Severe* (50%) and *Dys-Mild* (31%).

Table 2 presents the reading scores and other behavioral scores for the two *Dys* subgroups and their comparisons. Obviously, the 2 subgroups displayed significant differences in reading skills. Most importantly, they did not differ significantly in age or socioeconomic level. They differed on none of the other behavioral scores (all  $p > 0.29$ ), including scores of phonological awareness or verbal short term memory and working memory, but differed largely on the rapid automatized

**Table 2**

Mean of the standardized reading scores (i.e., z-scores) and corrected behavioral scores for the *Dys-Mild* and *Dys-Severe* subgroups and significance of their comparisons. Scores were standardized within the *Dys* group.

	<i>Dys-Mild</i> (n = 16)	<i>Dys-Severe</i> (n = 10)	p
Chronological age	10.38	10.01	0.40
non-verbal iq	111.71	110	0.71
socioeconomic status	6.07	6.20	0.90
Text (Alouette) reading accuracy	0.36	-0.58	<b>0.015</b>
Text (Alouette) reading speed	0.60	-0.96	<b>&lt; 0.0001</b>
Irregular word reading speed	0.62	-1.00	<b>&lt; 0.0001</b>
Regular word reading speed	0.67	-1.06	<b>&lt; 0.0001</b>
Pseudo-word reading speed	0.59	-0.95	<b>&lt; 0.0001</b>
Phoneme suppression	8.12	7.61	0.57
Phoneme fusion	7.87	7.51	0.59
Forward digit span	5.1	5.05	0.88
Backward digit span	3.7	3.67	0.91
RAN time (s)	20.85	30.04	<b>0.002</b>
TAP mean response time (ms)	627.55	625.02	0.95
TAP SD response time (ms)	132.11	151.82	0.29
TAP correct responses	15.6	15.54	0.78
TAP false responses	2.22	2.05	0.86



**Fig. 1.** Dispersion of normalized reading scores within and across subgroups of dyslexia. Circles indicate individual reading scores. Colored lines connect the five scores of each individual. Shaded areas provide a representation of score distribution for mild (left from middle lines in yellow-orange) and severe (right from middle lines in red-orange) subgroups of dyslexia.

naming (RAN) score ( $t_{24} = -3.5, p = 0.002, d = 0.71$ ). This is well in line with studies showing that RAN abilities remain central for reading acquisition, after reading initiation (Manis et al., 2000; Wimmer et al., 2000, 1998).

The same procedure was used to partition each of the two control groups. The *Ctrl-Age* group was split into one subgroup with high reading scores (*Ctrl-Age-High*;  $n = 12$ ; 5 females;  $10.2 \pm 1.1$  years) and one with low reading scores (*Ctrl-Age-Low*;  $n = 14$ ; 8 females;  $9.8 \pm 0.9$  years), which again did not differ on age ( $t_{24} = 0.96, p = 0.34, d = 0.20$ ) or socioeconomic level ( $t_{24} = 1.83, p = 0.08, d = 0.37$ ). Likewise, the *Ctrl-Read* group was split into a subgroup with high reading scores (*Ctrl-Read-High*;  $n = 12$ ; 6 females;  $7.82 \pm 0.56$ ) and a subgroup with low reading scores (*Ctrl-Read-Low*;  $n = 14$ ; 7 females;  $7.71 \pm 0.64$ ) not differing on age ( $t_{24} = 0.45, p = 0.66, d = 0.092$ ) or socioeconomic level ( $t_{22} = 0.60, p = 0.55, d = 0.13$ ). Importantly, three sets of comparisons demonstrated that each of the control subgroups remained a good control for its corresponding *Dys* subgroup: (i) there was no significant difference in age

between *Dys-Mild* and *Ctrl-Age-High* ( $t_{26} = 0.51, p = 0.61, d = 0.10$ ) nor between *Dys-Severe* and *Ctrl-Age-Low* ( $t_{26} = 0.50, p = 0.62, d = 0.098$ ), (ii) there was no significant difference in reading scores between *Dys-Mild* and *Ctrl-Read-High* ( $p > 0.17$  in all 5 comparisons) nor between the *Dys-Severe* and *Ctrl-Read-Low* ( $p > 0.21$  in all 5 comparisons), and (iii) there was no significant difference in socioeconomic level between *Dys-Mild* and the two control groups with high reading scores (*Ctrl-Age-High*,  $t_{26} = -1.89, p = 0.070, d = 0.37$ ; *Ctrl-Read-High*,  $t_{26} = -1.67, p = 0.11, d = 0.33$ ) nor between *Dys-Severe* and the two control groups with low reading scores (*Ctrl-Age-Low*,  $t_{22} = -0.24, p = 0.82, d = 0.051$ ; *Ctrl-Read-Low*,  $t_{22} = -0.22, p = 0.83, d = 0.047$ ).

Supplementary Fig. 1 presents the dispersion of the reading scores within and across subgroups of controls. The separation between *Ctrl-Read-High* and *Ctrl-Read-Low* was highly similar to that between *Dys-Severe* and *Dys-Mild*; that between *Ctrl-Age-High* and *Ctrl-Age-Low* was less clear. Most noticeably, both subgroups of *Ctrl-Age* had similar reading accuracy on the Alouette-R test ( $t_{24} = 0.51, p = 0.61, d = 0.10$ ), and were well separated on the reading speed for irregular and regular words but not for pseudo-words, hinting at a separation mainly based on the maturation of the lexical route (Coltheart et al., 1993, 2001). In any case, the partitioning of the control groups was conducted more for the practical purpose of having proper controls for *Dys-Severe* and *Dys-Mild* in our analyses than to highlight potential heterogeneity in reading abilities in typical readers.

### 2.3. Stimuli

**Fig. 2** illustrates the time-course of the video stimuli, which were exactly the same as in a previous study from our group (for more details, see Destoky et al., 2020). Video stimuli were derived from 12 audiovisual recordings of four native French speaking narrators (two females, three recordings per narrator) telling a story for approximately 6 min (mean  $\pm$  SD,  $6.0 \pm 0.8$  min). In each video, the first 5 s were kept unaltered to enable children to unambiguously identify the narrator's voice and face to which they were requested to attend. The remainder of the video was divided into 10 consecutive blocks of equal size that were assigned to nine conditions. Two blocks were assigned to the noiseless condition, in which the audio track was kept unaltered but the video was replaced by static pictures illustrating the story (mean  $\pm$  SD picture presentation time across all videos,  $27.7 \pm 10.8$  s). The remaining eight blocks were assigned to eight conditions in which the original sound was mixed with a background noise at 3 dB signal-to-noise ratio. There were four different types of noise, and each type of noise was presented once with the original video, thereby giving access to visual speech in-



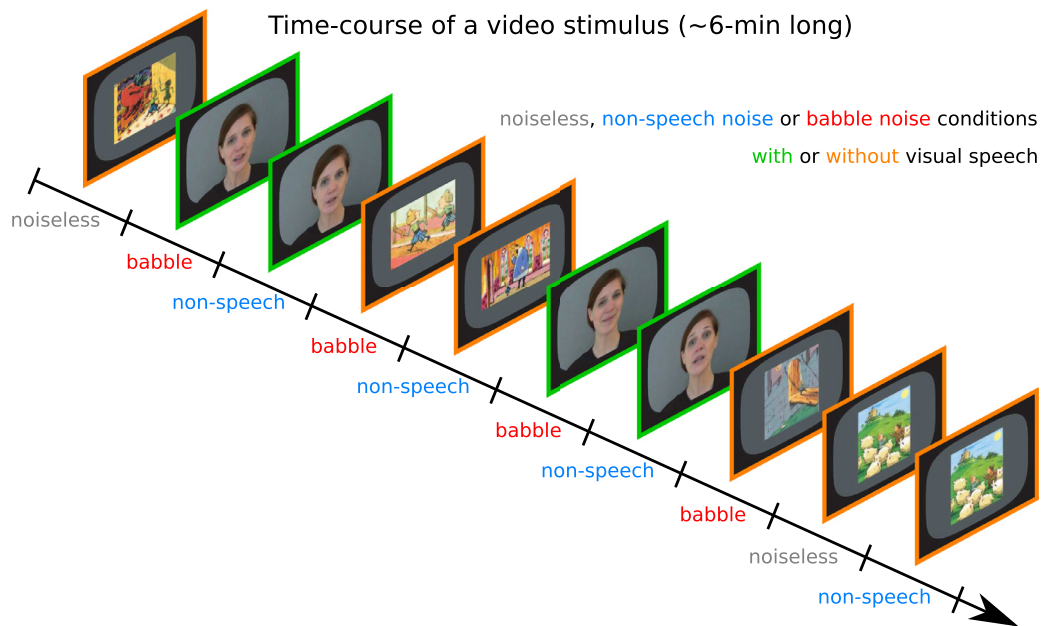


Fig. 2. Illustration of the time-course of a video stimulus.

formation, and once with the static pictures illustrating the story and hence without visual speech information. Here, as the aim was to use the most challenging listening condition, we report only on the data in which visual speech information was absent since it is already well documented that phrasal and syllabic CTS in noise is boosted when visual speech information is available (Destoky et al., 2020; Golumbic et al., 2013; Park et al., 2018, 2016). The different types of noise differed in the degree of energetic and informational interference they introduced (Pollack, 1975). Nevertheless, in our previous study on the same data (Destoky et al., 2020), we observed that the degree of energetic masking had little impact on CTS values. For this reason, we pooled the data and considered only the distinction between non-speech (non-informational) noises and babble (informational) noises. The non-speech noises were a white noise high-pass filtered at 10,000 Hz or a noise spectro-temporally matched to the narrator's voice. The babble noises were five-talker cocktail party noises of the same gender as the narrator or of the opposite gender. Individual noise components were obtained from a French audiobook database (<http://www.litteratureaudio.com>), normalized, and mixed linearly. The assignment of conditions to blocks was random. Ensuing videos were grouped into three disjoint sets featuring one video per narrator (total set duration: 23.0, 24.3, 24.65 min), and there were four versions of each set differing in condition random ordering.

#### 2.4. Experimental paradigm

Participants laid on a bed with their head inside a magnetoencephalography (MEG) helmet. Their brain activity was recorded while they were attending four videos of a randomly selected set presented in a random order (separate recording for each video), and finally while they were at rest (eyes opened, fixation cross) for 5 min. They were instructed to watch the videos attentively, listen to the narrators' voice while ignoring the interfering noise, and remain as still as possible. After each video, they were asked 10 yes/no simple comprehension questions. Videos were projected onto a back-projection screen placed vertically, approximately 120 cm away from the MEG helmet. The inner dimensions of the black frame were 35.2 cm (horizontal) and 28.8 cm (vertical), and the narrator's face spanned approximately 15 cm (horizontal) and approximately 20 cm (vertical). Participants could see the screen through a mirror placed above their head. In total, the optical path from the screen to participants' eyes was approximately 150 cm.

Sounds were delivered at 60 dB (measured at ear level) through a MEG-compatible, front-facing, flat-panel loudspeaker (Panphonics Oy, Espoo, Finland) placed approximately 1 m behind the screen.

#### 2.5. Data acquisition

During the experimental conditions, participants' brain activity was recorded with MEG at the CUB Hôpital Erasme (Brussels, Belgium). Neuro-magnetic signals were recorded with a whole-scalp-covering MEG system (Triux, MEGIN, Croton Healthcare, Helsinki, Finland) placed in a lightweight, magnetically shielded room (Maxshield, MEGIN, Croton Healthcare, Helsinki, Finland), the characteristics of which have been described elsewhere (De Tiège et al., 2008). The sensor array of the MEG system comprised 306 sensors arranged in 102 triplets of one magnetometer and two orthogonal planar gradiometers. Magnetometers measure the radial component of the magnetic field, whereas planar gradiometers measure its spatial derivative in the tangential directions. MEG signals were band-pass filtered at 0.1–330 Hz and sampled at 1000 Hz.

We used four head-position indicator coils to monitor the subjects' head position during the experimentation. Before the MEG session, we digitized the location of these coils and at least 300 head-surface points (on scalp, nose, and face) with respect to anatomical fiducials with an electromagnetic tracker (Fastrack, Polhemus).

Finally, subjects' high-resolution 3D T1-weighted cerebral images were acquired with a 3T hybrid PET-MR scanner (SIGNA, GE Healthcare, Milwaukee, Wisconsin, USA) after the MEG session.

#### 2.6. Data preprocessing

Continuous MEG data were first preprocessed off-line using the temporal signal space separation method implemented in MaxFilter software (MaxFilter, MEGIN; correlation limit 0.9, segment length 20 s) to suppress external interferences and to correct for head movements (Taulu et al., 2005; Taulu and Simola, 2006). To further suppress physiological artifacts, 30 independent components were evaluated from the data band-pass filtered at 0.1–25 Hz and reduced to a rank of 30 with principal component analysis. Independent components corresponding to heartbeat, eye-blink, and eye-movement artifacts were identified, and corresponding MEG signals reconstructed by means of the mixing matrix

were subtracted from the full-rank data. Of note, the investigator who identified the components to reject was blind to the group membership of the participant. An ANOVA revealed no significant difference between groups ( $F_{2,50} = 1.03, p = 0.36$ ) in the number of subtracted independent components (mean  $\pm$  SD; *Dys*,  $3.3 \pm 0.6$ ; *Ctrl-Age*,  $3.6 \pm 0.9$ ; *Ctrl-Read*,  $3.3 \pm 0.6$ ). Finally, time points at timings 1 s around remaining artifacts were set to bad. Data were considered contaminated by artifacts when MEG amplitude exceeded 5 pT in at least one magnetometer or 1 pT/cm in at least one gradiometer.

We extracted the temporal envelope of the attended speech (i.e., narrators' voice) using a state-of-the-art approach (Biesmans et al., 2017). Briefly, audio signals were band-pass filtered using a gammatone filter bank (15 filters centered on logarithmically spaced frequencies from 150 Hz to 4000 Hz), and sub-band envelopes were computed using Hilbert transform, elevated to the power 0.6, and averaged across bands.

## 2.7. CTS estimated globally for the left and right hemispheres

For each condition and participant, a global value of cortical tracking of the attended speech was evaluated for all left-hemisphere sensors at once and for all right-hemisphere sensors at once. Using the mTRF toolbox (Crosse et al., 2016), we trained a decoder on MEG data to reconstruct speech temporal envelope and estimated its Pearson correlation with real speech temporal envelope. This correlation is often referred to as the reconstruction accuracy, and it provides a global measure of CTS. In brief, electrophysiological data were band-pass filtered at 0.2–1.5 Hz (phrasal rate) or 2–8 Hz (syllabic rate) and a decoder for speech temporal envelope was built based on MEG data from –500 to 1000 ms (phrasal) or from 0 to 250 ms (syllabic) with respect to speech temporal envelope. The decoder used to estimate reconstruction accuracy in a given condition was built based on the data in all the other conditions, using 10-fold cross-validation to select the optimal regularization applied to limit the norm of the derivative of the reconstructed speech temporal envelope (Crosse et al., 2016). For a full description of the procedure, see our previous study (Destoky et al., 2020).

## 2.8. CTS estimated in the source space

As a preliminary step to estimate brain maps of CTS, MEG signals were projected into the source space. For that, MEG and MRI coordinate systems were co-registered using the 3 anatomical fiducial points for initial estimation and the head-surface points for further manual refinement. When a participant's MRI was missing ( $n = 24$ ; 5 *Dys*, 9 *Ctrl-Age* and 10 *Ctrl-Read*), we used that of another participant of roughly the same age, which we linearly deformed to best match head-surface points using the CPD toolbox (Myronenko and Song, 2010) embedded in Field-Trip (Donders Institute for Brain Cognition and Behavior, Nijmegen, The Netherlands, RRID:SCR\_004849; (Oostenveld et al., 2011)). The individual MRIs were segmented using the Freesurfer software (Martinos Center for Biomedical Imaging, Boston, MA, RRID:SCR\_001847; (Reuter et al., 2012)). Then, a non-linear transformation from individual MRIs to the MNI brain was computed using the spatial normalization algorithm implemented in Statistical Parametric Mapping (SPM8, Wellcome Department of Cognitive Neurology, London, UK, RRID:SCR\_007037; (Ashburner et al., 1997; Ashburner and Friston, 1999)). This transformation was used to map a homogeneous 5 mm grid sampling the MNI brain volume onto individual brain volumes. For each subject and grid point, the MEG forward model corresponding to three orthogonal current dipoles was computed using the one-layer Boundary Element Method implemented in the MNE software suite (Martinos centre for Biomedical Imaging, Boston, MA, RRID:SCR\_005972; (Gramfort et al., 2014)). The forward model was then reduced to its two first principal components. This procedure is justified by the insensitivity of MEG to currents radial to the skull, and hence, this dimension reduction leads to considering only the tangential sources. Source signals were then re-

constructed with Minimum-Norm Estimates inverse solution (Dale and Sereno, 1993).

We followed a similar approach to that used at the sensor level to estimate source-level CTS. For each grid point, we trained a decoder on the two-dimensional source time-series to reconstruct speech temporal envelope. Again, the decoder was trained on the data from all but one condition, and used to estimate CTS in the left-out condition. To speed up computations, the training was performed without cross-validation, with the ridge value retained in a sensor-space analysis run on all gradiometer sensors at once. This procedure yielded a source map of CTS for each participant, condition, and frequency range of interest; and because the source space was defined on the MNI brain, all CTS maps were inherently coregistered with the MNI brain. Hence, group-averaged maps were simply produced as the mean of individual maps within groups, conditions and frequency ranges of interest.

We further identified the coordinates of local maxima in group-averaged CTS maps. Such local maxima of CTS are sets of contiguous voxels displaying higher CTS values than all neighboring voxels (Bourguignon et al., 2012). We only report statistically significant local maxima of CTS, disregarding the extents of these clusters. Indeed, cluster extent is hardly interpretable in view of the inherent smoothness of MEG source reconstruction (Bourguignon et al., 2018; Hämäläinen and Ilmoniemi, 1994; Wens et al., 2015).

We also estimated the contrast of source maps between the different groups and identified the coordinates of local maxima therein.

## 2.9. Statistical analyses

### 2.9.1. Effect of hemisphere, group, subgroup, and noise on CTS

To test whether CTS is altered in dyslexia in comparison with controls in age or reading level, potentially in different ways in the left-versus right hemisphere (first research question), we ran a repeated measures ANOVA on CTS values in the noiseless condition with factors hemisphere and group (i.e., *Dys*, *Ctrl-Age* and *Ctrl-Read*), separately for phrasal and syllabic CTS.

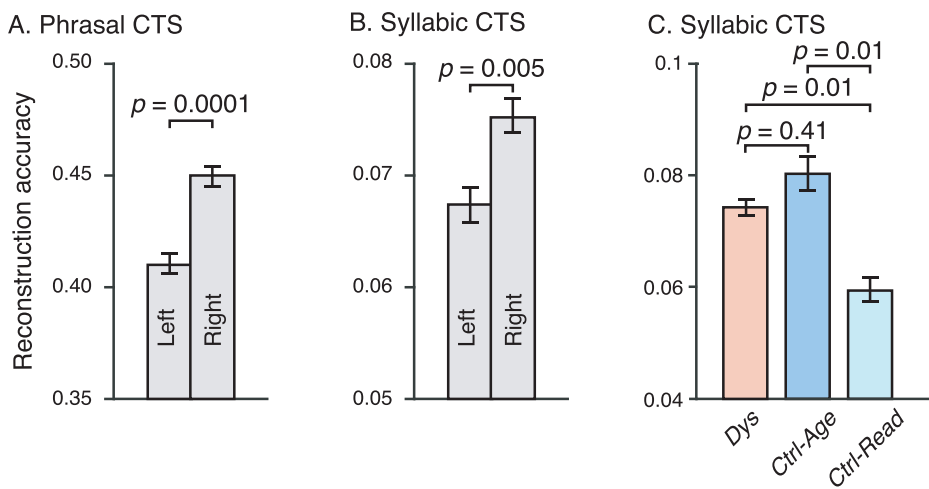
To test whether CTS is affected by the severity of the reading deficit in dyslexia (second research question), we ran the same analysis as above, but only on the data for *Dys*, with factors hemisphere and subgroup (*Mild* vs. *Severe*), separately for phrasal and syllabic CTS.

Finally, to test whether CTS alteration in dyslexia is most visible in SiN conditions (third research question), possibly depending on the severity of the reading deficit and on the hemisphere, we assessed with a linear mixed-effects analysis implemented in R (R Core Team, 2018) and lme4 (Bates et al., 2015) the effect of hemisphere, group, subgroup (*Mild/High* vs. *Severe/Low*) and noise (noiseless, non-speech, babble) on CTS values, separately for phrasal and syllabic CTS. An ANOVA could not be used here, because it cannot accommodate the clustering of participants in both groups and subgroups. We followed a step-up approach to iteratively identify all statistically significant effects. In brief, we started with a null model that included only a different random intercept for each subject. The model was iteratively compared with models incremented with simple fixed effects added one by one. At every step, the most significant fixed effect was retained until the addition of the remaining effects did not improve the model any further ( $p > 0.05$ ). The same procedure was then repeated to refine the ensuing model with the interactions of the simple fixed effects of order 2, 3 and then 4.

In all analyses, post-hoc t-tests were conducted to clarify the effects uncovered with the ANOVAs or linear mixed-effects analysis.

### 2.9.2. Significance of local maxima of CTS

The statistical significance of CTS local maxima observed in group-averaged maps for each group (i.e., *Dys*, *Ctrl-Age* and *Ctrl-Read*) and frequency range of interest (i.e., phrasal and syllabic rates) was assessed with a non-parametric permutation test that intrinsically corrects for multiple spatial comparisons (Nichols and Holmes, 2002). First, participant and group-averaged null maps of CTS were computed with MEG



**Fig. 3.** Phrasal (A) or syllabic (B,C) CTS estimated with reconstruction accuracy in each hemisphere (A,B) or group (C). Bars and vertical lines indicate mean  $\pm$  SEM values.  $P$ -values are provided for comparisons between hemispheres or groups.

and voice signals in each story rotated in time by about half of story length (i.e., the first and second halves were swapped, thereby destroying genuine coupling but preserving spectral properties). The exact temporal rotation applied was chosen to match a pause in speech to enforce continuity. Group-averaged difference maps were obtained by subtracting *genuine* and *null* group-averaged CTS maps. Under the null hypothesis that CTS maps are the same whatever the experimental condition, the labeling *genuine* or *null* are exchangeable prior to difference map computation (Nichols and Holmes, 2002). To reject this hypothesis and to compute a significance level for the correctly labeled difference map, the sample distribution of the maximum of the difference map's absolute value within the entire brain was computed from a subset of 1000 permutations. The threshold at  $p < 0.05$  was computed as the 95th percentile of the sample distribution (Nichols and Holmes, 2002). All supra-threshold local maxima of CTS were interpreted as indicative of brain regions showing statistically significant CTS and will be referred to as sources of CTS.

Permutation tests can be too conservative for voxels other than the one with the maximum observed statistic (Nichols and Holmes, 2002). For example, dominant CTS values in the right auditory cortex could bias the permutation distribution and overshadow weaker CTS values in the left auditory cortex, even if these were highly consistent across subjects. Therefore, the permutation test described above was conducted separately for left- and right-hemisphere voxels.

The same approach was used to assess the significance of local maxima in contrasts between group maps.

## 2.10. Data availability

The data and the code that support the findings of this study are available on the Open Science Framework at (<https://osf.io/4q3tz/>).

## 3. Results

### 3.1. Is CTS altered in French speaking children with dyslexia and how is this alteration associated with reading experience?

Fig. 3 presents the values of phrasal and syllabic CTS in the noiseless condition for both hemispheres and the 3 groups.

The ANOVA run on these phrasal CTS values revealed a significant effect of hemisphere ( $F_{1,75} = 16.75$ ,  $p = 0.0001$ ,  $\eta^2 = 0.05$ ), with higher right- than left-hemisphere CTS, no significant effect of group ( $F_{2,75} = 1.9$ ,  $p = 0.16$ ,  $\eta^2 = 0.03$ ) and no significant interaction between hemisphere and group ( $F_{2,75} = 1.29$ ,  $p = 0.28$ ,  $\eta^2 = 0.008$ ).

The ANOVA run on syllabic CTS values revealed a significant effect of hemisphere ( $F_{1,75} = 8.34$ ,  $p = 0.005$ ,  $\eta^2 = 0.02$ ), with higher right-

than left-hemisphere CTS, a significant effect of group ( $F_{2,75} = 4.62$ ,  $p = 0.013$ ,  $\eta^2 = 0.09$ ), and no significant interaction ( $F_{2,75} = 1.51$ ,  $p = 0.23$ ,  $\eta^2 = 0.006$ ). Post-hoc analyses revealed that CTS in *Ctrl-Read* differed significantly from that in *Dys* ( $t_{50} = 2.58$ ,  $p = 0.013$ ,  $d = 0.36$ ) and *Ctrl-Age* ( $t_{50} = 2.61$ ,  $p = 0.012$ ,  $d = 0.37$ ), without significant difference between *Dys* and *Ctrl-Age* ( $t_{50} = -0.83$ ,  $p = 0.41$ ,  $d = 0.12$ ) (see Fig. 3C).

In summary, at the sensor level, neither phrasal nor syllabic CTS in the noiseless condition were significantly altered in *Dys* compared with controls. The only significant difference between groups highlighted an increase in syllabic CTS with age.

Since a global analysis that distinguishes only between left- and right-hemisphere CTS may overlook subtle differences in specific brain regions, we also compared source-space CTS maps between groups.

Significant local maxima of phrasal CTS localized in all groups in posterior superior temporal gyrus (pSTG) bilaterally, less than 5 mm from the mean coordinate across groups (left, MNI coordinates  $[-46 -26 2]$  mm; right,  $[58 -21 0]$  mm), and in the right inferior frontal gyrus, less than 9 mm from the mean coordinate across groups ( $[54 20 3]$  mm; Fig. 4). The group comparisons revealed no significant difference between any of the groups in any of the hemispheres ( $p > 0.1$  for the 6 comparisons).

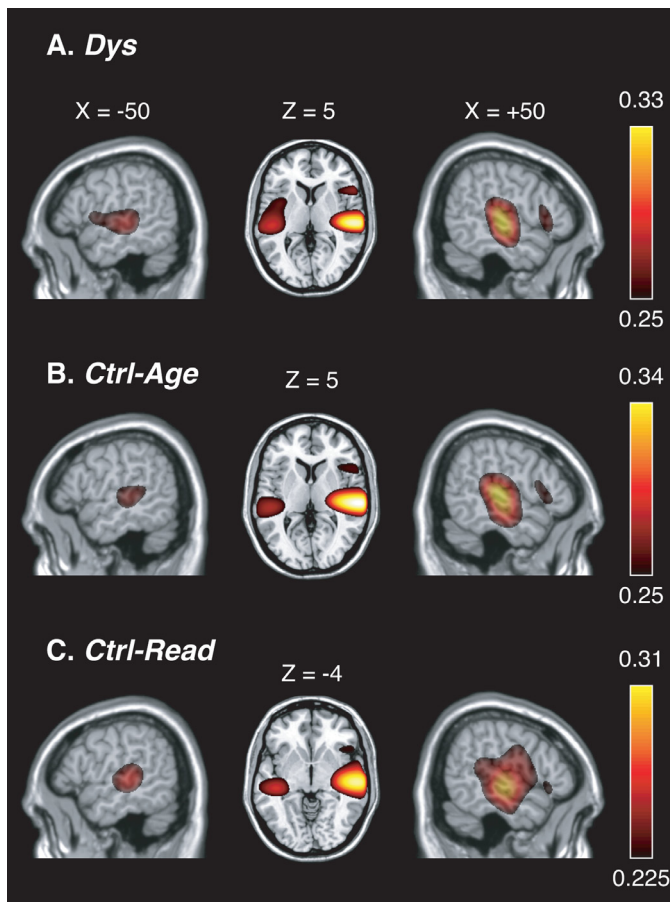
Significant local maxima of syllabic CTS localized in all groups in superior temporal gyrus (STG) bilaterally, less than 7 mm from the mean coordinate across groups (left,  $[-49 -18 8]$  mm; right,  $[57 -13 8]$  mm) and in inferior frontal gyrus bilaterally, less than 10 mm from the mean coordinate across groups (left,  $[-48 20 -7]$  mm; right,  $[52 28 0]$  mm) (Fig. 5). The group comparison, which was conducted for each hemisphere and pair of groups separately, revealed significantly higher CTS in the right hemisphere peaking in the STG in *Ctrl-Age* compared with *Dys* ( $p = 0.02$  at  $[65 -36 -1]$  mm) and *Ctrl-Read* ( $p = 0.001$  at  $[65 -30 10]$  mm). It also revealed a non-significant trend of higher CTS in *Dys* compared with *Ctrl-Read* ( $p = 0.07$ , peaking at  $[28 20 -2]$  mm), and no significant differences in the left hemisphere ( $p > 0.21$  for the 3 comparisons).

### 3.2. Does the severity of dyslexia impact CTS?

Fig. 6 presents the values of phrasal (Fig. 6A) and syllabic (Fig. 6B) CTS in both hemispheres and in both subgroups of dyslexic readers.

The ANOVA run on phrasal CTS revealed no significant effect of hemisphere ( $F_{1,25} = 0.56$ ,  $p = 0.46$ ,  $\eta^2 = 0.003$ ), no significant effect of subgroup ( $F_{1,25} = 0.1$ ,  $p = 0.76$ ,  $\eta^2 = 0.006$ ), but a significant interaction between hemisphere and subgroup ( $F_{1,25} = 6.79$ ,  $p = 0.016$ ,  $\eta^2 = 0.07$ ). Post-hoc analyses revealed that CTS hemispheric dominance in *Dys-Mild* differed from that in *Dys-Severe*. Indeed, in *Dys-Mild*, CTS values were





**Fig. 4.** Source-level maps of phrasal CTS in the noiseless condition. A-Maps for the Dys group. B-Maps for the Ctrl-Age group. C-Maps for the Ctrl-Read group. All maps are thresholded at statistical significance level corrected for multiple comparisons across each hemisphere.

higher in the right- compared with the left hemisphere ( $t_{15} = -2.48$ ,  $p = 0.02$ ,  $d = 0.64$ ) while there was no significant difference in *Dys-Severe* ( $t_9 = 1.43$ ,  $p = 0.19$ ,  $d = 0.48$ ). In light of this effect, and remembering that the 2 subgroups differed in RAN scores, we asked a posteriori if RAN abilities relate to hemispheric lateralization in phrasal CTS. Although RAN scores did not correlate significantly with the difference in CTS between left and right hemisphere ( $r = 0.31$ ,  $p = 0.12$ ), their correlation was significant with right-hemisphere CTS ( $r = -0.41$ ,  $p = 0.04$ ; Fig. 6C) but not with left-hemisphere CTS ( $r = -0.04$ ,  $p = 0.85$ ). Supplementary Results 1 present the comparison of phrasal CTS between subgroups for each hemisphere separately.

An ANOVA run on syllabic CTS revealed no significant effect of hemisphere ( $F_{1,25} = 1.8$ ,  $p = 0.19$ ,  $\eta^2 = 0.02$ ), no significant effect of subgroup ( $F_{1,25} = 0.0008$ ,  $p = 0.98$ ,  $\eta^2 < 0.0001$ ), and no significant interaction between the hemisphere and subgroup ( $F_{1,25} = 0.19$ ,  $p = 0.67$ ,  $\eta^2 = 0.002$ ).

In sum, we found that the severity of the reading deficit in dyslexia modifies the hemispheric dominance of phrasal CTS. The next subsection will clarify how these profiles compare with those in control groups.

### 3.3. Is CTS alteration in dyslexia most salient in challenging listening conditions?

Linear mixed-effects modeling of phrasal CTS values in all hemispheres, noise conditions, groups and subgroups revealed a statistically significant effect of noise ( $\chi^2(2) = 345$ ,  $p < 0.0001$ ), hemisphere ( $\chi^2(1) = 18.2$ ,  $p < 0.0001$ ), and group ( $\chi^2(2) = 8.75$ ,  $p = 0.01$ ), and significant interactions between hemisphere and noise ( $\chi^2(2) = 12.2$ ,

$p = 0.0022$ ), noise and group ( $\chi^2(4) = 9.61$ ,  $p = 0.047$ ), and hemisphere, group and subgroup ( $\chi^2(8) = 21.4$ ,  $p = 0.0062$ ).

Fig. 7A illustrates the interaction between hemisphere and noise. The interaction was explained by a right hemispheric dominance for phrasal CTS in *noiseless* ( $t_{77} = -4.08$ ,  $p = 0.0001$ ,  $d = 0.47$ ) and *non-speech* noise conditions ( $t_{77} = -3.88$ ,  $p = 0.0002$ ,  $d = 0.44$ ) but not in the *babble* noise condition ( $t_{77} = 0.46$ ,  $p = 0.65$ ,  $d = 0.054$ ). A pronounced effect of babble noise was also evident, with lower phrasal CTS in babble noise condition compared with noiseless and non-speech noise conditions ( $p < 0.0001$ ). These results replicate the finding that noise impacts more right- than left-hemisphere phrasal CTS (Destoky et al., 2020, 2019; Vander Ghinst et al., 2019, 2016). Supplementary Results 2 present the comparison of phrasal CTS between noise conditions for each hemisphere separately.

Fig. 7B illustrates the interaction between noise and group. The interaction was explained by significantly higher CTS in babble noise in *Ctrl-Age* compared with the two other groups (*Dys*,  $t_{50} = -3.11$ ,  $p = 0.0031$ ,  $d = 0.44$ ; *Ctrl-Read*,  $t_{50} = 3.81$ ,  $p = 0.0004$ ,  $d = 0.54$ ) for which there was no significant difference ( $t_{50} = 0.57$ ,  $p = 0.57$ ,  $d = 0.081$ ), while the groups did not differ significantly in *noiseless* nor in *non-speech* noise conditions ( $p > 0.08$  in all 6 comparisons; non-significant trend) though with non-significant trends for the difference between *Ctrl-Read* and *Ctrl-Age* (*noiseless*,  $t_{50} = 1.78$ ,  $p = 0.081$ ,  $d = 0.25$ ; *non-speech* noise,  $t_{50} = 1.70$ ,  $p = 0.096$ ,  $d = 0.24$ ). This indicates that the introduction of babble noise brought about a significant alteration in phrasal CTS in dyslexia and *Ctrl-Read* in comparison with *Ctrl-Age*. In other words, in reaction to babble noise, phrasal CTS in dyslexia is hindered much like in *Ctrl-Read*. Also worth noting, this effect was independent of the hemisphere and subgroup. Supplementary Results 3 present the comparison of phrasal CTS between noise conditions for each group separately.

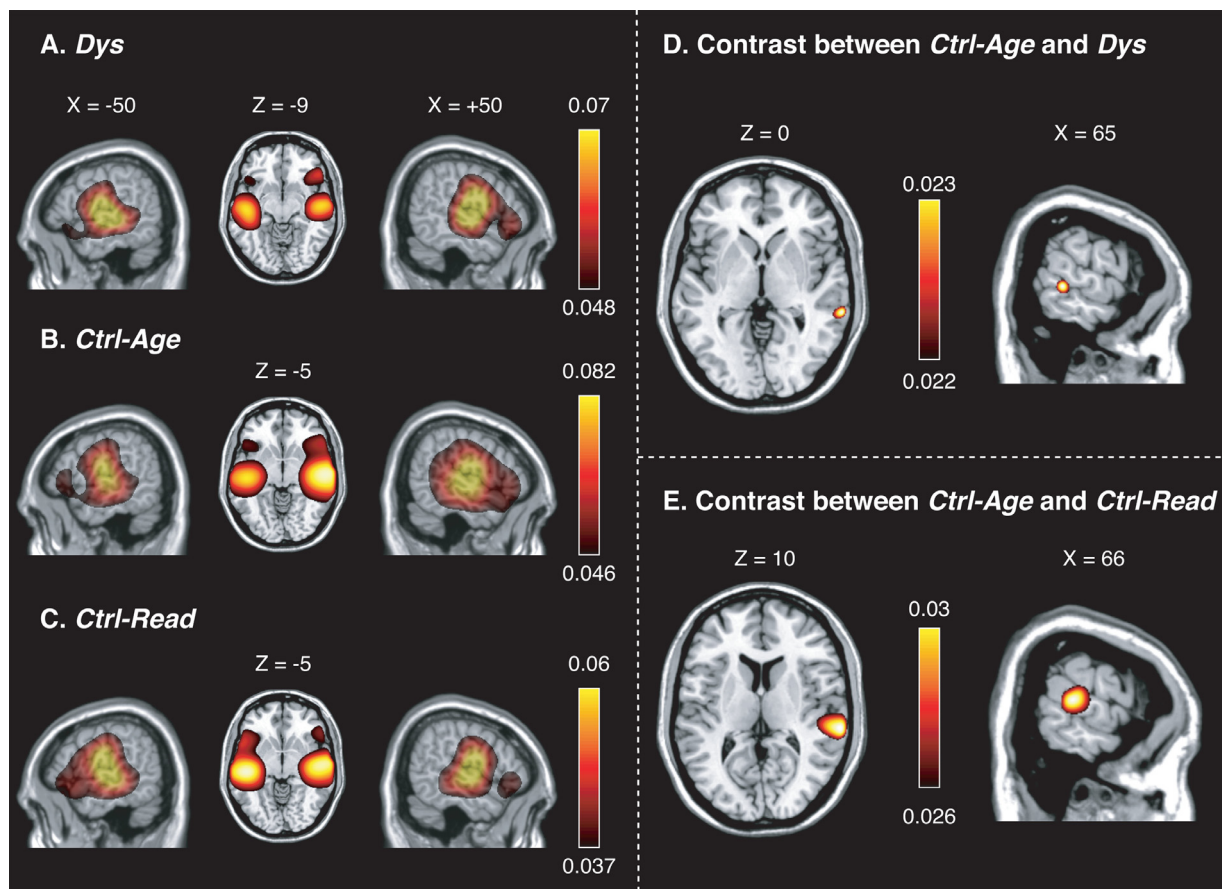
Fig. 7C illustrates the triple interaction between hemisphere, group and subgroup. This interaction indicates that the modulation in CTS hemispheric lateralization by reading proficiency seen in *Dys* (see previous section) differed between groups. Importantly, this effect did not interact with noise (no quadruple interaction;  $\chi^2(16) = 14.21$ ,  $p = 0.58$ ), indicating that noise did not exacerbate the impact of reading abilities on the hemispheric dominance in *Dys*. The interaction was driven by a difference in phrasal CTS between hemispheres that differed in *Dys-Severe* and *Ctrl-Read-High* from the 4 other groups. To substantiate this effect, we compared subgroups for their difference in CTS between right and left hemispheres (see Fig. 7D). As a result, the difference in *Dys-Severe* was significantly lower than in *Ctrl-Read-Low* ( $t_{22} = -2.43$ ,  $p = 0.024$ ,  $d = 0.52$ ) and in *Ctrl-Read-High* ( $t_{20} = -3.83$ ,  $p = 0.001$ ,  $d = 0.86$ ). Also, there were non-significant trends ( $p < 0.1$ ) for lower difference in *Dys-Severe* compared with *Dys-Mild* ( $t_{24} = 1.92$ ,  $p = 0.068$ ,  $d = 0.39$ ) and *Ctrl-Age-High* ( $t_{20} = -1.79$ ,  $p = 0.089$ ,  $d = 0.40$ ). Contrastingly, there was a non-significant trend ( $p < 0.1$ ) for higher difference in *Ctrl-Read-High* compared with *Ctrl-Age-High* ( $t_{22} = -1.99$ ,  $p = 0.059$ ,  $d = 0.42$ ) and *Ctrl-Read-Low* ( $t_{24} = 1.93$ ,  $p = 0.066$ ,  $d = 0.39$ ).

Linear mixed-effects modeling of syllabic CTS values iteratively revealed a statistically significant effect of noise ( $\chi^2(2) = 184$ ,  $p < 0.0001$ ), hemisphere ( $\chi^2(1) = 23.3$ ,  $p < 0.0001$ ) and group ( $\chi^2(2) = 11.9$ ,  $p = 0.0026$ ), and a significant interaction between hemisphere and group ( $\chi^2(2) = 6.77$ ,  $p = 0.03$ ). The absence of interaction involving noise indicates that phrasal CTS alteration in dyslexia is not more salient in noisy conditions.

Fig. 8 illustrates the effect of noise. The effect was explained by a significant reduction in syllabic CTS in babble noise condition compared with the two other conditions (*Noiseless*,  $t_{77} = 12.53$ ,  $p < 0.0001$ ,  $d = 1.43$ ; *Non-speech* noise,  $t_{77} = 12$ ,  $p < 0.0001$ ,  $d = 1.37$ ) for which there was only a non-significant trend of difference ( $t_{77} = 1.70$ ,  $p = 0.09$ ,  $d = 0.19$ ).

The interaction between hemisphere and group was similar to that described in Section 3.1, for it was not modulated by noise nor subgroup. Supplementary Results 4 present the comparison of syllabic CTS between groups for each hemisphere separately, and between hemispheres for each group separately.





**Fig. 5.** Source-level maps of syllabic CTS in the noiseless condition. A-Maps for the Dys group. B-Maps for the Ctrl-Age group. C-Maps for the Ctrl-Read group. D-Contrast between Ctrl-Age and Dys. E-Contrast between Ctrl-Age and Ctrl-Read. All maps are thresholded at statistical significance level corrected for multiple comparisons across each hemisphere.

#### 4. Discussion

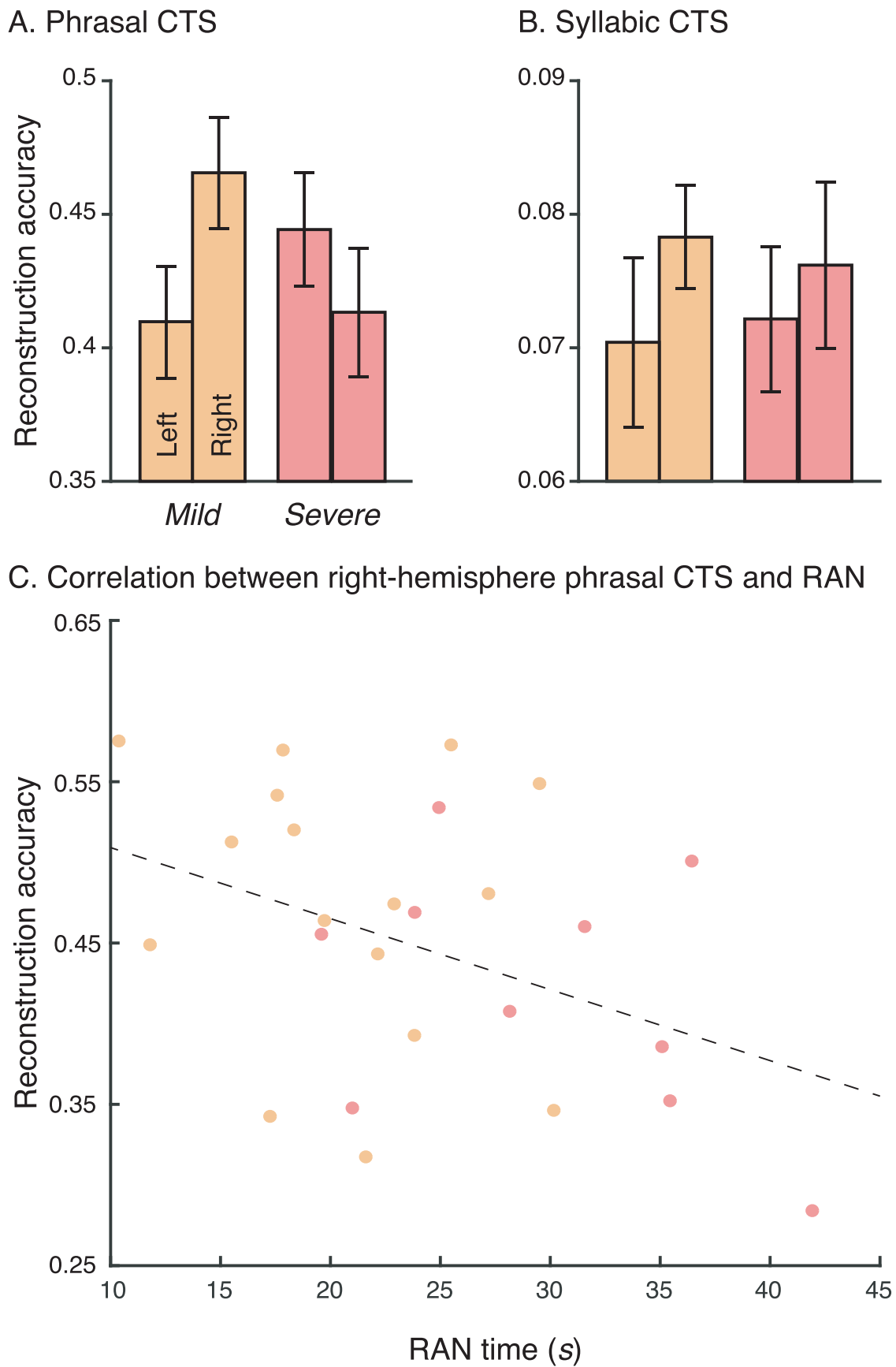
This study demonstrates that in French speaking children with dyslexia, (i) syllabic CTS in the right STG is altered in comparison with age-matched controls, but not with reading-level-matched controls, (ii) phrasal CTS hemispheric lateralization is abnormal in the most severe form of dyslexia in relation with low RAN abilities, and (iii) phrasal CTS is altered, but only in babble noise, and again, only in comparison with age-matched controls and not with reading-level-matched controls. Overall, these data provide novel insights into the neurobiology of dyslexia that explain the contradictions between previous reports of altered/preserved CTS in dyslexia.

##### 4.1. Abnormal syllabic CTS in dyslexia

Our source level results suggest that syllabic CTS in the right STG is reduced in children with dyslexia in comparison with age-matched but not reading-level-matched controls. Although an absence of difference between children with dyslexia and reading-level-matched controls could be due to higher metacognitive abilities in children with dyslexia that would mask a deficit, it is classically ascribed to reduced reading experience (Goswami, 2015). Indeed, individuals with dyslexia tend to have less scheduled reading time compared with typical readers (Finucci et al., 1985; Sun et al., 2013), and learning to read fosters cerebral development by providing intensive training for sensory (Dehaene et al., 2015) and attentional processes (Goswami, 2015). For example, literacy acquisition improves early visual processes which leads to a reorganization of the ventral occipito-temporal pathway

(Szwed et al., 2014) and also modifies phonological coding by strengthening the functional and anatomical link between graphemic and phonemic representations (Dehaene et al., 2015) leading to a reciprocal link between phonology and reading development (Castles and Coltheart, 2004). In the sphere of language, literacy enhances the cerebral activation seen in response to spoken language (Dehaene et al., 2010; Monzalvo and Dehaene-Lambertz, 2013; Nation and Hulme, 2011). Accordingly, reading acquisition improves sensory and attentional brain processes much like maturation does. It is therefore difficult to tell apart the effect of reduced reading experience from that of a developmental disorder itself on sensory or attentional skills. In other words, such deficits can be direct or indirect causes or consequences of dyslexia. In our study, the inclusion of—and comparison with—a group of controls matched for reading level was crucial to indicate that reduced syllabic CTS in the right hemisphere in dyslexia is associated with a proxy of reduced reading experience (reading level) rather than with dyslexia itself.

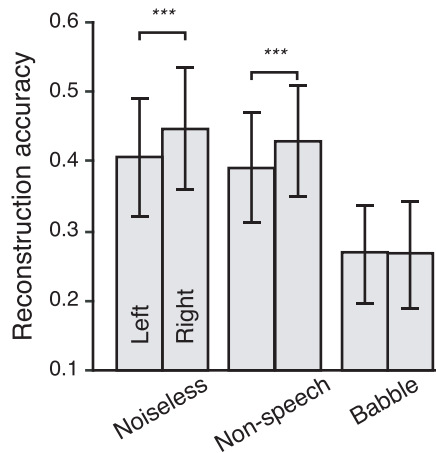
Syllabic CTS is often associated with low-level auditory processing (Molinero and Lizarazu, 2018) or phonemic processing (Destoky et al., 2020; Di Liberto et al., 2015; Mai et al., 2016). Phonemic processing and hence phonemic awareness have long been suggested as causal factors of dyslexia (Tallal, 1980). In contrast, the temporal sampling framework for developmental dyslexia posits that abnormal sampling of speech would be the underlying cause, leading to a deficit in both reading abilities and phonological processing. Our finding that the deficit in syllabic CTS in dyslexia was associated with reduced reading abilities does not provide clear support for or against abnormal sampling at syllabic rate. In fact, recent evidence suggests that syllabic CTS in dyslexia is similar to that in age-matched controls right after speech edges, but decays



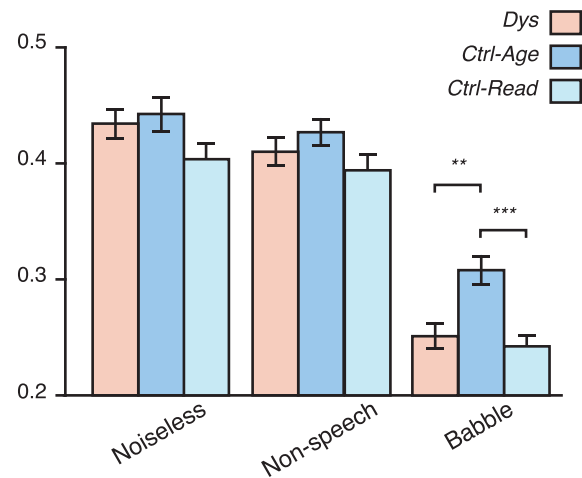
**Fig. 6.** Effect of the reading deficit in dyslexia on CTS. A and B-Phrasal (A) and Syllabic (B) CTS in both hemispheres for the two dyslexic subgroups (Mild and Severe). Bars and vertical lines indicate mean  $\pm$  SEM values. C-Correlation between right-hemisphere phrasal CTS and RAN scores.

## Phrasal CTS

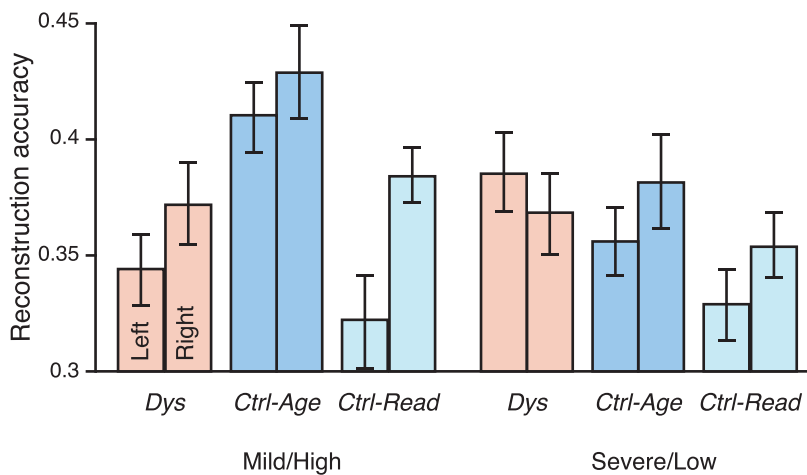
A. Effect of noise and hemisphere



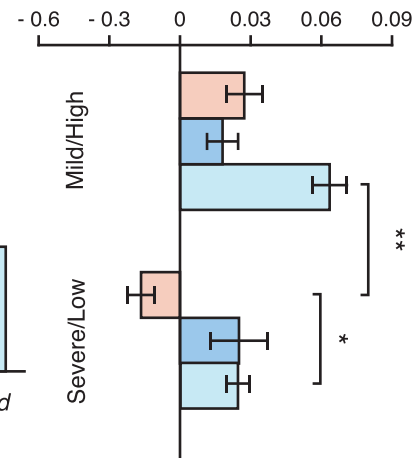
B. Effect of noise and group



C. Effect of group, subgroup and hemisphere



D. Difference between hemispheres



**Fig. 7.** Effect of hemisphere, noise, group and subgroup on phrasal CTS. A-Phrasal CTS averaged across groups. B-Phrasal CTS averaged across hemisphere and subgroups. C-Phrasal CTS averaged across noise conditions. D-Difference between right- and left-hemisphere phrasal CTS further averaged across noise conditions. Bars and vertical (A-C) or horizontal (D) lines indicate mean  $\pm$  SEM values. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

faster shortly thereafter (Lizarazu et al., 2020); further studies should tell how such decline in syllabic CTS relates to reading abilities.

### 4.2. Altered phrasal CTS lateralization in severe but not mild dyslexia

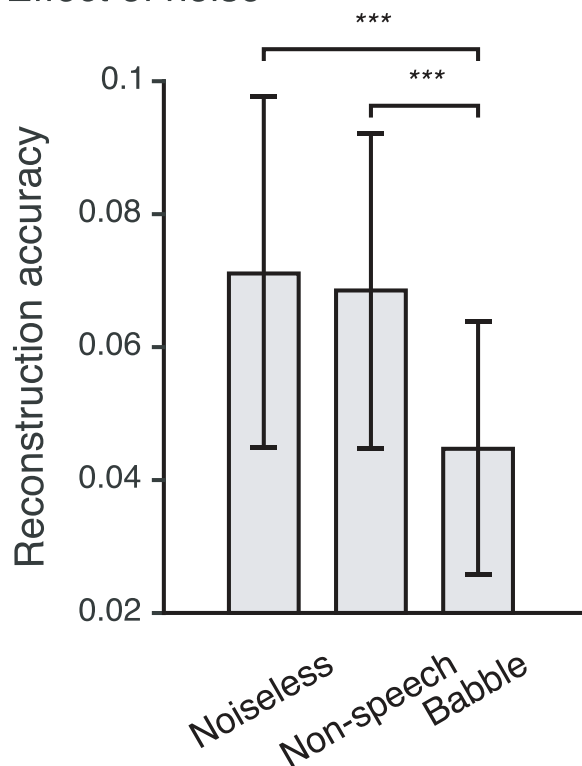
This study indicates an effect of the severity in reading deficit on the hemispheric dominance of phrasal CTS. Phrasal CTS lateralized to the right hemisphere in children with mild dyslexia while there was no significant dominance in children with severe dyslexia. Moreover, both control groups showed the same right-hemisphere lateralization for phrasal CTS, indicating that children with severe dyslexia stood out from better readers and younger children with the same reading level with their atypical phrasal CTS lateralization. Their hemispheric lateralization for phrasal CTS is more akin to that previously reported in pre-readers (Ríos-López et al., 2020). The right hemispheric dominance seen in both control groups and in mild dyslexia is in accordance with the asymmetric sampling in time hypothesis, which argues that prosodic and syllabic information of the linguistic signal are preferentially processed in the right hemisphere, while phonemic information (i.e., information at faster rates) would be processed in the left hemisphere or bilaterally (Poepfel, 2003). That hemispheric lateralization was altered in severe dyslexia indicates departure from typi-

cal development. In fact, atypical brain hemispheric lateralization is commonly reported in dyslexia, and it has been considered as a potential cause of dyslexia (Abrams et al., 2009; Giraud and Poeppel, 2012; Goswami, 2011; Molinaro et al., 2016). Anatomically, the planum temporale is larger in the left hemisphere compared with the right in about 70% of the population (Geschwind and Levitsky, 1968; Steinmetz et al., 1991), but this asymmetry appears to be different, perhaps even absent, in individuals with dyslexia (Altarelli et al., 2014; Galaburda et al., 1985; Hynd et al., 1990; Larsen et al., 1990; Ramus et al., 2018). Functionally, typical readers were reported to present a right-hemispheric dominance for delta and theta band oscillations and a left-hemispheric dominance for gamma band oscillations during an audiovisual perception task, while dyslexic readers of the same age did not present any specific lateralization (Lehongre et al., 2013). This atypical hemispheric lateralization is in line with the temporal sampling framework for developmental dyslexia (Goswami, 2011). This framework argues that the primary neural deficit in dyslexia is impaired phase locking by right-lateralized auditory cortical oscillations at phrasal and syllabic frequencies. Impaired low frequency mechanisms would ultimately hamper the integration of different acoustic features contributing to phonemic perception. Our data suggests that abnormal lateralization is only apparent in children with severe dyslexia. Alternatively, severe dyslexia in our



# Syllabic CTS

## Effect of noise



**Fig. 8.** Effect of noise on syllabic CTS. Syllabic CTS was averaged across hemispheres and groups. \*\*\*,  $p < 0.001$ .

study could actually reflect true dyslexia, while mild dyslexia would encompass misdiagnosed children who were just slow learners that eventually caught up with their peers, or children with good compensatory skills. If one embraces this view, our data can be taken as strongly supportive of the hypothesis of abnormal temporal sampling of speech at phrasal rate in the right hemisphere in dyslexia (Goswami, 2011). In any case, the distinction between subgroups of dyslexia (in a broad sense) highlights the importance of factoring in the heterogeneity of the disorder (McArthur et al., 2013), to better understand the neuronal correlates of its multiple etiology (Jednoróg et al., 2014) and severity. The fact that most studies do not follow such an approach may explain discrepancies in the existing literature.

Our results indicate a central role of RAN abilities in the behavioral and neuronal correlates of dyslexia: children with severe- compared with mild dyslexia were characterized by specifically altered RAN abilities, and phrasal CTS in the right hemisphere correlated negatively with the time taken by children with dyslexia to perform a RAN task. RAN alteration in severe dyslexia can be explained in two ways. First, noting that all our participants with dyslexia underwent speech therapy, as is customary in Belgium thanks to limited cost to the parents, children with severe dyslexia could have a pre-existing RAN deficit that made speech therapy less efficient. This view is well in line with the double deficit theory of dyslexia according to which dyslexia results from a deficit in phonological awareness or in RAN, and that a simultaneous deficit in both abilities leads to a severe reading deficit (Wolf and Bowers, 1999). Alternatively, the RAN deficit could result from poor reading acquisition. However, this latter view is incompatible with the well-documented fact that RAN abilities in pre-readers predict upcoming reading fluency (Bowey, 2008; Norton and Wolf, 2012).

Studies of the neuronal basis of RAN abilities highlighted the activation of the left inferior frontal gyrus, left posterior middle frontal gyrus, and bilateral inferior occipital areas (Misra et al., 2004; Norton and Wolf, 2012). Importantly, activation in the left inferior frontal gyrus during RAN correlates with reading abilities (Cummine et al., 2015). Besides, it has been reported that children with dyslexia have impaired phrasal CTS in the right auditory cortex and impaired feedforward effective coupling therefrom to the left inferior frontal gyrus (Molinaro et al., 2016). In light of this, our data could suggest that altered phrasal CTS in the right hemisphere leads to reduced training of the left inferior frontal gyrus, a structure that is central to both RAN and reading for its role in lexical access (Hagoort, 2005; Krieger-Redwood and Jefferies, 2014). Indeed, a reason why RAN predicts upcoming reading abilities could be that both abilities require efficient lexical access (Georgiou et al., 2018). Moreover, lexical access was convincingly shown to contribute to CTS since speech devoid of amplitude modulation at the phrasal (and sentential) level still elicits cortical tracking of its phrasal and sentential structure (Ding et al., 2016).

### 4.3. Impact of noise on phrasal CTS in dyslexia

Our results support the well-documented detrimental effect of background babble noise on speech processing in dyslexia (Calcutt et al., 2015; Dole et al., 2012; Ziegler et al., 2009). Indeed, phrasal CTS was reduced in dyslexia in comparison with controls in age only in the babble noise condition and not in noiseless and non-speech noise conditions. This therefore indicates that the alteration in phrasal CTS seen in Spanish or English speaking children with dyslexia (Abrams et al., 2009; Giraud and Poeppel, 2012; Goswami, 2011; Molinaro et al., 2016) is also seen in French, but only in challenging listening conditions. It has already been posited that different languages impact differently on some aspects of CTS because of differences in their properties (Lallier et al., 2017). For example, French speakers may tune less strongly their neural oscillations than Spanish or English speakers to slow speech modulations, in particular in the delta (i.e. phrasal) and theta (i.e. syllabic) frequency bands, as a consequence of differences in lexical stress pattern (Lallier et al., 2017). This is because lexical stress in French is totally predictable as it always falls on the last syllable. In contrast, lexical stress in Spanish and English changes depending on the word itself and is used to differentiate between words made of the exact same sequence of phonemes. The perfect predictability of stress in French leads to a “stress deafness” in native speakers (Dupoux et al., 1997), which ultimately results in underrepresentation of stress in the lexical phonological memory (Dupoux et al., 2010). This French “stress deafness” led us to hypothesize that atypical right-hemisphere neural oscillatory sampling for the low frequencies seen in English and Spanish dyslexic readers would be less severe in French dyslexic readers (Lallier et al., 2017), which is exactly what we have observed. Still, more cross-linguistic studies are warranted to fully determine to which extent language specifics determine the interrelation between reading abilities and the range of language brain functions subtended by CTS.

Notwithstanding the above, the impact of babble noise on phrasal CTS was similar in children with dyslexia compared with their controls in reading level. This, again, suggests that the deficit in phrasal CTS in noise seen in children with dyslexia is associated with reduced reading experience rather than with dyslexia.

Reading experience could impact phrasal CTS in noise through its effect on general lexical knowledge (Destoky et al., 2020). Indeed, reading improves lexical knowledge because new words are more often encountered during reading than listening activities. This effect is commonly called the “Matthew effect” (Morgan et al., 2008). In turn, lexical knowledge influences SiN comprehension (Carroll et al., 2016; Kaandorp et al., 2016; Lewis et al., 2010; Mattys and Wiget, 2011), tentatively through top-down mechanisms that leverage such lexical knowledge to facilitate identification of phonemes by retuning phonemic categories (McClelland et al., 2006). Since the level of phrasal CTS in noise

is an electrophysiological correlate of SiN comprehension (Peelle et al., 2013; Riecke et al., 2018; Vanthornhout et al., 2018), we can surmise the causal chain as follows: reading acquisition develops lexical knowledge which itself boosts the level of phrasal CTS in noise.

#### 4.4. Limitations and perspectives

A recurring problem in studies investigating CTS in dyslexia concerns the sample size usually included and the absence of controls in reading level. Indeed, all of these studies included at most 20 dyslexic readers (Di Liberto et al., 2018; Lizarazu et al., 2021; Molinaro et al., 2016; Power et al., 2016), some of them mixing child and adult populations. Also, half of these studies used age-matched controls but no reading-level matched controls. Our study did slightly better in terms of sample size, and, more importantly, did include appropriate controls in reading level (78 children; 26 children with dyslexia and their controls in age and reading level), making it possible to dissociate associations with a proxy of reading experience from associations with dyslexia. Despite having included a larger population, we did not identify any potential core alteration in dyslexia that would have been seen in comparison with both control groups. Also, the potential genuine differences we might have missed (false negatives) should have an effect size small enough to dismiss them as non-core deficits in dyslexia (Friston, 2012). Moreover, even for our analysis involving subgroups of participants, where the sample size was substantially reduced, we still had sample sizes (10–16 participants) roughly comparable to the number of children with dyslexia included in previous studies (Power et al., 2016: 13; Di Liberto et al. 2018: 13; Molinaro et al., 2016: 10). Future studies should gather even more participants to identify alterations in multiple subgroups (or subtypes) of dyslexia (Saksida et al., 2016).

Not all participants took part in the MRI acquisition, mainly due to fear of the scanner or reluctance of the parents to learn about potential abnormalities in their child's brain. For each of the participants for whom we lacked MRI (20–40% depending on the group), source reconstruction was performed based on another participant's MRI linearly deformed to match the digitized head surface. Using a well-matched MRI was reported to lead to maximal errors of about 1 cm (Gohel et al., 2017). However, since the direction of the error is expected to be inconsistent across participants, the overall effect of missing MRIs on group-level maps of CTS should be very limited.

Comparability of studies assessing oscillatory cortical activity in dyslexia can be somewhat limited due to mere methodological differences. For example, tracking might be different for language stimuli (Destoky et al., 2020, 2019; McHaney et al., 2020; Riecke et al., 2018; Vander Ghinst et al., 2016) and non speech stimuli like amplitude modulated white noise (De Vos et al., 2017; Lehongre et al., 2011). The analysis methods is another factor, the most commonly used being coherence analysis (Destoky et al., 2019; Molinaro et al., 2016; Molinaro and Lizarazu, 2018), reconstruction accuracy (Destoky et al., 2020; Power et al., 2016), and phase locking value (Hämäläinen et al., 2012; Lizarazu et al., 2020, 2015). It would be important in future studies to characterize to which extent these methodological specificities explain differences across studies.

It is important to highlight that the correlation between RAN and right-hemisphere phrasal CTS we identified in dyslexic children awaits replication. Indeed, the correlation analysis was conducted a posteriori, based on the incidental finding that mild and severe dyslexia subgroups differed on RAN abilities. The correlation is also partly redundant with the presence of a difference in both RAN and CTS hemispheric lateralization between subgroups of dyslexia.

## 5. Conclusion

This study demonstrates that altered CTS in dyslexia is associated with reduced reading level, hinting at an association with reduced reading experience rather than with the disorder itself. Moreover, children

with “severe dyslexia” did not show the typical right-hemisphere lateralization for phrasal tracking seen in children with “mild dyslexia” and other controls, tentatively linked to reduced RAN abilities. This abnormal lateralization pattern lays support to the hypothesis of abnormal temporal sampling of speech at the phrasal rate in the right hemisphere in dyslexia, provided “severe dyslexia” in our study can be assimilated to true dyslexia. Finally, we demonstrate that phrasal CTS is not altered in French speaking children dyslexia, in contrast with reports on Spanish or English speaking children. However, the alteration becomes evident in challenging SiN conditions, but again, in association with reduced reading level.

#### Data availability

The MEG data as well as analysis code are available at <https://osf.io/4q3tz/>.

#### Declaration of Competing Interest

None of the authors disclose any potential conflict of interest.

#### Credit authorship contribution statement

**Florian Destoky:** Visualization, Data curation, Formal analysis, Writing – original draft, Investigation, Writing – review & editing. **Julie Bertels:** Writing – review & editing, Visualization, Data curation. **Maxime Niesen:** Writing – review & editing, Data curation. **Vincent Wens:** Writing – review & editing, Data curation. **Marc Vander Ghinst:** Writing – review & editing, Visualization. **Antonin Rovai:** Writing – review & editing, Data curation. **Nicola Trotta:** Writing – review & editing, Data curation. **Marie Lallier:** Writing – review & editing, Visualization. **Xavier De Tiège:** Writing – review & editing, Visualization. **Mathieu Bourguignon:** Writing – review & editing, Visualization, Formal analysis, Data curation.

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#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2022.119061](https://doi.org/10.1016/j.neuroimage.2022.119061).

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