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OSCILLATORY ‘TEMPORAL SAMPLING’ AND DEVELOPMENTAL DYSLEXIA: TOWARDS AN OVERARCHING THEORETICAL FRAMEWORK

Topic Editors
Usha Goswami, Alan J. Power, Marie Lallier and Andrea Facoetti

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Topic Editors:
Usha Goswami, University of Cambridge, United Kingdom
Alan J. Power, University of Cambridge, United Kingdom
Marie Lallier, Basque Center on Cognition Brain and Language, Spain
Andrea Facoetti, University of Padua, Italy

Children with developmental dyslexia fail to acquire efficient reading and spelling skills despite adequate tuition and an absence of overt sensory and/ or neural deficits. Learning to read and spell requires linguistic skills, auditory skills and visual skills. Oscillatory 'temporal sampling' theory links the development of sensory and linguistic processes. The auditory system 'samples' acoustic information at different temporal rates, which for speech processing suggests that temporal information encoded by delta, theta and gamma oscillations is bound together in the final speech percept. Temporal sampling theory proposed a possible deficit in dyslexia in auditory sampling of the speech signal at syllable-relevant rates (< 10 Hz, delta and theta). This would hypothetically affect prosodic development prior to reading and syllable-based parsing, which would affect efficient linguistic skills and consequently reading development across languages. The visual system also samples information in the visuo-spatial field. In theory atypical visual oscillatory sampling could therefore be related to some of the visual features of developmental dyslexia. In this special issue, we bring together visual and auditory sensory processing studies around the general theme of oscillatory temporal sampling. Contributors were encouraged to discuss their findings within a temporal sampling perspective. The resulting studies cover a wide range of sensory processes, with findings both supporting and contradicting the theory. It is also important to note that studies covered a wide range of languages, and that the behavioural manifestations of a sampling impairment may differ both with language and over the course of development. Nevertheless, it is encouraging to see such diverse findings considered within a single theoretical framework, even if at the same time, it is apparent that an over-arching theoretical framework encompassing both visual and auditory deficits in dyslexia is yet to be achieved.

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EDITORIAL
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Oscillatory "temporal sampling" and developmental dyslexia: toward an over-arching theoretical framework

***Usha Goswami*[1]*, Alan J. Power*[1]*, Marie Lallier*[2] *and Andrea Facoetti*[3]**

[1] *Department of Psychology, Centre for Neuroscience in Education, University of Cambridge, Cambridge, UK*
[2] *Basque Centre on Cognition, Brain and Language, San Sebastian, Spain*
[3] *General Psychology, University of Padua, Padua, Italy*
**Correspondence: ucg10@cam.ac.uk*

Edited by:
Hauke R. Heekeren, Freie Universität Berlin, Germany

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Human cognitive systems such as language represent the sensory world as unitary. For example, the "speech signal" is perceived as a single auditory stimulus, and different visual features and textures in the visual field are perceived holistically as unitary objects. Yet sensory neuroscience demonstrates the diversity of encoding in the neural systems supporting sensory perception. Different aspects of sensory information are processed in parallel, often at different timescales and by different populations of neurons. Further, research into the function of *neuronal oscillations* (e.g., Buzsáki and Draguhn, 2004) reveals a key role in processing sensory information. In this special issue, we investigate the developmental implications of one neuroscientific theory based on oscillations that is relevant to reading education and developmental dyslexia, the "temporal sampling" framework (hereafter TSF, Goswami, 2011). The TSF identifies specific oscillatory mechanisms that may be impaired in dyslexia. We expect that deeper understanding of neural mechanisms of information-processing will eventually enable deeper understanding of developmental disorders of learning, such as dyslexia. Developmental dyslexia is a disorder in the acquisition of successful reading and spelling skills that is found in ~7% of children across cultures.

The ability to read and write—the achievement of literacy—is one of the most complex and sophisticated cognitive skills developed by the brain. Literacy skills develop as a result of direct teaching, usually in childhood, and become fluent during years of practice. By adulthood, most brains have read millions of words. This makes it difficult to disentangle cause from effect when studying sensory and neural factors. Dyslexia is usually only diagnosed after 2–3 years of schooling, when the brain has already had considerable experience of reading and reading tuition. Dyslexia is diagnosed when children who are receiving adequate teaching and who have no overt sensory or neurological problems fail to develop fast, efficient and age-appropriate reading and spelling.

The TSF was proposed as the neural basis for the extraction of phonological information from speech via auditory oscillatory encoding (Goswami, in press). Based on work by Poeppel, Greenberg, Giraud, Ghitza and many others (Giraud and Poeppel, 2012, for a recent summary), the TSF linked "sampling" of the speech stream by auditory cortical networks operating at different timescales or oscillatory frequencies (delta, theta, gamma) to the emergence of phonological (linguistic) coding of speech by children. Poeppel and others argued that cortical oscillations enabled the representation of different temporal rates of amplitude modulation in the complex speech signal. These temporal frequency bands yield complementary "windows" of information relating to cognitive linguistic units such as syllables (theta rate) and phonemes (gamma rate, see Poeppel, 2003). Accordingly, the TSF proposed that atypical oscillatory sampling at one or more temporal rates in children with dyslexia could cause phonological difficulties in specifying linguistic units such as syllables.

Phonological difficulties in dyslexia are related to difficulties in the accurate perception of amplitude "rise time" (related to modulation rate). The TSF proposed that atypical oscillatory entrainment at *syllable-relevant* rates of amplitude modulation (delta [~ stressed syllable rate], theta [~ syllable rate]) could be one neural cause of the "phonological deficit" found in children and adults with dyslexia across languages and orthographies. This theory is about early developmental mechanisms, nevertheless impaired oscillatory sampling in auditory cortex could, over developmental time, lead to atypical functioning of the left-lateralized "reading network" identified in many fMRI studies of older children (Richlan, 2012, for a recent overview; Clark et al., 2014, for a relevant longitudinal study). This should be true across languages. Indeed, rise time perception is impaired in English, French, Spanish, Hungarian, Finnish, Chinese, and Dutch dyslexic children (see Goswami and Leong, 2013, for an overview). The "phonological deficit" in dyslexia is found in all of these languages, and manifests as difficulties in oral tasks such as recognizing prosodic stress, counting syllables, and counting or deleting *phonemes* (the smallest phonological units in a language; Ziegler and Goswami, 2005, for a cross-language review). These and other phonological tasks are considered by some of the auditory-based contributions to the special issue (Lehongre et al., 2013; Power et al., 2013; White-Schwoch and Kraus, 2013; Sela, 2014 this issue).

The aim of this special issue, however, was to simultaneously invite colleagues who work on visual sensory processing to consider whether atypical oscillatory "temporal sampling" may explain the pervasive visual processing deficits in dyslexia reported in many orthographies (e.g., Facoetti et al., 2010; Lallier and Valdois, 2012). Visual and auditory sensory theories of dyslexia are typically considered to compete with each other, indeed a recent review counted 12 competing theories of developmental dyslexia (Ramus and Ahissar, 2012). The act of reading of course depends upon many visual processes. Examples are (for alphabetic orthographies) serial letter recognition, visual grouping of repeating letter patterns in familiar words, and the left-to-right (or in some orthographies, right-to-left) horizontal linear tracking of print. Practice in reading (reading experience) will obviously train the brain in aspects of visual processing related to reading. Such visual practice is necessarily reduced in children with dyslexia (reading is effortful, so the child reads less). Disentangling the effects of reading experience on the brain across the many different sensory and cognitive components that support the development of reading and writing is thus experimentally challenging. Nevertheless, by studying particular aspects of non-linguistic visual processing in isolation (such as magnocellular function, or eye movements), research can begin to disentangle cause from effect in developmental dyslexia.

In this special issue, a number of the different aspects of impaired visual and visuo-spatial attentional processing found in dyslexia are studied and possible relations with oscillatory temporal sampling are considered (see De Luca et al., 2013; Lallier et al., 2013; Conlon et al., 2013; Gori et al., 2014; Ruffino et al., 2014; Varvara et al., 2014 this issue). Theoretically, these contributions consider whether spatiotemporal sampling of information by the visual system may be impaired in dyslexia (see Pammer, 2014; Vidyasagar, 2013 this issue). Indeed, Vidyasagar argues that a visual sampling impairment may be *primary* to the auditory difficulties in dyslexia documented by other contributors, a provocative claim which requires longitudinal studies. In fact, in order to establish the possible causal role of different visual and auditory sensory processes to reading development, and to identify their sequential contributions during the developmental learning trajectory, a range of developmental research designs are required.

At minimum, evidence is required that:

1. the sensory/neural deficit precedes being taught to read
2. the sensory/neural deficit affects aspects of cognitive development other than reading (e.g., musical development for auditory deficits, conceptual development for visual deficits) in predictable ways
3. the sensory/neural deficit can be demonstrated when children with dyslexia are compared to younger children whose *reading skills* are matched with the dyslexics (this research design aims to equate the effect of reading experience on the brain; the *reading level match* research design)
4. developmental trajectories are followed in longitudinal studies, exploring the complex interplay of auditory and visual sensory/neural and cognitive processes during the development of reading, thereby establishing the developmental primacy of the candidate deficit
5. the sensory/neural deficit is consistent across different languages and orthographies
6. training the candidate deficit has demonstrable effects upon subsequent reading development

Longitudinal studies, beginning before reading is taught and carried out across languages, are enormously important to the field (e.g., Boets et al., 2011; Franceschini et al., 2012). Sensory/neural deficits may change over developmental time. Perhaps a sensory factor critical for early development becomes less relevant when studying older children, or is no longer apparent when studying adults. Sensory/neural deficits may also *manifest* differently in different languages, for example as a consequence of factors such as orthographic grain size (e.g., the phonemic grain size is practiced by readers of alphabetic languages, whereas Japanese readers practice the syllable grain size) or phonology (e.g., rhythmic or phonetic differences, such as whether a language has many sonorant phonemes and is syllable-timed, such as Spanish, or many plosive phonemes and is stress-timed, such as English). Reading difficulties may be comorbid with other difficulties such as attention-deficit-hyperactivity disorder (ADHD); the possible effects of co-morbid disorders on sensory processing must be taken into account (Thaler et al., 2009). The studies in this special issue document and calibrate some of these aspects of auditory and visual processing that seem to be important in developmental dyslexia. Incorporating all of these aspects of sensory processing into oscillatory studies will be the next task for developmental research into dyslexia.

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Physiologic discrimination of stop consonants relates to phonological skills in pre-readers: a biomarker for subsequent reading ability?†

Travis White-Schwoch[1,2] **and Nina Kraus**[1,2,3,4,5] *****

[1] *Auditory Neuroscience Laboratory, Northwestern University, Evanston, IL, USA*
[2] *Department of Communication Sciences, Northwestern University, Evanston, IL, USA*
[3] *Institute for Neuroscience, Northwestern University, Evanston, IL, USA*
[4] *Department of Neurobiology and Physiology, Northwestern University, Evanston, IL, USA*
[5] *Department of Otolaryngology, Northwestern University, Chicago, IL, USA*

Edited by:
Marie Lallier, Basque Center on Cognition Brain and Language, Spain

Reviewed by:
Willy Serniclaes, Université Libre de Bruxelles, Belgium
Jenny Thomson, University of Sheffield, UK

****Correspondence:***
Nina Kraus, Auditory Neuroscience Laboratory, Northwestern University, 2240 Campus Drive, Evanston 60208, IL, USA
e-mail: nkraus@northwestern.edu

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Reading development builds upon the accurate representation of the phonological structure of spoken language. This representation and its neural foundations have been studied extensively with respect to reading due to pervasive performance deficits on basic phonological tasks observed in children with dyslexia. The subcortical auditory system – a site of intersection for sensory and cognitive input – is exquisitely tuned to code fine timing differences between phonemes, and so likely plays a foundational role in the development of phonological processing and, eventually, reading. This temporal coding of speech varies systematically with reading ability in school age children. Little is known, however, about subcortical speech representation in pre-school age children. We measured auditory brainstem responses to the stop consonants [ba] and [ga] in a cohort of 4-year-old children and assessed their phonological skills. In a typical auditory system, brainstem responses to [ba] and [ga] are out of phase (i.e., differ in time) due to formant frequency differences in the consonant-vowel transitions of the stimuli. We found that children who performed worst on the phonological awareness task insufficiently code this difference, revealing a physiologic link between early phonological skills and the neural representation of speech. We discuss this finding in light of existing theories of the role of the auditory system in developmental dyslexia, and argue for a systems-level perspective for understanding the importance of precise temporal coding for learning to read.

Keywords: reading, dyslexia, temporal sampling, phase locking, brainstem, phonological awareness, temporal coding

INTRODUCTION

Learning to read scaffolds on the development of more basic language skills. One such primitive is phonological awareness, the knowledge that spoken language is made up of smaller units such as syllables and phonemes (Sandak et al., 2004; Kovelman et al., 2012; Pugh et al., 2013). Phonological processing has been an area of keen interest in the study of reading for years due to the observation of pervasive performance deficits in dyslexics on basic phonological tasks (Swan and Goswami, 1997; Pugh et al., 2013; Ramus et al., 2013). Theories of developmental dyslexia, and theories of reading more generally, must therefore account for the biological mechanisms supporting phonological processing and related language skills.

Developmental dyslexia affects approximately 5–10% of children and is characterized by a failure to develop effective reading skills despite typical intelligence and adequate support from parents, teachers, and caregivers (Démonet et al., 2004). As a group, children (and adults) with dyslexia have a constellation of deficits in auditory processing. There are, for example, extensive performance gaps between dyslexic and typically developing children on a variety of basic auditory tasks (Wright et al., 1997; Goswami et al., 2002; Ahissar et al., 2006). Children with dyslexia have difficulty coding rapidly changing frequency content in speech such as formant transitions in consonant–vowel syllables (Tallal and Piercy, 1975; Tallal, 1980). Dyslexics also have difficulty tracking amplitude envelope modulations in speech, such as in syllable onsets (Goswami et al., 2002, 2011). However, it remains unknown whether these deficits are each observed within an individual or if there are variable manifestations of developmental dyslexia.

Neurophysiologic deficits associated with dyslexia include increased variability in neural firing as observed in auditory midbrain in humans (Hornickel and Kraus, 2013) and cortex in a rat model of dyslexia (Centanni et al., 2013), in addition to decreased auditory cortical phase-locking to the acoustic envelope (Abrams et al., 2009; Lehongre et al., 2011). Our own group has identified a number of deficits in speech coding throughout the central auditory system that are linked to poor reading (Kraus et al., 1996; Wible et al., 2005; Abrams et al., 2009; Banai et al., 2009; Chandrasekaran et al., 2009; Hornickel and Kraus, 2013).

In light of the wide variety of auditory deficits identified in dyslexics, a plethora of theories as to the disorder's biological origin have emerged, each of which has tried to identify a "core deficit." Although these theories are not necessarily mutually exclusive, there is little accord in the literature (cf. Livingstone et al., 1991; Wright et al., 2000; Stein, 2001; Ahissar, 2007; Vidyasagar and Pammer, 2010; Goswami, 2011; Lallier et al., 2013). Many theories have centered on a core deficit in phonological processing and, consequently, a number of neurophysiologic investigations have characterized the biology underlying this skill and deficits thereof. Neuroimaging studies have identified diminished activity in left-lateralized language networks in dyslexic children performing phonological tasks (Kovelman et al., 2012; Pugh et al., 2013). Lehongre et al. (2011) used magnetoencephalography to measure neural entrainment to amplitude modulated noise bursts, and found that dyslexics had poorer phase-locking in the "low gamma" range (~30 Hz), correlating with poor performance on phonological tasks. Finally, the discrimination of stop consonants in auditory midbrain is linked to reading ability in school age children (Hornickel et al., 2009).

While these studies (in addition to many others) have offered insight into the pathophysiology underlying phonological and/or reading deficits, they are complicated by the reciprocal relationship between phonological processing and reading. For although phonological awareness likely bootstraps reading development, the first years of reading themselves influence phonological awareness (Castles and Coltheart, 2004). Therefore, here, we assessed the relationship between phonological awareness and neurophysiologic discrimination of stop consonants in a group of typically developing 4-year-old children. We hypothesized that early phonological awareness is linked to the precision of physiologic speech sound discrimination. To test this hypothesis, we measured neural responses to a pair of speech stimuli previously shown to vary systematically with phonological processing in school-age children (Hornickel et al., 2009). By assessing physiologic processing of speech in pre-school age children we hope to gain insight into the developmental trajectory of reading development. Moreover, we may identify a potential biomarker to predict subsequent reading ability.

MATERIALS AND METHODS

SUBJECTS

Four-year-old children ($N = 26$, 14 female) were recruited from the Chicago area to participate in a developmental study at Northwestern University. No child had a history of a neurologic or otologic condition, second language experience, or a diagnosis of autism spectrum disorder. Four children had immediate family histories of dyslexia (parent or sibling). All children passed a brief screening of peripheral auditory function (normal tympanometry and distortion product otoacoustic emissions at least 6 dB above the noise floor for octaves from 1–8 kHz). Additionally, all children had normal click-evoked auditory brainstem responses (Wave V latency < 6.0 ms, measured by a 100 μs click presented at 80 dB SPL to the right ear at 31.25 Hz).

Although we consider these children too young to have attained fully developed reading skills, and so refer to them as "pre-readers," we note that many of them may have begun some explicit instruction. We did not formally evaluate their reading skills and acknowledge this as a limitation. Nevertheless, we suggest that our cohort represents children who have either not yet begun to learn to read, or are only in the first stages, and so offers novel insight into the relationship between phonological processing and auditory-neurophysiologic responses to speech early in life.

Parents provided informed consent for their children to participate in the study, and the subjects provided verbal assent. The Institutional Review Board of Northwestern University approved all procedures and children were paid $10/hr for their participation.

BEHAVIORAL MEASURE – PHONOLOGICAL AWARENESS

Phonological awareness was measured with the Clinical Evaluation of Language Fundamentals Preschool, 2nd edn., phonological awareness subtest (CELF 2; Wiig et al., 2004). The test evaluates a child's knowledge of the sound structure of the English language and measures a child's ability to manipulate sound through: compound word and syllable blending, sentence and syllable segmentation, and rhyme awareness and production. Raw scores are computed and were used for analysis. The maximum score is 24, and higher scores correspond to better performance. All children met the age-appropriate "criterion" cutoff, indicating that they are within the range of typically developing children. Therefore our data represent a cohort of children with developmentally appropriate performance on the phonological awareness test but with a large range of variability.

NEUROPHYSIOLOGY: STIMULI

Auditory brainstem responses were elicited in response to the stop consonants [ba] and [ga]. Both consonant–vowel (CV) syllables were 170 ms stimuli that have been described previously (Hornickel et al., 2009). Briefly, both begin with a 5 ms stop burst and have a 50 ms transition from the consonant to the vowel. The vowel is sustained for 120 ms. Both stimuli have a flat fundamental frequency ($F_0 = 100$ Hz) and during the 50 ms transition the first three formant frequencies shift. The [ba] and [ga] differ only in the F_2 onset frequency ($F_{2\text{OF[ba]}} = 900$ Hz; $F_{2\text{OF[ga]}} = 2480$ Hz) but are identical in F_2 frequency for the vowel portion ($F_{2\text{VOWEL}} = 1240$ Hz; see **Figure 1**). The remaining formants are identical ($F_1 = 400–720$ Hz; $F_3 = 2580–2500$ Hz) with F_{4-6} steady through the 170 ms stimuli ($F_4 = 3300$ Hz, $F_5 = 3750$ Hz, $F_6 = 4900$ Hz). Stimuli were presented monaurally to the right ear at 80.4 dB SPL through electromagnetically shielded insert earphones (ER-3, Etymotic Research, Elk Grove Village, IL, USA). Stimulus presentation was controlled by E-Prime 2.0 (Psychology Software Tools, Inc., Sharpsburg, PA, USA) and stimuli were presented in alternating polarity with an 81 ms interstimulus interval. 4200 sweeps of each stimulus were presented, and the presentation order was randomized for each subject.

NEUROPHYSIOLOGY: RECORDING AND DATA PROCESSING

Brainstem responses were collected using a BioSEMI Active2 recording system with ABR module. Active electrodes were placed at Cz and each ear with CMS/DRL placed on the forehead, one-half centimeter on either side of Fpz. Only ipsilateral (Cz-A2) responses are used in analysis. Responses were digitized at

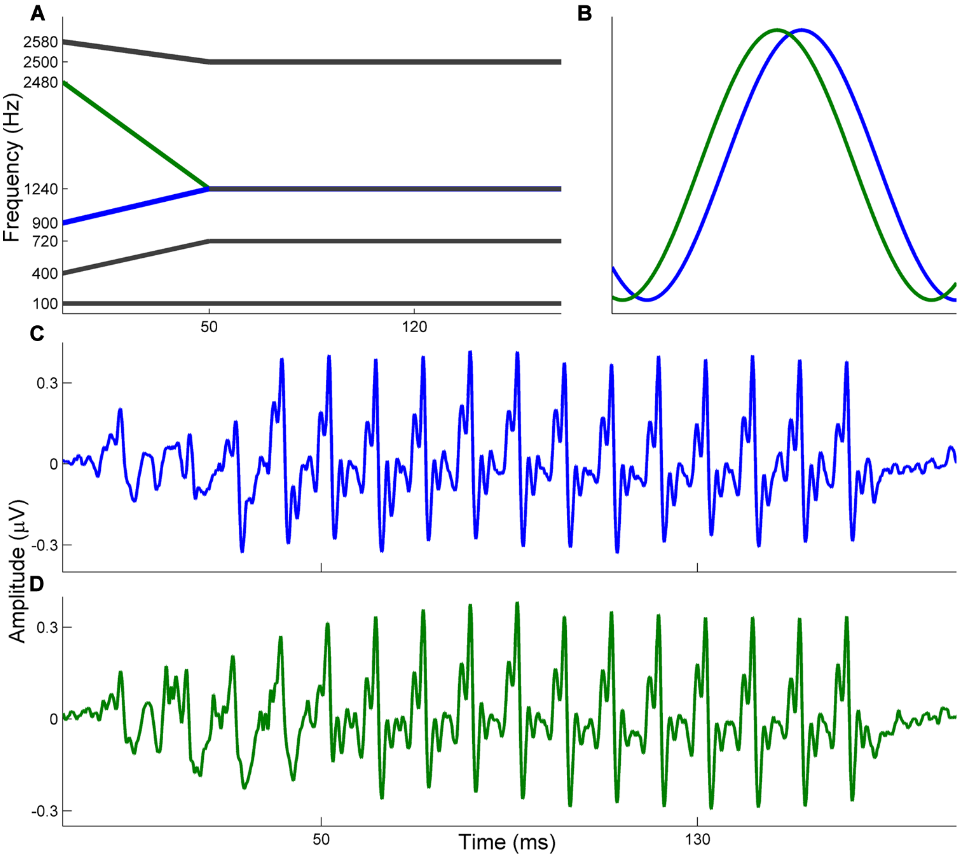

FIGURE 1 | (A) Schematic illustrating formant information for the [ba] and [ga] stimuli. The F_0, F_1, and F_3 are identical. The stimuli differ in F_2 onset frequencies with [ba] (blue) ascending and [ga] (green) descending to stabilize for the vowel portion. **(B)** Schematic illustrating the expected phase relationship between brainstem responses to the [ba] and [ga]. Since the [ga] (green) has a higher F_2 onset frequency it is expected that brainstem responses to [ga] phase lead those to [ba]. **(C,D)** Grand average waveforms are displayed for the [ba] (top, blue) and [ga] (bottom, green).

16.384 kHz and collected with online filters from 100–3000 Hz (20 dB/decade roll-off) in the BioSEMI ActiABR and recorded into LabView 2.0 (National Instruments, Austin, TX, USA). Since speech-evoked brainstem responses are ideally filtered with a high-pass of 70 Hz (Skoe and Kraus, 2010), in MATLAB responses were offline amplified in the frequency domain with an inverse power ramp, 20 dB per decade for 3 decades below 100 Hz (i.e., from 0.1 to 100 Hz, then flat from 0.1 Hz down to DC). Next, a bandpass filter (70–2000 Hz, Butterworth filter, 12 dB/octave roll-off) was applied to frequency-amplified responses. Responses were epoched from −40–213 ms (stimulus onset at 0 ms) and baseline corrected. Artifact rejection was set at ± 35 µVs. Final responses comprised 2000 artifact-free sweeps of each polarity, and responses from alternating polarities were added to emphasize the envelope-following brainstem response while minimizing the influence of stimulus artifact and cochlear microphonic (Campbell et al., 2012).

NEUROPHYSIOLOGY DATA ANALYSIS: PHASE DISTINCTION BETWEEN RESPONSES

Due to the tonotopicity of the ascending auditory system, stimuli that differ in frequency elicit brainstem responses which are out of phase (Gorga et al., 1988). Therefore, it is expected that responses to [ba] and [ga] begin out of phase from each other (during the transition portion) and are phase-aligned during the vowel, when the stimuli are acoustically identical. In this regard, the relative phases of the two responses are used as proxies for the relative timing of the responses at each frequency. A schematic illustrating this expected relationship is presented in **Figure 1**.

The phase relationship between responses to [ba] and [ga] was measured using custom routines in MATLAB (Skoe et al., in press). Responses were divided into overlapping 20 ms windows from −40–170 ms (1 ms separating each adjacent window) and ramped with a 20 ms Hanning window. The cross-power spectral density function (cspd) was applied between brainstem responses, and power estimates were converted to phase angles to index alignment of the two signals. A larger phase angle (in radians) indicates that the responses are farther out of phase and, therefore, that there is a larger timing lag between responses at a given frequency. A three dimensional "cross-phaseogram" figure is constructed illustrating time (ms, x-axis), frequency (Hz, y-axis), and phase angle (radians, colorbar). During the transition region positive phase angles indicate better neural consonant distinction, as this indicates that

[ga] phase-leads [ba], the expected relationship since [ga] has a higher F_{2OF}.

SUBJECT GROUPS

Scores on the CELF formed a normal distribution with a mean score of 18.96 (SD, 3.80; Kolmogorov–Smirnov $D(26) = 0.146$, $p = 0.160$). Children were grouped based on their performance on the CELF with a median split defining the top phonological awareness "Top PA" (CELF > 19, $N = 14$, 6 female) and bottom phonological awareness "Bottom PA" (CELF < 19, $N = 12$, 6 female) groups. Five subjects in the Top PA performed at ceiling on the test (scores of 24). Each group included two children with a family history of dyslexia. Groups did not differ in distribution of males and females ($\chi^2 = 0.154$, $p = 0.70$) nor on non-verbal intelligence (matrix reasoning subtest, Wechsler Preschool and Primary Scale of Intelligence, Revised; Wechsler, 1989; $p = 0.35$). As expected, the groups did statistically differ in performance on the CELF, $t(24) = 9.11$, $p < .001$, Cohen's $d = 3.56$. Summary statistics for the two groups are presented in **Table 1**.

RESULTS

SUMMARY OF RESULTS

Group average cross-phaseograms are presented in **Figure 2**. The Top phonological awareness group (Top PA) evinces a large phase distinction corresponding in time to the transitions in the stimuli, which occurs in the responses from approximately 300–700 Hz (indicated by a large orange–red swatch) and a more moderate phase shift from approximately 750–1000 Hz. Conversely, relatively small phase distinctions were observed in the bottom group (Bottom PA) suggesting that the frequency difference between the stimuli was not strongly represented in these children. Phase distinctions for individual subjects are presented in **Figure 3**, along with group means. No phase distinctions were observed in the response region corresponding to the steady state vowel in either group, as is expected since the stimuli are acoustically identical in the vowel portions.

PHASE DISTINCTIONS IN THE CONSONANT-VOWEL TRANSITION, 300-700 Hz

Mean phase angle distinctions were calculated for the lower frequency region (15—55 ms × 300—700 Hz). This was the primary region of interest, since it corresponds best to previous reports (Skoe et al., in press; Parbery-Clark et al., 2012). In the Top PA there was a larger mean phase distinction than in the Bottom PA group, $t(24) = 2.61$, $p = .015$, Cohen's $d = 1.07$. See **Table 2** for descriptive statistics. Since there was a slightly skewed distribution in the Top PA group, this comparison was repeated, and confirmed, with the non-parametric Mann–Whitney U test ($p = 0.015$).

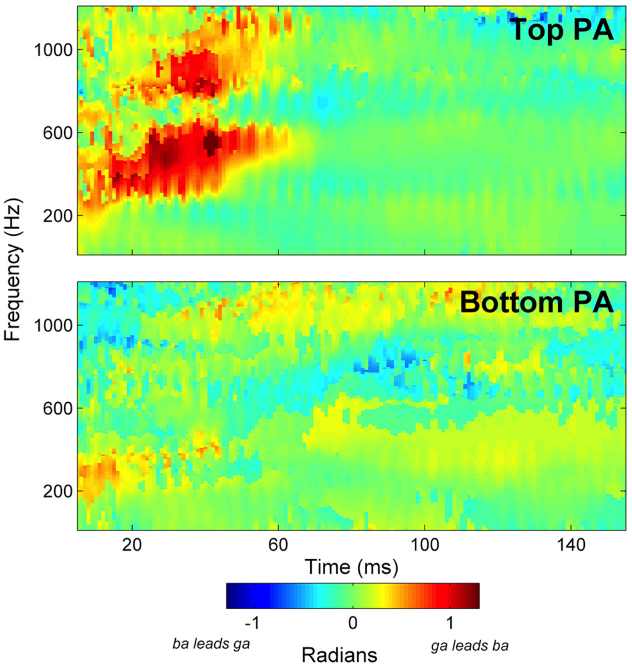

FIGURE 2 | Group average cross-phaseograms are presented for the Top phonological awareness (PA) and Bottom PA groups. The Top PA more strongly codes the difference between the [ba] and [ga] stimuli, as indicated by the large red–orange swatches in response to the CV transition.

Individual phase distinctions for each group are presented in **Figure 3**. The majority of subjects in the Top PA group had positive phase distinctions whereas most subjects in the Bottom PA group had either very small phase distinctions or distinctions in the opposite of the expected direction (i.e., responses to [ba] phase lead those to [ga]). It is also noteworthy that the magnitude of the largest phase distinctions in the Top PA group exceeds those observed in the Bottom PA group.

Finally, a trending correlation between CELF score and phase distinction was observed (Spearman's $\rho(26) = 0.38$, $p = .056$) with higher scores on the CELF corresponding to larger phase distinction. We suspect that with a larger subject group, and relatively fewer subjects at ceiling on the CELF, this relationship would be stronger.

PHASE DISTINCTIONS IN THE CONSONANT-VOWEL TRANSITION, 750-1000 Hz

To further explore group differences, and to ensure that there were no phase distinctions in response to the vowel, additional analyses were pursued. The first analysis focused on the higher frequency phase distinction (25—55 ms × 750—1000 Hz). As indicated in

Table 1 | Demographics for the top and bottom phonological awareness groups are summarized.

	Top PA ($N = 14$)	Bottom PA ($N = 12$)
Males	6	6
Family history of dyslexia	2	2
CELF cutoff	≥ 20	≤ 18
CELF (raw score)	22.0 (1.7)	15.4 (2.0)
Non-verbal IQ (percentile)	70.8 (24.6)	79.4 (19.9)

Groups are matched on all criteria except CELF score. The number of males and number of subjects in each group with a family history of dyslexia are reported. Means (with SDs) are reported for the CELF and for the non-verbal IQ test (Matrix Reasoning sub-test of the WPPSI)

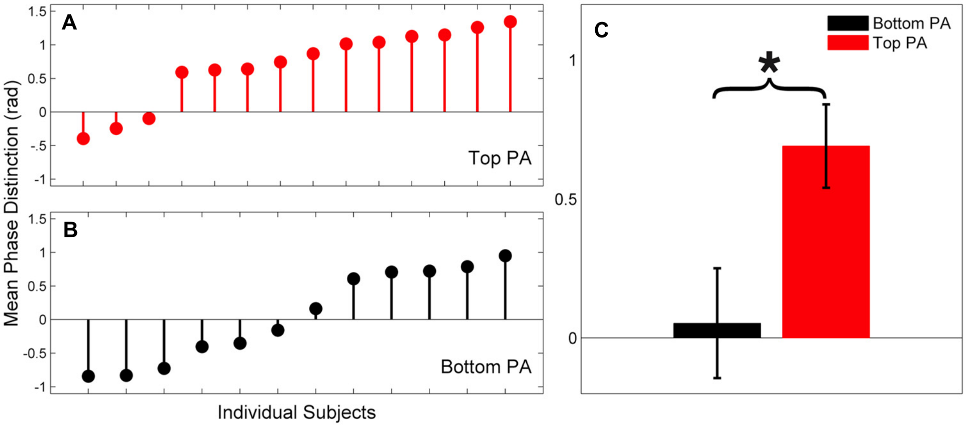

FIGURE 3 | (A,B) Phase distinctions for individual subjects (15–55 ms × 300–600 Hz) are presented for the Top PA (Panel A, red) and Bottom PA (Panel B, black) groups. **(C)** Group means are presented. Error bars, ± 1 SEM; $^*p < 0.05$.

Table 2 | Mean phase distinctions for the two frequency ranges are reported for each group (in rad, with SDs).

		Top PA	Bottom PA
300–700 Hz	Transition	0.690 (0.56)	0.053 (0.69)
	Vowel	−0.041 (0.16)	0.084 (0.56)
750–1000 Hz	Transition	0.551 (0.50)	0.074 (0.74)
	Vowel	−0.075 (0.34)	−0.144 (0.29)

Figure 2, the Top PA group had a larger mean phase distinction than the Bottom PA group, $t(24) = 2.00$, $p = 0.06$, Cohen's $d = 0.82$.

PHASE DISTINCTIONS IN THE VOWEL REGION

Since the [ba] and [ga] stimuli are identical in the steady state vowel portions no phase distinction is expected in this region. This is reflected in **Figure 2** where green indicates a phase difference of about 0 rad. To confirm this statistically, mean phase angles were calculated for the same frequency regions as in the transition from 60 to 155 ms. There were no group differences in phase distinction for the lower frequency region (300–700 Hz; $t(24) = 0.81$, $p = 0.427$) or higher frequency region (750–1000 Hz, $t(24) = 0.55$, $p = 0.589$).

DISCUSSION

We assessed the physiologic discrimination of stop consonants in a group of 4-year-old children and reveal a link between this discrimination and phonological awareness. Children with higher phonological awareness had superior neural discrimination of the stop consonants [ba] and [ga], as inferred by far-field electrophysiology. Conversely, children who performed worse on the phonological awareness test, on average, did not robustly distinguish these speech sounds. This relationship has previously been observed in school age children, with neural speech discrimination varying in concert with phonological awareness (Hornickel et al., 2009). By demonstrating this relationship in pre-school children too young to have attained full reading competence we can begin to trace the developmental trajectory of the primitives necessary for complex language-based tasks such as reading. However, we do not know if these children with weak consonant differentiation will soon develop a strong neural differentiation and end up as normal readers, or if they will face challenges as they learn to read. The latter possibility would suggest that these children are at risk for a reading disorder. Regardless, this relationship highlights the role of central auditory processing in developing language skills, and complements phonological deficit theories of reading.

One interpretation of the current results is that they reflect different levels of maturation. The auditory system undergoes rapid developmental plasticity through the first several years of life, and this is reflected in subcortical (Johnson et al., 2008; Skoe et al., in press) and cortical evoked potentials (Choudhury and Benasich, 2011). Individual differences in this rate of maturation may explain the variability in the [ba]-[ga] phase distinction. We do not think this vitiates the link between subcortical auditory function and phonological processing, however. After all, slower maturation of the neural processes important for phonological development may set certain children at a disadvantage when they begin learning to read. Nevertheless, the functional developmental consequences of this maturation for reading (dis)ability remain to be seen.

TEMPORAL SAMPLING: A SYSTEM-WIDE PERSPECTIVE

Goswami (2011) has proposed a theoretical framework to understand developmental dyslexia, the "temporal sampling framework" (TSF). Under TSF, the core deficit in dyslexia is phonological and is due to impaired oscillatory phase locking for low frequency temporal coding in auditory cortex. An attractive feature of TSF is that it resolves many apparent discrepancies between competing theories of developmental dyslexia. Support for TSF may be found in a large series of psychophysical and neurophysiologic investigations (Witton et al., 1998; Goswami et al., 2002, 2011; Serniclaes et al., 2004; Noordenbos et al., 2012, 2013; Leong and Goswami, 2013; Power et al., 2013).

Although TSF predicts deficient slow cortical phase locking in dyslexia (at rates < 30 Hz; Goswami, 2011), our demonstration of a link between high frequency phase locking in the subcortical auditory system and phonological processing may also be consistent with TSF. While TSF predicts superior *cortical* phase locking at fast rates for dyslexics, and here we report a deficit for high frequency temporal coding in auditory midbrain, we advocate for a systems-level perspective with different "optimal" rates of phase locking as a function of the physiology of the site of interest along the auditory pathway. We see this as compatible with TSF because our view is that the auditory system is best thought of as an integrated circuit that interacts dynamically with cognitive, reward, and other sensory systems (Kraus and Nicol, in press; Kraus and Chandrasekaran, 2010; Bajo and King, 2012; Anderson et al., 2013). The subcortical evoked response we analyzed in the current paper (and others from our group) is generated predominantly by inferior colliculus (IC; for review see Chandrasekaran and Kraus, 2010). Most IC neurons phase lock in the range of 100–1000 Hz (Liu et al., 2006) which is 10-fold the range of the impaired theta and delta oscillatory phase locking in auditory cortex observed in dyslexia (Goswami, 2011). Optimal phonological coding may rely on the interaction of rapid temporal sampling in IC with relatively slow sampling in auditory cortex. Indeed, Abrams et al. (2006) reported that subcortical timing was linked to the temporal integrity of auditory cortical speech coding. Wible et al. (2005) reported correlated subcortical and cortical neural synchrony in representing speech, both of which were diminished in children with language-based learning problems.

That said, relatively little is known about the temporal coding of low frequency information in IC (i.e., < 30 Hz), which may in fact be deficient in dyslexics. Recordings from cat IC do demonstrate phase locking as low as 10 Hz (Langner and Schreiner, 1988), however, the lower limits of phase locking in human IC, and more broadly the oscillatory dynamics of IC, remain an avenue for future research. Temporal coding at multiple rates may occur in parallel through the auditory pathway; evidence from a guinea pig model suggests that a paralemniscal thalamocortical pathway relays slow temporal information to auditory cortex in parallel with fast temporal information relayed through a lemniscal pathway (Abrams et al., 2011). Therefore, a full elucidation of the relationship between auditory phase locking and reading ability on a system-wide level will likely have to accommodate simultaneous temporal coding at multiple rates.

Further support for this integrated view of system-wide temporal coding comes from the rhythm perception literature, which has connected poor reading with an impaired ability to entrain to an external beat and impoverished perception of musical meter (Thomson et al., 2006; Huss et al., 2011; Tierney and Kraus, 2013b). This rhythmic entrainment seems to rely on auditory cortical phase locking (Power et al., 2012). However, the ability to entrain to an external beat is also linked to rapid *subcortical* phase locking and neural synchrony (Tierney and Kraus, 2013a), again suggesting that phase locking across multiple temporal rates may support perceptual skills linked to reading, if not phonological processing itself. An overarching theoretical framework for reading, then, may have to include relatively rapid subcortical phase locking as a key component that interacts with slower cortical oscillatory sampling. Both rapid and slow sampling likely rely on the synchronous firing of neurons in the auditory system, which supports precise representation of transient sounds (McGinley et al., 2012), 0.1 ms precision timing (Anderson et al., 2012), and speech discrimination (Engineer et al., 2008). And once again, dyslexia has been linked to deficits in neural synchrony as observed in humans (Hornickel and Kraus, 2013) and a rat model (Centanni et al., 2013).

This view would be also consistent with the Rapid Auditory Processing theory of developmental dyslexia (RAP; Tallal, 1980; Benasich and Tallal, 2002). Decreased sensitivity to rapidly changing phonological features could drive the impoverished distinction between speech sounds. Previous work has demonstrated that lengthening formant transitions in speech can improve the *cortical* discrimination of speech sounds (Bradlow et al., 1999; Steinschneider and Fishman, 2011), but it is unknown what effect this has on *subcortical* discrimination. Finally, we note that these our findings would be broadly consistent with the view that there are general, non-linguistic sensory deficits in dyslexia (Wright et al., 1997; Stein, 2001; Ahissar et al., 2006). Future work, therefore, should consider the interactions of acoustics, phonemics, and behavioral relevance in subcortical temporal processing.

A BIOMARKER FOR SUBSEQUENT READING ABILITY?

Although it is important to develop and refine empirically based theories of reading, it is also important to develop methods to identify children at risk for reading disorders. Previous neurophysiologic studies have identified cortical predictors of dyslexia, such as slower right hemisphere polarity shifts in evoked responses to speech (Guttorm et al., 2005; for review, see Leppänen et al., 2012). The structural integrity and volume of left articulate fasciculus is diminished in young children with poor phonological awareness (Saygin et al., 2013). Performance on speech perception tasks is also predictive (Benasich and Tallal, 2002), in addition to oscillatory dynamics in the infant brain (Gou et al., 2011). While the current analysis is not longitudinal, the techniques employed here may one day be useful for predicting future reading ability, either independently or as a complement to existing techniques. In fact, the children in the current study will be tracked over the next several years in hopes of identifying early predictors of subsequent reading ability. We note that the CELF phonological awareness test combines many subskills under the phonological awareness construct (Wiig et al., 2004); it is unknown if group differences are driven primarily by one or two of these subskills, and future investigation is warranted to look specifically at which aspects of phonological awareness are linked to auditory system development.

There are a number of attractive features of the "cross-phaseogram" as a potential biomarker. For one, it is a fast and objective automated procedure. Moreover, as we illustrate here, this measure relates to individual differences in language-based skills. Subcortical evoked responses to speech are relatively easy to obtain and meaningful in individuals (Skoe and Kraus, 2010). From a practical standpoint, responses may be elicited when a child is sleeping or watching a video, thereby eliminating the need for subject compliance in task-related physiologic measurements. And by following the children in this study longitudinally, we may be able to explore individual differences in neurophysiology that distinguish between individual presentations of dyslexia.

DYSLEXIA, TREATMENT, AND THE SEARCH FOR A CORE DEFICIT

A number of short-term interventions have been employed to improve phonological abilities and reading skills, and these offer further insight into the biological foundations of reading. Some of these studies have focused on perceptual deficits related to poor phonological processing (Tallal et al., 1996; Temple et al., 2003). Other interventions have been broader, such as assistive listening devices that improve classroom signal-to-noise ratios by directing attention to meaningful sound – and in fact also improve neural synchrony in response to speech (Hornickel et al., 2012). Non-speech training such as playing action video games, which improve attentional abilities (Green and Bavelier, 2012), can also improve reading skills (Franceschini et al., 2013), suggesting a role for non-auditory mechanisms in reading development and/or remediation.

Music training, which engenders a host of auditory perceptual and cognitive benefits, may also hold promise. Since precise temporal coding of sound supports fundamental reading skills, and this coding is strengthened by musical experience, it stands to reason that music training may promote the development of reading-related skills (Tierney and Kraus, 2013c). In fact, music experience has been directly linked to improved phonological skills and reading (Moreno et al., 2009; Besson et al., 2011), in addition to physiologic discrimination of speech sounds, as presented in the current study (Parbery-Clark et al., 2012; Strait et al., 2013). Given the established link between rhythm skills and phonological abilities, the rhythmic components of music training may be especially important for developing language-based skills. In fact, Bhide et al. (2013) reported that a comprehensive rhythm training regimen improves phonological skills.

To understand the biological bases of reading, and develop strategies that engender reading skills and remediate dyslexia, it is important to identify which skills to target. In this regard, the quest for the core deficit is important. That said, this search may at times cloud the principal problem, namely, that certain children have tremendous difficulty learning to read. Moreover, the possibility remains that no single deficit accounts for every child who has difficulty reading. Our view is that even without a full understanding of the pathophysiology of dyslexia it is important to identify children at risk as early as possible. Here we have identified a neural correlate of early phonological awareness in pre-school age children. Due to the importance of precise phonological representations for reading this correlate may indicate a biological bottleneck certain children face when they begin to learn to read.

AUTHOR CONTRIBUTIONS

Travis White-Schwoch and Nina Kraus designed the study; Travis White-Schwoch oversaw data collection and analyzed the data; Travis White-Schwoch and Nina Kraus wrote the paper.

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Neural entrainment to rhythmic speech in children with developmental dyslexia

Alan J. Power*, Natasha Mead, Lisa Barnes and Usha Goswami

Department of Psychology, Centre for Neuroscience in Education, University of Cambridge, Cambridgeshire, UK

Edited by:
Andrea Facoetti, Università di Padova, Italy

Reviewed by:
April A. Benasich, Rutgers University, USA
Gabriella Musacchia, Montclair State University, USA (in collaboration with April A. Benasich)
Chiara Cantiani, IRCCS Eugenio Medea, Italy

****Correspondence:***
Alan J. Power, Department of Psychology, Centre for Neuroscience in Education, University of Cambridge, Downing Street, CB23EB Cambridgeshire, UK
e-mail: ajp218@cam.ac.uk

A rhythmic paradigm based on repetition of the syllable "ba" was used to study auditory, visual, and audio-visual oscillatory entrainment to speech in children with and without dyslexia using EEG. Children pressed a button whenever they identified a delay in the isochronous stimulus delivery (500 ms; 2 Hz delta band rate). Response power, strength of entrainment and preferred phase of entrainment in the delta and theta frequency bands were compared between groups. The quality of stimulus representation was also measured using cross-correlation of the stimulus envelope with the neural response. The data showed a significant group difference in the preferred phase of entrainment in the delta band in response to the auditory and audio-visual stimulus streams. A different preferred phase has significant implications for the quality of speech information that is encoded neurally, as it implies enhanced neuronal processing (phase alignment) at less informative temporal points in the incoming signal. Consistent with this possibility, the cross-correlogram analysis revealed superior stimulus representation by the control children, who showed a trend for larger peak *r*-values and significantly later lags in peak *r*-values compared to participants with dyslexia. Significant relationships between both peak *r*-values and peak lags were found with behavioral measures of reading. The data indicate that the auditory temporal reference frame for speech processing is atypical in developmental dyslexia, with low frequency (delta) oscillations entraining to a different phase of the rhythmic syllabic input. This would affect the quality of encoding of speech, and could underlie the cognitive impairments in phonological representation that are the behavioral hallmark of this developmental disorder across languages.

Keywords: neural entrainment, developmental dyslexia, low frequency oscillations, temporal sampling, audio-visual

INTRODUCTION

Temporal coding is a critical aspect of speech processing and is fundamental to phonological representation, the mental representation of the sound structure of human languages. Temporal coding is thought to be accomplished in part by the synchronous activity of networks of neurons in auditory cortex that align their endogenous oscillations at different preferred rates with matching temporal information in the acoustic speech signal (Poeppel, 2003; Lakatos et al., 2008; Giraud and Poeppel, 2012). Speech involves auditory, visual and motor modalities, and both auditory and visual information in speech unfold over multiple timescales. Accordingly, oscillating networks of neurons in auditory *and visual* cortices are thought to "phase lock" or "phase align" their ongoing activity with matching modulation rates in the input (Luo et al., 2010). For human speech, the visuo-spatial information generated by face, cheek and mouth movements is temporally predictive of the production of speech sounds, and may "reset" auditory cortex to the optimal phase for processing succeeding vocalizations (Schroeder et al., 2008). *Multi-time resolution models* (MTRMs) of speech processing capitalize on these neurophysiological processes (e.g., Poeppel, 2003; Ghitza and Greenberg, 2009), and argue that the neural entrainment of these oscillatory networks is occurring at multiple temporal rates in both visual and auditory cortices, with hierarchical and interdependent cross-modal phase interactions, resulting in a coherent representation of the signal and enabling communication between human listeners.

A large literature suggests that temporal coding in both the auditory and visual modalities may be atypical in individuals with developmental dyslexia, a specific learning difficulty affecting reading and spelling that affects approximately 7% of children across languages (e.g., Witton et al., 1998; Snowling et al., 2000; Ziegler and Goswami, 2005; Lallier et al., 2009; Facoetti et al., 2010; Goswami et al., 2011; Hämäläinen et al., 2012a). Developmental dyslexia is not due to low intelligence, poor educational opportunities, or overt sensory or neurological damage. The primary cognitive difficulty found in dyslexia across languages is a difficulty in the accurate neural representation of phonology, the sound structure of words. Children with dyslexia are poorer than age- and reading-level matched controls at identifying and manipulating phonological units in words, for example, they are poorer at counting *syllables* (e.g., 3 syllables in "popsicle"), at identifying *rhymes* (e.g., "cat" and "hat" rhyme, "cat" and "hot" do not rhyme), and at recognizing shared *phonemes* (the smallest speech sounds that change meaning, e.g., "clip" and "quip" share the initial phoneme,/k/; see Ziegler and Goswami, 2005, for review). Children with dyslexia are also significantly impaired compared to younger reading level controls in prosodic awareness tasks, such as tasks requiring the identification of syllable stress (Goswami et al., 2013). These difficulties with phonology appear to precede learning to read (Lyytinen et al., 2001), and are also found in children with dyslexia who are learning non-alphabetic scripts. For example, Japanese Kana uses orthographic characters that represent syllables rather than phonemes, and Japanese children with dyslexia find syllable reversal tasks difficult (Kobayashi et al., 2003). Given the importance of neuronal oscillations for speech processing as revealed by multi-time resolution models, it is plausible that the phonological deficits found in dyslexia across languages could be related to impaired or atypical oscillatory mechanisms at one or more temporal rates in either auditory cortex, visual cortex or during audio-visual integration.

Accordingly, and building on the prior work noted above on MTRMs for speech processing, a "temporal sampling" framework (TSF) for developmental dyslexia has been proposed. The TSF suggests that the phonological deficit found in dyslexia across languages might be due in part to impaired or functionally atypical entrainment mechanisms for phonology in auditory cortex, particularly oscillations at the slower temporal rates (theta and delta) that are relevant to syllabic and prosodic processing (Goswami, 2011). As syllable awareness in children develops before phonological awareness of rhymes and phonemes (Ziegler and Goswami, 2005), and as syllables are the primary processing unit in all human languages (Greenberg et al., 2003), atypical entrainment mechanisms related to syllabic phonology would have effects throughout the phonological system in all languages, consequently affecting the phonological representation of smaller units such as rhymes and phonemes. According to multi-time resolution models of speech processing (Giraud and Poeppel, 2012), identification of phonetic segments is related to faster temporal modulations (gamma rate, 30–80 Hz), identification of syllables is related to slower modulations at the theta rate (4–10 Hz), and information relating to syllable stress and prosodic patterning is related to modulations at the delta rate (1.5–4 Hz). Here we provide the first direct test of the TSF with children with developmental dyslexia, utilizing a rhythmic speech paradigm previously developed for typically-developing children (Power et al., 2012b) to measure oscillatory entrainment to phonological information in dyslexia.

Oscillatory entrainment in humans has so far been measured by EEG in rhythmic paradigms, as by hypothesis endogenous oscillations should phase-reset their activity to the rhythmic information in the input, synchronizing cell activity so that peaks in excitation co-occur with stimulus delivery, thereby enhancing neural processing (Lakatos et al., 2005; Canolty et al., 2006). Whereas early studies of oscillatory entrainment in EEG utilized rhythmic streams of non-speech stimuli, such as tones or flashes of light (Lakatos et al., 2008; Stefanics et al., 2010; Gomez-Ramirez et al., 2011), we (Power et al., 2012b) designed a *speech* paradigm based on rhythmic repetition of the syllable "ba" by a female speaker. The repetition rate was 2 Hz, and participating 13-year-old children either saw a "talking head" so that both visual and auditory information was present (audio-visual or AV condition), saw the talking head without sound, so that only visual information was present (visual [V] condition), or heard the stimulus stream in the absence of visual stimulation (auditory [A] condition). The children were asked to detect occasional rhythmic violations in each condition (A, V, AV), when the syllable was slightly late and therefore out of time. We found significant entrainment at the stimulation rate (delta, 2 Hz) in all conditions, and also significant entrainment at the *theta* rate in the auditory and AV conditions. Consistent with the predictions of MTRMs of speech processing, therefore, theta entrainment was important in processing this syllabic input. Furthermore, individual differences in the strength of theta entrainment (measured by inter-trial coherence or phase consistency) were related to measures of phonological processing and reading in this typically-developing child sample. Higher phase consistency was associated with higher behavioral performance. Further, the preferred phase of auditory entrainment was altered by congruent visual information (AV condition), suggesting that visual speech information modulated auditory oscillations to the optimal phase for speech processing in these 13-year-old participants, consistent with Schroeder et al. (2008).

The TSF proposes that auditory oscillatory entrainment to phonological information at both delta and theta rates may by atypical in developmental dyslexia, and that atypical auditory entrainment might also have consequences for visual oscillatory entrainment to speech via cross-modal and cross-frequency phase alignment. The rhythmic speech paradigm that we developed (Power et al., 2012b) can also be used to study entrainment in children with dyslexia. Accordingly, we recruited a group of children with dyslexia, and matched their performance as a group to that of a sub-set of the typically-developing children who had participated in our previous study. The TSF enables a number of plausible predictions with respect to our dyslexic group. The simplest possibility is that the children with dyslexia should show significantly less entrainment to the auditory stimulus stream, at both delta and theta rates (reduced inter-trial coherence or phase consistency). Once cross-modal information is available, however, it is plausible that children with dyslexia may show strength of entrainment that is *equivalent* to typically-developing children (as visual information may modulate auditory oscillations to the optimal phase for speech processing). Indeed, children with dyslexia may rely *more* on visual speech information than typically-developing children, in order to *compensate* for their impaired auditory processing skills. A recent study of audio-visual processing of noise vocoded speech by adults with and without dyslexia produced some evidence for atypical visual processing of low frequency modulations in those with dyslexia in a non-rhythmic paradigm (Megnin-Viggars and Goswami, 2013). Nevertheless, the same study also produced some data suggestive of visual compensation. Other studies of rhythmic entrainment in adults with dyslexia have focused on the auditory modality.

In one relevant study utilizing MEG, we (Hämäläinen et al., 2012b) played amplitude-modulated white noise at 4 temporal rates (2, 4, 10, 20 Hz) to adults with and without dyslexia in an unattended listening paradigm (the participants were watching a silent video). On the basis of the TSF, we expected group differences in neuronal oscillatory entrainment at the slower AM rates (2 Hz, 4 Hz). The data showed significantly less entrainment by the participants with dyslexia in right hemisphere auditory networks to the 2 Hz rate only. There was also significantly weaker entrainment overall (adding across modulation rates) in the right hemisphere for those with dyslexia. As the right hemisphere is thought to prefer slower temporal rates (delta, theta, see Poeppel et al., 2008), these results were considered to be consistent with the TSF. Hamalainen et al. also found that the dyslexic group also showed significantly stronger entrainment to the 10 Hz rate in the *left* hemisphere, a finding which was not predicted. This could indicate compensatory entrainment at faster temporal rates. In a second study investigating dyslexia using EEG and an attended paradigm, we (Soltesz et al., 2013) compared rhythmic entrainment in adults with and without dyslexia to a tone stream delivered at 2 Hz (Soltesz et al., 2013). The task was to press a button whenever white noise replaced a tone in the stream, as in a standard auditory oddball paradigm. In this study, the strength of entrainment as measured by inter-trial coherence (ITC) was significantly reduced in the participants with dyslexia, even though they were as fast and as accurate as the controls in the button-press paradigm. Whereas response time in controls was significantly related to the instantaneous phase of the delta oscillation, with faster responses in the rising phase of the oscillation, participants with dyslexia showed no such relationship. This suggests that the oscillatory function of low frequency brain rhythms may be atypical in dyslexia (Soltesz et al., 2013).

However, an alternative oscillatory framework for dyslexia has been developed by Giraud and her colleagues, who have proposed that a single auditory anomaly, phonemic sampling in left auditory cortex, accounts for the three major aspects of impaired phonological processing in dyslexia (which are impaired phonological awareness, impaired rapid automatized naming [RAN], and impaired phonological memory, see Lehongre et al., 2011; Giraud and Poeppel, 2012). In a passive listening study with adults with dyslexia using MEG, Lehongre et al. (2011) presented amplitude-modulated white noise at rates that increased incrementally from 10 to 80 Hz, and measured the auditory steady state response (ASSR) while participants watched a silent video. Of particular theoretical interest were oscillations in the low gamma band (25–35 Hz), thought to reflect optimal phonemic encoding. Both dyslexic and control participants showed significant phase locking as measured by the ASSR, but hemispheric differences were found between groups, with left-dominant entrainment shown by the control participants only. When faster temporal rates were considered (>50 Hz), then those with dyslexia showed stronger entrainment bilaterally than controls. Lehongre and colleagues then computed the degree of leftward asymmetry shown by each participant at the low gamma rate for ASSR power, and correlated this measure with the phonological measures. Significant relations with phonological processing (a global construct measure made up of Spoonerisms, digit span and nonword repetition) and rapid naming were found when the dyslexics were considered alone, but not for controls alone nor for the total sample. Lehongre et al. (2011) argued that their data suggested a focal (left-lateralized) impairment of selective extraction and encoding of phonemic information, which would not be expected to affect global sensitivity to amplitude modulation. Phonemic oversampling was also proposed by Giraud and Poeppel (2012) to underpin the phonological "deficit" in dyslexia. The oscillatory nesting observed between theta/delta phase and gamma power (Schroeder and Lakatos, 2009; Canolty and Knight, 2010) was argued by Lehongre et al. (2011) to provide a means by which information at the phonemic (gamma) rate is integrated at the syllabic rate.

In the only neuroimaging study of which we are aware to *compare* slow rate (<10 Hz) and faster rate (20 Hz) oscillatory entrainment in dyslexia, the auditory steady state response was recorded to speech-weighted noise stimuli amplitude modulated at either 4 Hz, 20 Hz or 80 Hz (Poelmans et al., 2012). Participants were dyslexic and control adults, the task was passive listening, and EEG recordings were analyzed at parietal and mastoid electrodes only. No group differences were found for the ASSRs to the 80 Hz and 4 Hz stimuli, but a significant group × laterality effect was found for the 20 Hz stimulus. For 20 Hz AM noise, dyslexic adults showed less power at left hemisphere electrodes compared to controls. Phase coherence *between and within hemispheres* was also computed, and a main effect of group was found at the 20 Hz rate for both measures. Adults with dyslexia demonstrated lower inter- and intra-hemispheric coherence than controls. Note that this phase measure is not related to the stimulus *per se*, rather the between-hemisphere results show that the relationship between the phase pattern at the selected electrodes is less similar for participants with dyslexia. As the 20 Hz rate yielded the only significant group differences, Poelmans et al. (2012) concluded that cortical processing of phoneme-rate modulations was impaired in dyslexia.

However, a series of studies with dyslexic adults based on nursery rhymes (rhythmically-produced speech) by Leong and Goswami (2013) has compared rhythmic entrainment in dyslexia at slower and faster rates using behavioral measures (tapping or speaking to a beat). Using modeling developed by Leong (2012), these nursery rhyme studies explored the role of *phase relations* between amplitude modulation at different rates in the speech signal in the perception and production of rhythmic speech. Building on MTRMs of speech processing and the oscillatory hierarchy (Poeppel, 2003; Schroeder et al., 2008; Giraud and Poeppel, 2012), Leong (2012) modeled entrainment to different AM rates in the speech signal using an *amplitude modulation phase hierarchy* (AMPH) approach. Leong assumed that the modulation hierarchy within the speech signal followed the oscillatory hierarchy, with the slowest rates *highest* in the hierarchy. In Leong's models, the slower rates (delta and theta) hence temporally constrain entrainment at the faster rates, such as gamma (for detail regarding these novel AMPH models of the speech signal, see Leong, 2012). Leong and Goswami (2013) demonstrated that participants used the *phase relationship* between delta- and theta-rate AMs (2 Hz and 4 Hz AM rates) to calibrate their rhythmic behavior. Importantly, Leong and Goswami found that adults with dyslexia showed an *earlier* preferred phase angle for theta entrainment compared to control participants. Individual differences in both theta and delta preferred AM phase were correlated with phonological awareness in a Spoonerisms task, and with reading development.

Concerning rhythmic speech *production* (measured by asking participants to speak rhythmically in time with a metronome beat at 2 Hz), Leong and Goswami (2013) reported that the two groups showed equivalent *strength* of entrainment in terms of internal phase locking between delta- and theta-AMs, and between theta- and gamma-AMs (stressed syllable, syllable and phoneme rates, respectively). However, the participants with dyslexia again preferred a different phase alignment of the AMs conveying syllable and phoneme information, respectively (theta- and gamma-AMs). A difference in phase locking *angle* implies a difference in how speech information at different temporal rates is bound together in the final speech percept (Poeppel, 2003). Leong and Goswami (2013) argued that the significant difference in phase-locking angle between syllable- and phoneme-relevant information in speech was consistent with the large behavioral database indicating that phonological information is represented *differently* in the dyslexic mental lexicon.

In the current study, participants are also perceiving rhythmic speech in an attended paradigm, and neuronal oscillatory entrainment can be measured *directly* at both the delta and theta rates of AM (whereas when tapping and speaking in time are the dependent measures, the measurement of entrainment is necessarily indirect because of additional motor demands). Given the preferred phase angle differences found in the studies with adults (Leong and Goswami, 2013), it is therefore possible that the preferred *phase of entrainment* will differ between dyslexic and control children in the current study, at least in the auditory condition, for either delta or theta phase (or both). The phase of entrainment of neuronal oscillation relative to a presented stimulus has been shown to be central to stimulus processing. It has been shown that oscillations entrain to stimuli at differing preferred phases (anti-phase, in fact) depending on whether they are being attended to or being ignored (Lakatos et al., 2008; Besle et al., 2011; Horton et al., 2013). Furthermore, the phase of pre-stimulus delta activity has been shown to be related to reaction times in a task where the target probability was manipulated, suggesting that efficiency of stimulus processing is related to oscillatory phase (Stefanics et al., 2010). EEG phase patterns have also been shown to reflect the selectivity of neural firing with single neurons more likely to fire at specific phases in response to an auditory stimulus (Ng et al., 2013). *These studies suggest that there is an optimal or preferred phase of entrainment which is necessary for accurate and efficient stimulus processing.* If preferred delta and/or theta phase is different for participants with dyslexia, then speech units such as syllables will occur at a sub-optimal phase, and will not be processed optimally. The result will be a degraded representation or encoding of the speech stimulus.

In order to see whether such potential differences in preferred phase would be related to the quality of children's phonological representations, two strategies were employed. First, a phoneme deletion task was administered to participants as a measure of phonological awareness, and was correlated with the entrainment measures. Secondly, a correlogram approach was used to measure the fidelity of the neuronal representation to the envelope information in the speech signal. The speech stimulus is a stream of syllables repeated rhythmically enabling the stimulus envelope to be cross-correlated with the envelope of the averaged neural response. The peak *r*-value from the cross-correlogram gives us an estimate of the strength of stimulus representation in the EEG. The lag at which this peak occurs gives a measure of the timing of stimulus envelope processing (this is a similar approach to Abrams et al., 2009). If the brain is representing a speech syllable with high fidelity but at a different temporal phase with respect to entrainment to the ongoing stimulus, group differences in peak lag would occur, which would again have implications for the overall quality of the phonological representation via the binding together of temporal information at different rates in the speech signal.

To summarize, phase values (entrainment strength or ITC and phase angle), peak *r*-values (correlation strength), and peak lag values (temporal phase measure) might be expected to differ between dyslexic and control participants at delta and theta rates according to the TSF. According to the model based on anomalous temporal sampling at the low gamma rate proposed by Lehongre and colleagues, no such differences might be expected. In contrast, it has also been proposed that dyslexic children are developing high-quality mental representations of speech, and that the cognitive "phonological deficit" found in dyslexia arises as a result of problems in *accessing* the mental lexicon (see Ramus and Szenkovits, 2008). If the neural phonological representations themselves are precise, then on this "intact representations" hypothesis no group differences in these neural measures of representational quality would be expected.

MATERIALS AND METHODS

PARTICIPANTS

We studied 21 typically-developing children and 11 children with a history of developmental dyslexia (mean ages of 165.57 ± 12.71 months and 166.73 ± 13.72 months, respectively). All children were taking part in a longitudinal behavioral study of auditory processing (Goswami et al., 2011). All participants and their guardians gave informed consent for EEG in accordance with the Declaration of Helsinki, and the study was approved by the Psychology Research Ethics Committee of the University of Cambridge. All participants were free of any diagnosed learning difficulties aside from dyslexia (i.e., dyspraxia, ADHD, autistic spectrum disorder, speech and language impairments) and spoke English as their first language.

STANDARDIZED TESTS OF READING, NONWORD READING, VOCABULARY AND IQ

Psychometric tests were given for the purposes of group matching and also exploring possible relations between entrainment and the development of spoken and written language skills. The psychometric tests comprised the British Ability Scales (BAS) (single word reading, Elliott et al., 1996); the single word reading (SWE) and phonemic decoding efficiency (PDE) measure of non-word reading from the TOWRE (Torgesen et al., 1999); the British Picture Vocabulary Scales (BPVS receptive vocabulary, Dunn et al., 1982); and one subtest of the Wechsler Intelligence Scale for Children (WISC-III, Wechsler, 1992): picture arrangement. Performance on these measures is shown in **Table 1**.

EXPERIMENTAL PHONOLOGICAL TASKS

In order to see whether individual differences in entrainment would relate to individual differences in phonological processing between children, participants were administered a phoneme

Table 1 | Group differences in Age, IQ, and behavior.

Measure	CA	DY	$F_{(1, 30)}$	*p*
Age (months)	165.57 ± 12.71	166.73 ± 13.72	0.057	0.814
IQ	112.76 ± 13.31	114.64 ± 14.07	0.138	0.713
BAS standard score	109.29 ± 11.86	86.18 ± 15.5	22.729	<0.001
Reading age (months)	177.00 ± 20.7	134.55 ± 27.52	24.186	<0.001
TOWRE word reading	103.48 ± 10.33	87.91 ± 7.82	19.125	<0.001
TOWRE non-word reading	107.62 ± 11.21	81.55 ± 10.99	39.559	<0.001
BPVS not aligned	107.71 ± 13.28	100.1 ± 19.48	1.604	0.215
RAN TOTAL	34.67 ± 3.95	38.91 ± 8.88	3.5830	0.070
pSTM	45.81 ± 11.25	35.91 ± 12.55	5.170	0.03
Phoneme deletion	16.48 ± 3.17	12.91 ± 3.89	7.825	0.009

deletion task, an experimental measure of phonological short-term memory (PSTM) and an experimental measure of rapid automatized naming (RAN). Further details for each task are given in Power et al. (2012b).

RHYTHMIC ENTRAINMENT TASK

Rhythmic speech comprising multiple repetitions of the syllable "BA" was presented at a uniform repetition rate of 2 Hz. There were three conditions: auditory (A), visual (V), and audio-visual (AV). Further details of the task can be found in Power et al. (2012b). **Figure 1** summarizes the paradigm.

EEG PREPROCESSING

This was exactly as in Power et al. (2012b).

EEG ANALYSIS

For all analyses, the first three observations in each entrainment period were discarded to ensure that rhythmicity had been established (following the approach employed in Gomez-Ramirez et al., 2011). Here we are interested in entrainment to a uniform stimulus repetition rate, and so responses in the violation and "return to isochrony" periods (see **Figure 1**) were not analyzed. Furthermore, sequences in which a target was not detected were discarded, as were catch trials. As accuracy was ~79% and 75 target sequences were presented per condition, the analysis included ~60 trials per subject per condition. In order to identify frequency bands of interest we examined the phase-locked power (i.e., the power of sequence averages in the time period of interest) in the three conditions (see **Figure 2**). Phase locked power was obtained as in Power et al. (2012b). Given the peaks evident in the spectra, with the highest phase-locked power present for delta and theta, we deemed the delta (~2 Hz) and theta (~4 Hz) frequency bands to be of interest (for further details see *Results* and *Discussion*). Frequency band activity was obtained using FIR filters designed using the Parks-McClellan algorithm (Parks and McClellan, 1972). The delta band filter had corner frequencies of 1 and 3 Hz and the theta band filter had corner frequencies of 3 and 5 Hz. Both had a 40 dB attenuation in the stop band. In order to examine whether auditory entrainment differed for the A and AV conditions, we subtracted an estimate of phase-locked visual activity from each AV trial (AV-V), and compared the remaining A and (AV-V) activity. The estimate of visual activity was obtained from the time-locked average activity in the visual condition.

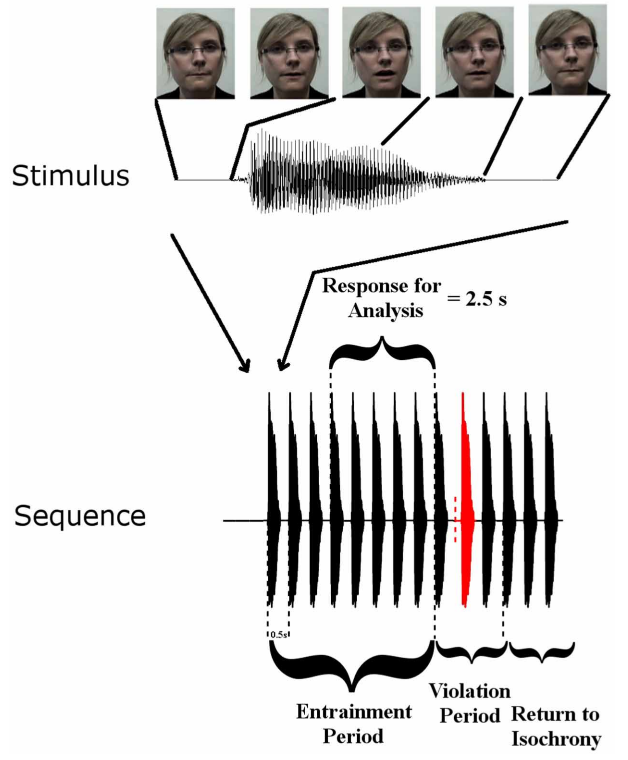

FIGURE 1 | Stimulus Setup: top panel shows one auditory "Ba" token and corresponding frames of the visual stimulus at five time points. Visual movement initiates 68 ms before auditory onset. The lower panel shows a stimulus sequence consisting of the entrainment period with SOA of 500 ms, and the violation period where SOA is disrupted, followed by 3 re-entrainment stimuli ("Return to Isochrony"). The red stimulus is the violator, whose position in the violation period is chosen at random (i.e., either the first, second, or third stimulus can violate the rhythm). The vertical dashed red line indicates where the stimulus would have onset if it had adhered to the isochronous stimulation rate. Also shown is the "Response for Analysis" period over which EEG responses were analyzed.

Power analysis

We wished to investigate possible differences in overall power between conditions and groups. This is important both in terms of potentially different EEG power in response to the various conditions, but also for interpreting differences in strength of phase locking. Higher inter-trial coherence (ITC) values may only be interpreted as improved phase consistency over trials if they are accompanied by no change in response power. If higher ITC is accompanied by a change in response power, it is possible that this is due to a stronger additive response as opposed to increased consistency over trials. To obtain the overall total power we calculated the FFT of the broadband responses for each trial for each subject and took the average. Thus, both phase-locked and non-phase locked power are included in the measure. Delta and theta power were extracted by taking the power at 2 and 4 Hz, respectively, from the overall broadband frequency representation.

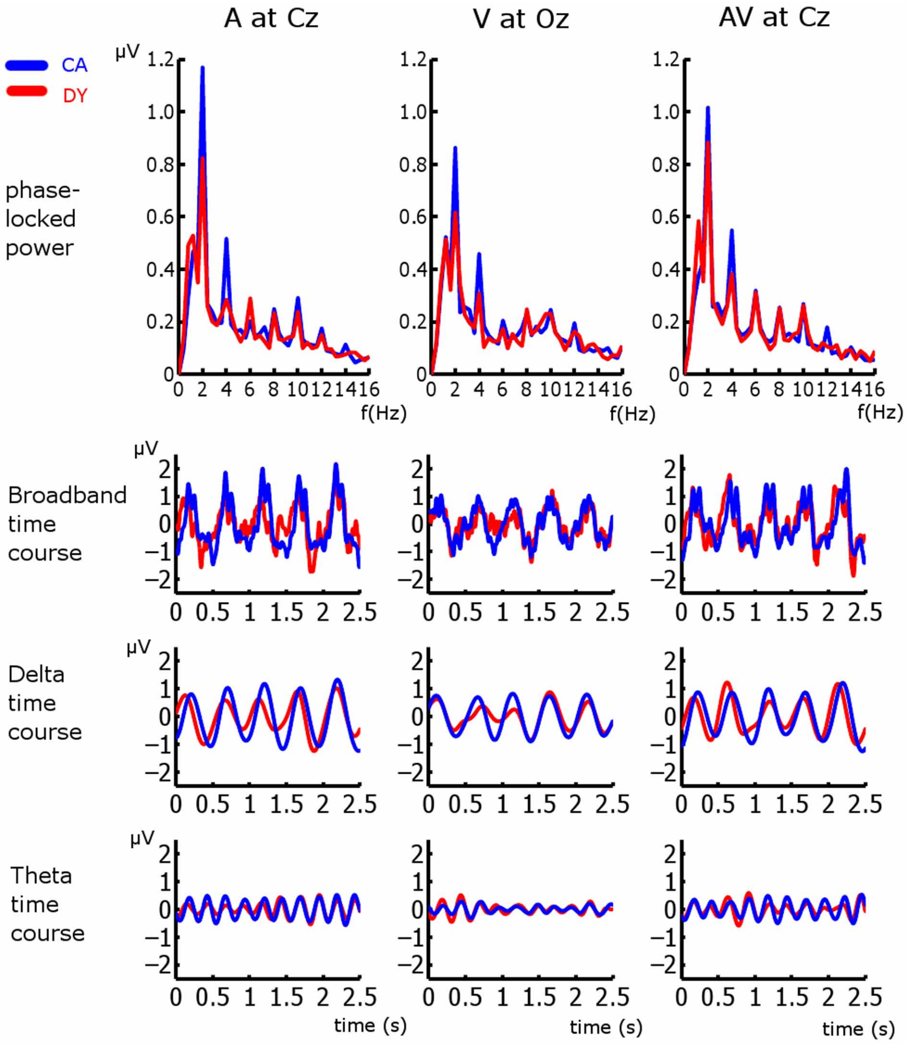

FIGURE 2 | Frequency spectra and broadband, delta, and theta time courses for all three conditions at representative electrodes. CA responses are in blue and DY response are in red.

Assessing phase-locking

The pre-stimulus phase of the last 5 stimuli in the entrainment period was obtained. The pre-stimulus phase is defined here as the phase at the onset of the visual element of the stimulus in the AV condition. This time point is kept consistent for all conditions (i.e., for the auditory condition phases are extracted at the time point where the visual stimulus would have onset, had the visual element of the stimulus accompanied the auditory information, this is 68 ms before auditory stimulus onset). Only sequences where the rhythmic violation was correctly identified are analyzed. These phase values were pooled across sequences and subjects. Given that 75 target sequences were presented to each subject and accuracy was ~79%, the number of phase observations was 6270, 6355, and 6155 (~60 sequences × 5 stimuli × 21 participants) observations for the control group for the auditory, visual and AV conditions, respectively. Similarly 3185, 3210, and 3250 observations were tested for the dyslexic group in the three conditions, respectively (~60 sequences × 5 stimuli × 11 participants). Pre-stimulus phase distribution histograms for each condition were obtained (see **Figure 3**). The phase values were extracted by obtaining the *analytic signal* of the filtered responses via the Hilbert transform. The *analytic signal* is complex, i.e., it has real and imaginary components, and thus the instantaneous phase can be extracted. To test if pre-stimulus phase distributions differed from uniformity, the distributions for the three conditions were tested against the null hypothesis of uniformity using the Rayleigh statistic at three representative electrodes (Fz, Cz, and Oz). A critical p-value of 0.001 was selected to minimize type I error. Statistical difference from uniformity suggests a preferred concentration of phase values, which is indicative of entrainment (Stefanics et al., 2010; Gomez-Ramirez et al., 2011).

Inter-trial coherence (ITC) was then used to compared strength of entrainment across groups, conditions, and channels. ITC is a measure of phase alignment and can have

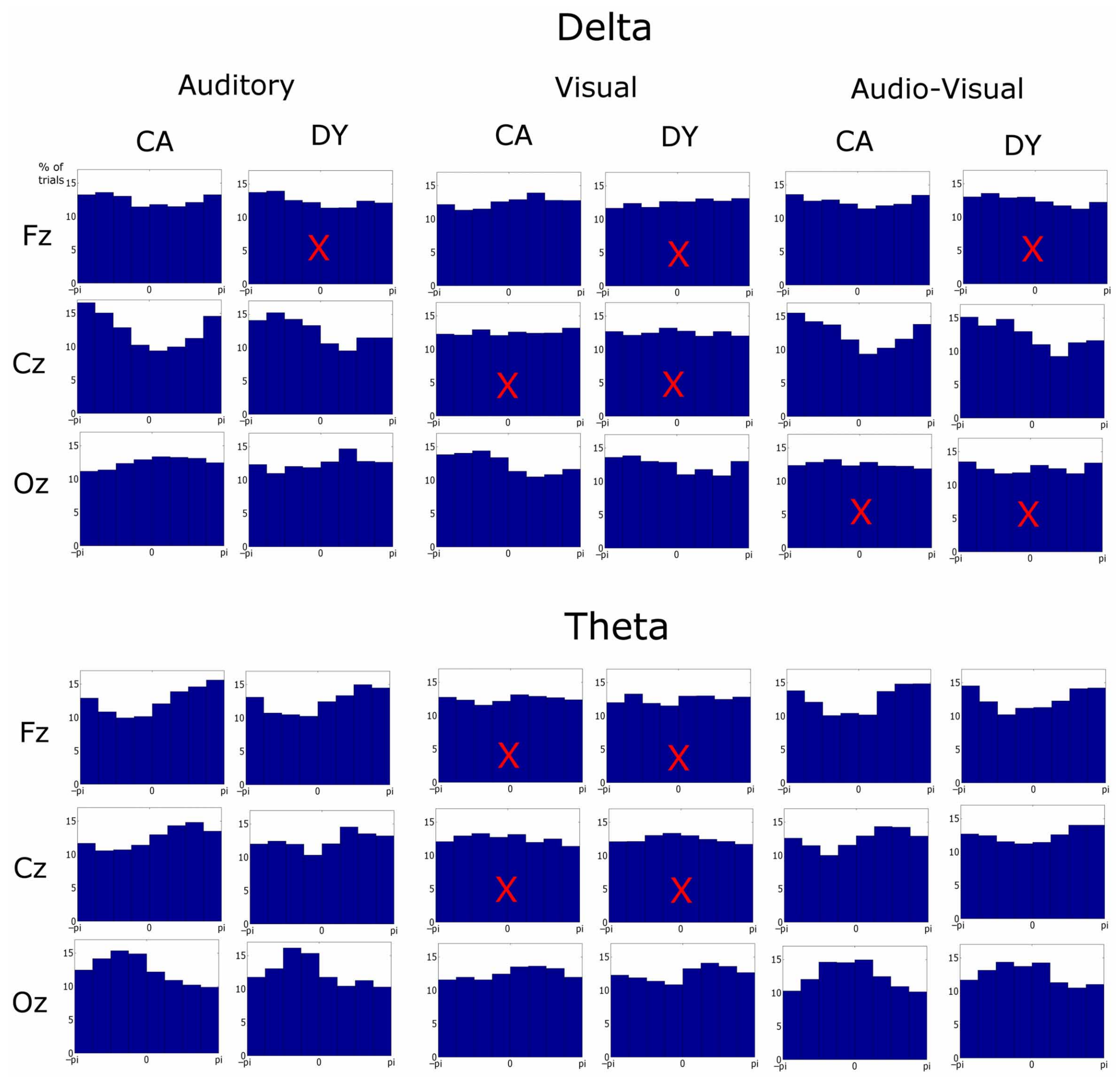

FIGURE 3 | Phase distributions at stimulus onset at representative frontal, central, and occipital electrodes in each condition, frequency band, and group. The *x*-axis is phase ranging from -π to π and *y*-axis represents the percentage of trials. Most distributions differed from uniformity when tested against the Rayleigh statistic at a critical *p*-value of 0.001. Distributions with a superimposed X did not result in significant entrainment.

values ranging from 0 to 1. 1 indicates perfect phase alignment and 0 indicates no phase alignment. ITC was calculated for the same pre-stimulus phase values that were submitted to the Rayleigh test. Preferred phase of entrainment between groups and conditions was also investigated (shown in **Figure 4**). The preferred phase of entrainment for each participant is obtained by calculating the mean pre-stimulus phase for that individual. Mean preferred phase for each group is then calculated for each condition (A, V, AV). If the phase at which the low frequency oscillations (delta, theta) entrain is different between the groups, this implies that the information encoded is different (neurons are firing at the "wrong" time, thus selectively encoding information at a sub-optimal point in the stimulus).

Cross-correlogram analysis of entrainment and laterality

Finally, in order to obtain converging evidence for entrainment, the relationship between the stimuli and the neural responses was also assessed using cross-correlations (see **Figure 5**). We then sought to relate measures of stimulus representation in the EEG data, obtained from these cross-correlations, to the behavioral data. To do this we employed peak *r*-values and the lags at which those peaks occurred. Peak *r*-values are a measure of the strength of stimulus representation in the EEG, and peak-lags are a measure of stimulus-response timing. We also tested potential hemispheric differences in the strength and timing of auditory encoding, following Abrams et al., 2009. To do this we found peak *r*-values and the lags at which those peaks occurred at three pairs of temporal electrodes. The temporal electrode

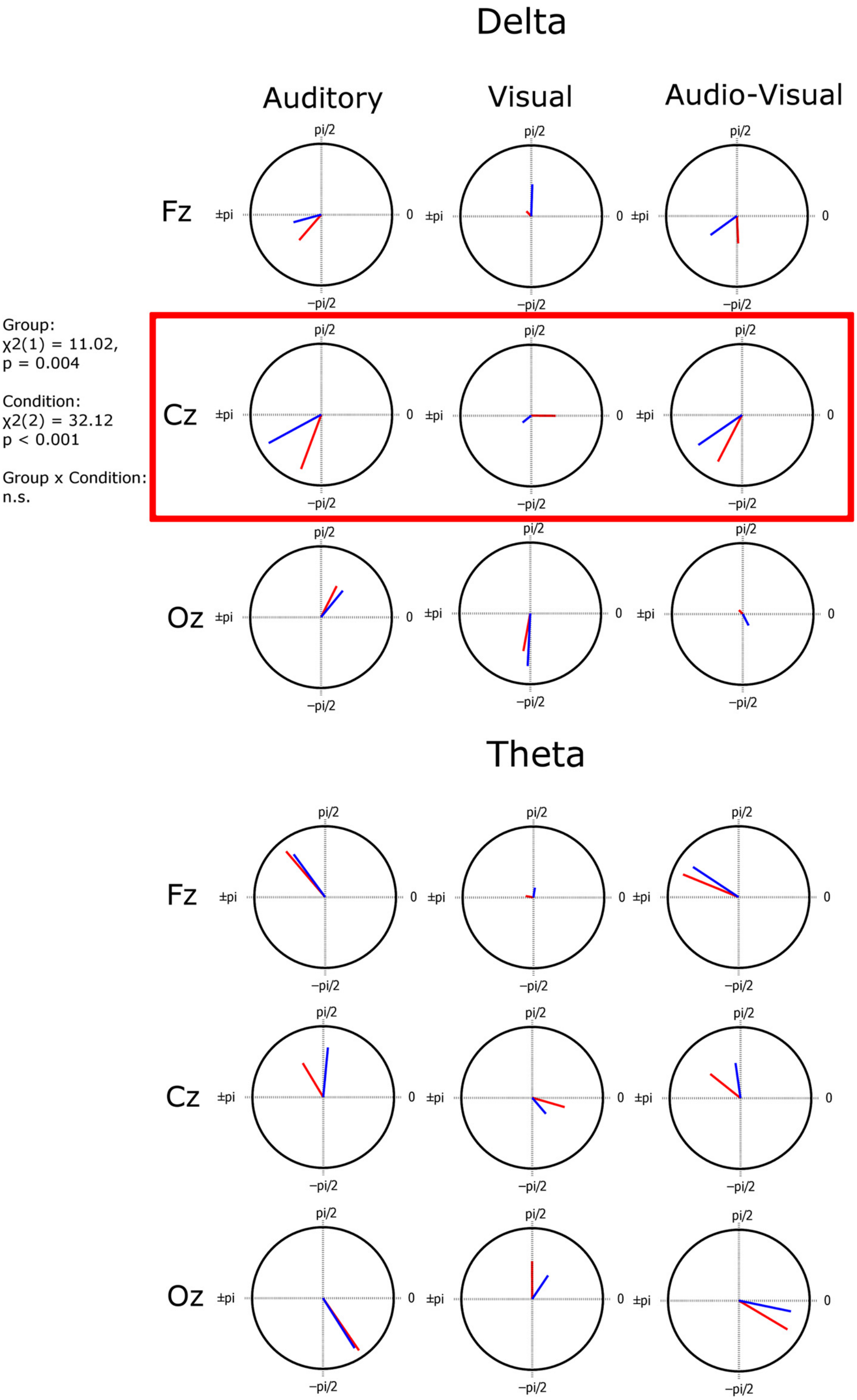

FIGURE 4 | Mean resultant vector plots indicating the coherency of preferred phase across subjects (the length of the vector) and the preferred angle of entrainment (the vector angle) plotted on a unit circle. A significant group difference in preferred angle was found in the delta band at electrode Cz.

pairs were electrodes at (T3, T4), (T5, T6) and (Tp7, Tp8) of the 10–20 system. The first electrode of each pair was in the left temporal region and the second was in the right temporal region.

Phase re-setting of auditory oscillatory activity by visual information

Finally, we sought to investigate the impact of the accompanying visual stimulation on auditory entrainment. The pre-stimulus phase values (at auditory stimulus onset) for the AV and (AV-V) responses were extracted in the same manner as outlined above for the separate conditions. We then looked at the topography of the strength of entrainment. To do this we plotted the pooled phase values at each electrode (shown in **Figure 7**). These topographies show a common region of strong entrainment, indicative of entrainment in auditory areas (see **Figure 7**). Subsequent analysis was thus confined to the pooled activity of electrodes in this region of interest (ROI). The electrodes chosen for this ROI are shown in **Figure 7**. We compared the extent of phase alignment as obtained using ITC and the preferred pre-stimulus phase. Once again an estimate of the preferred phase was determined for each subject by finding the mean pre-stimulus phase.

RESULTS

BEHAVIORAL ENTRAINMENT TASK

In order to assess whether there were significant behavioral differences between conditions, 2 Two-Way mixed design ANOVAs with a between-subject factor of Group and a within-subject factor of Condition were carried out. The dependent variables in the separate ANOVAs were the EEG task (79.4% accuracy) behavioral threshold in ms in each condition and response time (RT) in ms in each condition, respectively. If the assumption of sphericity was violated the Greenhouse–Geisser corrected degrees of freedom are reported. The ANOVA for *threshold* showed a main effect of Group that approached significance, $F_{(1,\ 30)} = 4.006$, $p < 0.054$, $\eta_p^2 = 0.118$. There was a significant main effect of condition, $F_{(1.57,\ 47.089)} = 97.9$, $p < 0.001$, $\eta_p^2 = 0.765$. *Post-hoc* inspection of the means (Bonferroni corrected) showed that the threshold for the visual condition was significantly higher than the thresholds for the auditory and AV conditions (both p's < 0.001). The thresholds in the auditory and AV conditions did not differ from each other ($p > 0.05$). The Group × Condition interaction approached significance [$F_{(1.57,\ 47.089)} = 2.602$, $p = 0.097$]. *A priori*, we had expected potential group differences in benefit accrued in presenting AV over A or V alone and also a possible differential benefit by group of A over V (those with dyslexia worse in A and better in V). Therefore, we carried out three planned exploratory *post-hoc* t-tests probing group effects in differences between conditions: (DY_A-DY_AV) vs. (CA_A-CA_AV), (DY_V-DY_A) vs. (CA_V-CA_A), (DY_V-DY_AV) vs. (CA_V-CA_AV). With Bonferroni corrections, a significance threshold of $p = 0.05/3 = 0.016$ was applied. Results of these *post-hoc* tests showed that dyslexics gained significantly more benefit in the AV condition compared to the auditory alone condition ($p = 0.014$). The difference in benefit from visual alone to AV did not differ between groups ($p = 0.057$). Therefore, the *post-hoc* t-tests suggest that dyslexics accrued more benefit than controls when stimuli were presented audio-visually rather than as auditory-alone. The same pattern was not found for AV presentation over visual-alone. The advantage of auditory alone over visual alone presentation was not significantly different between the groups ($p = 0.802$).

The ANOVA for *response time* showed a main effect of condition, [$F_{(1.638,\ 49.139)} = 39.24$, $p < 0.001$, $\eta_p^2 = 0.567$], but no significant group effects [$F_{(1,\ 30)} = 0.035$, $p > 0.05$] nor interaction [$F_{(1.638,\ 49.139)} = 0.118, p > 0.05$]. *Post-hoc* inspection of the significant condition effect (Bonferroni corrected) showed that RT in the visual condition was significantly faster than RT for the auditory and AV conditions (both p's < 0.001). Differences in RT between the auditory and AV conditions approached significance ($p = 0.054$), suggesting that although the AV condition did not result in an improved detection threshold over auditory information alone, some facilitation of RT was occurring. Performance on the behavioral entrainment task is shown in **Table 2**.

Table 2 | Response times and 79.4% detection threshold (in ms) for the EEG behavioral task.

	CA	DY
RT auditory (ms)	352.44 ± 45.48	358.52 ± 44.31
RT visual (ms)	303.27 ± 48.82	303.76 ± 43.45
RT audio-visual (ms)	337.71 ± 41.29	339.61 ± 40.02
EEG behavioral threshold auditory (ms)	51.39 ± 19.34	80.01 ± 62.15
EEG behavioral threshold visual (ms)	131.21 ± 26.44	138.56 ± 38.69
EEG behavioral threshold audio-visual (ms)	56.00 ± 17.85	62.41 ± 28.68

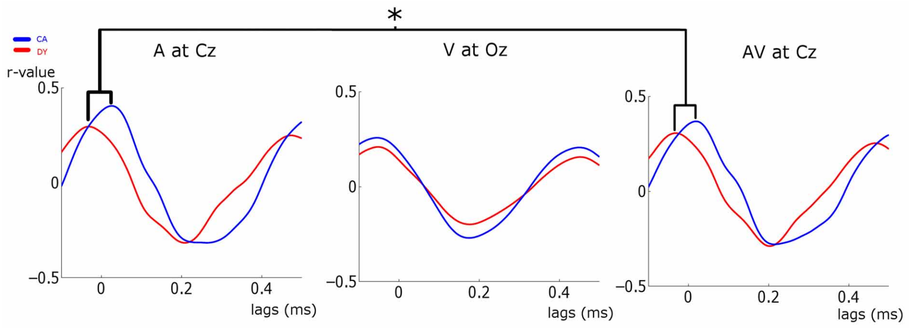

FIGURE 5 | Stimulus-Response cross-correlation analysis. The plots show the cross-correlation analysis between the stimulus and the responses at representative electrodes. Average CA data is plotted in blue and DYs in red. A very strong representation of the temporally extended stimulus is seen in the response. Significant peak timing differences are indicated. $^*p < 0.05$.

Finally, to check that individual differences in the thresholds for the 3 conditions were correlated with the behavioral, reading, and phonological measures, partial correlations across all subjects controlling for age and IQ were computed (see **Table 3**). Most of the correlations were significant, suggesting that the task is tapping into mechanisms that are relevant to reading and reading development. The top panel of **Figure 6** shows a scatter plot and regression line of the auditory threshold in the EEG behavioral task plotted against performance in the phoneme deletion task.

EEG DATA: TOTAL RESPONSE POWER

To assess potential group differences in *total response power*, we carried out separate ANOVAs for each frequency band of interest (delta, theta) with the between-subject factor of group and within-subject factors of condition and channel. For the delta band ANOVA we found no main effect of group [$F_{(1,\ 30)} = 0.104$, $p = 0.75$, $\eta_p^2 = 0.003$]. There were significant main effects of condition [$F_{(2,\ 60)} = 9.932$, $p < 0.001$, $\eta_p^2 = 0.249$] and channel [$F_{(2,\ 60)} = 10.062$, $p < 0.001$, $\eta_p^2 = 0.251$]. The condition effect was driven by larger delta power in the A and AV conditions than the V condition. Power in the A and AV conditions did not differ. The main effect of channel was driven by higher delta power at Fz than at Cz and Oz. There was no difference in delta power between Cz and Oz. The was also a significant group × condition interaction [$F_{(2,\ 60)} = 3.428$, $p < 0.039$, $\eta_p^2 = 0.103$]. *Post-hoc* tests showed that this was driven by higher delta power in the A than V condition for controls, compared with no difference for those with dyslexia. In contrast, those with dyslexia had higher delta power for the AV condition than the V condition; this was not the case for controls.

In the theta band ANOVA we again found no main effect of group, suggesting that overall theta power was similar between the groups [$F_{(1,\ 30)} = 0.233$, $p = 0.633$, $\eta_p^2 = 0.008$]. Once again there were significant main effects of condition [$F_{(2,\ 60)} = 7.116$, $p = 0.002$, $\eta_p^2 = 0.192$] and channel [$F_{(2,\ 60)} = 3.875$, $p < 0.026$, $\eta_p^2 = 0.114$]. The condition effect was again driven by larger delta power in the A and AV conditions than in the V condition. Power in the A and AV conditions did not differ. The main effect of channel was driven by higher delta power at Fz

Table 3 | Partial correlations across all subjects controlling for age and IQ between EEG behavioral task thresholds and reading and phonology measures.

Measure	Auditory threshold	Visual threshold	Audio-visual threshold
BAS (SS)	$r = -0.579^{**}$	$r = -0.508^{**}$	$r = -0.383^{*}$
Reading age	$r = -0.522^{**}$	$r = -0.475^{**}$	$r = -0.305$
TOWRE word reading	$r = -0.434^{*}$	$r = -0.441^{*}$	$r = -0.306$
TOWRE non-word reading	$r = -0.538^{**}$	$r = -0.533^{**}$	$r = -0.389^{*}$
RAN	$r = 0.193$	$r = 0.265$	$r = 0.216$
pSTM	$r = -0.044$	$r = -0.114$	$r = 0.153$
Phoneme deletion	$r = -0.407^{*}$	$r = -0.123$	$r = -0.313$

$^{**}p < 0.01$, $^{*}p < 0.05$.

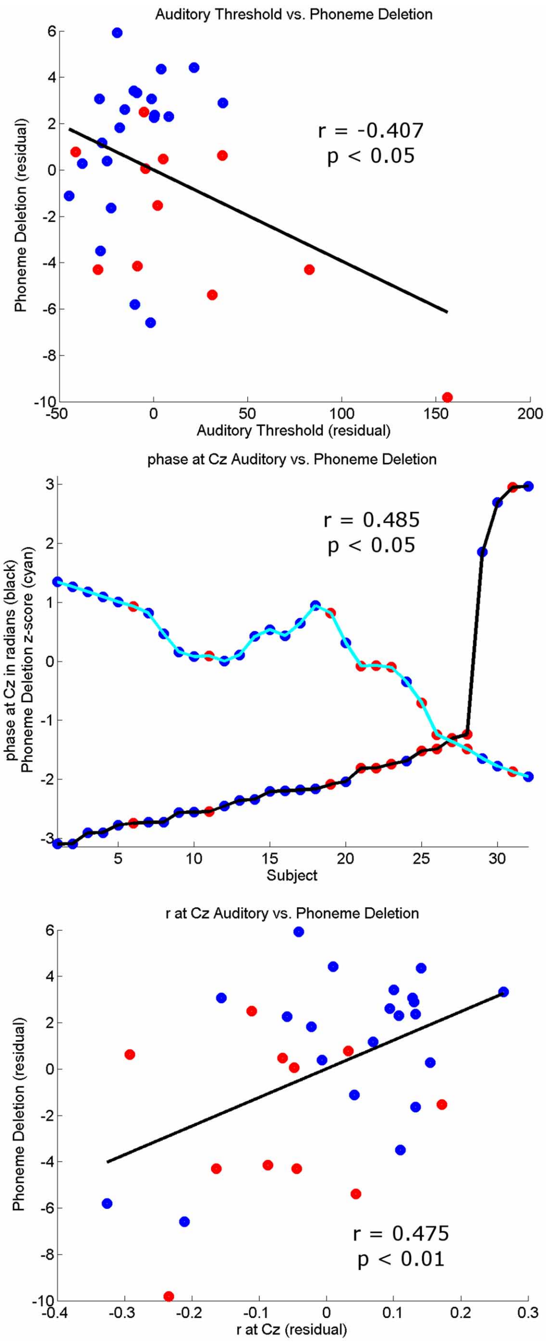

FIGURE 6 | Correlation plots. The **top panel** shows the partial correlation plot controlling for age and IQ of the Auditory Threshold on the EEG behavioral task with phonology (phoneme deletion). The **middle panel** shows the relationship between the circular variable preferred phase of entrainment (black trace) and the linear variable phoneme deletion *z*-score (cyan). For visualization purposes the phoneme deletion trace has been smoothed using a 12-point averaging window. Higher phoneme deletion scores occur when a subject has a preferred phase in the region ($-\pi$, $-\pi/2$) and lower scores in the region ($\pi/2$, π). The **bottom panel** shows the partial correlation plot controlling for age and IQ of strength of auditory stimulus representation at Cz (*r*) with phonology (phoneme deletion). Controls subjects are identified by blue dots and dyslexics by red dots in all panels.

than at Oz. There was also a significant group × channel interaction [$F_{(2,\ 60)} = 4.459$, $p < 0.026$, $\eta_p^2 = 0.129$]. *Post-hoc* testing revealed that this was driven by larger theta power at Fz than Cz for DYs only. There was also a significant channel × condition interaction [$F_{(2.974,\ 89.229)} = 5.036$, $p = 0.003$, $\eta_p^2 = 0.144$]. This is to be expected, as different channels should respond differently to different conditions e.g., Cz would respond more strongly to auditory than visual stimulation.

EEG DATA: PHASE CONSISTENCY

We next explored entrainment in the pre-stimulus phase distributions of the delta and theta activity (see **Figure 3**). Here three representative electrodes were chosen for analysis: Fz, Cz, and Oz, identifying responses from frontal, central, and occipital regions, respectively. Significant phase locking (i.e., significant differences from a uniform random distribution) were investigated using the Rayleigh statistic, and a critical *p*-value of 0.001 was chosen in order to minimize Type I errors.

In the *auditory* condition, significant entrainment was found at both delta and theta rates at all three channel locations, with one exception, the Fz channel for dyslexic participants (A$_\delta$_DY_Cz: $Z = 36.76$, $p << 0.001$; A$_\delta$_DY_Oz: $Z = 7.27$, $p << 0.001$; A$_\delta$_CA_Fz: $Z = 14.30$, $p << 0.001$; A$_\delta$_CA_Cz: $Z = 124.55$, $p << 0.001$; A$_\delta$_CA_Oz: $Z = 36.76$, $p << 0.001$; A$_\theta$_DY_Fz: $Z = 28.43$, $p << 0.001$, A$_\theta$_DY_Cz: $Z = 9.60$, $p << 0.001$; A$_\theta$_DY_Oz: $Z = 35.97$, $p << 0.001$; A$_\theta$_CA_Fz: $Z = 73.58$, $p << 0.001$; A$_\theta$_CA_Cz: $Z = 49.58$, $p << 0.001$; A$_\theta$_CA_Oz: $Z = 75.38$, $p << 0.001$). Regarding delta activity at Fz for the dyslexics, the entrainment did approach significance (A$_\delta$_DY_Fz: $Z = 6.73$, $p = 0.0013$). Therefore, as would be expected on MTRMs of speech processing, theta entrainment to the syllable stimulus was present in both groups and at all electrodes. Significant delta entrainment was also present in both groups at all electrodes, as would be expected in our paradigm.

In the *visual* condition, entrainment was significant in occipital areas only, as would be expected (V$_\delta$_DY_Oz: $Z = 8.81$, $p << 0.001$; V$_\delta$_CA_Oz: $Z = 46.28$, $p << 0.001$; V$_\theta$_DY_Oz: $Z = 10.01$, $p << 0.001$; V$_\theta$_CA_Oz: $Z = 13.30$, $p << 0.001$). No significant entrainment was found at Cz in either band (V$_\delta$_DY_Cz: $Z = 0.56$, $p > 0.05$; V$_\delta$_CA_Cz: $Z = 0.41$, $p > 0.05$; V$_\theta$_DY_Cz: $Z = 3.78$, $p > 0.05$; V$_\theta$_CA_Cz: $Z = 5.22$, $p > 0.05$). While significant entrainment was not found in either band at Fz for dyslexics (V$_\delta$_DY_Fz: $Z = 0.70$, $p > 0.05$; V$_\theta$_DY_Fz: $Z = 0.51$, $p > 0.05$), controls did show significant entrainment at Fz in the delta band (V$_\delta$_CA_Fz: $Z = 13.09$, $p < 0.001$) but not the theta band (V$_\theta$_CA_Fz: $Z = 2.04$, $p > 0.05$).

The pattern of entrainment for the *audio-visual* condition was somewhat more complex. Both groups showed significant entrainment in the theta band at Fz, Cz and Oz (AV$_\theta$_DY_Fz: $Z = 21.10$, $p << 0.001$, AV$_\theta$_CA_Fz: $Z = 75.50$, $p << 0.001$; AV$_\theta$_DY_Cz: $Z = 9.78$, $p << 0.001$; AV$_\theta$_CA_Cz: $Z = 35.83$, $p < 0.001$; AV$_\theta$_DY_Oz: $Z = 21.03$, $p < 0.001$; AV$_\theta$_CA_Oz: $Z = 66.55$, $p < 0.001$). In the delta band, however, both groups showed significant entrainment at Cz only (AV$_\delta$_DY_Cz: $Z = 34.43$, $p << 0.001$; AV$_\delta$_CA_Cz: $Z = 78.22$, $p < 0.001$). Controls also showed significant entrainment at Fz (AV$_\delta$_CA_Fz: $Z = 9.50$, $p << 0.001$), whereas for the dyslexics entrainment only approached significance at Fz (AV$_\delta$_DY_Fz: $Z = 6.64$, $p = 0.0013$). Neither group showed significant entrainment at Oz (AV$_\delta$_DY_Oz: $Z = 1.58$, $p > 0.05$; AV$_\delta$_CA_Oz: $Z = 2.11$, $p > 0.05$). The Oz data is likely due to volume conduction from auditory areas. As can been seen from **Figure 3**, activity at Oz in the auditory condition tends to entrain in opposite phase to the visual condition. This would lead to a balancing of the audio-visual phase distribution at Oz.

EEG DATA: PHASE LOCKING STRENGTH (ITC)

In order to examine potential group differences in the degree of phase locking *consistency* for each group we carried out separate mixed factor ANOVAs by group for each frequency band of interest. The with-in group factors were condition (A vs. V vs. AV), and channel (Fz vs. Cz Vs. Oz). Once again, if the assumption of sphericity was violated the Greenhouse–Geisser corrected degrees of freedom are reported. In the *delta band* ANOVA there was no main effect of group [$F_{(1,\ 30)} = 0.519$, $p = 0.477$, $\eta_p^2 = 0.017$], hence the strength of entrainment did not differ between the groups. There was a significant effect of condition [$F_{(2,\ 60)} = 8.294$, $p = 0.001$, $\eta_p^2 = 0.217$]. Bonferroni corrected *post-hoc* analysis showed this to be driven by stronger entrainment in the auditory and audio-visual conditions than in the visual condition. Strength of entrainment was equivalent between auditory and audio-visual conditions. There was also a main effect of channel [$F_{(2,\ 60)} = 14.74$, $p < 0.001$, $\eta_p^2 = 0.329$]. *Post-hoc* analysis found this to be driven by stronger entrainment at Cz then at either Fz or Oz. Finally, there was a significant condition × channel interaction [$F_{(4,\ 120)} = 9.474$, $p < 0.001$, $\eta_p^2 = 0.240$]. This interaction suggests that strength of entrainment at the electrodes depends on the experimental condition. This is to be expected, e.g., we would expect Cz to show stronger entrainment to the auditory and audio-visual stimuli than the visual stimulus. This can be seen in **Figure 4**. No other significant effects or interactions were found in the delta band.

In the theta band ANOVA the main effect of group approached significance [$F_{(1,\ 30)} = 3.264$, $p = 0.081$, $\eta_p^2 = 0.098$]. This suggests that the strength of theta entrainment tends to be greater for controls than those with dyslexia. A main effect of condition was also found [$F_{(2,\ 60)} = 5.916$, $p = 0.005$, $\eta_p^2 = 0.165$]. As in the delta band *post-hoc* analysis (Bonferroni corrected), entrainment in the auditory and audio-visual conditions was significantly stronger than in the visual condition. There was also a main effect of channel [$F_{(1.468,44.031)} = 5.576$, $p = 0.013$, $\eta_p^2 = 0.157$]. Bonferroni *post-hoc* tests showed this to be driven by stronger entrainment at Oz than Cz, No significant interactions were found (all p's > 0.05).

EEG DATA: PREFERRED PHASE OF ENTRAINMENT

Having assessed both presence of entrainment (significant phase locking, ITC) and potential differences in strength of entrainment for each group (degree of consistency in phase locking), we sought to investigate potential group differences in the *preferred phase* of entrainment. Although consistency of phase (strength of phase locking) did not differ between groups, this does not mean that both groups entrained at the *same* phase. The preferred phase of entrainment has been shown to be a crucial contributor to stimulus processing (Lakatos et al., 2008; Ng et al., 2013). Preferred phase angles can be seen in **Figure 4**. The length of the vector in **Figure 4** represents the inter-subject coherence; the greater the magnitude of the vector, the more similar the phase at which all subjects entrain. Conversely the shorter the vector, the less consistent (or more variable) the phase across subjects. In order to investigate whether preferred phase differed between groups, we carried out 6 group × condition ANOVAs, one for each frequency band/channel combination (Cz and delta, Cz and theta, Fz and delta, Fz and theta, Oz and delta, Oz and theta). This was done using the Harrison-Kanji two-factor ANOVA test (HK ANOVA) for circular variables (Harrison and Kanji, 1988). This test is not carried out using repeated measures. Also, the reported statistic depends on the width, or concentration factor kappa, of the Von Mises distribution applied to the data. If it is low (<2), a Chi-squared statistic is reported, but if it is high, an F-statistic is reported. A significant group effect was found only for Cz in the delta band ANOVA ($\chi^2_{(1)} = 11.02, p = 0.004$). A significant main effect of condition was also found in this ANOVA ($\chi^2_{(2)} = 32.12$, $p < 0.001$). The group × condition interaction was not significant ($p > 0.05$). Since the entrainment analysis and **Figure 3** showed that activity at Cz in the visual condition was not significantly entrained, and thus the preferred phase for this condition at this channel is not informative, we carried out a further exploratory group (CA vs. DY) × condition (A vs. AV) HK ANOVA for Cz and delta band activity, leaving out the potentially confounding visual condition. Again we found a significant main effect of group [$F_{(1,\ 63)} = 9.08, p = 0.0038$]. There was, however, no longer an effect of condition ($p > 0.05$) and no significant interaction ($p > 0.05$). This suggests that the two groups differ in their preferred phase of entrainment in the auditory and audio-visual conditions at Cz, and that the preferred phase for each group does not differ between these conditions. Activity at Cz is broadly indicative of auditory processing in this task.

SUMMARY OF EEG DATA

Regarding our hypotheses about potential group differences in entrainment, these data suggest that there were no overall group differences in response power or in the consistency of phase across trials (ITC). However, there were important group differences in the *preferred phase of entrainment*, which differed at Cz in the delta band in the Auditory and AV conditions. This points toward a potentially very important difference between the groups in the oscillatory processes supporting speech encoding, one that may have significant implications for the quality and type of information that is encoded. In particular, if the different preferred phase of entrainment has a negative effect on speech encoding by children with dyslexia, this should be reflected in relationships between individual differences in preferred phase and the behavioral measures of reading and phonology. To investigate whether this was the case, circular-linear correlations between the preferred phase of delta entrainment and the behavioral measures were computed, and are shown in **Table 4**. For the auditory condition, significant correlations are shown for all the measures of reading and for phoneme deletion, with a trend toward significance ($p < 0.10$) for the phonological memory and rapid naming measures. Clearly, preferred phase is significantly related to the quality of the phonological representations in the mental lexicons of our participants. A plot outlining the relationship between preferred phase of entrainment at Cz in the auditory condition and performance in the phoneme deletion task can be seen in the middle panel of **Figure 6**. This important result is considered further in the Discussion.

Table 4 | Circular-linear correlation between preferred delta phase of entrainment and reading and phonology measures.

Measure	Preferred phase for A at Cz	Preferred phase for V at Oz	Preferred phase for AV at Cz
BAS(SS)	0.532*	0.322	0.322
BAS(AS)	0.570**	0.213	0.294
Reading age	0.388*	0.245	0.356
TOWRE word reading	0.510*	0.200	0.323
TOWRE non-word reading	0.465*	0.324	0.271
RAN (combined)	0.405+	0.290	0.447*
pSTM combined	0.412+	0.312	0.424+
Phoneme deletion	0.485*	0.144	0.389+

*The pattern of correlations mirrors that of the peak lag correlations in this table emphasizing that both measures tap into similar mechanisms (that is the timing of the EEG activity in response to the stimulus). **$p < 0.01$, *$p < 0.05$, +$p < 0.1$.*

QUALITY OF THE STIMULUS REPRESENTATION: CROSS-CORRELOGRAMS

The analyses conducted so far have investigated differences in EEG responses between the groups. Now we investigate the direct relationship between the EEG response and the entraining stimulus for each group. To ascertain this relationship, we calculated the cross-correlogram between the stimulus envelope and the neural response. Following Abrams et al. (2009), we did not partition the EEG into sub-bands for this analysis, but used the broadband response. The peak r-values of the cross-correlogram indicate the strength of stimulus envelope representation in the EEG response. The lags at which the peak r-value occurs indicate the timing/phase at which the greatest representation of the stimulus occurs. Given the significant differences in preferred phase found in the EEG, peak lag values in particular might be expected to differ between those with dyslexia and the control group.

The strength of stimulus representation was investigated using a mixed factor ANOVA with the between-subject factor of group (CA vs. DY) and the within-subject factors of condition (A vs. V vs. AV) and channel (Fz vs. Cz vs. Oz). The dependent variable was the peak r-values. The main effect of group approached significance [$F_{(1,\ 30)} = 2.999$, $p = 0.094$, $\eta^2_p = 0.091$]. There was a significant main effect of condition [$F_{(2,\ 60)} = 6.675$, $p = 0.002$, $\eta^2_p = 0.182$]. Bonferroni corrected *post-hoc* analysis showed that this was driven by larger r-values in the A and AV conditions than in the visual condition ($p = 0.024$ and $p = 0.016$, respectively). The peak r-values in the A and AV conditions did not differ ($p > 0.05$). There was also a significant effect of channel [$F_{(2,\ 60)} = 11.328$, $p = 0.001$, $\eta^2_p = 0.274$]. *Post-hoc* analysis revealed this to be driven by larger r-values at Cz than at both Fz and Oz ($p < 0.001$ and $p = 0.01$, respectively). A significant condition × channel interaction was also found [$F_{(4,\ 120)} = 7.304$, $p < 0.001$, $\eta_p^2 = 0.196$]. This would be expected, as stimulus representation should differ at each channel in different experimental conditions. The stimulus-response cross-correlation has a period of ~500 ms (see **Figure 5**). This suggests that it is dominated by delta band activity.

To investigate the *timing* of maximal response representation, we extracted the lags for which peak *r*-values occurred for each participant at each channel and in each condition (a subset of which is plotted in **Figure 5**). We then took the lags at each channel as the dependent variable in 3 separate ANOVAs, each with the between-subject factor of group and the within-subject factor of condition (A vs. V vs. AV). The ANOVA for Fz showed a main effect of condition [$F_{(2,\ 60)} = 59.09$, $p < 0.001$, $\eta_p^2 = 0.653$]. There was no significant effect of group, nor was there a significant group × condition interaction. Similar results were found for the Cz ANOVA [main effect of condition: $F_{(2,\ 60)} = 33.808$, $p < 0.001$, $\eta_p^2 = 0.53$]. However, given that the analysis of entrainment had shown that visual activity at Cz was not significantly entrained, we also carried out an exploratory Two-Way ANOVA for Cz omitting the visual condition, with factors of group (CA vs. DY) and condition (A vs. AV). Here we found a significant main effect of group [$F_{(1,\ 30)} = 5.859$, $p = 0.022$, $\eta_p^2 = 0.163$], paralleling the results found at Cz for the preferred phase of entrainment analysis. *Post-hoc* analysis of the group effect revealed that it was driven by controls having a *longer* peak-lag than the dyslexic group. Although the timing of peak stimulus representation (as identified by the peak lags) does not measure the same thing as preferred pre-stimulus phase, both are measures of the timing of the relevant oscillatory response activity. Indeed, the results of this peak-lag analysis mirror those of the preferred phase of delta entrainment analysis carried out above, as both analyses point to atypical timing of response entrainment and atypical response representation in participants with dyslexia. Both the strength of stimulus representation and response timing are likely to be crucial factors in phonological development.

Converging evidence for a potentially important role for the neural timing of auditory responses in phonological development and reading development was sought by exploring correlations between these two measures of the quality of stimulus representation and the behavioral measures. Peak *r*-values and peak lags at Cz in the three conditions were correlated with the various reading and phonology measures, partialling out age and IQ (see **Table 5**). A series of significant correlations were found, most notably in the Auditory condition, and the correlations were positive, suggesting that a stronger stimulus representation (higher peak *r*-value) and a longer peak lag were related to higher scores on the behavioral tasks. As shown in **Table 5**, peak *r*-values were significantly correlated with reading age, non-word reading and phoneme deletion in the Auditory condition, while peak lag was significantly correlated with reading standard score and reading age (The bottom panel of **Figure 6** shows a scatter plot and regression line for the relationship between peak *r*-values at Cz in the auditory condition vs. performance in the phoneme deletion task) For the AV condition, peak *r*-values were significantly correlated with phonological awareness, while individual differences in peak lag were significantly correlated with reading age and RAN. As those with dyslexia showed *shorter* lags than controls, the more *"control-like"* the peak lag, the better the behavioral performance.

Overall, the partial correlations suggest that the typically-developing children had stronger neural representations of the speech stimulus "ba," and that the strongest representation occurred later in time compared to those with dyslexia. These results provide converging evidence for the importance of the *phase* of low frequency oscillations in stimulus encoding. The participants with dyslexia appear to be entraining to a sub-optimal phase, and this is reflected in both timing differences in their neural responses and also a difference in the quality of stimulus representation as measured by the correlograms.

To investigate potential effects of hemisphere on the strength of auditory stimulus representation and timing, we subjected the peak *r*-values and lags to separate 2 × 3 × 2 ANOVAs with a between-subject factor of group and within-subject factors of electrode pair (T3,T4 vs. T5,T6 vs. Tp7,Tp8) and hemisphere (left vs. right). The peak *r*-value ANOVA found no significant effects, suggesting that the strength of auditory stimulus representation does not differ by group in temporal regions.

Table 5 | Partial correlations across all subjects controlling for age and IQ between reading and phonology measures and peak *r*-value and peak lag at Cz in the Auditory condition, Oz in the visual condition, and Cz for the audio-visual condition.

Measure	*r*-value for A at Cz	Peak lag for A at Cz	*r*-value for V at Oz	Peak lag for V at Oz	*r*-value for AV at Cz	Peak lag for AV at Cz
BAS(SS)	0.402*	0.409*	0.076	−0.003	0.182	0.308
BAS(AS)	0.401*	0.429*	0.079	0.008	0.171	0.31
Reading age	0.324^{+}	0.388*	0.088	0.038	0.116	0.373*
TOWRE word reading	0.281	0.356^{+}	0.068	0.07	−0.043	0.354^{+}
TOWRE non-word reading	0.385**	0.356^{+}	0.131	−0.087	0.033	0.241
RAN	−0.167	−0.322^{+}	−0.111	−0.006	0.193	−0.467**
pSTM	−0.054	0.060	0.127	−0.133	−0.2	0.357^{+}
Phoneme deletion	0.475**	0.229	0.094	0.064	0.466*	−0.107

$^{**}p < 0.01$, $^{*}p < 0.05$, $^{+}p < 0.1$.

Furthermore, no hemispheric difference or interactions were found, suggesting that the strength of stimulus encoding is similar in both hemispheres. The lag ANOVA showed a main effect of Group [$F_{(1,\ 30)} = 4.37, p = 0.045, \eta_p^2 = 0.127$]. No other contrasts resulted in significant effects. This timing difference was again driven by children with dyslexia having a shorter peak lag than children in the control group.

PHASE RESETTING: EFFECTS OF VISUAL STIMULATION ON AUDITORY ENTRAINMENT

Following Power et al. (2012b), our final question was whether there would be group differences in the degree to which visual speech information would reset the phase of auditory oscillations so that they were optimally timed to encode the speech signal. Given behavioral data (e.g., Megnin-Viggars and Goswami, 2013), we expected that the dyslexic group might accrue greater benefit from visual phase-resetting than controls. Following Power et al. (2012b), **Figure 7** shows ITC topographies for the A and (AV-V) conditions averaged across groups. The fronto-central distribution in both conditions is indicative of entrainment in auditory cortical areas. **Figure 7** also shows the phase distributions for delta and theta for the pooled activity in the ROI for both groups and conditions. Rayleigh tests revealed significant entrainment in both conditions at both frequencies (A_δ_DY: $Z = 403.43$, $p << 0.001$; AV-V_δ_DY: $Z = 265.87$, $p << 0.001$; A_θ_DY: $Z = 441.16$, $p << 0.001$; AV-V_θ_DY: $Z = 376.69$, $p << 0.001$; A_δ_CA: $Z = 1247.30$, $p << 0.001$; AV-V_δ_CA: $Z = 684.82$, $p << 0.001$; A_θ_CA: $Z = 1220.5$, $p << 0.001$; AV-V_θ_CA: $Z = 704.96$, $p << 0.001$). This would be expected given the way in which the ROI was determined.

To assess possible group differences in the effects of visual speech cues on the auditory oscillations, we first investigated whether the level of auditory entrainment (inter-trial coherence, ITC) was affected by the visual cues. The ITC values were submitted to two 2 × 2 ANOVAs (one each for delta and theta), with the between-subject factor of group (CA vs. DYS) and within-subject factor of condition [A vs. (AV-V)]. The ANOVAs showed no main effect of group nor condition in either frequency band (all p's > 0.05), suggesting that the strength of auditory phase locking in both bands was similar whether visual cues were present or not. There was also no significant group × condition interaction in either band (both p's > 0.05).

Mirroring the previous ITC analysis, we next carried out a similar 2 × 2 ANOVA for each frequency band taking the overall response power as the dependent variable. In the delta band, we found no main effect of group, but a significant group × condition interaction [$F_{(1,\ 30)} = 5.809, p = 0.022, \eta_p^2 = 0.162$]. *Post-hoc* inspection revealed that the interaction was driven by higher delta power in the A than in (AV-V) for the control children only. There was no difference in power between the two conditions for those with dyslexia. The theta band ANOVA showed similar results, with no main effect of group, but a significant group × condition interaction [$F_{(1,\ 30)} = 5.048$, $p = 0.032$, $\eta_p^2 = 0.144$]. *Post-hoc* inspection revealed that this was again driven by higher power in A than AV-V for the control children only.

Taking these results together, typically-developing children showed a significant difference between auditory oscillatory activity to auditory stimuli alone (A) and auditory oscillatory activity when visual cues were present (AV-V), in both delta and theta power. The children with dyslexia did not. This may indicate that

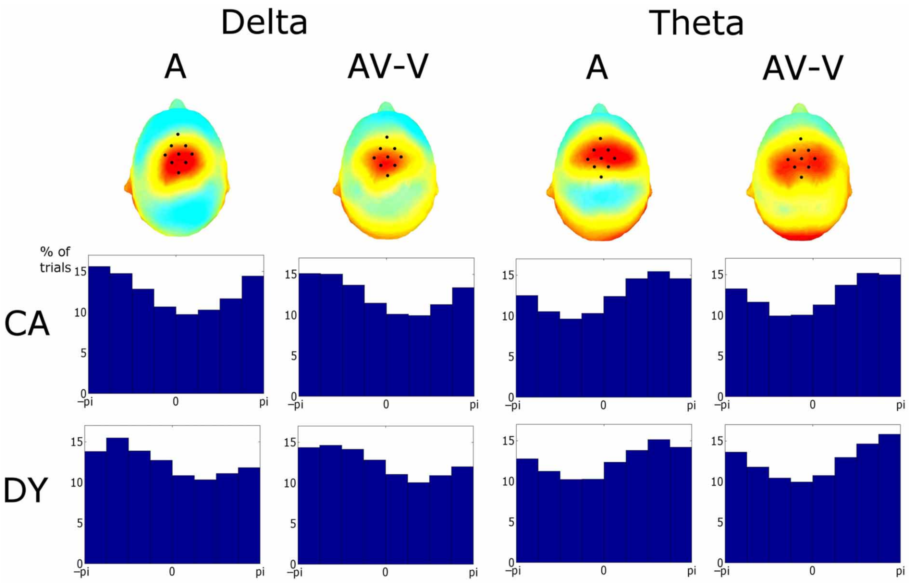

FIGURE 7 | Upper Panel: Topographies of the ITC for phase at stimulus onset. The similarity of these topographies established a particular fronto-central region of interest coinciding with the area of strongest entrainment. **Lower Panel:** phase distributions for the conditions and frequency bands in the region of interest (ROI). Activity in the ROI showed significant entrainment, as tested using the Rayleigh statistic, in both frequency bands and for both response types and both groups. Tests on the preferred phase of entrainment showed that auditory delta phase differed between groups. Auditory theta phase differed between conditions and was thus affected by visual cues.

auditory cortex in typical development does not have to work as "hard" to process speech stimuli when they are presented multimodally. The results also show that the consistency of auditory phase is not affected for either group by whether stimuli are only auditory or whether they are audio-visual.

PREFERRED PRE-STIMULUS PHASE

To assess whether the information from visual speech affected the phase of auditory entrainment similarly for each group, we tested for preferred phase differences in each frequency band using two 2-way circular ANOVAs (HK ANOVA as before). Each ANOVA had group as the between-subjects factor (CA vs. DY) and condition [A vs. (AV-V)] as the within-subjects factor. In the delta band ANOVA there was a significant main effect of group [$F_{(1,\,63)} = 11.06$, $p = 0.0015$]. This mirrors the differences in preferred phase found by group at Cz for the auditory condition. There was no significant effect of condition ($p > 0.05$) and there was no significant interaction ($p > 0.05$). In the theta band ANOVA we found a significant main effect of condition [$F_{(1,\,63)} = 7.97$, $p = 0.0065$] but no significant main effect of group ($p > 0.05$) and no significant interaction ($p > 0.05$). This suggests that for theta the preferred auditory phase in the ROI is altered by audio-visual information. The absence of a significant interaction with group in both ANOVAs suggests that the preferred phase of entrainment in both frequency bands is similarly affected by visual speech information in both groups, with no phase alteration in the delta band but a significant phase alteration in the theta band. Nevertheless, the preferred delta phase at which auditory responses entrain is different between the groups. Overall these data suggest that for theta band entrainment, which by hypothesis is primary in syllable-level processing (Poeppel, 2003), accompanying visual speech information does alter the preferred phase of entrainment, for both groups. Therefore, accompanying visual information results in a more optimal theta phase than when auditory information is presented alone, and both groups are *similarly* affected by visual speech information. There is no evidence for enhanced use of visual speech information by participants with dyslexia. In contrast, group differences in the preferred delta band phase persist in spite of the visual speech information. This suggests that *sub-optimal phase of entrainment* still occurs in the AV condition for participants with dyslexia.

DISCUSSION

Here we compared neuronal oscillatory entrainment in children with and without dyslexia in the delta and theta bands to a rhythmic speech stimulus, the syllable "ba" repeated at a 2 Hz (delta) rate. The speech stimulus was either presented in the auditory modality only, the visual modality only, or audio-visually (AV). On the basis of the temporal sampling framework for developmental dyslexia (TSF, Goswami, 2011), we predicted group differences in entrainment in the auditory modality. Given the prior literature on oscillatory entrainment in dyslexia (adult studies, Hämäläinen et al., 2012b; Soltesz et al., 2013), delta band oscillations seemed the most likely to reveal group differences in the current study. On the basis of previous behavioral studies of entrainment (tapping measures) with adults and children, we again expected group differences in the delta band (Thomson et al., 2006; Thomson and Goswami, 2008). Finally, on the basis of recent studies of behavioral entrainment in adults with dyslexia to rhythmic speech, we predicted possible group differences in preferred phase alignment (Leong and Goswami, 2013).

Here the data in the auditory entrainment condition showed no difference in phase consistency (ITC) over trials between the groups, and no difference in response power between groups. However, significant differences were indeed found in the *timing* of auditory stimulus encoding. Timing differences were revealed both by a significant group difference in the *preferred phase* of neuronal entrainment in the delta band, in both the auditory and AV conditions, and by the timing of maximal stimulus encoding as measured by cross-correlating the stimulus envelope with the neural response. The cross-correlation approach revealed a significant group difference in peak lag value, with typically-developing children showing later peak lags than children with dyslexia. There was also a trend toward higher *r*-values in controls, indicating better stimulus envelope representation. Regarding laterality, we found no differences in peak *r*-values by group or hemisphere, although longer peak lags were found in both hemispheres in controls. This is discussed further below. Individual differences in both the preferred delta phase measure and the cross-correlation measures were significantly correlated with behavioral measures of reading and phonology (**Tables 4**, **5**). The preferred delta phase measure in the auditory condition showed a particularly consistent set of relations, with significant correlations for all the measures of reading and the phoneme deletion measure.

The suboptimal phase of encoding demonstrated for the participants with dyslexia in the delta band is likely to have significant consequences for the quality of their phonological representations. According to MTRMs of speech encoding (e.g., Luo and Poeppel, 2007; Ghitza and Greenberg, 2009), speech input is encoded most efficiently by the brain when endogenous cortical neuronal oscillations phase-align with temporal modulations (amplitude or frequency modulations) in the input signal, so that maximal neuronal responses occur at the most informative points. If the phase of peak neural responding is consistently misaligned with the modulation peaks in the input, then the signal will be encoded in suboptimal fashion. This will result in differently-specified phonological representations for words in the mental lexicon. The cross-correlation analyses in the current study (which cross-correlated the neural response with the stimulus envelope) provided congruent evidence for significantly different neural timing (peak lag measure) and lower quality neuronal representation of the speech envelope for "ba" (peak *r*-value measure) by the children with dyslexia. These delta band findings suggest that the highest level in the amplitude modulation hierarchy, the delta band, which carries information about prosodic structure, is encoded less efficiently by the dyslexic brain. This would have cascading effects for the encoding of the other levels of phonological structure that are nested within the delta band, including syllable-level (theta band) AM information and phoneme-level (gamma band) AM information. The difference in preferred phase in the current study was 12.8 ms between groups (0.1613 radians at 2 Hz). Acoustic changes in this timescale would be in the gamma range, suggesting that the consistent timing difference in preferred delta phase shown by our participants with dyslexia would have cascading consequences for the optimal encoding of gamma-rate or phonetic information. Some of these faster gamma transitions would be occurring in a sub-optimal temporal window, contributing to the impairments in phonological encoding found at every grain size (prosodic, syllabic, onset-rhyme and phonemic) in developmental dyslexia (Snowling et al., 2000; Ziegler and Goswami, 2005; Goswami et al., 2013).

Hemispheric differences were not found in the cross-correlation measures, in contrast to an earlier study by Abrams et al. (2009). Abrams and colleagues employed three stimulus types: clear speech, conversational speech and compressed speech. A right hemisphere dominance in stimulus encoding (peak r-value) was found for the clear and conversational speech in good and poor readers, whereas for time-compressed speech (a more challenging listening condition), the right hemisphere dominance was only found for good readers. Encoding was represented symmetrically across hemispheres for the poorer readers. Although we found no hemispheric differences in encoding, there are some possible reasons for the differing results. Crucially, Abrams et al. (2009) employed a paradigm in which stimuli were presented to the right ear only. Subjects were instructed to ignore the sentences and to attend to a movie whose soundtrack was presented to the left ear. It has been shown that spatial attention in a speech environment suppresses the neural representation of the ignored stimulus (Horton et al., 2013). It has also been reported that stronger speech suppression takes place in the left hemisphere than in the right under such conditions Power et al. (2012a). The interplay between attention and hemispheric bias is not addressed in Abrams et al. (2009), and it is possible that attentional influence may contribute to the reported right hemisphere bias. For example, the fact that the stimulus is being actively ignored may suppress stimulus representations in the left hemisphere more than in the right. The fact that our stimuli are presented rhythmically, and thus timing is entirely predictable from syllable to syllable, is a further important difference with Abrams et al. (2009), where the speech stimulus envelope was not periodic. Indeed, the fact that the Group × Hemisphere interaction was only seen in their compressed speech condition suggests that the hemispheric interaction effect may be only apparent when the auditory system attempts to entrain to a taxing stimulus whose envelope is variable.

Abrams et al. (2009) also found a significant group × hemisphere interaction for peak lags in all three speech conditions. Poor readers had earlier r-value peaks in the left hemisphere and later peaks in the right hemisphere. It is of note that our results mirror the left hemisphere timing findings of Abrams et al. (2009). The lack of Group × Hemisphere interactions in our study may be due in part to the predictable nature of our stimuli. If the right hemisphere does preferentially encode low frequency activity, as hypothesized by Poeppel (2003), and if this right hemisphere encoding network is the primary impairment in dyslexia, as hypothesized by our group (Goswami, 2011), then we can argue that in a case where the right hemisphere network's capacity to follow low frequency fluctuations is not heavily taxed (as with a rhythmic and predictable stimulus), hemisphere differences may not be found. However, when difficulty increases (such as with non-periodic speech), the unaffected right hemisphere of control participants can facilitate processing, resulting in a decreased peak lag. In contrast, the impaired right hemisphere network of participants with dyslexia will struggle to cope, and so the peak lag increases. Taken together, the results of both studies converge in showing impaired processing of low frequency information by poor readers, both in terms of strength of stimulus representation and response timing. Further research is required, however, to tease apart the delicate contributions of attention and stimulus parameters.

Indeed, a recent study exploring how new acoustic representations are learned by the adult brain (Luo et al., 2013) has shown that neuronal phase patterns in *low-frequency oscillatory responses* below 8 Hz (i.e., in the delta and theta bands) are critical to the learning process. Distinguishably-different low-frequency oscillatory phase patterns were shown by Luo and colleagues to form gradually over learning time, thereby differentiating novel noise patterns as individual auditory objects for successful learners. If a similar learning mechanism underpins the learning of the acoustic patterns which are words, then the phase differences in dyslexia in the delta band revealed here would have serious consequences for the quality of the phonological representations of word forms developed by affected children. Oscillatory phase patterns may be more important than oscillation amplitude in terms of informational encoding. Ng et al. (2013) used natural animal sounds to investigate the encoding of acoustic stimuli in macaque auditory cortex, examining neural firing directly by recording local field potentials inside the brain. Ng and colleagues showed that stimulus-selective firing patterns imprinted on the *phase* rather than the *amplitude* of slow oscillations (<8 Hz), with phase patterns rather than oscillation power carrying discriminative information. A comparable result was reported for human EEG to the same naturalistic stimuli, and Ng and colleagues noted that these naturalistic stimuli could be discriminated on the basis of their phase patterns *without* any increases in oscillatory power. The emerging importance of phase suggests that the brain capitalizes on both power (firing rate) and phase (the timing of firing) when encoding and developing neuronal representations for a complex stimulus like human speech. Therefore, the neural timing differences revealed in the current study could carry important implications for the *quality* of phonological encoding. Note that earlier ASSR studies measuring differences in response *power* between adult participants with and without dyslexia did not measure phase consistency across trials (Lehongre et al., 2011; Poelmans et al., 2012). The identified difference in grand averaged power in those studies may hence be due to inconsistent phase alignment across trials. Both firing rates and phase patterns tend to be sensitive to the same acoustic features (Ng et al., 2013). Hamalainen et al. did investigate both phase and power in their ASSR study, and in their MEG study the group differences between participants with dyslexia and controls at 2 Hz were caused by differential phase consistency and not by differential response power. Note further that in the non-speech study reported by Soltesz et al. (2013), phase *was* examined, and those with dyslexia did show an earlier preferred phase in the 2 Hz entrainment condition compared to the control group; however, this effect was not significant. Nevertheless, it is important to note that none of these earlier dyslexic studies used the speech signal as input.

Contrary to prediction, we did not find any significant differences in *visual entrainment* between children with dyslexia and control children. As noted earlier, differences between dyslexic and control children have been found in visual attention shifting tasks (e.g., Facoetti et al., 2010) and in visual attention span measures (e.g., Lallier and Valdois, 2012), while adults with dyslexia have been reported to show *superior* perception of and memory for low-frequency visual features in natural scenes (Schneps et al., 2012). Our task explored the neural processing of natural dynamic visual cues to speech perception, which incorporate both low-frequency (e.g., jaw movement) and high-frequency (e.g., lip shape) visuo-spatial information, and by hypothesis should be directly related to the quality of phonological encoding. However, in the visual alone condition, dyslexics and controls showed equivalent entrainment strength and equivalent preferred phase, while in the AV condition the dyslexic group again showed an earlier preferred phase in the delta band compared to control participants, mirroring the findings for the auditory alone condition. When we explored how visual speech information affected the phase of auditory entrainment, we found that in the theta band visual information did alter preferred auditory phase, but to the same extent for both groups. Visual speech information is thought to reset auditory theta phase to the optimal alignment for processing upcoming speech (Schroeder and Lakatos, 2009). The only significant group difference was again in the delta band. As in the auditory alone condition, when computed for (AV–V), preferred phase of entrainment was significantly earlier for the dyslexic group. Hence despite the accompanying visual information, in the AV condition the participants with dyslexia were again entraining to a suboptimal phase. As previously, this suggests that the slower delta oscillations are not providing the dyslexic brain with an efficient temporal reference frame for auditory information encoding. In the theta band, by contrast, both groups showed efficient phase resetting of auditory oscillatory activity by congruent visual information.

In fact, given the earlier study by Power et al. (2012b) using the current paradigm, which reported a significant relationship between theta power and reading development in typically-developing children, the absence of significant group differences in theta band entrainment in the current study is somewhat surprising. Theta entrainment is thought to be central to speech processing on multi-time resolution models (syllable-level entrainment, e.g., Luo and Poeppel, 2007). However, our failure to find group differences in theta power or phase could be task-related. The participants were required to process a delta-rate rhythm (2 Hz), and to detect violations of that rhythm, and thus task demands did not focus on theta entrainment or phase. If stimuli had been delivered instead at a rhythmic rate within the theta band (e.g., 5 Hz), group differences in theta activity may have emerged. Nevertheless, the current violation detection task is likely to be more informative than the passive entrainment tasks used in prior studies with adult dyslexics (Lehongre et al., 2011; Hämäläinen et al., 2012b; Poelmans et al., 2012). With a passive listening paradigm it is impossible to quantify how the different groups are approaching the task, for example whether those with dyslexia and controls are using similar processing strategies. Furthermore, prior oscillatory studies suggest that when a stimulus is continuous (rather than rhythmic, as utilized here), the brain uses a continuous mode of processing, which maximizes gamma activity (e.g., Schroeder and Lakatos, 2009). Hence the gamma findings in prior studies using non-speech and continuous stimuli (Lehongre et al., 2011; Poelmans et al., 2012), indicating that gamma power was significantly lower in the dyslexic group when processing AM noise, could reflect task demands rather than stimulus-specific processing differences between participants with dyslexia and controls.

In conclusion, this study provides direct neural evidence for the "phonological representations" hypothesis of developmental dyslexia, according to which the neural representations underpinning word recognition in children with dyslexia are impaired or atypical in their phonological characteristics. The current study suggests that one mechanism contributing to atypical development of the dyslexic mental lexicon is auditory oscillatory entrainment to speech at a different preferred phase of the delta band, which consequentially affects the quality of the information encoded at all phonological levels including the phonemic level. Concurrent visual speech information as in natural listening conditions is not sufficient to ameliorate this difference in preferred auditory phase, as shown by the AV condition in the current study. Nevertheless, converging evidence is required regarding the developmental salience of delta band information for developing high-quality phonological representations, ideally investigating the entrainment to, and encoding of, auditory and speech stimuli in the dyslexic brain under various task demands.

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Impaired auditory sampling in dyslexia: further evidence from combined fMRI and EEG

Katia Lehongre*[1]*, Benjamin Morillon*[2]*, Anne-Lise Giraud*[3] *and Franck Ramus*[4]**

[1] Research Center of the Brain and Spine Institute (CRICM), Hôpital de la Pitié-Salpêtrière, Paris, France
[2] Department of Psychiatry, Columbia University Medical Center, New York, NY, USA
[3] Department of Neuroscience, University of Geneva, Geneva, Switzerland
[4] Laboratoire de Sciences Cognitives et Psycholinguistique, Ecole Normale Supérieure, EHESS, CNRS, Paris, France

Edited by:
Usha Goswami, University of Cambridge, UK
Andrea Facoetti, Università di Padova, Italy
Marie Lallier, Basque Center on Cognition Brain and Language, Spain
Alan J. Power, University of Cambridge, UK

Reviewed by:
Jarmo Hamalainen, University of Jyvaskyla, Finland
Hanne Poelmans, KU Leuven, Belgium

****Correspondence:***
Franck Ramus, Laboratoire de Sciences Cognitives et Psycholinguistique, Ecole Normale Supérieure, 29 rue d'Ulm, 75005 Paris, France
e-mail: franck.ramus@ens.fr

The aim of the present study was to explore auditory cortical oscillation properties in developmental dyslexia. We recorded cortical activity in 17 dyslexic participants and 15 matched controls using simultaneous EEG and fMRI during passive viewing of an audiovisual movie. We compared the distribution of brain oscillations in the delta, theta and gamma ranges over left and right auditory cortices. In controls, our results are consistent with the hypothesis that there is a dominance of gamma oscillations in the left hemisphere and a dominance of delta-theta oscillations in the right hemisphere. In dyslexics, we did not find such an interaction, but similar oscillations in both hemispheres. Thus, our results confirm that the primary cortical disruption in dyslexia lies in a lack of hemispheric specialization for gamma oscillations, which might disrupt the representation of or the access to phonemic units.

Keywords: dyslexia, auditory sampling, phonemic processing, gamma oscillation, theta oscillation, delta oscillation, EEG-fMRI

INTRODUCTION

Developmental dyslexia is a specific difficulty in the acquisition of reading skills that is not accounted for by mental age, visual acuity deficit or inadequate schooling (WHO, 2011). It is thought to affect between 3 and 7% of the population (Lindgren et al., 1985), although estimates vary widely depending on cut-off criteria on reading performance scales.

While there remains a great diversity of theoretical outlooks on dyslexia (Ramus and Ahissar, 2012), it is now widely agreed that the majority of dyslexic individuals share difficulties in one or several aspects of phonological processing, including paying attention to and mentally manipulating speech sounds (phonological awareness), storing phonological material for a few seconds (verbal short-term memory), and rapidly retrieving long-term phonological representations (Wagner and Torgesen, 1987; Vellutino et al., 2004). Debates persist on whether this phonological deficit (i) follows from an underlying primary auditory processing deficit (Tallal, 1980; Goswami et al., 2011), (ii) arises from a degradation of phonological representations or in difficulties accessing them (Ramus and Szenkovits, 2008), and (iii) is sufficient by itself to account for learning disability or merely a risk factor (Pennington, 2006).

At the anatomo-functional level, while the issue remains debated (Richlan et al., 2011), the vast majority of findings from functional and structural brain imaging and post-mortem dissection converge on a disruption of left perisylvian cortical networks, which are involved in speech processing and recruited for reading acquisition (Galaburda et al., 1985; Eckert, 2004; Richardson and Price, 2009; Linkersdorfer et al., 2012). Genetic variations associated with dyslexia further point to structural and functional variations in the perisylvian language network (Darki et al., 2012; Pinel et al., 2012; Giraud and Ramus, 2013).

A new theoretical framework for the cortical organization of speech processing sheds a new light on the neural basis of developmental dyslexia. According to "asymmetric sampling in time" (AST) theory (Poeppel, 2003), left and right auditory cortices show cortical oscillations at different preferred rates: low gamma (25–45 Hz) in the left hemisphere and delta-theta (1–7 Hz) in the right. Gamma and theta oscillations are assumed to play a role in the segmentation of the sound stream into units of the corresponding sizes, which may be optimal for the analysis of phonemes by the left auditory cortex and syllables and prosodic cues by the right one (around 25 and 200 ms, respectively). While this hypothesis has received empirical support from neuroimaging and neurophysiological studies (Giraud et al., 2007; Abrams et al., 2008; Telkemeyer et al., 2009; Morillon et al., 2010), its implications for developmental dyslexia are not so clear. On the one hand, Giraud and Poeppel (2012) have hypothesized that dyslexic individuals might not show the typical left-hemisphere specialization for the gamma rate, which would explain their specific difficulties with the processing of phonemic units. On the other hand, Goswami (2011) has hypothesized that dyslexic individuals might rather show atypical cortical oscillations in the theta

(4–7 Hz) or in the delta (1–4 Hz) frequency band, thereby leading to processing deficits at the syllable and more generally at the prosodic level, which are also proposed to be causally linked to reading disability (Goswami et al., 2010).

In a previous study, we used magnetoencephalography (MEG) to measure auditory steady-state responses (ASSRs) to an amplitude-modulated white noise in dyslexic and control individuals. We found the expected left dominance of ASSRs in the *planum temporale* in the gamma range (25–35 Hz) in controls, but not in dyslexic participants who displayed no or a reversed asymmetry (Lehongre et al., 2011). These results, that are supported by another study that also measured ASSRs [using electroencephalography (EEG)] and found group differences at 20 Hz in the left hemisphere (Poelmans et al., 2012), were consistent with the hypothesis of a left-hemisphere-based gamma oscillation disruption, but did not explicitly test the delta/theta alteration hypothezis. In the delta/theta range, one study found no group difference at 4 Hz using EEG-ASSR (Poelmans et al., 2012), and another one exploring MEG-ASSRs at 2, 4, 10 and 20 Hz found a right-hemisphere dominance at 2 Hz in controls but not in dyslexic participants and no further group difference at any other frequency (Hamalainen et al., 2012). Using more naturalistic speech stimuli, an EEG study found that poor readers, in contrast to good readers, did not present the natural dominance of the right hemisphere to follow the speech envelope. They presented a more bilateral pattern, but this was the case only when speech was compressed to 50% of its original duration (Abrams et al., 2009). Finally, anomalies in the alpha rhythm have also been found in children with dyslexia or with language impairments (Heim et al., 2011; Babiloni et al., 2012; Han et al., 2012).

In the context of these conflicting results, the goals of the present study were twofold: Firstly, to replicate and extend the results of our previous study, using more naturalistic stimuli and an entirely different methodology; secondly, to directly compare the predictions of the two main theories by testing cortical oscillations in the gamma, theta and delta ranges in auditory cortices. For this purpose, rather than using a simple amplitude-modulated noise, we exposed participants to an audiovisual documentary movie featuring more ecological conversational speech, thereby including the whole range of amplitude modulations relevant to language.

We used simultaneous EEG and functional magnetic resonance imaging (fMRI) to measure the activity of the auditory cortex at both high temporal (millisecond) and spatial (millimeter) resolution. Changes in Blood-oxygen-level-dependent (BOLD) are associated with changes in the spectral profile of neuronal activity (Rosa et al., 2010b), and EEG and fMRI do not capture exactly the same signals. Only a small fraction of the BOLD signal reflects synaptic activity involving pyramidal cells (Lee et al., 2010; Logothetis, 2010), which we hypothesize here to work as a sampling device. By combining delta, theta and low-gamma power variations and BOLD activity we expect to capture the part of the BOLD activity that is explained out by circuits involving pyramidal cells, which generate these rhythms. Furthermore, simultaneous EEG/fMRI recordings are well suited to study oscillations in continuous recordings with uncontrolled states as it has been demonstrated in several studies [see for review: (Herrmann and Debener, 2008; Rosa et al., 2010a; Laufs, 2012)].

MATERIALS AND METHODS

PARTICIPANTS

Thirty-two normal-hearing, French–native-speakers participated in a simultaneous EEG and fMRI experiment (with approval of the local ethics committee; biomedical protocol C08–39). Seventeen participants reported a history of reading disability, scored at or below the expected level for ninth graders in a standardized reading test, and at least 90 in non-verbal IQ. The remaining 15 participants were normal readers matching dyslexic participants with respect to age, gender, handedness, and non-verbal IQ, but scoring above the ninth grade reading level. Demographic and psychometric data, as well as the results of a larger battery (Soroli et al., 2010) of literacy and phonological tests are reported in **Table 1**.

BEHAVIORAL TEST BATTERY

Non-verbal intelligence was assessed in all participants using Raven's matrices (Raven et al., 1998). Their receptive vocabulary was assessed with the EVIP test (Dunn et al., 1993), a French adaptation of the Peabody picture vocabulary scale. They were included on the basis of performance on the Alouette test (Lefavrais, 1967), a meaningless text that assesses both reading accuracy and speed, yielding a composite measure of reading fluency. Orthographic skills were assessed using a computerized orthographic choice task, and a spelling-to-dictation test. Phonological tests: we used the WAIS digit span as a measure of verbal working memory (Wechsler, 2000). Phonological awareness was assessed using a computerized spoonerism task, in which participants heard pairs of words, and had to produce them swapping the initial phonemes. Finally, rapid automatized naming was assessed using the object and digit sheets from the PhAB (Frederickson et al., 1997) and two custom-made color sheets modeled on the object sheets, with five different colors repeated 10 times each, one replacing each object. The dependent variable is the total time taken to name all items on each sheet, irrespective of errors.

MRI ACQUISITION

Subjects were either asked to rest with closed eyes or to pay attention to an audiovisual movie (Morillon et al., 2010). The movie, a scientific documentary on an ecological topic, included three speakers (2 men). Data were acquired in three sessions with session 1: 10 min of rest; sessions 2 and 3: 10 min of movie followed by 11 min of rest. The scanner produced a constant auditory signal during data acquisition presumed not to interfere with our analyzes, given that its modulation frequencies are outside our frequencies of interest (See supplemental data p. 1, Morillon et al., 2010).

The three sessions yielded 1560 echoplanar fMRI image volumes (Tim-Trio; Siemens, 40 transverse slices, voxel size = $3 \times 3 \times 3$ mm; repetition time = 2 s; echo time = 50 ms; field of view = 192). A 7-min anatomical T1-weighted magnetization-prepared rapid acquisition gradient echo sequence (176 slices, field of view = 256, voxel size = $1 \times 1 \times 1$ mm) was acquired at the end of scanning.

Table 1 | Summary of behavioral tests.

	Controls (15 subjects)			Dyslexics (17 subjects)		
	n	Mean	sd	*n*	Mean	sd
Males	7			9		
Right handed	10			12		
Age	15	24.09	3.54	17	23.79	4.04
Non-verbal IQ	15	112.07	13.43	17	111.35	10.73
EVIP Vocabulary	15	123.07	2.94	15	120.67	5.26
Reading fluency (nb of correct words/min)***	15	196.16	36.98	17	113.53	24.70
Spelling (%)**	15	94.22	4.67	12	81.25	11.81
Orthographic choice accuracy (%)	14	95.07	5.47	15	89.60	9.82
RAN of objects (sec)**	15	61.80	10.23	17	78.37	17.85
RAN of digits (sec)***	15	31.87	6.56	17	44.78	12.34
RAN of colors (sec)**	15	54.33	9.15	17	71.21	18.80
Spoonerisms accuracy**	15	0.75	0.10	15	0.50	0.26
Digit span (%)***	15	10.73	1.58	17	7.35	2.85

As indicated by the number of participants, some values were missing for some tests.

*Sec: seconds; Stars indicate significant differences between controls and dyslexics (independent t-test, ** for p < 0.01, *** for p < 0.001, uncorrected).*

MRI PREPROCESSING

We used statistical parametric mapping (SPM8; Wellcome Department of Imaging Neuroscience, UK; www.fil.ion.ucl.ac.uk) for fMRI standard preprocessing, which first involved realignment of each subject's functional images and coregistration with structural images. Structural images were segmented, spatially normalized to Montreal Neurological Institute stereotactic space to $3 \times 3 \times 3$ mm and finally spatially smoothed with a 10-mm full-width half-maximum isotropic Gaussian kernel to compensate for residual variability after spatial normalization.

EEG ACQUISITION

Continuous EEG data were recorded at 5 kHz from 62 scalp sites (Easycap electrode cap) using MR compatible amplifiers (BrainAmp MR and Brain Vision Recorder software; Brainproducts). Two additional electrodes (electro-oculograph, EOG and electrocardiograph, ECG) were placed under the right eye and on the collarbone. FCz was set as reference for the acquisition of all electrodes. Impedances were kept under 10 kΩ and EEG was time-locked with the scanner clock, which helps to have a very reproducible, more easily removed MRI artifact, thus resulting in higher EEG quality in the gamma band (Mandelkow et al., 2006).

EEG PREPROCESSING

Gradient and pulse artifacts were first detected and marked using in-house software (wiki.cenir.org/doku.php/datahandler). Detection was achieved by correlating the data with automatically (for gradient) or manually (for pulse) defined templates. We used the raw signal of channel FC2 for gradient artifacts, and the raw ECG signal filtered between 0.5 and 10 Hz for pulse artifacts. In a second step, artifacts were corrected using two software: FASST v111017 (www.montefiore.ulg.ac.be/~phillips/FASST.html) for gradient artifacts and EEGlab v.9 (sccn.ucsd.edu/eeglab) for pulse artifacts. In both cases we used the principal component analyses methods implemented in the software. Blinks and vertical eye movements were corrected using independent component analyses as described in EEGlab's tutorial. Data were subsequently down-sampled to 250 Hz and re-referenced to a common average reference. The original reference electrode was recalculated as FCz, generating a total of 63 cortical electrodes.

For each subject, periods with head movement artifacts were detected by visual inspection, for rejection purposes as described below. As our interest was in auditory activity, we focused the analyses described below on the temporal channels that best captured the activity of our ROIs, i.e., where we observed the highest correlation between EEG and BOLD: T7, T8, FT7, FT8, TP7, TP8, TP9, and TP10.

ANALYZES

Analyzes are reported for the movie condition, as our interest was to explore brain oscillation properties during natural speech processing. Analyzes were also conducted on rest sessions but did not yield any significant result, in particular no group effect.

TIME-FREQUENCY ANALYZIS

For each movie session, we performed time-frequency (TF) analyzes with a Morlet wavelets approach using Fieldtrip (Oostenveld et al., 2011) at each channel for frequencies from 1 to 48 Hz bands, with a frequency step of 1 Hz and a time step of 0.1 s. For each frequency and channel, the previously detected periods of movement were rejected by replacing values by NaNs (Not A Number). The power time courses were converted to Z-scores, which, when larger than 4, were replaced by NaNs to remove residual artifacts. The transformed signal was then averaged over the eight temporal channels, Z-transformed a second time and averaged across frequency bands of interest: 1–3 Hz (delta), 4–7 Hz (theta) and 25–35 Hz (gamma). Finally NaNs were replaced by zeros. We removed (on average across all subjects) around 40 s of signal per movie condition (mean +/− s.e.m: controls: 36 +/− 8 s; dyslexics: 45 +/− 18 s; independent t-test: $t = -0.44$, $p = 0.65$).

REGIONS OF INTEREST (ROI)

In accordance with AST theory we focused our analysis on the auditory cortex. We used three regions of interest (ROI) within Heschl's gyrus (Te1.0, Te1.1, and Te1.2), and the *planum temporale*: Te3 (**Figure 1**), all defined from cytoarchitectonic criteria using the SPM anatomy toolbox v.1.6. BOLD time courses were averaged over voxels using MarsBar (Brett et al., 2002).

CORRELATION BETWEEN BOLD TIME COURSE OF ROIs AND EEG POWER SPECTRUM

For each ROI and frequency band (delta, theta and gamma), we built a design matrix to perform a partial correlation between the BOLD time course of the ROI and the EEG power. The EEG time courses (averaged across all eight electrodes) of each frequency band were convolved with the hemodynamic response function (HRF) and downsampled to 0.5 Hz, i.e., the fMRI sampling rate. This analyzis was meant to capture the degree to which each ROI oscillates in each frequency band. A positive correlation indicates that the EEG power fluctuations in any given frequency band are reflected in the modulations of local synaptic activity as detected with fMRI (Laufs et al., 2003). Such correlations allow us to exploit the spatially detailed BOLD effect to precisely localize widespread EEG effects, resulting in a finer localization of oscillatory activity than with EEG only (Rosa et al., 2010a). We averaged over the whole set of temporal electrodes (left and right hemisphere) to avoid hemispheric biases in the EEG. Using this approach, asymmetries arise from specific correlations with the BOLD effect (Giraud et al., 2007). Our statistical model also included the motion parameters, their derivatives, the averaged signal of three brain compartments (white-matter gray-matter and CSF), and of all out-of-brain voxels, as nuisance covariates, as well as a regressor modeling the sessions. For normalization purposes the entire matrix was Z-transformed in time.

GROUP LEVEL STATISTICS

A repeated-measures ANOVA (with Greenhouse-Geisser corrections when appropriate) was performed with SPSS (IBM Corp. Released 2012. IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY), with the Fisher transformed partial correlation coefficients between EEG power and BOLD time courses as dependent variables, the 4 areas, 3 frequency bands and 2 hemispheres as within-subject factors, and group, sex and handedness as between-subject factors. All factors were entered as main effects in the model, as well as the 2nd, 3rd, and 4th order interactions of the 3 within-subject factors and group. Effect sizes were estimated for some measures of within or between group differences with Cohen's formula: $d = (M_1–M_2)/SD_{pooled}$, with M_1 = mean of group 1, M_2 = mean of group 2, $SD_{pooled} = \sqrt{[(SD_1^2 + SD_2^2)/2]}$, SD_1 = standard deviation of group 1, SD_2 = standard deviation of group 2. All other analyses were done using Matlab (version 2011/2012) (The MathWorks Inc., Natick, Massachusetts, USA).

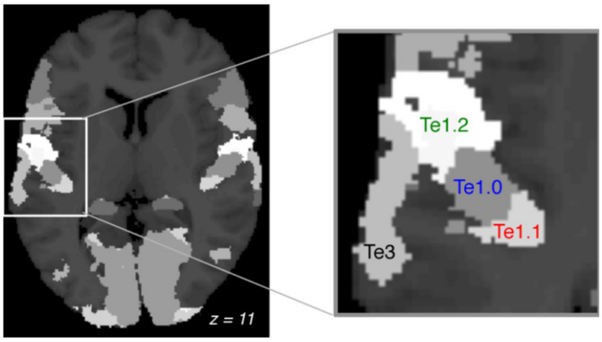

FIGURE 1 | Regions of interest. Cortical cytoarchitectonic areas defined by the anatomy toolbox (axial plane, MNI: z = +11). Focus on the left auditory cortex and the four ROIs: Te1.1, Te1.0, Te1.2, Te3. Te1 is Heschl's gyrus and Te3 is the *planum temporale*.

RESULTS

The repeated-measures ANOVA yielded significant main effects of area and hemisphere, and a group × frequency × hemisphere interaction.

Across groups, frequencies and hemispheres, there was a main effect of area [$F_{(2.2,\ 26.8)} = 7.45$, $p = 0.001$]. Correlations between EEG and fMRI were overall strongest in area Te1.2 and weakest in area Te1.1. This suggests that different regions of the auditory cortex show differential strength of responses in the frequency bands of interest, however, the specific correlation pattern observed here does not suggest any obvious interpretation. We also observed a main effect of hemisphere, with overall higher correlations in the right than in the left hemisphere [$F_{(1,\ 28)} = 8.28$, $p = 0.008$], an effect that seems to be carried by the delta and theta bands [$F_{(1,28)} = 10.15$, $p = 0.004$ and $F_{1,28} = 7.04$, $p = 0.013$ respectively, see **Figure 2**].

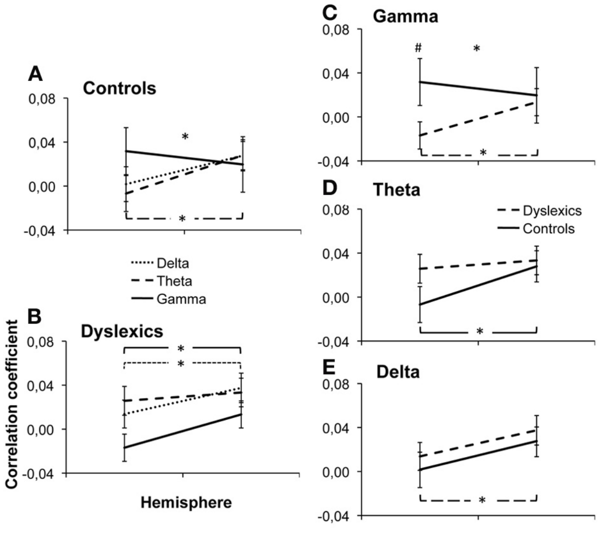

FIGURE 2 | Group × Frequency × Hemisphere interaction. Individual beta values were averaged over ROIs and plotted along the different dimensions of the interaction: Frequency × Hemisphere interaction in controls **(A)** and dyslexics **(B)** and Frequency × Group interaction in the gamma **(C)**, delta **(D)** and theta **(E)** bands. Error bars represent the s.e.m. *indicates a significant interaction or difference with $p < 0.05$. #indicates a marginally significant difference, $p = 0.066$.

Table 2 | Mean values of partial correlations.

	Controls ($n = 15$)				Dyslexics ($n = 17$)			
	Left		Right		Left		Right	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Gamma	0.03	0.08	0.02	0.10	−0.02	0.06	0.01	0.05
Theta	0.00	0.06	0.03	0.06	0.03	0.05	0.03*	0.05
Delta	0.01	0.06	0.03*	0.05	0.01	0.05	0.04*	0.06

Averaged partial correlation over areas in left and right hemispheres of both groups.

Stars indicate values significantly different from 0 (p < 0.05).

Most interestingly, we observed a group × hemisphere × frequency band interaction [$F_{(1.90,\ 27.10)} = 6.56$, $p = 0.003$, **Figure 2**, **Table 2**. Controls presented a frequency × hemisphere interaction [$F_{(1.76,\ 11.24)} = 5.21$, $p = 0.017$, **Figure 2A**], with right dominance for theta [$F_{(1,\ 12)} = 8.71$, $p = 0.012$]. The delta and gamma bands showed no significant asymmetry [$F_{(1,\ 12)} = 3.10$, $p = 0.104$; $\mathrm{F}_{1,\ 12} = 0.51$, $p = 0.487$, respectively]. Conversely, dyslexics showed the same correlation patterns across frequencies [frequency × hemisphere: $F_{(1.93,\ 13.07)} = 1.32$, $p = 0.288$; **Figure 2B**], but overall stronger correlations in the right than in the left hemisphere [$\mathrm{F}_{(1,\ 14)} = 6.83$, $p = 0.020$], carried mostly by the gamma and delta bands [$F_{(1,\ 14)} = 5.16$, $p = 0.039$; $F_{(1,\ 14)} = 8.94$, $p = 0.010$ respectively]. Thus, the control group presented a hemispheric division of labor consistent with that predicted by Poeppel (2003) and observed by Giraud and collaborators (Giraud et al., 2007; Morillon et al., 2010), while the dyslexic group did not.

To further interpret this triple interaction, we first compared the neural organization for each frequency band between groups by testing group × hemisphere interactions for each frequency band. For the gamma band (**Figure 2C**), there was a hemisphere × group interaction [$F_{(1,\ 28)} = 5.30$, $p = 0.029$], with a marginally significant group difference in the left [Controls > Dyslexics, $F_{(1)} = 3.66$, $p = 0.066$, effect size: $d = 0.71$] but not in the right hemisphere [$F_{(1)} = 0.29$, $p = 0.867$]. However, the theta and delta bands (**Figures 2D,E**) showed no significant group × hemisphere interaction [$F_{(1,\ 28)} = 2.80$, $p = 0.105$ and $\mathrm{F}_{1,\ 28} = 0.001$, $p = 0.937$, respectively]. Thus, the difference between the two groups lies primarily in the lateralization of cortical responses to the gamma band.

Finally, in order to fully describe the triple interaction, we tested the group × frequency interaction, hemisphere by hemisphere. In the left hemisphere, we observed a group × frequency interaction [$F_{(1.43,\ 27.57)} = 4.39$, $p = 0.030$], with marginally stronger correlations for the gamma band in controls than in dyslexics as described in the paragraph above. However, in the right hemisphere we observed no group × frequency interaction [$F_{(1.52,\ 27.48)} = 0.17$, $p = 0.781$]. This suggests that the cortical disorganization of the auditory cortex in dyslexia affects the left more than the right hemisphere.

Because hand preference is to some extent linked with language laterality, we also investigated hand preference effects. We found an area × hemisphere × hand preference interaction [$F_{(2.20,\ 26.80)} = 6.035$, $p = 0.003$), reflecting over both groups stronger right than left correlations between EEG power and the BOLD signal for right-handers in area Te1.0 and Te1.2 [$F_{(1,\ 19)} = 8.35$, $p = 0.009$; $F_{(1,\ 19)} = 13.87$, $p = 0.001$, respectively], and stronger right than left correlations for left-handers in area Te1.1 and Te3 [$F_{(1,\ 7)} = 5.67$, $p = 0.049$; $F_{(1,\ 7)} = 10.06$, $p = 0.016$, respectively]. There was also a hemisphere × hand preference interaction in Te1.2 [$F_{(1,\ 28)} = 9.12$, $p = 0.005$], with a trend in the left hemisphere for stronger correlations in left handed than in right handed subjects [$F_{(1)} = 3.56$, $p = 0.069$].

Finally, because of the suspicion that males and females might have partly different brain bases for dyslexia (Humphreys et al., 1990; Altarelli et al., 2013; Evans et al., 2013) we checked whether there was any sex effect. No main effect of sex and no significant interaction involving this factor were observed, whether groups were considered together or apart. Thus, the results obtained seem to hold equally across males and females.

DISCUSSION

In a previous study (Lehongre et al., 2011) we observed that dyslexic subjects had disrupted ASSRs at phoneme-relevant rates (low gamma around 30 Hz). While controls presented a left dominance in low-gamma range oscillations, in accordance with AST theory (Poeppel, 2003), dyslexic individuals showed no asymmetry or a right dominance. However, that study relied on the processing of an unnatural sound, a white noise that was modulated in amplitude. Furthermore, that the noise was modulated from 10 to 80 Hz made it impossible for us to test brain responses in frequency bands beyond this range. In particular, we could not test Goswami (2011) hypothesis that oscillations at syllable-relevant rates (delta and theta, 1–7 Hz) were disrupted. In the current study, we used more ecological audiovisual stimuli in which sounds were essentially natural conversational speech that better reflects situation outside the laboratory, and we were able to analyze at once the whole range of frequencies that are suspected to be altered in dyslexia, in Heschl's gyrus and the *planum temporale*. By using natural speech we preferentially induce those oscillations that are prominent in speech envelope (delta/theta), and periodically reset by speech onsets. As gamma power is both evoked by speech edges and controlled by theta modulations, it also follows speech modulations in primary auditory cortex (Giraud and Poeppel, 2012).

While our results do not show a clear-cut group difference in all of the conditions examined, they do show significant interactions that, in our view, constitute stronger results than a group difference in a single hand-picked condition. Our main finding is a group × hemisphere × frequency interaction, indicating that dyslexics differ from controls in the way the processing of the three target frequency bands is distributed across the two hemispheres. While control subjects show a frequency × hemisphere interaction, with a right dominance only for theta oscillations, dyslexic subjects show the same correlation patterns across the three bands, with a global dominance of the right hemisphere, suggesting a different pattern of hemispheric specialization.

With respect to the two target hypotheses on dyslexia, we find that dyslexic individuals' auditory cortical function differs from controls more in the left than in the right auditory cortex (group × frequency interaction in the left hemisphere only), and more for the gamma than for the delta and theta bands (group × hemisphere interaction for the gamma band only). The present results hence are consistent with our previous conclusion (Lehongre et al., 2011), that dyslexia reflects a primary disruption of left-hemisphere based gamma band oscillations.

Exploring low frequency oscillations in the delta (1–3 Hz) and theta ranges (4–7 Hz), we confirmed a right dominance for delta-theta oscillations in the auditory cortex of both controls and dyslexics (Poeppel, 2003). However, as there was neither a group × hemisphere interaction for the delta and theta bands, nor any hint of a group difference in the right hemisphere, the present results do not lend much support to the hypothesis of a right-hemisphere based, delta or theta oscillation disruption (Goswami, 2011).

One possibility to explain the conflicting results between studies might be a language difference. Indeed studies reporting group differences in delta-theta frequency bands were carried out in English only (Abrams et al., 2009; Hamalainen et al., 2012). It might be that speakers of a stress-timed language like English acquire stronger sensitivity to delta and theta rhythms than those of a syllable-timed language like French. However, this hypothesis is not consistent with the results obtained in (stress-timed) Dutch speakers by Poelmans et al. (2012). Another parameter to take into account is that the BOLD signal is described as mostly driven by oscillations in the beta/gamma band (Magri et al., 2012). This might induce both greater EEG/BOLD correlations and a better signal/noise ratio for this frequency band than for the delta/theta range, and therefore increase our statistical power to detect group differences in the gamma band. However, we do not find in our data any evidence of greater correlations in the gamma than in the delta-theta bands.

Our study also differs from the other EEG/MEG studies, as we did not analyze simple EEG power spectrum. The reason is that our stimulus being conversational speech, there is no multiply-repeated stimulus that enables a well-defined spectro-temporal analyzis of the evoked response. We did not analyze the phase locking with the speech envelope either, because this would provide information about low frequencies (Howard and Poeppel, 2012), but not the gamma band, and we wanted to compare both frequency bands. Our analysis of correlations between the EEG power time course and the BOLD signal allowed us to estimate the degree to which activations in specific brain regions reflect cortical oscillations in given frequency bands. The EEG signal alone lacks spatial resolution, and the BOLD signal alone reflects much more than cortical oscillations. Here we were able to interrogate auditory cortex very precisely, as variations in EEG/BOLD correlations presumably reflect variations in cortical oscillations in the specific areas of interest, that are probably related to the fluctuations in amplitude of the speech envelope modulations.

To what extent do our results depend on the naturalistic audio-visual stimuli used here, as opposed to amplitude-modulated sounds used in previous studies? Our exclusive focus on primary and secondary auditory cortex makes it unlikely that we should observe direct responses to either the higher-level linguistic information, or the visual information. However, it is plausible that the access to semantic information and the presence of synchronized visual information (lip movements) may have served to enhance the responses to the auditory stimuli, thereby improving the signal/noise ratio.

As described by other functional and anatomical studies, many measures highlight a weak or reversed brain lateralization related to language in dyslexics, including in the *planum temporale*, labeled Te3 here (Galaburda et al., 1985, 1987; Altarelli et al., submitted). The lack of hemispheric specialization for delta, theta, and gamma oscillations could affect the efficiency of the auditory processing based on a dual-scale temporal integration (Poeppel, 2003). One possible consequence of this deficit of low gamma oscillations in dyslexics' left hemisphere is to lead them to segment the auditory input into non-standard phonemic units, hence distorting the very format of their phonological representations. This would be consistent with the general understanding of the phonological deficit in dyslexia (Mody et al., 1997; Adlard and Hazan, 1998; Serniclaes et al., 2004; Vellutino et al., 2004). Another possibility would be that such cortical oscillations do not directly affect the format of phonological representations, but their salience or their availability for downstream cognitive processes. Thus, the disruption of phoneme-relevant cortical oscillations is also compatible with the view that dyslexics' phonological representations are essentially normal, but that phonemic units are more difficult to rapidly access, to pay attention to, and to manipulate for dyslexic individuals (Ramus and Szenkovits, 2008; Ramus and Ahissar, 2012; Giraud and Ramus, 2013).

CONCLUSION

In this study, we used a combined EEG-fMRI paradigm to measure the oscillations of auditory cortical areas in response to speech stimuli in dyslexic and in control adult participants, in three frequency bands of interest: gamma (25–35 Hz), theta (4–7 Hz) and delta (1–3 Hz). We first confirmed the presence of an auditory sampling impairment in dyslexia, using natural speech listening conditions. Secondly, we further confirmed that this impairment consisted mainly in a in a reduced responsiveness of left auditory cortex to gamma oscillations. On the other hand, we found little evidence for a disruption in auditory sampling in the delta and theta rates. Our results are consistent with a large literature showing the difficulties of dyslexic individuals with the representation, processing, or access to phonemic units, and provide a possible brain basis for this phenomenon.

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Visual and auditory synchronization deficits among dyslexic readers as compared to non-impaired readers: a cross-correlation algorithm analysis

Itamar Sela*

Edmond J. Safra Brain Research Center for the Study of Learning Disabilities, University of Haifa, Haifa, Israel

Edited by:
Marie Lallier, Basque Center on Cognition Brain and Language, Spain
Usha Goswami, University of Cambridge, UK
Andrea Facoetti, Università di Padova, Italy
Alan J. Power, University of Cambridge, UK

Reviewed by:
Thomas Lachmann, University of Kaiserslautern, Germany
Manon Wyn Jones, Bangor University, United Kingdom

****Correspondence:***
Itamar Sela, Edmond J. Safra Brain Research Center for the Study of Learning Disabilities, University of Haifa, Mount Carmel, Haifa 31905, Israel
e-mail: isela01@campus.haifa.ac.il

Visual and auditory temporal processing and crossmodal integration are crucial factors in the word decoding process. The speed of processing (SOP) gap (Asynchrony) between these two modalities, which has been suggested as related to the dyslexia phenomenon, is the focus of the current study. Nineteen dyslexic and 17 non-impaired University adult readers were given stimuli in a reaction time (RT) procedure where participants were asked to identify whether the stimulus type was only visual, only auditory or crossmodally integrated. Accuracy, RT, and Event Related Potential (ERP) measures were obtained for each of the three conditions. An algorithm to measure the contribution of the temporal SOP of each modality to the crossmodal integration in each group of participants was developed. Results obtained using this model for the analysis of the current study data, indicated that in the crossmodal integration condition the presence of the auditory modality at the pre-response time frame (between 170 and 240 ms after stimulus presentation), increased processing speed in the visual modality among the non-impaired readers, but not in the dyslexic group. The differences between the temporal SOP of the modalities among the dyslexics and the non-impaired readers give additional support to the theory that an asynchrony between the visual and auditory modalities is a cause of dyslexia.

Keywords: dyslexia, asynchrony, crossmodal integration, EEG, ERP, cross-correlation analysis

INTRODUCTION

According to a widely accepted definition of developmental dyslexia, a dyslexic reader is one who exhibits slow and inaccurate reading performance unrelated to his/her IQ level or educational opportunities (British Psychological Society, 1999; Lyon and Shaywitz, 2003; Shaywitz and Shaywitz, 2008). An abundance of research into phonological deficits has indicated that the primary source of the difficulties experienced by dyslexic readers lies in word decoding accuracy (Liberman and Shankweiler, 1991; Badian, 1997). Some studies have found that disabled readers demonstrate a fundamental orthographic deficit (Stanovich and West, 1989; Cunningham and Stanovich, 1990; Zecker, 1991; Barker et al., 1992; Morris et al., 1998).The reading deficits of developmental dyslexia persist into adulthood (Bruck, 1992; Leonard et al., 2001). A large number of studies have shown deficient phonological processing as a core deficit in developmental dyslexia. The leading theory, the phonological deficit theory of developmental dyslexia (Stanovich, 1988; Share, 1994; Snowling, 1995), suggests that dyslexic readers may suffer from an (unspecified) dysfunction in peri-sylvian brain regions, which leads to difficulties in generating and processing accurate and efficient phonological representations of speech sounds (Stanovich, 1988; Temple et al., 2001).

In addition, researchers are still debating whether dyslexic readers are characterized by impairment in basic auditory and/or visual processing (Amitay et al., 2002a,b; Vellutino et al., 2004; Lachmann et al., 2005; Groth et al., 2011). In the auditory domain, data has indicated dyslexics' inability to discriminate between temporal rapidly changing tones and consecutive acoustic events (Tallal, 1980; Tallal et al., 1993, 1998). Difficulties locating the origin of sounds and blending them were also found (Stein, 1993). In the visual domain, findings have indicated that dyslexic readers have smaller and fewer neurons in the magnocellular layers of the Lateral Geniculate Nucleus (LGN) (Livingstone, 1991) suggesting fundamental deficiencies of the magnocellular system and pathways of the visual cortex that are responsible for motion, contrast sensitivity (Stein and Walsh, 1997; Stein and Talcott, 1999; Stein, 2001; Stein et al., 2001) and fast sequential processing (Ben-Yehudah and Ahissar, 2004). Based on the aforementioned studies regarding the presumed low-level visual and/or auditory sensory deficit among dyslexic readers, it was recently demonstrated, using the Pair Associate Learning paradigm (Hulme et al., 2007), that dyslexic readers exhibited a crossmodal association difficulty (Jones et al., 2013). Previous data (Breznitz, 2002, 2003, 2006) has found that the gap in the speed of processing (SOP) between the visual and auditory modalities is wider among dyslexic readers than non-impaired readers. This gap prevents the precise integration over time (Berninger et al., 1990; Wolf and Bowers, 2000) of the cross-modal information necessary for accurate word decoding and leads to the asynchrony phenomenon. Breznitz (2006) suggested that the asynchrony phenomenon in the word-decoding process occurs when there is time gap resulting in a mismatch between the grapheme and its phoneme correspondent.

It was previously suggested that different frequency ranges are important to speech perception (Luo and Poeppel, 2007; Ghitza and Greenberg, 2009). The temporal sampling framework for developmental dyslexia (Goswami, 2011) proposes that at the basic level of auditory perception processing, dyslexic readers have difficulties distinguishing between different frequency ranges, an impairment that leads to a slower and less accurate speech perception (Goswami et al., 2010). It is reasonable to assume that an impairment in sensory temporal processing that can be identified at the frequency domain may be also expressed at the time domain. Thus, it is important to study whether dyslexic readers exhibit an abnormal basic sensory (auditory or visual) information processing. Here, the dyslexic readers' ability to process fundamental sensory input is investigated by using a time-based cross-correlation analysis.

The synchronization hypothesis proposes that for accurate information processing to occur, it is crucial that the information that arrives from more than one modality be integrated in both content (Fujisaki and Nahida, 2005; Ghajar and Ivry, 2008; Neil et al., 2011) and time (Llinas, 1993; Breznitz, 2001, 2002, 2003, 2006; Breznitz and Misra, 2003; Breznitz et al., 2013). The act of reading relies on the information processing system and during the word decoding process both the visual and the auditory modalities are activated. Word decoding accuracy can be achieved only when the activation within and between modalities is synchronized (Breznitz, 2008). It was found that the time gap between the visual and auditory Event Related Potential (ERP) component of P1 of the dyslexic readers was larger than 100 ms, whereas the non-impaired readers exhibited an insignificant time gap of 15–30 ms only (Breznitz, 2008). A similar trend of results was found when the time gap between the auditory and visual ERP of N1 was analyzed. Moreover, it was shown that the between-modalities time gap has developmental constraints: while the auditory components of N1 and P1 had shorter latency as compared to visual ones among dyslexic children, the opposite was found among adult dyslexic readers (Breznitz, 2008). The author argued that these results support the notion that a deficit within the visual modality affects decoding ability, a claim that was supported by evidence of a significant correlation between the between-modalities time gap and reading performance (fluency and reading errors).

The visual-orthographic and auditory-phonological systems are the core systems activated temporally during the word-decoding process. However, during a normal course of processing, both systems differ not only in the structure and length of their neural networks, but are also located in different parts of the brain (Saito et al., 2005) and operate in a different manner and at different speeds (Breznitz, 2002, 2003, 2006). Data has indicated that auditory information arrives (Mishra et al., 2007) at the auditory cortex, about 30 ms after stimulus presentation (Heil et al., 1999), whereas visual information arrives (Mishra et al., 2007) at the visual cortex about 70 ms after stimulus presentation (Schmolesky et al., 1998). This suggests that when a stimulus includes both visual and auditory representations, the auditory stimuli arrive in the brain faster than the visual stimuli. However, at the word-decoding level, the auditory-phonological channel perceives and processes the information in a temporal-serial manner (Rosenzweig and Bennet, 1996), whereas the visual-orthographic channel process information in a spatial, holistic manner (Breznitz, 2006). This suggests that visual processing at this level might be faster than auditory processing. Yet, an effective word decoding process requires an exact integration of graphemes and phonemes (Adams, 1990; Berninger, 2001). In other words, the two systems need to be synchronized for appropriate crossmodal integration to occur. The focus of the current study is to quantify the synchronization of the two modalities among non-impaired and dyslexic readers.

Earlier studies that verified the relationships between visual and auditory processing among non-impaired readers suggested that presenting a visual pattern prior to an auditory one eases inter-sensory correspondence while the presentation of an auditory pattern prior to a visual one increases correspondence errors (Botuck and Turkewitz, 1990). It has been suggested that either the information might be received more accurately through the visual as opposed to the auditory modality, or it is more difficult to register information arranged temporally than information arranged spatially in memory (Botuck and Turkewitz, 1990). Furthermore, Ben-Artzi and Marks (1995) examined whether and how stimulus type influences visual-auditory interaction. In Ben-Artzi and Marks' study (1995), participants were asked to classify sound levels and spatial locations on two types of tasks: uni-dimensional and bi-dimensional. Data indicated that visual identification is not only faster (see also Melara and O'Brien, 1987) but also dominant (Egeth and Sager, 1977) over the auditory identification. Posner et al. (1976) suggested that visual dominance is, in fact, a compensation for the visual system's limited capacity to arouse internal attention. According to this approach, the increases in sound level in the auditory system arouse attention automatically. However, the arousal of attention in the visual system requires specific controlled effort and the brain learns to allocate attention to visual stimuli. Furthermore, it has been suggested that the existence of the visual system, which can allocate attention to spatial stimuli, enables the ear to relate to its relevant stimuli (Posner et al., 1976). By using fMRI imaging techniques, recent studies have indicated that during crossmodal activation, when both visual and auditory information are presented, the visual modality is dominant at the pre- response level whereas the auditory is more dominant at the response level (i.e., Koppen et al., 2009; Chen and Zhou, 2013). Thus, all the above support the notion that a deficit in the visual modality might be involved in dyslexia. In light of the assumption that the visual modality has dominancy over the auditory modality, it is important to investigate the relationship and interaction between the two sensory modalities.

The basic assumption of this study is that exposing a participant to either a visual or an auditory stimulus triggers sequential information processing which has an effect on ongoing ERP activity. Furthermore, visual-only or auditory-only information processing is carried out in a similar fashion irrespective of whether the stimulus is solely visual or accompanied by an auditory stimulus presented at the same time (crossmodal presentation). Therefore, the first hypothesis of this study is that the ongoing

ERP of the crossmodal condition will contain visual and auditory elements that will also be found in each of the unimodal conditions (Marchant and Driver, 2013). It should be noted that the current study does not assume that an apparent correlation between the unimodal and crossmodal ERPs stems solely from the presence of the unimodal element within the crossmodal ERP. It is proposed that to a certain extent, the two datasets share a common factor which may be explained as a specific unimodal brain reaction.

The second hypothesis asserts that although the information processing of a unimodality (specific-visual or auditory) will be similar under the two conditions of the unimodal stimulus type and under the two modalities stimulus type, the crossmodal processing will affect the SOP of the uni (specific) modality. Thus, if the data were to be looked at in an individual time window for the unimodal condition, it is assumed that a similar pattern of the component (factor) will be found in a corresponding time window for the crossmodal condition, but not necessarily in exactly the same time location, as it may appear earlier or later [this is defined as Delta Time (DT)]. The polarity of DT indicates either an acceleration (negative DT) or deceleration (positive DT) in one modality's SOP as a result of the presence of the second modality.

As the SOP of the two different modalities was shown to differ (Saito et al., 2005) the third hypothesis of the current study is that differences will be found between the size of the interaction between the visual and auditory modalities and the influence of one modality on the other. Moreover, as dyslexic readers' ability to process uni (visual or auditory) and crossmodal sensory information was found deficient (Lachmann et al., 2005; Breznitz, 2006; Jones et al., 2013), the fourth hypothesis of the current study is that differences between the two-reading-level groups will be found. Specifically, it is assumed that the results of the current study would show a negative effect of one modality (visual or auditory) on the SOP of the other modality among the dyslexic readers.

METHODS

PARTICIPANTS

Nineteen dyslexic readers (age 25.5 ± 2.91) and 17 non-impaired readers (age: 24.52 ± 2.29) were included in the study [$t_{(35)} = 0.191, p = 0.242$]. None of the participants had a history of neurological or emotional disorders, and no differences were found between dyslexics and non- impaired readers in attention ability as measured by the d2 test for adults [$t_{(35)} = -0.222, p = 0.825$] (Brickenkamp, 1981). The dyslexic readers were diagnosed with dyslexia during childhood, and their diagnosis was confirmed as adults by achieving one standard (−1) score or below on the Hebrew "MATAL" normative reading test (MATAL Battery, 2007). The non-impaired readers were recruited via notices posted on campus bulletin boards. Individuals with dyslexia were recruited through the Student Support Service at the University of Haifa. All participants were native Hebrew speakers from a middle-class background, right-handed, and screened for normal hearing. All participants displayed normal or corrected-to-normal vision in both eyes. All participants gave their informed written consent prior to inclusion in the study, and all were paid as compensation for their time. The experiment was approved by the University of Haifa Ethics Committee (Number, 1991) according to the Helsinki Declaration.

The classification of participants into non-impaired readers and dyslexic readers groups was based on the following behavioral measures (For more details see Breznitz and Misra, 2003; Breznitz et al., 2013).

Intelligence

Intelligence was tested by the *Block Design* (performance) and the Similarities sub-tests (verbal) from the WAIS-III (Wechsler, 1997).

Decoding skills

One Minute Tests (Breznitz and Misra, 2003) comprised a battery of two subtests one for words and the other for pseudowords in which the participants were asked to read single words or pseudowords as quickly and as accurately as possible within the space of 1 min.

Reading rate and accuracy of connected text

Oral reading time and accuracy of a narrative text comprising 247 words (MATAL Battery, 2007. See also Breznitz and Misra, 2003). Reading time was defined as the mean reading time for each word read correctly.

Reading rate and comprehension

A Reading Comprehension Test (MATAL Battery, 2007), comprising 412 words. The participants were asked to silently read a passage as quickly as possible and then answer 18 comprehension questions. Reading time was based on the mean reading time per word. Comprehension scores were based on the total number of correct answers.

Memory

In the Digit Span (WAIS III, Wechsler, 1997), the standard scores of each participant were recorded.

Speed of processing (SOP)

Two tests were used to assess SOP: The Digit Symbol Task and Coding Task-Speed Factor (WAIS III, Wechsler, 1997).

Table 1 presents the means, standard deviations, and *t* values for the reading and the cognitive background measures. The dyslexic readers achieved significantly lower scores than the non-impaired readers in reading accuracy and time parameters but not for silent reading comprehension. In addition the dyslexic readers also obtained significantly lower scores compared to the non-impaired readers in the SOP and working memory measures but not in the intelligence measures (see **Table 1**).

APPARATUS

Two computer sets were used in this study. The first computer was used to present the task stimuli (visual as well as auditory, using a screen, and a pair of speakers) and to record participant's responses. The electrophysiological data was collected using a Bio-Logic Brain Atlas IV computer system (2nd computer set) with 20 electroencephalographic (EEG) activity reception channels. The data collection from the scalp began at approximately

Table 1 | Reading and cognitive measures for dyslexic and non-impaired readers.

	Non-impaired readers group		Dyslexic readers group		*t*
	Mean	***SD***	**Mean**	***SD***	
One minute test—number of words read correctly	111.04	16.99	65.63	20.71	−8.87***
Pseudowords per minute—number of correct Pseudowords read	59.89	15.68	27.50	11.05	−8.70***
Oral reading (per letter reading rate)	0.69	0.18	0.41	0.09	6.19***
Silent text reading rate—total reading time	212.05	54.69	128.83	30.12	−6.89***
Reading comprehension (correct answers out of 18 questions)	16.67	2.40	15.54	4.70	1.06
Digit symbol SD score	12.60	10.75	8.23	15.16	−2.63**
Coding SD Score	13.87	10.86	8.90	5.98	5.57***
General ability similarities	12.01	3.86	11.90	2.91	1.57
Block design	12.67	2.29	12.85	1.66	1.21
Digit span—standard score	12.42	3.08	9.00	2.76	−4.38***

***$p < 0.01$; ***$p < 0.001$.*

1000 ms prior to the beginning of the experimental task. The sample rate was 256 Hz and was carried out using a full array of electrodes placed according to the International 10/20 system (Jasper, 1958) utilizing an Electro-cap (a nylon cap fitted over the head with 9 mm tin electrodes sewn within).An electrooculogram (EOG) was recorded with an electrode extension that was located under the left eye. A ground electrode was placed on the left mastoid. All electrodes were maintained at an impedance of 5 KΩ or less. Brain activity was sampled directly from 19 scalp electrodes (Fp1, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, O2).

TASK DESIGN

A visual, auditory, and crossmodal processing task (Breznitz and Misra, 2003; Meyler and Breznitz, 2003) was administered. This task consisted of 150 stimuli presented to the participants in three different conditions: auditory alone (50 tones occurring at 1000 Hz with a time length of 200 ms), visual alone (50 white rectangle shape stimuli, presented at the middle of a black screen for duration of 200 ms), and crossmodal (50 tones and flashes occurring simultaneously). The 150 stimuli were presented in a randomized order. The between trials interval, i.e., the time from the beginning of one trial to the beginning of the next trial was set to 2 s. The participants were asked to press one of three computer keys—One key to indicate the appearance of an auditory tone stimulus alone, one key for the visual rectangle-like flash, and the another key to indicate when the two stimuli occurred simultaneously. Off-line analysis differentiated between the auditory, visual, and simultaneous segments. All stimuli were presented to the participants on a PC computer. Participants were seated 0.5 m from the computer screen and heard the tones via speakers.

PROCEDURE

During data collection, participants were seated in a sound attenuated room. The experiment took place during two sessions of about 2 h each. The first part of data collection consisted of gathering the behavioral measures, and in the second part the experimental tasks ERP measures were incorporated.

DATA ANALYSIS

For each participant and for each of the three task conditions, both the mean value of Reaction Time (RT) for correct responses and accuracy were computed. The EEG data were segmented into 1945 ms epochs (one per trial) and by three different conditions based on the trial type (1-visual-only, 2-auditory-only, 3-crossmodal stimulus). Data of one trial started 445 ms prior to stimulus presentation and ended 650 ms following presentation. The data was corrected for eye movements using the Orgil Medical Equipment (1997), normalized by comparing cognitive activity time with inactive time for each electrode, separately, for each participant, filtered using a low pass 20–24 Hz filter, and averaged by stimulus type (Orgil software, 1997) prior to beginning the cross-correlation analysis.

CROSS-CORRELATION ANALYSIS

In order to verify the research hypotheses, a cross-correlation analysis was obtained. Cross-correlation analysis is a procedure used in signal processing by which the similarity between two signals is measured. The algorithm analysis output is a series of correlation coefficients between two signals according to time, i.e., one correlation coefficient is calculated for successive time points according to a specific temporal increment (Woody, 1967; Nelson-Wong et al., 2009). Previously, the cross-correlation technique was used as part of a tool aimed at overcoming the limitations of the traditional ERP averaging method and to categorize participants based on their ERP data (Sela et al., 2008). Similar to the work of Sela et al. (2008), the current study algorithm obtained and compared data time windows taken from participants' ERPs. These data time windows included all 19 electrodes within the selected time areas. In the following algorithm, the term "unimodal" refers to either visual- or auditory-only ERP datasets. The term "crossmodal" refers to the synchronized visual-auditory stimulus's ERP.

TIME WINDOW ANALYSIS—CREATION OF A CROSS-CORRELATION GRAPH

The following algorithm was used on three different datasets: visual-only ERP, auditory-only ERP, and crossmodal ERP. The explanation below describes the process in which a cross-correlation graph is computed.

1. A unimodal time window was constructed by taking the values (amplitude) of all electrodes from the unimodal dataset across a certain time window (**Figure 1**). Thus, a time window is defined as a two-dimensional dataset with electrodes as rows and time samples as columns. The time window's location is defined as the center of the specific time window. For example, a time window taken at the time area of 150 ms

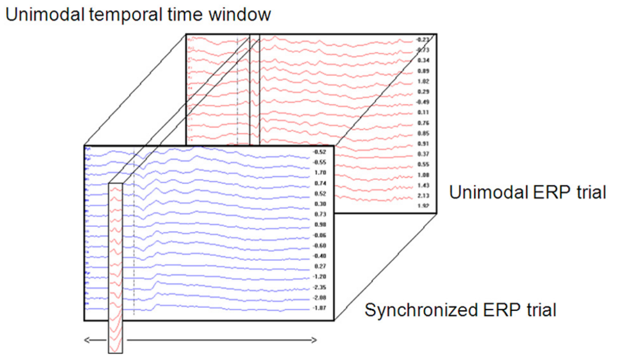

FIGURE 1 | Cross-correlation analysis between a unimodal time window throughout the crossmodaltrial.

is defined as the amplitude data of all electrodes between 100 and 200 ms (see Temporal implementation of Phases A and B for an explanation of the choice of time window location).

2. A cross-correlation loop between the above time window and the crossmodal ERP was applied as follows:
   a. A crossmodal ERP time window of the same duration of the unimodal ERP time window constructed in Phase 1 was computed. The first crossmodal ERP time window used in the algorithm was from 0 to 100 ms. Note that the algorithm takes into account a time window of all electrodes altogether.
   b. The correlation strength between the two time windows was calculated and resulted in a number within the range of −1 and 1. A value of zero indicates no correlation. A correlation value that approaches −1 indicates a strong negative correlation and a value that approached 1 indicates a strong positive correlation.
   c. A new crossmodal ERP time window was then constructed which was located one successive time frame (3.9 ms) after the crossmodal ERP time window constructed in Phase 2a.
   d. This procedure was repeated until the end of the crossmodal ERP trial duration (see **Figure 1**).
3. The result of the algorithm is a series of correlation coefficients computed for each unimodal ERP time window location every 10 ms, from the beginning of the ERP trial to the end.
   If assumption 1 is correct, then the cross-correlation graph should appear as in **Figure 2**.
   Thus, for most of the iterations (Phases 2b to 2d) the correlation between the unimodal ERP window and the crossmodal ERP should be relatively low, but at a particular time, the correlation strength should increase and reach a relatively high peak. The peak's location is the point in time at which the ERP data of the unimodal window have their maximum similarity to the crossmodal ERP. This notion can be understood as two pictures that look almost the same.
4. The DT between the peak time and the center of the unimodal window was measured. DT is the parameter used as the basis for the next phase of analysis.

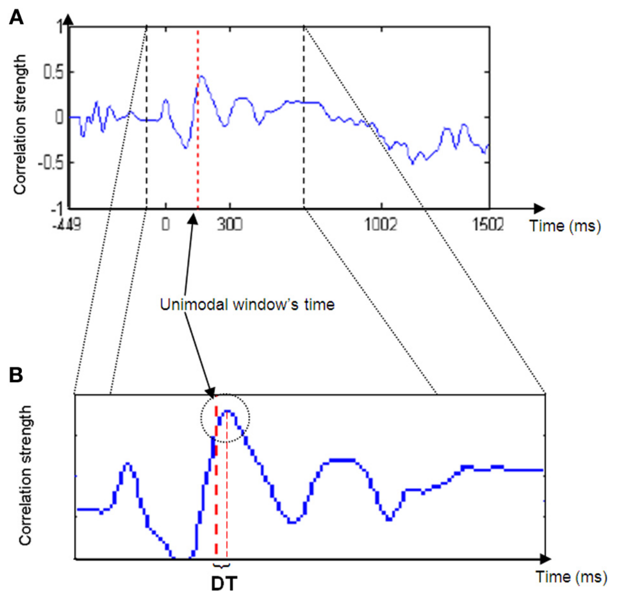

FIGURE 2 | Cross-correlation strength graph. Note the peak in graph strength in the area of the unimodal time window (right red dashed line in **B**) and the delta time (DT) between the line and the peak maximum.

DELTA TIME (DT) PARAMETER

The dependent variable in the proposed algorithm consists of the DT between the unimodal window's location and the correlation peak's time location. If the unimodal time window represents a temporal fraction of information processing and there is a relatively strong correlation between the window and a window similar in size from the crossmodal ERP, then the algorithm suggests that the same temporal fraction of information processing occurred in both ERPs. In addition, if there is a DT between the peak location and the unimodal window, then the fraction of information processing occurred earlier or later, depending upon the DT polarity. Thus, a negative DT indicates early occurrence of the information processing fraction, or in other words, the second modality influenced and accelerated the process of the first modality. In contrast, a positive DT indicates late occurrence of the information processing fraction, which means that the second modality decelerated the SOP of the first modality.

The algorithm found the DT for each participant between the peak's location and the center of the unimodal time window. A *t*-test assessed whether there was a significant difference on DT values between the two groups of participants.

TEMPORAL IMPLEMENTATION OF PHASES A AND B

The phases described above (A and B) focus on a particular time window (for example, between 100 and 200 ms). However, SOP rate can change throughout time. In addition, it is reasonable to assume that the second modality's degree of influence is varied at different time locations. Therefore, the last phase of the algorithm runs across the entire unimodal time course. In other words, the DT for each time window's location for each participant was calculated between the location of the unimodal window and the location of the correlation peak with the crossmodal ERP. For each of the time windows, an average DT was computed for each group. It has been suggested (Goswami, 2011) that dyslexic individuals suffer from difficulties at processing information presented at rates corresponding to the occurrence of syllabic information in speech, and critical for speech comprehension (4–7 Hz, Giraud and Poeppel, 2012). Information at these frequencies arrive to the brain every 142–250 ms. Therefore, it is reasonable to assume that in the current study, where the task was to react to a single event stimulus (visual, auditory, or crossmodal type), the DT of each of the groups would differ statistically within this time area. To verify this assumption, a series of *t*-test analyses was run on the DT parameter (that was computed based on each of the time windows taken from the time area of 140–250 ms) to assess whether there was a significant difference between the two groups.

IMPLEMENTATION OF PHASE C ON BOTH MODALITIES

The procedure was run twice, once for each modality. The window locations were set between 50 and 650 ms. Each successive time window was moved in increments of 10 ms (i.e., the second time span was centered at 60 ms, the third at 70 ms, etc.; see **Figure 3** for a full flowchart description of the cross-correlation algorithm).

RESULTS

EXPERIMENTAL BEHAVIORAL MEASURES:

In order to investigate task accuracy and RT when processing visual, auditory and crossmodal integration, an analysis of variance (ANOVA) in a 2 × 3 design (Group (dyslexic

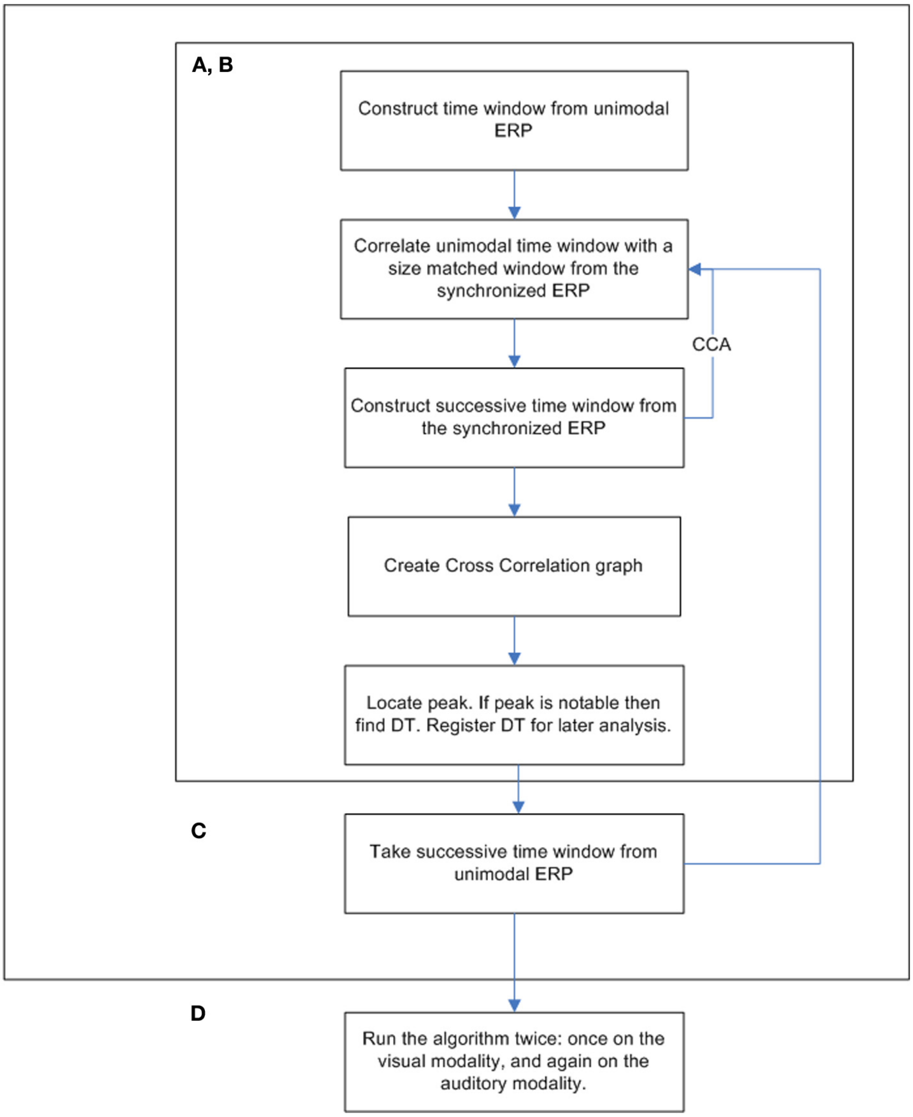

FIGURE 3 | The cross-correlation algorithm flow chart.

Xnon-impaired readers) × conditions (visual-only × auditory-only × crossmodal) was employed for RT and Accuracy separately. No significant between-group differences were found in accuracy [$F_{(1,\ 34)} = 2.48$, $p > 0.05$]. A significant Condition effect was obtained [$F_{(2,\ 68)} = 50.2$, $p < 0.001$] which stemmed from a lower performance under the auditory only condition for both groups (**Table 2**). No significant group by Condition interaction was found [$F_{(2,\ 68)} = 0.22$, $p > 0.05$].

The analysis of the RT data revealed a significant group effect [$F_{(1,\ 34)} = 4.45$, $p < 0.05$], but no significant condition effect [$F_{(2,\ 68)} = 1.2$, $p > 0.05$] and no significant group by condition interaction [$F_{(2,\ 68)} = 1.44$, $p > 0.05$].

ERP CROSS-CORRELATION ANALYSIS RESULTS

In order to investigate the influence of the presence of one modality on the SOP of the other modality, several cross-correlation analyses were obtained on averaged on-going ERP. The first analysis was obtained in order to investigate the influence of the auditory modality on the SOP of the visual one and the second analysis investigated the influence the visual modality on SOP of the auditory one. The cross-correlation analysis was run between sequential time windows taken from each unimodal condition and the crossmodal condition. The cross-correlation analysis outcome measure, the visual and auditory DT, was then used to compare between-modalities' influence and between group differences.

Table 2 | Mean (and Standard Deviation) for the dyslexic and non-impaired readers of the behavioral reading and experimental measures.

	Dyslexic readers	Non-impaired readers	t	p
Visual correct responses (%)	73 (20.8)	83 (16)	1.43	n.s
Auditory correct responses (%)	65 (19.5)	73 (16.3)	1.02	n.s
Visual + Auditory correct responses (%)	71.8 (18.7)	83.3 (14.2)	1.68	n.s
Visual reaction time (ms)	669 (115)	565 (122)	2.23	<0.05
Auditory reaction time (ms)	692 (110)	586 (129)	2.29	<0.05
Visual + auditory reaction time (ms)	639 (136)	587 (66)	1.12	n.s

Based on the size of the correlation between the unimodal data and the crossmodal ERP data within an allotted time frame, it can be inferred that a given time window from the unimodal condition exists in the crossmodal ERP data (see **Figure 4**).

For most participants, a notable peak could be identified (see **Figure 4A**), though results should be interpreted with caution as the graph's shape did not always indicate successful correlation strength (see **Figures 4B,C**). For example, iteration B's dataset is too noisy to determine the peak's location because of an artificial waveform and iteration C's is very local and low. Therefore, inclusion conditions were developed and applied: only cross-correlation graphs which had a peak which was located no more than 50 ms before or after the time of the unimodal window were included in the computation of the DT average. The time window total width of 100 ms (50 ms before and after the time window location) was based on previous evidence that asserted that the variance of ERP component time locations is normally distributed in a time area of less than 50 ms before and after the component mean time location (for example, see Simon et al., 2007; Maurer et al., 2008; Spironelli and Angrilli, 2009). In addition, the graphs could not contain more than 3 additional local peaks within the given time window. These criteria kept distorted datasets out of the further analysis (see Phase B). **Figure 5** shows the percentage of participants included in the process in every time window location. **Figures 5A,B** reveal the percentage of participants included in each time window analysis throughout the visual and auditory information process analysis, respectively. Overall, a relatively low number of participants from both groups were included in the visual analysis in the time areas of 50–150 and 450 ms to the end (**Figure 5A**). It is interesting to note that toward the end of the trial, the percentage of dyslexic readers included in the analysis decreased more slowly than the percentage of included non-impaired readers. In the auditory analysis (**Figure 5B**), the percentage rate of included participants in both groups remained constant from the beginning of the trial until about 500 ms.

In order to investigate the influence of one modality's activation on the SOP of the other modality, a DT for each of the participants and for each of the time windows was computed (**Figure 6**). A t-test analysis was applied for time windows located within the time area of 140–250 ms (**Table 3**), to determine if there was a between-group difference in each of the

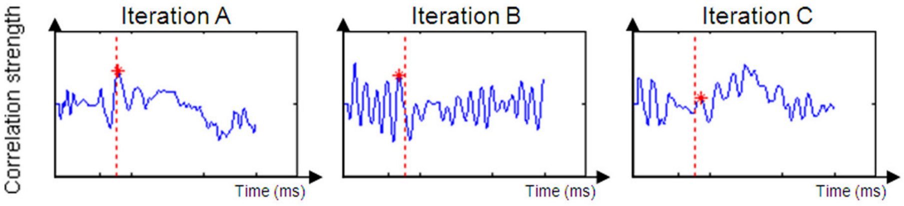

FIGURE 4 | Examples of a successful correlation result (Iteration A) and unsuccessful correlation result (Iterations B and C). Iteration **(A)** produced a positive peak near the original time of the unimodal window. Iteration **(B)**'s dataset is too noisy to suppose that the value of DT is reliable. Iteration **(C)**'s peak is to low and expresses a weak correlation between the two datasets.

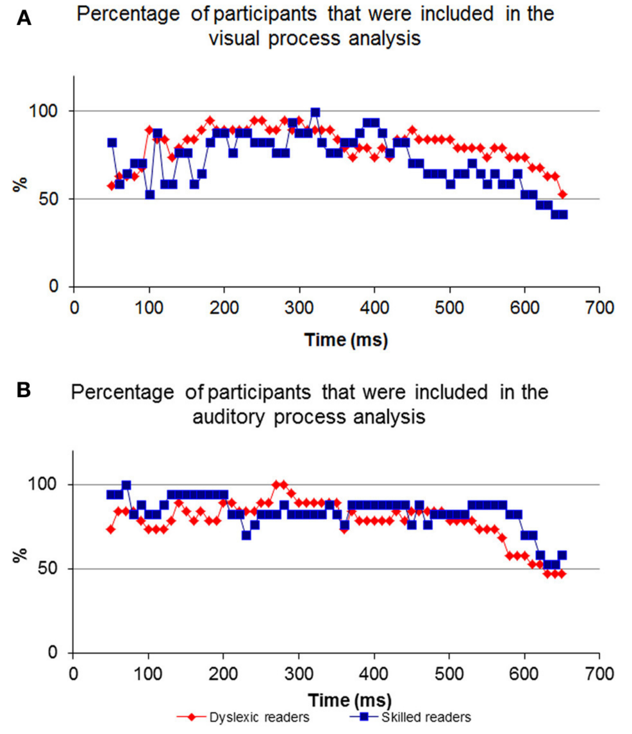

FIGURE 5 | The percentage of participants included in every comparison. Note the inverted 'U' shape of the visual process graph where at the beginning and end of the process the percentage of participants is relatively low compared to the middle. In contrast to the visual process's graph, the auditory graph is stable at the beginning.

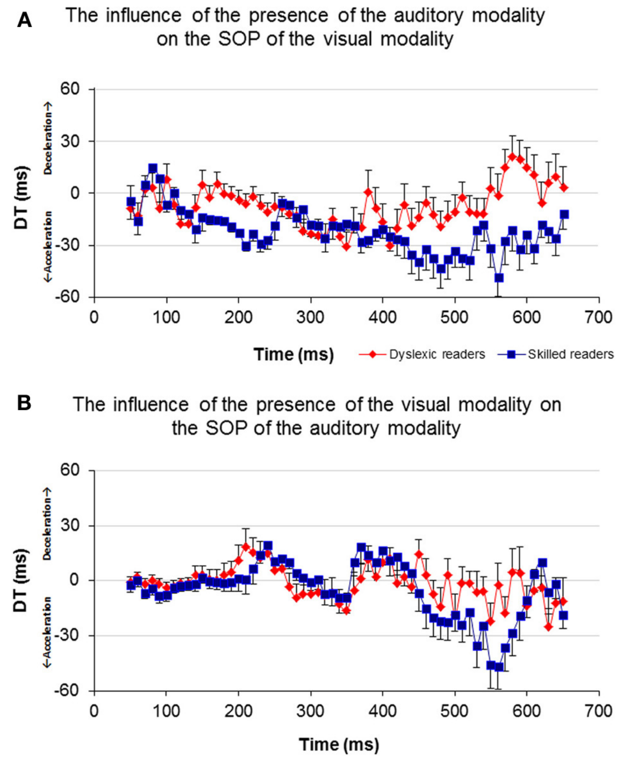

FIGURE 6 | Average DT of the two groups for each time window. Axis X represents time and axis Y represents DT. **(A)** The DT results of the visual-only and the crossmodal ERPs. **(B)** The DT results of the auditory-only and the crossmodal ERPs.

time windows (it is important to note here that a *t*-test was used to assess between-group differences rather than repeated measures analysis of variance (rmANOVA) due to the number of degrees of freedom and the relatively insufficient number of participants in this study). When the DT was based on the influence of the auditory modality on the SOP of the visual modality, significant between-group differences were found in the time area of 170 ms through 240 ms (**Figure 6A**, **Table 3**). In contrast, no significant between-group differences were found when the DT was based on the influence of the visual modality on the SOP of the auditory modality (**Figure 6B**). Nevertheless, note the positive peak (de-acceleration) in the value of the non-impaired readers' DT in the time area of 240 ms, and of the dyslexic readers' similarly shaped peak occurring at 210 ms.

Table 3 | The comparison between the groups' DT computed from the Visual modality time windows taken from the time area of 140–250 ms.

Window location (ms)	$t_{(35)}$	*p*
140	1.157	0.258
150	1.595	0.122
160	1.426	0.167
170	2.506	0.019
180	2.553	0.016
190	2.872	0.007
200	3.033	0.005
210	3.645	0.001
220	3.022	0.005
230	2.7	0.011
240	2.199	0.036
250	1.022	0.315

DISCUSSION

The purpose of this experiment was to investigate the effect of one modality on the SOP of the second modality. Stimuli of visual and auditory modalities were employed in a unimodal and crossmodal presentation. Overall, our results support the notion that there is in fact an interaction between modalities during information processing, consistent with previous research. Furthermore, the significant differences that were found between dyslexic and non-impaired readers highlight the difficulty which dyslexic readers face in synchronizing processing between the visual and auditory modalities.

Hypothesis 1 suggested that the ERP data of the crossmodal condition would contain unimodal visual and auditory elements. It is suggested that the peak in the correlation graph results supports this assumption (**Figure 2A**). As described previously, a cross-correlation analysis computing successive correlation coefficients between unimodal ERP within a specific time window and successive crossmodal ERP time windows sliding along the entire crossmodal trial was implemented. More specifically, the current algorithm took a fraction (i.e., 100 ms) of the temporal information processing from a unimodal ERP trial and searched for a matching fraction of information processing throughout the crossmodal ERP trial. It is apparent from **Figure 2A** that throughout the sequence, the correlation strength was mainly low and randomized. However, at a particular point in time, an increase in the correlation strength appeared, usually a short distance in time from the time location of the unimodal window. It may be argued that this constitutes evidence for the presence of the same fraction of information processing that occurs in the crossmodal ERP. A short while after the correlation strength reaches its peak, it starts to decline as the unimodal window passes its identical fraction of information processing and continues toward the time area in which low and randomized similarity appear.

Hypothesis 2 implied that the presence of a second modality will have an effect on the SOP of a first modality. **Figure 2B** reveals that the correlation graph's peak location is not in the exact location of the unimodal time window. Furthermore, data analysis across the entire time domain and across participants revealed that the correlation peak location may appear shortly before or after the unimodal window's time location. It is suggested that the time difference between the two locations (i.e., DT) is a reflection of the degree of influence of the second modality on the first modality's SOP when presented simultaneously. If the closest matching fraction of information processing taken from a unimodal ERP was found at a later time location (i.e., DT is positive), then this comparison indicates that there was a delay in the processing of the modality in the crossmodal ERP, meaning that SOP decelerated. Conversely, if the DT was negative, then the location of the same fraction of information processing existed at an earlier point of time in the crossmodal ERP compared to the unimodal ERP. Consequently, this constitutes evidence of SOP acceleration in the modality.

The neurobiology of the visual system is considered to be constructed from two major pathways (the dorsal and ventral), where visual information enters the retina and travels to the visual cortex. Information reaches the visual cortex about 100–150 ms post visual stimulus presentation. Auditory processing begins at the ear and initial auditory information reaches the auditory cortex through several pathways about 70–100 ms post stimulus presentation (see Breznitz, 2006 for review). Both modality pathways prepare initial sensory information for higher cognitive processing. As the pathways process information rapidly and in areas deep within the brain, it is expected that their operations will not have a strong impact on EEG data. Therefore, comparing the visual-only ERP and the crossmodal ERP during the first 150 ms of data collection will result in a relatively lower "success" rate when locating the visual information processing fraction in the crossmodal ERP (**Figure 5A**). However, as time progresses and processing moves from deeper brain areas to higher cortical structures, the size of the common components in the two ERP sets increases. Therefore, the algorithm has more success in finding common visual components 150 ms post stimulus presentation. As a result, a higher percentage of participants are included in the analysis from 150–450 ms. When finding the common components between the auditory-only ERP and crossmodal ERP, a higher "success" rate was found at an earlier time frame (50 ms post stimulus presentation) as initial auditory processing is faster than initial visual processing (**Figure 5B**).

Shifting our focus to the end of processing within the visual modality, a differential between the dyslexic reading group and non-impaired readers is apparent beginning at around 450 ms post stimulus presentation (**Figure 5A**). The differential begins at this point in time due to the decrease in the percentage of non-impaired readers included in the analysis. The percentage of dyslexic readers included in the analysis remains high for a longer period of time. The decrease in the percentage rate of included participants for analysis implies that among the non-impaired readers, the shared elements of the two ERPs end at that point. Thus, the duration of visual information processing is approximately 450 ms, and, as such, the ERP data appearing after 450 ms no longer deals with visual information, which results in a lower "success" rate of finding a sufficient correlation between the two datasets. However, visual information processing lasts longer in the dyslexic group and as such, the percentage of participants starts to decrease approximately 50 ms later. This is an important difference between the two groups as it provides evidence for slow speed of visual processing among the dyslexic readers as compared to non-impaired readers.

As can be seen in **Figure 6A**, non-impaired readers' visual processing "benefits" from the presence of the auditory synchronized stimulus as the value of DT is negative almost throughout the entire timeline (i.e., their SOP of visual information is accelerated). A similar but lower effect was observed among the dyslexic readers. Furthermore, a significant difference was found between the values of DT appearing around 170 and 240 ms where the DT of the non-impaired readers was more negative than that of the dyslexic readers. This time area is considered to be related to perception and has been suggested by previous research to be related to the dyslexia phenomenon (Maurer et al., 2006, 2008). On the other hand, processing within the auditory modality was not affected by the presence of a visual stimulus appearing from about 50–200 ms in both groups (**Figure 6B**). The non-impaired readers began to decelerate their auditory SOP around 210 ms. Similar deceleration was observed among the dyslexic readers but 40 ms earlier. Based on the reasoning that visual processing is slower than auditory processing, we provide additional evidence that in the normal information processing sequence, whenever there is a need to synchronize the two modalities, the brain accelerates processing within the visual modality and decelerates processing within the auditory modality. Unlike the non-impaired readers, the dyslexic readers do not accelerate their visual SOP to the same degree (**Figure 6A**). Moreover, they decelerated their auditory processing too early (**Figure 6B**). It is possible that this leads to asynchrony within the two modalities and to an overall slowness of information processing.

Failure at the level of lower sensory processing, which was the focus of the present study, may accumulate in the higher order levels of processing such as processing letters, syllables, words, sentences, and general reading comprehension. As reading activates sequential parallel visual and auditory processes, synchronization between the two modalities is necessary for successful reading accuracy and rate. The results obtained in the current study concerning common elements between single modality and crossmodal processing lend support to the synchronization hypothesis (Breznitz and Misra, 2003).

Prior studies in the field of temporal processing have been focused on the ability of the brain to process input at different frequencies (Buzsaki and Draghun, 2004; Luo and Poeppel, 2007; Power et al., 2012). Specifically, the temporal sampling framework of dyslexia (Goswami, 2011) suggests that the dyslexic reader may suffer from atypical processing of information occurring at frequencies between 4 and 7 Hz, i.e., every 142–250 ms (theta band, and possibly lower frequencies). The current results indicate an apparent failure of dyslexic readers in processing information occurring within the specific time area of 150–250 ms following a single event stimulus (**Figure 6**). The non-impaired readers demonstrated a non-symmetric effect of one modality on the other, in which the occurrence of bimodal information processing accelerated the SOP of the visual modality and decelerated the SOP of the auditory modality at the time area of 170–250 ms. This concurrent change in the two modalities' SOP was not obtained among the dyslexic readers as their visual modality's SOP did not accelerate in the presence of auditory information processing (**Figure 6**). It could be that, as proposed by the temporal sampling framework of dyslexia (Goswami, 2011), atypical neural oscillations at the theta frequency band for auditory processing among the dyslexic readers impact negatively the SOP of their visual modality processing, by preventing it from accelerating adequately. Thus, it may be suggested that these results provide additional support for the difficulty of the dyslexic individual to process a 4–7 Hz inflow of information and moreover, support the temporal sampling framework of dyslexia (Goswami, 2011; Power et al., 2012).

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Reading into neuronal oscillations in the visual system: implications for developmental dyslexia

***Trichur R. Vidyasagar*[1,2] ***

[1] *Visual and Cognitive Neuroscience Laboratory, Department of Optometry and Vision Sciences, University of Melbourne, Parkville, VIC, Australia*
[2] *Melbourne Neuroscience Institute, University of Melbourne, Parkville, VIC, Australia*

Edited by:
Usha Goswami, University of Cambridge, UK
Andrea Facoetti, Università di Padova, Italy
Marie Lallier, Basque Center on Cognition Brain and Language, Spain
Alan J. Power, University of Cambridge, UK

Reviewed by:
Kyle E. Mathewson, University of Illinois, USA
Biao Han, Centre de Recherche Cerveau et Cognition, France

****Correspondence:***
Trichur R. Vidyasagar, Department of Optometry and Vision Sciences, The University of Melbourne, Alice Hoy Building, Room 429, Parkville, VIC 3010, Australia
e-mail: trv@unimelb.edu.au

While phonological impairments are common in developmental dyslexia, there has recently been much debate as to whether there is a causal link between the phonological difficulties and the reading problem. An alternative suggestion has been gaining ground that the core deficit in dyslexia is in visual attentional mechanisms. If so, the visual aetiology may be at any of a number of sites along the afferent magnocellular pathway or in the dorsal cortical stream that are all essential for a visuo-spatial attentional feedback to the primary visual cortex. It has been suggested that the same circuits and pathways of top-down attention used for serial visual search are used for reading. Top-down signals from the dorsal parietal areas to primary visual cortex serially highlight cortical locations representing successive letters in a text before they can be recognized and concatenated into a word. We had shown in non-human primates that the mechanism of such a top-down feedback in a visual attention task uses synchronized neuronal oscillations at the lower end of the gamma frequency range. It is no coincidence that reading graphemes in a text also happens at the low gamma frequencies. The basic proposal here is that each cycle of gamma oscillation focuses an attentional spotlight on the primary visual cortical representation of just one or two letters before sequential recognition of letters and their concatenation into word strings. The timing, period, envelope, amplitude, and phase of the synchronized oscillations modulating the incoming signals in the striate cortex would have a profound influence on the accuracy and speed of reading. Thus, the general temporal sampling difficulties in dyslexic subjects may impact reading not necessarily by causing phonological deficits, but by affecting the spatio-temporal parsing of the visual input within the visual system before these signals are used for letter and word recognition.

Keywords: developmental dyslexia, neuronal oscillations, posterior parietal cortex, primary visual cortex, top-down attention, reading

INTRODUCTION

For nearly three decades, the dominant model to explain the reading difficulties experienced by those with developmental dyslexia (DD) was one that was phonologically based (Bradley and Bryant, 1983; Goswami and Bryant, 1990; Stanovich, 1998; Shaywitz and Shaywitz, 2005; Ziegler and Goswami, 2005; Goswami, 2011). This was supported not only by the profound deficits in phonological skills and in phonemic awareness commonly found to be associated with dyslexia, but also by the findings of temporal processing difficulties in the auditory system that provided a possible neuronal basis for the phonological theory (Tallal, 1980; Ahissar et al., 2000; Temple et al., 2000; Breier et al., 2001). Recently, these findings were integrated with a host of studies on neuronal oscillatory mechanisms that are relevant for temporal sampling of speech and were applied to DD in a model termed the "temporal sampling framework" (TSF) by Goswami (2011). This was a fresh new approach in the field and brought a sound neurophysiological perspective to the phonological model of dyslexia. In essence, in line with the new understanding of the possible role of neuronal oscillations in speech perception (Luo and Poeppel, 2007; Poeppel et al., 2008), Goswami (2011) suggests that deficits in syllabic perception at delta/theta (4–10 Hz) frequencies form the critical basis for the reading impairment in DD. However, the TSF could be applied to the various stages of processing within the visual system as well, prior to the information entering the phonological processing stage. This leads one to consider how oscillatory activity may influence visual processing. The following account proposes a mechanism that underpins reading, based upon recent neurophysiological demonstrations of how visual cortical areas communicate with each other and the biophysical limitations surrounding such communication. It leads with an introduction to how these factors influence a function long established in phylogeny, namely visual attention, which could hold the key for our ability to read.

THE ROLE OF TOP-DOWN FEEDBACK SIGNALS FROM PARIETAL CORTEX IN SERIAL VISUAL SEARCH

An alternative to the phonological basis for dyslexia has been the suggestion that the core deficit is in visuo-spatial attentional mechanisms that may be crucial to reading (Ans et al., 1998; Vidyasagar, 1999, 2001; Facoetti et al., 2000; Valdois et al., 2004; Pammer and Vidyasagar, 2005; Vidyasagar and Pammer, 2010). A number of studies have shown significant impairments in visual attention in children with DD (Casco and Prunetti, 1996; Hari et al., 1999; Vidyasagar and Pammer, 1999; Facoetti et al., 2000, 2008; Facoetti and Molteni, 2001; Bednarek et al., 2004; Kinsey et al., 2004; Valdois et al., 2004; Strasburger, 2005; Bosse et al., 2007; Roach and Hogben, 2007; Solan et al., 2007; Dhar et al., 2008; Jones et al., 2008; Kevan and Pammer, 2008; Bosse and Valdois, 2009; Facoetti et al., 2010; Ruffino et al., 2010). However, why should such a deficit in spatial attention cause dyslexia? This leads one to consider what may be the neural processes that nature has evolved that humans exploit in reading and what may be the neurophysiological constraints that these processes impose on our reading abilities. It has been proposed (Vidyasagar, 1999) that reading uses a circuit that the visual system had evolved to deal with the common problem of recognizing a target in a cluttered world. The visual system faces two major challenges in real visual scenes that are usually populated by myriad objects of different sizes, forms, colors, etc. These are:

1. Neurons in the ventral cortical stream that mediate object recognition exhibit progressively larger receptive fields (**Figure 1**) but yet display position invariance, i.e., they respond to the optimum stimulus, say a face, a car, or a letter, irrespective of their location within the large receptive field (Boussaoud et al., 1991). This and the various other invariances such as for retinal size and angle of view constitute an essential property for any object recognition system, so as to avoid the combinatorial problem of having neurons specific for a feature or object for every possible location, viewpoint, etc. However, the loss of location information will be an impediment in a number of situations, including that of reading a text, since the spatial sequence of letters within a word is vital for word recognition.
2. Different attributes of an object, such as color, form, depth, movement, etc are processed in separate cortical areas and there are over 30 of these in the primate cerebral cortex (Felleman and van Essen, 1991). How can these attributes be bound together so that the objects can be correctly identified?

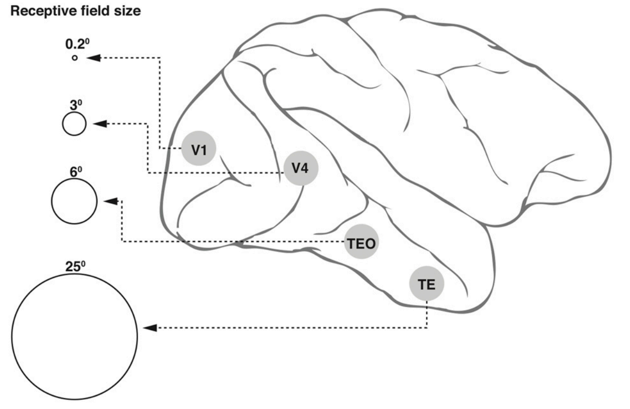

FIGURE 1 | Receptive field (RF) sizes along the ventral cortical stream in the primate. While the degree of complexity of processing may increase, the RF size at any one eccentricity also increases dramatically along the various cortical areas from V1 into the temporal pole. The circles shown in the figure are not drawn to scale, but the numbers above the circles indicate approximate relative sizes of the RF diameters.

One widely accepted solution to this double conundrum, supported by a long and continuing series of experiments using *visual search* paradigms, is that a spotlight of attention highlights one location at a time and the attributes of each object get bound by the coincident processing of its features (Treisman and Gelade, 1980; Treisman, 1988). The neuronal basis of this solution is likely to be a feedback from the parietal cortical region back to earlier visual areas, area V5/MT and still further back to V1, from where the two cortical streams originate (Vidyasagar, 1999). Many studies have now identified attentional facilitation of discrete locations in area MT (Saalmann et al., 2007) and the primary visual cortex (Vidyasagar, 1998; Brefzynski and DeYoe, 1999; Gandhi et al., 2001; McAdams and Reid, 2005; Simola et al., 2009). When only a small location of the visual scene on the primary visual cortex, pertaining to say one object, gets preferentially highlighted for a short period, the signals from this area will lead to unambiguous object identification despite the large receptive fields of neurons in the ventral stream; also, the different attributes of the object get bound together due to the coincidence of activation in different areas that process each of these attributes.

VISUAL SEARCH AND READING

The earliest scripts in recorded history are only about 6000 years old and many human communities did not have any written language until recently but all have the capacity to read and write. For this reason, it has been repeatedly pointed out that, during reading, we are using or "recycling" neural circuits that evolved over hundreds of thousands of years for other reasons (e.g., Vidyasagar, 1999; Dehaene and Cohen, 2007). What could these circuits be? It is now well established that the Visual Word Form area (VWFA), that shows specific activation during reading and dubbed the "letterbox area" of the brain (Cohen and Dehaene, 2004; Dehaene, 2009; Dehaene and Cohen, 2011), is one of the subdivisions in the ventral occipitotemporal region involved in object recognition (Puce et al., 1996; Kanwisher et al., 1997; Ishai et al., 1999; Haxby et al., 2001; Malach et al., 2002). This happens to be an area that codes for visual images of a particular spatial scale and when humans learn to read, the VWFA seems to be responsible for stringing letters together into words. In fact, literacy training in childhood even causes this area to expand at the cost of adjoining areas of the ventral visual cortex that code for objects at other spatial scales (Dehaene et al., 2010). Given such impressive plasticity of this ventral region, the core deficit in DD is unlikely to be a lesion here, unless one finds comparable deficits in object recognition of all types, which is not the case. However, prior to the stage of word recognition at VWFA, there are many steps in visual processing which are all critical for reading. Beyond the stage of initial processing of elementary contours such as lines and edges, a vital hurdle to be overcome is the conundrum described in the previous section. Written text such as the one you are reading now is almost certainly the most frequent and crowded visual scene at a fine spatial scale that we are confronted with in modern civilization. How do we manage to identify each letter and combine them in the appropriate sequence to form words despite the limitations mentioned earlier? One solution that has been proposed (Vidyasagar, 1999, 2001; Vidyasagar and Pammer, 1999, 2010) was that during reading we exploit the same circuits and processes that we had evolved for visual search and object identification in a cluttered world. It was hypothesized that during the periods of eye fixation in reading a text, each lasting approximately 250 ms, feedback signals to V1 sweep a spotlight of covert attention across the letters of individual words and this temporal sequence of identified letters leads to their concatenation into the spatial sequence subsequent to their serial recognition in the ventral stream. Given this scenario, reading may well be the most challenging task for the visuo-spatial attentional mechanisms in a visual world dominated by the printed text and any deficit of these attentional resources can lead to the impairment in what is possibly one of the most sensitive of all our brain functions, namely reading.

Many studies had implicated a deficit in the magnocellular pathway in dyslexia (e.g., Lovegrove et al., 1980; Livingstone et al., 1991; Cornelissen et al., 1995; Eden et al., 1996; Stein and Walsh, 1997; Pammer and Wheatley, 2001; Solan et al., 2004). Such a deficit can potentially be the basis of the attentional impairment (Vidyasagar and Pammer, 1999), since the visual inputs to the dorsal stream, the putative driver of the attentional feedback, is dominated by magnocellular signals. However, the magnocellular deficit has not always been found to be associated with dyslexia as reviewed by Skoyles and Skottun (2004). This discrepancy in the literature is not entirely surprising, for two reasons: (1) A visuo-spatial attentional deficit and consequent reading impairment can be caused not only by a lesion in the visual magnocellular pathway, but also in the dorsal stream structures themselves or in the feedback pathways to the striate cortex. (2) For a magnocellular deficit to manifest as dyslexia, it needs to be at the critical visual field site, namely a small region near the center of the fovea where covert attention is used for letter identification as described above. Unless a magno deficit involves this region, a reading difficulty need not be expected. That almost none of the studies have paid attention to this confounder, could be a contributory factor to the discrepancy in the literature on the relationship between magnocellular dysfunction and the reading impairment.

THE ROLE OF NEURONAL OSCILLATIONS IN VISUAL SEARCH AND READING

If, as suggested above, top-down feedback is essential for serial letter recognition in reading, what could be the neuronal mechanism that makes such feedback modulation and parsing of letters possible? The answer to this question may come from the recent realization that oscillatory activity of neurons is fundamental for organizing and integrating information in the brain (for review, Buzsáki, 2006). Recent studies into the role of synchronized oscillations in visual attention (Saalmann et al., 2007; Gregoriou et al., 2009; Miller and Buschman, 2013), and speech perception (Giraud and Poeppel, 2012) provide an insight into how neuronal oscillations might also mediate the top-down feedback process in visual search and reading.

Humans analyze speech in essentially two integration windows: one at ∼150 ms and above, i.e., at delta-theta band for syllabic segmentation and one at ∼30 ms and below, i.e., at low gamma range for phonemic segmentation (Giraud et al., 2007; Abrams et al., 2009; Lehongre et al., 2011; Giraud and Poeppel, 2012). Processing of human speech indicates that weak gamma oscillation at rest (30–40 Hz) gets stronger with auditory input and individual neurons tuned for specific acoustic frequencies tend to fire more at a particular phase at each cycle (Giraud and Poeppel, 2012). In this scenario, acoustic energy concentrated in formants in the feedforward input at delta-theta range is itself conceived to lead to nesting of the higher gamma frequencies.

These sampling principles in the time domain with acoustic speech signals can be applied also to the visual system, which has to perform a spatiotemporal sampling of the visual input. While modulation frequencies in the delta-theta (3–10 Hz) band are crucial in speech perception for syllabic segmentation of the amplitude envelope, there is no reason at all for segmentation at these rates to be crucial for the visual system in deciphering individual letters or for that matter concatenating them into a word. There is no actual physical modulation at the syllabic level in the visual input arising from a text. The critical visual segmentation is primarily at the level of graphemes, which in English, are the alphabetic letters. Regular, periodic, segmentation at the word level is impractical since word lengths vary considerably. This is not the case with letters which usually occupy approximately the same physical space and can be sampled in a nearly periodic fashion by a spatiotemporal sampling process.

The one naturally occurring process in the brain that could be exploited for parsing the neuronal signals related to letters in a text that arrive at the primary visual cortex is in fact the top-down signals that are usually used for serially highlighting items in a visual search task. Such modulation of early areas is now known to be mediated by synchronized neuronal oscillations (Fries, 2005; Saalmann et al., 2007). In visual search, one can envisage a small group of cells in the posterior parietal cortex (PPC) oscillating in synchrony when they mediate focal spatial attention (Saalmann et al., 2007), either due to the relative saliency of the sensory input or in response to top-down signals from the prefrontal executive regions (Buschman and Miller, 2009). The frequency of the neuronal synchrony of the top-down signals from PPC have been identified to be 25–45 Hz (Saalmann et al., 2007) and the ones from prefrontal cortex to PPC to be 22–34 Hz (Buschman and Miller, 2007).

Oscillations can potentially either define the periods when and how often a set of post-synaptic neurons would fire in response to inputs that otherwise are too weak to reach threshold or enhance responses to a specific set of input signals, or do both. By the same token, the lack of oscillatory modulation of the membrane potential may by default act as suppression, since it would require a much stronger input to lift the membrane potential to threshold. The feedback pathways are known to be excitatory in nature (Anderson et al., 2011), but local inhibitory connections could cause suppression of unattended stimuli (Miller and Buschman, 2013).

It is not unlikely that the top-down signals from the PPC to MT and further to V1 (Vidyasagar, 1998; Brefzynski and DeYoe, 1999; Gandhi et al., 2001; McAdams and Reid, 2005) that are essential for serial visual search might also be exploited for reading. The same oscillatory nature of the modulation can be used for scanning the printed text during reading and process one letter (or two) at a time. One could conceive of each cycle of an oscillating wavelet in the low gamma range highlighting one of the salient locations on the visual field representation (**Figure 2**). This permits discrete chunks of information, just from one location or object, to be processed concurrently in the ventral stream for perceptual binding and object identification. For this to work in serial visual search, one would expect the salient locations on the parietal priority map to be activated in sequence with each cycle of a gamma wavelet switching to a different spatial location. There is evidence for this from the work of Buschman and Miller in macaques (2009; 2010), which showed spatial attention in a serial search task being directed by FEF in the frontal cortex with the fronto-parietal synchrony serially activating object locations in LIP. In fact, monkeys were found to shift their covert attention every 40 ms and the neural correlate of such shifts were observed in the oscillations of local field potentials in the FEF synchronized to 25 Hz. In learning to read, I suggest that the fronto-parietal network gets trained to do a similar serial, but *spatially sequential*, switching of top-down focal attention signals.

A consequence of the above framework is that any sampling process that humans use for reading an alphabetic text such as English is likely to have a temporal frequency roughly related to the rate at which readers sample individual letters or small groups of letters (say, in twos or threes as most words have upwards of two or three letters in them). I propose that if reading exploits the same mechanisms that we employ for visual search, both reading speed, and print sizes would fall within limits that are ultimately determined by the low gamma frequency range used by the visual search mechanism for top-down gating of visual signals arriving at V1. Thus, the speed of both these processes—visual search and reading—measured as items or characters (alphabets) processed in unit time—will be within the major frequency band of the synchrony between these areas during periods of focal spatial attention. Most common visual search paradigms yield a slope of 20–45 ms/item depending upon task demands (e.g., Wolfe et al., 1998; Wolfe and Horowitz, 2004), whose reciprocal, namely frequency, in cycles per second is between 22.2 and 50 Hz. This is in fact very similar to the range (25–45 Hz) of low gamma frequencies that the parietal cortex has been shown to use for top-down modulation of early visual areas (Saalmann et al., 2007).

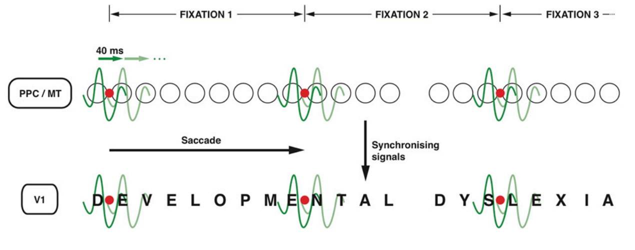

FIGURE 2 | Neuronal oscillations underlying the spotlight of attention that enables sequential letter processing during reading. A wavelet of low gamma frequency (say around 25 Hz, i.e., with a period of 40 ms) sweeps across the retinotopic map in posterior parietal cortex and MT leading to sequential shift of the locus of top-down facilitation in V1 through interareal synchrony. The letters in the bottom row (DEVELOPMENTAL DYSLEXIA) represent the bottom-up sensory signals in V1 corresponding to each letter of the text that is being read. The fine grain representation of the visual world in V1 preserves the form of each letter, even though they are not coded as "letters" in V1. The circles in the middle row represent the loci of activities in LIP and MT that code for letter locations in the text. The letter representations highlighted by each subsequent cycle of the gamma wavelet are hypothesized to be processed and recognized individually and in sequence in the ventral stream. Only two cycles are shown for each fixation but they are presumed to sweep across the letters away and to the right of the fixation point to cover 7–8 letter-spaces during each fixation. The red dot represents the point of eye fixation. The top row indicates the periods of fixation, each lasting 250–300 ms.

With most instances of visual search, the main immediate task may be only object identification, but in the case of reading, the cognitive load is considerably beyond simple identification of letters and words. After the letters are concatenated into words, the words need to be semantically interpreted, strung together in to a sentence and the overall meaning of sentences and the passage comprehended. Furthermore, there is the necessity of having to proceed along a specific spatial gradient (left to right in the horizontal direction in English) to the exclusion of all other directions. Therefore, for a function such as reading that is forced to use an evolutionarily older process (visual search) whose sampling bandwidth is limited to a range of 22.2–50 Hz, it would be best to use the slowest possible speed within that range, thus, parsing letters at the lower end of this range to prevent the subsequent cognitive processing stages from being overloaded.

How well are these predictions borne out by data on reading speeds? In a major study (Rubin and Turano, 1992), the average reading speed was found to be in fact a maximum of 303 words/min. This translates, in English which has an average of 4.5 letters to a word, to about 23 alphabetic characters per second (23 Hz) or nearly 44 ms per letter. This is almost precisely the lower end of the neuronal oscillation range for the top-down signals from PPC that mediate focal spatial attention (Saalmann et al., 2007). A further testable prediction from the above framework is that the variation in reading speed seen in the population may roughly reflect the variation between individuals in the speed of visual search. In fact, recent experiments (Verghese et al., under review) indicate a significant positive correlation between these two variables. Valdois and colleagues, investigating further their earlier finding that reading performance was influenced by visual attention span (Bosse and Valdois, 2009), also found that reading speed was affected by only one component of visual attention capacity, namely visual processing speed (Lobier et al., 2013). These observations follow directly from the above theory that the speed determined by the gamma frequency oscillation is the essential rate-limiting step in reading.

PHYSIOLOGICAL CONSTRAINTS ON OSCILLATIONS, VISUAL SEARCH AND READING

If visual search and reading are dependent on oscillating signals that mediate the essential cortical interactions, they are inevitably locked into a narrow range of speeds that are related to the low gamma range of the neural synchrony that underpins the interactions. In turn, there are compelling biophysical and physiological reasons why the frequency of oscillations themselves fall within a particular range (Buzsáki, 2006). Frequency of rhythmically discharging GABAergic neurons and the resonance properties of pyramidal cells determined by their time constants allow only a relatively narrow window of frequencies of oscillations that could facilitate within-area and between-areas synchrony (Hutcheon and Yarom, 2000; Markram et al., 2004; Economo and White, 2012). This may be the reason why the commonly encountered neuronal oscillations are in the gamma frequency range, 20–70 Hz, which resonate best with neurons, which all tend to have integration times between 15 and 50 ms. While within-area synchrony may be largely driven by relatively higher gamma frequencies, typically in the 35–85 Hz range, as for example for stimulus driven synchrony of V1 cells (Eckhorn et al., 1988), between-area synchronization is usually slower, being 25–45 Hz for the LIP (an area within the macaque PPC) to MT feedback (Saalmann et al., 2007). This may be related to the type of post-synaptic cells that receive the feedback, the local circuitry that could influence the active properties of the cells and their time constants. While the frequency of the feedback to V1 from area MT mediating focal attention has not yet been directly measured, we already know that the MT cells fire at 25–45 Hz during focal spatial attention (Saalmann et al., 2007).

The intrinsic properties of neurons—some of them subject to dynamic changes, such as conductance of ion channels and others not subject to changes such as the size of the cell itself that sets the outer limits to input resistance—can potentially play a fundamental role in the emergence of neuronal oscillations and to what frequencies in the input signals that the neuron will resonate most. These variables are reflected in the range of low gamma oscillations seen in interareal synchrony. **Figure 3** is a putative model of the top-down modulation of V1 activity by a feedback from area MT at low gamma frequencies, whose range is determined by the resonance properties of the post-synaptic V1 cells and the circuitry they are embedded in.

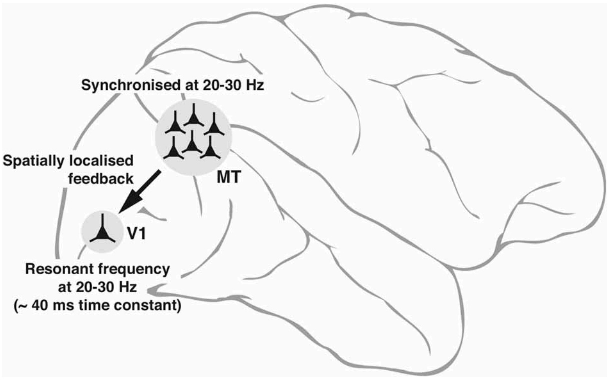

FIGURE 3 | Schematic diagram, explaining the neuronal basis of feedback oscillations. Local network properties and biophysical parameters such as time constants of neurons determine the synchronizing frequencies of neurons in MT that provide feedback to V1 and the resonant properties of neurons in V1. It is suggested that a group of neurons representing a single location (of say, an object) in the parietal saliency map sending its signals via the corresponding group of neurons in MT can set the membrane potential of the spatially equivalent group of neurons in V1 (only 1 shown) to oscillate at its resonant frequency. Such an oscillation would facilitate the V1 neurons to respond to a sensory input more readily as the input signals ride on the top of the depolarizing crests in membrane potential.

While there are a number of cortical areas involved in reading such as the VWFA in the ventral cortex (for reviews, Dehaene, 2009; Wandell, 2012), there have been few electrophysiological studies so far that have identified the frequencies that mediate cortical interactions between these areas. The account presented in this paper has largely concentrated on the feedback within the dorsal stream for two reasons. First, there is relevant electrophysiological data available that provide us with some real numbers. Second, since the neural process mediating visual search is essential for parsing of letters in a text and determines reading speed, the neuronal oscillations in the dorsal feedback are likely to have a more decisive influence on the speed of orthographic processes than the oscillatory activities within the ventral stream.

SYNCHRONIZED OSCILLATIONS AND DEVELOPMENTAL DYSLEXIA

There has been much controversy recently whether the core deficit in dyslexia is in phonological processing or in visuo-spatial attention (for reviews, see Ramus, 2003; Vidyasagar and Pammer, 2010; Goswami, 2011). Though there are profound phonological deficits in most cases of DD, the causality has not been established (Castles and Coltheart, 2004; Vidyasagar and Pammer, 2010; Vidyasagar, 2012), whereas there are now many studies claiming visual attentional deficits as the critical causative factor (e.g., Vidyasagar and Pammer, 1999; Facoetti et al., 2000, 2008; Facoetti and Molteni, 2001; Valdois et al., 2004; Bosse et al., 2007; Kevan and Pammer, 2008; Bosse and Valdois, 2009). In an attempt to anchor the aetiology of dyslexia in basic neurophysiology, Goswami (2011) attributed the phonological deficits and by inference the reading impairment to possible alteration of the syllabic sampling of speech (Goswami, 2011). The nesting of phonemic sampling at the low gamma rates of around 20–30 Hz within the low delta/theta syllabic frequency of around 4 Hz implies that altered sampling at syllabic rates could be the basis of the poor sensitivity of dyslexic children to low frequencies in the amplitude modulated acoustic input (Lorenzi et al., 2000). However, in a recent study of auditory steady state cortical responses (ASSR) to an amplitude modulated noise spectrum measured using magnetoencephalography and MRI (Lehongre et al., 2011), a significant deficit was seen in dyslexic subjects only for low gamma (phonemic) frequencies (20–30 Hz) in the left planum temporale. This appears at odds with the idea of a core deficit in syllabic (delta/theta) frequencies suggested by Goswami (2011), unless the low frequency transitions reset the neuronal activity occurring at gamma frequencies as suggested for selective attention by Schroeder and Lakatos (2009).

The sensory stimulus for the study by Lehongre et al. (2011) was acoustic, but I suggest that the deficit may be one that is more general across other modalities as well and the use of visual stimuli might expose deficits in visual areas, particularly those involved in visuo-spatial attention. As mentioned earlier, the critical sampling rate for visual search is indeed in the same range of low gamma frequencies and not the much slower delta/theta rate, which in fact shows no deficit in the study by Lehongre et al. (2011). The sampling rate that is used by the visuo-spatial attentional process for sequential reading of letters in a word is also the low gamma rate. The core deficit in DD may thus be an impairment in sampling at this rate. The deficits in speech perception and phonological processing may be a consequence of poorer sampling of the acoustic signals, but the reading deficit itself may be a consequence of similar impaired sampling at low gamma frequencies in the visual domain. In this scheme, the essential deficit in dyslexia is entirely within the visual system. The phonological deficits occur in parallel and to some extent they could also be partially the result of poor orthographic processing.

It should be noted that the sampling rate that we generally use for reading is not one that evolution had selected for reading but one that had possibly been selected for visual search and as noted above, this range is itself under certain constraints. However, reading comprehension, unlike reading speed, depends upon the working memory and cognitive capacities of the individual and the demands placed on them by the semantic content of the text. It is thus, most likely that as one learns to read, the brain uses the speed at the low end of the gamma range used for visual search (namely around 20–25 Hz), so that sufficient time can be spent on each grapheme and the subsequent processing stages. It is possible that due to the biophysical and network parameters that determine the limited range of frequencies for neuronal oscillations, the rate that one uses for reading may differ between individuals and this may explain the variance seen in reading speeds. Every reader ultimately gets "locked" into a particular narrow range of speeds, which makes slower or faster parsing of letters in a text inefficient. For complex material, the sampling rate one is locked into may turn out to be "too fast" for some. In fact, adult dyslexics, who are "compensated" may actually have a better reading comprehension scores even though their reading speeds will be slower than controls. On the flip side, fast readers (and hyperlexics), who are essentially "locked" into this higher speed, may have a gamma range for top-down modulation that is shifted toward higher frequencies, as indeed seen in their faster visual search (Verghese et al., under review). This shifted range will enable faster reading, but reading comprehension will be compromised due to overloading of the subsequent working memory and semantic stages.

The basic deficit in DD may be either an impairment (e.g., lower amplitude of oscillation) of the sampling at low gamma frequencies that affects visual search and reading and/or a slowing down of this rate. A change in amplitude or frequency of the synchronized oscillations is likely to affect the efficiency of modulation of V1 by the top-down feedback. Lower power will lead to poorer facilitation of sensory signals arriving in V1 and alteration in frequency would lead to a mismatch with the resonant frequencies of the V1 cells with subsequently poorer oscillations of the membrane potential. In either case, reading speed will be affected, but when there is some slowing down of the sampling rate, reading comprehension may in fact be better.

One interesting observation made by Lehongre et al. (2011) was that the dyslexics do not always show a general slowing of temporal processing as originally proposed by Tallal (1980). In fact the dyslexic subjects also show an increase in the 40 Hz activity in the right hemisphere to the acoustic stimuli. However, in the scheme proposed here, both slower and faster sampling would have consequences—slower by reducing reading speed and faster by overloading the working memory capacity and the time needed for semantic interpretation of the text.

Buzsáki (2006) has argued that the oscillating frequency of a cluster of neurons will be slower when the spatial extent of the group is larger. This has implications for the framework proposed here that involves a discrete moving spotlight of attention that is represented by a spatial sequence of small groups of neurons on the parietal priority map, that each fire in synchrony. Thus, if the spotlight of attention is larger and spans more than one letter at a time (as it could happen with experienced readers who may identify sets of two or even three letters at each gamma cycle), the rhythm may be slower. Thus, the reading speed may not be very much faster with a larger span, leading to a fairly narrow range of optimum font sizes in print. In fact, the distribution of print sizes in many types of publications all fall within a range that was indeed found optimal for reading (Legge and Bigelow, 2011).

It should not, however, be interpreted that the above scheme discounts the role of delta and theta frequencies that have been suggested as being critically important in reading and for speech recognition (Goswami, 2011; Power et al., 2012). In fact, the saccadic eye movements in reading occur on average at about 4 Hz, i.e., a saccade approximately every 250 ms (Rayner, 1998). One could argue that the sensory inputs get parsed at this rate, which is close to the word and syllabic reading speeds, a frequency range that has been implicated in the aetiology of DD (Goswami, 2011). However, the critical information processing essential for decoding a printed text is the parsing and identification of letters, which for most readers occurs at low gamma rates. In fact, this process may itself determine the saccade frequency. The decreasing strength of covert attention at increasing distance from the center of the fovea and the individual's preferred gamma frequency will limit in time and space the number of letters that can be sequentially identified during a single period of fixation and can even trigger the subsequent saccade. That the efferent oculomotor signals lead to saccades at the delta/theta frequency during reading does not imply that the afferent stream also gets segmented at the same rate for purposes of detailed sensory processing. Thus, the critical parsing of the afferent signals for grapheme recognition may be restricted largely to the low gamma range.

Low frequency oscillations in human cortical areas have also been reported in a number of other situations, for example with regard to sustained visual attention (Busch and VanRullen, 2010), speech recognition (Giraud and Poeppel, 2012; Power et al., 2012), auditory syntactic processing (Schmidt-Kassow and Kotz, 2008), and modulation of visual awareness (Mathewson et al., 2012). Taken together, these studies suggest the existence of a number of different time scales at which neural oscillations are linked to cognitive processes, ranging from the delta frequencies in decoding speech (Giraud and Poeppel, 2012) to the 12 Hz seen with visual awareness (Mathewson et al., 2012). As remarked earlier, the range of oscillating frequencies depend upon the network dynamics of the respective circuitry and the resonance properties of the cells in the network. Unlike the above instances, in the case of reading, the critical frequency used in specific decoding of the text may be the low gamma frequencies. These frequencies are known to be used in shifting the loci of attention in visual search tasks (Buschman and Miller, 2009, 2010) and are also impaired in DD (Lehongre et al., 2011).

It is worth stressing that reading a text is a very different process from speech recognition. Speech decoding is dictated by external inputs and has to be dynamic and flexible, occurring not only at multiple time scales (syllabic and phonetic), but also at the different frequencies that the speaker outputs, with the listeners having little choice in the sampling required of them. In reading this is not a problem, since the rate that is most optimal for the reader's perceptual and cognitive systems can be employed by every individual reader without any external constraint. Thus, the temporal characteristics associated with speech recognition need not necessarily determine the processing speeds of the visual system in the case of reading.

PREDICTIONS OF THE SCHEME

A few testable predictions that specifically follow from the scheme outlined in this paper are summarized below:

1) Reading speed will show a positive correlation with the speed of visual search.
2) Reading speed will also show a positive correlation with the frequency of interareal synchrony between the dorsal stream and primary visual cortex.
3) Those with slower reading speeds, including many compensated adult dyslexics, will have better reading comprehension than faster readers.
4) As each individual is locked into a narrow range of sampling, one cannot force oneself to a slower reading speed by parsing letters more slowly, without seriously affecting reading comprehension.
5) In DD, the use of periodic visual stimuli will reveal an impairment in the low gamma frequencies in the visual cortical areas, similar to that seen in auditory areas with acoustic stimuli.

At this juncture, one might attempt to predict the consequences of the scheme for non-alphabetic languages such as Chinese. Even though in Chinese, there are only 1.5 characters per word on average (Sun et al., 1985), as against 4.5 letters to a word in English, it does not follow that the reading speed would be three times faster and it is not. The approximately 6000 Chinese characters cannot be taken as equivalent to the set of 26 alphabetic characters in English. A more appropriate level of parsing is by radicals which constitute a smaller set of 214 elemental units that go to form any one of the 6000 characters. As there are on average 2.6 radicals to a character (Shi et al., 2003) and the reading rate in horizontally written Chinese is 580 characters per minute (Sun et al., 1985), the speed of parsing would be ca. 40 ms/radical (25 Hz). This is in the same ballpark as in English (44 ms/letter on average).

The above argument can be extended also to difficult visual searches, where search speeds can be much slower, i.e., much longer than the 40–44 ms/item indicated above for reading. When searching for targets that are more complex than conjunction of elementary features such as lines and colors as in the case of a face in a crowd, a car in parking lot, or a book on a cluttered desk, the situation is more akin to that of reading Chinese characters. Thus, a process of parsing at low gamma frequencies across the details of each complex object would yield larger slopes per object. Unless there is a unique feature in the target that can lead to pop-out, complex objects would yield larger search slopes proportionate to the number of elementary features that they are composed of. However, parsing of these elementary features would *always* occur at the same low gamma frequency. This is a strong and testable prediction from the scheme proposed here.

CONCLUSION

The development of writing and reading was a cultural programme in human history that happened to exploit a mechanism that had evolved for covert serial visual search. Top-down signals from a fronto-parietal network that uses neuronal synchrony for interareal attentional gating have been found to function at low gamma frequencies, with each cycle of the oscillation shifting to a different location during serial search. It is proposed here that this same mechanism is used for sequential scanning of individual letters during reading. This explains the fact that the reading speed of graphemes in a text is also in the same gamma range. This is consistent with the findings that with acoustic stimuli, there is an impairment of oscillations in the low gamma range in DD (Giraud and Poeppel, 2012).

Most genetic markers of DD seem to be involved in development of cortical laminae and migration of neurons (for review, Paracchini et al., 2007) and consistent with these, morphological changes in sizes of neurons and cytoarchitecture have been found in many regions of the brain including the visual system (for review, Galaburda and Livingstone, 1993; Galaburda, 1994). One important consequence of such changes in cell morphology and circuitry will be a change in the resonance properties of neurons and thus, the frequency and amplitudes of neuronal oscillations in the brain. Mild impairments of such brain rhythms may not affect most behavioral functions except those that are most sensitive to the disruption. As argued earlier, reading is one of the most challenging tasks in present civilization for visual attentional mechanisms, as the parsing of the text is done within a narrow spatiotemporal range. Thus, with any mild impairment of the attentional mechanisms, reading may be compromised, while for most other cognitive functions which also use top-down attentional processes, the deficit may not be so disabling.

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Investigating the role of visual and auditory search in reading and developmental dyslexia

Marie Lallier[1]*, Sophie Donnadieu[2,3] and Sylviane Valdois[2,4]

[1] Basque Center on Cognition Brain and Language, Donostia-San Sebastian, Spain
[2] Laboratoire de Psychologie et NeuroCognition, UMR CNRS 5105, Grenoble-Chambéry, France
[3] Faculté de Psychologie, Université de Savoie, Chambéry, France
[4] Centre National pour la Recherche Scientifique, Paris, France

Edited by:
Alan J. Power, University of Cambridge, UK

Reviewed by:
John J. McDonald, Simon Fraser University, Canada
Donatella Spinelli, Università di Roma "Foro Italico," Italy

***Correspondence:**
Marie Lallier, Basque Center on Cognition Brain and Language, Paseo Mikeletegi 69, Planta 2, Donostia-San Sebastian, 20009, Spain
e-mail: m.lallier@bcbl.eu

It has been suggested that auditory and visual sequential processing deficits contribute to phonological disorders in developmental dyslexia. As an alternative explanation to a phonological deficit as the proximal cause for reading disorders, the visual attention span hypothesis (VA Span) suggests that difficulties in processing visual elements simultaneously lead to dyslexia, regardless of the presence of a phonological disorder. In this study, we assessed whether deficits in processing simultaneously displayed visual or auditory elements is linked to dyslexia associated with a VA Span impairment. Sixteen children with developmental dyslexia and 16 age-matched skilled readers were assessed on visual and auditory search tasks. Participants were asked to detect a target presented simultaneously with 3, 9, or 15 distracters. In the visual modality, target detection was slower in the dyslexic children than in the control group on a "serial" search condition only: the intercepts (but not the slopes) of the search functions were higher in the dyslexic group than in the control group. In the auditory modality, although no group difference was observed, search performance was influenced by the number of distracters in the control group only. Within the dyslexic group, not only poor visual search (high reaction times and intercepts) but also low auditory search performance (d') strongly correlated with poor irregular word reading accuracy. Moreover, both visual and auditory search performance was associated with the VA Span abilities of dyslexic participants but not with their phonological skills. The present data suggests that some visual mechanisms engaged in "serial" search contribute to reading and orthographic knowledge via VA Span skills regardless of phonological skills. The present results further open the question of the role of auditory simultaneous processing in reading as well as its link with VA Span skills.

Keywords: dyslexia, reading, visual search, auditory search, attention, temporal processing, visual attention span, phonology

INTRODUCTION

Developmental dyslexia is a neurocognitive disorder reflected by severe and persistent reading difficulties in individuals who have been provided with appropriate schooling, present a non-verbal IQ within the normal range, and do not suffer from any sensory or psychiatric disorders. A number of neuroimaging and behavioral studies now suggest that reading difficulties in dyslexia may not stem from a unique but rather multiple origins (Ramus and Ahissar, 2012; Koyama et al., 2013; van Ermingen-Marbach et al., 2013). Developmental dyslexia in this context is seen as a multifactorial and heterogeneous disorder. For example, the visual attention span (VA Span, hereafter) hypothesis describes at least two cognitive impairments (phonological and visual attentional) that can equally but independently lead to developmental dyslexia (Bosse et al., 2007). Looking at two large samples of French and English dyslexic children, Bosse et al. (2007) report that the reading difficulties of dyslexic children were either accompanied by a single phonological disorder (i.e., phonological awareness, phonological short term memory, phonological fluency), a single VA Span deficit (without phonological problems), or a combination of those two. Importantly, Peyrin et al. (2012) found that the biological bases for those two dyslexic cognitive subtypes were independent: they found that a dysfunction located within the left inferior frontal gyrus characterized dyslexia associated with a phonological disorder whereas a dysfunction of the superior parietal lobules bilaterally was seen in the VA Span dyslexic subtype.

The VA Span is defined as the number of visual elements that can be processed simultaneously (at a glance) in a visual multi-element array, regardless of the verbal or non-verbal nature of those elements (Lobier et al., 2012). VA Span skills are thought to tap into perceptual attention (i.e., attention skills which enhance perceptual encoding and its clarity) and be specifically critical for (i) processing simultaneously all the letters within whole-word visual forms, (ii) building-up lexical orthographic knowledge and (iii) enhancing the recognition of previously unfamiliar words

(Bosse and Valdois, 2009; Bosse et al., 2013). Moreover, VA Span skills have been shown to play a significant role at various stages of typical reading development by contributing to reading variance independently from phonological skills (Bosse and Valdois, 2009).

For the VA Span hypothesis, the simultaneous dimension of visual perceptual attention plays a central role in reading development independently of phonology. Contrastively, the sequential dimension of visual perceptual attention has been proposed as a significant contributor to dyslexia associated with phonological difficulties (sluggish attentional shifting theory of dyslexia, Hari and Renvall, 2001). Supporting the claims of both the VA Span and the sluggish attentional shifting theories, Lallier et al. (2010a) showed that a dyslexic adult with a severe phonological deficit but preserved VA Span skills was impaired on visual sequential attentional skills. This suggests that phonological, and visual sequential processing disorders can co-occur in dyslexia regardless of visual simultaneous processing problems, i.e., VA Span deficits. Along the same lines, some studies showed that dyslexic participants exhibited visual impairments on paradigms where stimuli were presented sequentially but not simultaneously (Ben-Yehudah and Ahissar, 2004; Conlon et al., 2004; Ram-Tsur et al., 2006), or the opposite (Yap and Van der Leij, 1993; Lassus-Sangosse et al., 2008).

These studies suggest that the dissociation between sequential and simultaneous visual processing deficits in dyslexia essentially depend on the stimulus presentation mode of the task. However, the link between sequential presentation paradigms and the sequential dimension involved in ecologic reading is rather indirect: orthographic units never appear and disappear sequentially at a unique fixation point (*externally driven* sequential processing). Rather, the self-paced visual attentional captures within and between words generate the sequential dimension present in the reading activity (*internally driven* sequential processing). Conversely, simultaneous visual processes such as VA Span skills are directly involved in ecologic reading since they reflect visual attention skills at play during an ocular fixation (Prado et al., 2007).

Visual search paradigms have been proposed to reflect both sequential (Vidyasagar and Pammer, 1999, 2010; Vidyasagar, 2004) and simultaneous (Marendaz et al., 1996) visual perceptual attention at play in reading. In those paradigms, participants are presented with a stimulus display where a target presented simultaneously with a set of distracters has to be detected as fast as possible. Within the framework of the "Feature Integration Theory" (Treisman and Gelade, 1980) two types of search tasks, in which the type of stimuli presented varies, are generally administered and require distinct visual processes. In the so-called "parallel" search, the target possesses only one feature which differentiates it from all the distracters (e.g., "Q" among "O"s). In this condition reaction times (RT) for target detection are not affected by the number of distracters: a pre-attentive "pop-out" effect for the target occurs because a battery of visual analyzers, specialized for detecting that unique feature, automatically captures the attentional focus. In the so-called "serial" search, the target is characterized by the conjunction of two features (e.g., "O" among "Q"s). In that case, RTs for target detection increase linearly as a function of the number of distracters because an effortful sequential screening, thought to engage controlled attention, occurs to search for the target. When assessed on visual search paradigms, dyslexic children (Casco and Prunetti, 1996; Marendaz et al., 1996; Vidyasagar and Pammer, 1999) and adults (Iles et al., 2000; Buchholz and McKone, 2004; de Boer-Schellekens and Vroomen, 2012) are repeatedly found to be impaired on the "serial" search condition, suggesting a visual attention deficit in this population. Typically, dyslexic participants present a higher search slope coefficient than skilled readers, indicating that they process a smaller amount of stimuli per second in the display.

To explain these deficits, two hypotheses regarding the nature of visual attention problems have been suggested: Marendaz et al. (1996) suggest the hypothesis of a reduction of the number of elements that dyslexic individuals can encode simultaneously under fixation whilst searching for the target (i.e., reduced VA Span). Alternatively and according to the feature integration theory of visual search, Vidyasagar (2004, Vidyasagar and Pammer, 1999), proposes that reading problems and difficulties on the visual "serial" search task in dyslexia are both caused by a failure in monitoring sequential spatial attentional shifts under fixation (see also Franceschini et al., 2012). This idea finds support from the neurophysiology of the visual system and the fact that visual information flux arriving from the retina to the visual primary cortex separates into two cortical pathways: (i) the dorsal or "magnocellular" pathway subtending fast/transient processing and object motion encoding and (ii) the dorsal or "parvocellular" pathway subtending slow/sustained visual processing and object identification mechanisms. According to Vidyasagar, the dorsal stream monitors rapid spatial attentional shifts screening serially each of the 7 or 8 letters falling under fixation, therefore facilitating their identification by the ventral system. Like the VA Span hypothesis, this proposal suggests that the key mechanism of visual attention for reading acquisition would occur within an ocular fixation and regardless of the phonological skills of participants (see Pammer et al., 2004, 2005; Vidyasagar and Pammer, 2010)[1].

In the present study, we present dyslexic and age-matched skilled reader children with a visual task and an auditory one that involve the simultaneous presentation of multiple stimuli. Our first aim was to determine whether deficits classically observed on the "serial" search task in developmental dyslexia were restricted to dyslexia associated with VA Span deficits. Our second aim was to investigate whether any impairment observed on the visual "serial" search task in dyslexia would also occur on an auditory search task. Indeed, since reading requires multimodal resources, it would not be surprising if perceptual attentional deficits in dyslexia were not restricted to only one sensory modality, but also tapped into an amodal pool of resources (Facoetti et al.,

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[1] The theoretical nuance between the two theories is that Vidyasagar proposes that these visual attentional resources are serial (since it would be governed by the dorsal stream) whereas the VA Span hypothesis assumes that they are parallel (since they would be subtended by brain areas playing a role attention devoted to multi-element processing: Peyrin et al., 2012). Another difference between the two theories is that Vidyasagar defines the visual attentional resources in terms of spatiality whereas in the VA Span hypothesis, they are defined in terms of quantity.

2003, 2005, 2010; Lallier et al., 2009, 2010a,c). Moreover, a perceptual asymmetry, which is similar to the one found in visual search tasks, takes place in auditory search tasks. Cusack and Carlyon (2003) presented participants with a task in which a frequency modulated (FM) sound had to be detected among non-modulated sounds (steady sounds), and a task in which the opposite had to be done. No auditory pop-out effect was found for either of the two tasks; however, the participants' accuracy in detecting the FM sound among steady sounds was less affected by the number of distracters than their ability to accurately detect the steady sound among FM distracters was. The authors concluded that auditory search reflected systems specialized for certain auditory features, as well as the limited capacity of attentional resources to process the auditory set, and that the two conditions engaged various degrees of difficulty.

We reasoned that if search mechanisms require simultaneous perceptual attention, and simultaneous perceptual attention reflected in VA Span skills taps into an amodal pool of resources, poor VA Span skills should be associated with poor visual and auditory search performance. Support for this hypothesis comes from a recent study showing that dyslexic children with a VA Span disorder were impaired on simultaneous auditory attention assessed in a dichotic listening task designed to be comparable to the task measuring VA Span abilities (Lallier et al., 2012). Also found that simultaneous auditory attention was unrelated to the phonological awareness and short term memory skills of the participants. Here, we therefore expected that if detecting an auditory target presented simultaneously among auditory distracters involves simultaneous perceptual attention, performance should not be related to the phonological abilities of participants but rather to their VA Span skills.

MATERIALS AND METHODS

PARTICIPANTS

Thirty-two French children took part in the present study. A group of 16 dyslexic children (10 boys) was compared to a group of 16 control children (3 boys). All children attended school regularly and had French as native language. They had normal or corrected-to-normal vision, normal hearing level, and no history of neurological or psychiatric disorders.

The 16 dyslexic children were recruited at the "Reference Center for Specific Learning Disorders" of the Pediatric Department of the Hospital of Grenoble and the Neuropediatric Department of the Kremlin-Bicêtre Hospital in Paris where the diagnosis of developmental dyslexia was primarily established by practitioners in charge (i.e., neuropsychologists or neuropediatricians) using both inventories and testing procedures in accordance with the guidelines of the ICD-10 classification of Mental and Behavioral disorders. All the dyslexic participants had normal IQ (full IQ superior to 85 on the WISC-III or WISC-IV, or a score superior to the 25th percentile on the Raven's Progressive Matrices; Raven et al., 1998). Although the two groups were matched for age [controls: 128 ± 5 months; dyslexics: 133 ± 10 months, $t_{(30)} = 1.7$, $p = 0.09$], control children were older regarding reading age [139.2 ± 16 months; dyslexics: 85.7 ± 6.4 months, $z = 4.8$, $p < 0.001$] as measured by the "Alouette" reading test (Lefavrais, 1967).

READING SKILLS ASSESSMENT IN THE CONTROL AND THE DYSLEXIC CHILDREN

Reading performance of the 32 participants were assessed using reading lists including a list of 20 words, a list of 20 irregular words and a list of 20 pseudowords, taken from the ODEDYS battery (Jacquier-Roux et al., 2002). Items between lists were matched for letter and syllable lengths, grammatical class and frequency. The 20 pseudowords were legal pseudowords without lexical neighbors. Participants were instructed to read aloud each of the three lists as quickly and as accurately as possible. Both accuracy and reading rate were taken into account.

PHONOLOGICAL AND VA SPAN SKILLS SCREENING OF THE DYSLEXIC CHILDREN

Dyslexic children were presented with some additional tasks in order to determine the cognitive disorder associated to their dyslexia at the individual level. Phonological processing was quantified with two tasks: a phonemic deletion task (phonemic awareness) and a pseudoword repetition task (phonological short-term memory). The two phonological tasks were taken from the EVALEC battery (Sprenger-Charolles et al., 2005) in which pseudowords are presented to participants through headphones. The visual whole report and visual partial report tasks (e.g., Bosse et al., 2007; Bosse and Valdois, 2009) were further administered to dyslexic children in order to quantify their VA Span skills.

Phonemic awareness

Twelve pseudowords with a tri-phonemic consonant-consonant-vowel structure (CCV) were presented to the children via headphones. The children were instructed to remove ("eat") the first sound of the pseudoword and say the remaining part. The score corresponded to the percentage of correct answers.

Phonological short-term memory

Children were asked to repeat pseudowords as accurately as possible without any time constraint. The task included 24 pseudowords varying in length from three to six syllables. The score corresponded to the percentage of pseudowords accurately repeated.

VA span skills

Prior to the visual whole report task, children were administered a control letter identification task. Children were presented with a single letter (each of the 10 consonants presented for the two report tasks described below) in the center of the screen during varying durations (33, 50, 67, 84, and 101 ms) immediately followed by a mask. They were asked to name the letter immediately after being presented.

The whole report task included 20 black consonant strings (composed of 10 consonants, upper-case Arial font, 18 pt). The center-to-center distance between each adjacent consonant was 1.2° so that lateral masking effects were minimized. Stimuli did not include the same letter twice and were not French word skeletons (e.g., C M P T R for "compter"). At the start of each trial, a central fixation point was displayed for 1000 ms followed by a blank screen for 50 ms. Consonant strings were presented horizontally during 200 ms at the center of the screen. Immediately after the string presentation, participants had to recall as many letters as possible. The score corresponded to the percentage of letters accurately reported (identity not location).

In the partial report task, participants were required to orally report a single cued letter presented before briefly within a 5-consonant string. Fifty 5-letter strings were built from the same 10 consonants used in the whole report condition and with the same characteristics as the whole report task. The probe indicating the letter to be reported was a vertical bar presented for 50 ms, 1° below the target letter presented in the string. Each letter was used as target once in each position. Like in the whole report task, a central fixation point was presented for 1000 ms followed by a blank screen for 50 ms. The 5-letter string was then presented at the center of the screen for 200 ms. At the offset of the letter string, the bar probe appeared for 50 ms. Participants were asked to report the cued letter only and to be as accurate as possible and no time pressure. The score corresponded to the percentage of cued letters accurately reported.

VISUAL AND AUDITORY SEARCH TASKS

The two search tasks used in the present study were created from two tasks in the visual (Marendaz et al., 1996) and the auditory (Cusack and Carlyon, 2003, Experiment 3) modalities which previously showed a perceptual asymmetry for search performance as a function of target type and number of distracters.

Visual stimuli

As in Marendaz et al. (1996), the visual search configurations were composed of two types of capital letters (O and Q, Helvetica font, 28 pts) subtending an average angular size of 0.8°. The letter search display covered a surface of 10.2° by 11.4° (height and width) from a viewing distance of 45 cm. The minimum distance separating two stimuli was never twice as much as the letter size in order to avoid grouping effects. In the "parallel" search condition, children had to detect the target letter "Q" among distracter letters "Os" whereas in the "serial" search condition, they had to detect the target letter "O" among distracter letters "Qs."

Auditory stimuli

Following Experiment 3's procedure of Cusack and Carlyon (2003), the auditory search configurations were composed of 250 ms-long tones randomly distributed over a 1-s window[2] and across a logarithmic frequency scale (262–4192 Hz), with the constraint that two simultaneously occurring tones had to be separated from at least one third of an octave. In a first condition, children had to detect a FM tone target (described as a "moving sound"), which was modulated at a depth of 5% (0.84 semitones) among pure tones, and in a second condition, they had to detect a steady tone (described as a "non-moving sound") within FM tones. The sounds were presented over headphones (Earthquake, TS 800) at a level of 70 dB SPL approximately.

Procedure

Henceforth, the two search conditions for each modality will be referred to as the "O target" and "Q target" conditions in the visual modality, and "FM target" and "Steady target" conditions in the auditory modality. In both the visual and the auditory tasks, eight search configurations of 4, 10, and 16 stimuli were created, yielding a total of 48 trials for each condition. For each condition, the configurations with various stimulus set sizes were presented randomly and the target was present in half of the trials. Children were instructed to determine whether the target was present or not: in the visual task, they had to press "P" on the keyboard as fast they could as soon as they detected the target, or press "A" when they did not detect any target. In the auditory task, they were instructed to wait until the 1-s auditory configuration finished before pressing the response key when a question about the presence or absence of the target appeared on a white screen.

In the visual modality (**Figure 1A**), children were first presented with a mask subtending the size of the following letter display for 2000 ms. Then, a blank screen was presented for 1000 ms followed by a fixation cross at the center of the screen for 900 ms. A blank screen then appeared for 200 ms and one of the eight visual configurations was presented. After the response of the subject a blank screen then appeared for 1000 ms before the presentation of the mask of the following trial. In the auditory modality (**Figure 1B**), a fixation cross appeared on a blank screen for 1000 ms and the auditory search configuration was displayed for 1000 ms whilst the cross remained on the screen. After the auditory sequence, a question appeared on the screen asking whether the target was present or not. Before the auditory search task, an identification task composed of 40 trials was administered to the children in order to make sure they could identify both types of sound. On this control task, all children were at ceiling,

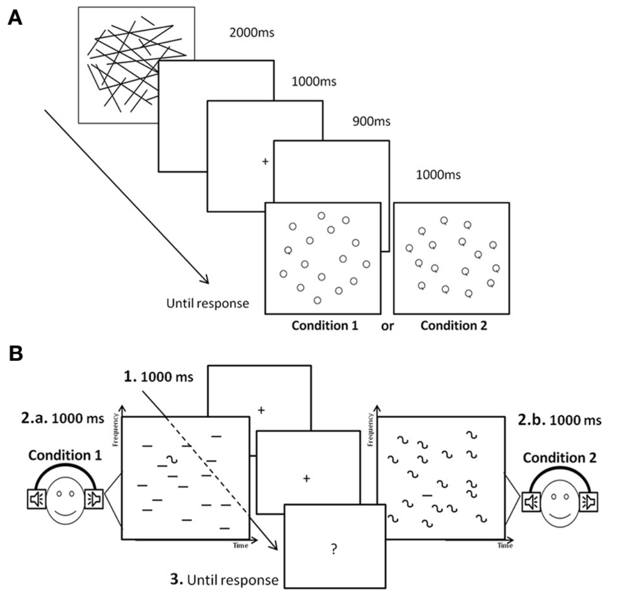

FIGURE 1 | Illustration of the visual (A) and the auditory (B) search tasks.

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[2] In Cusack and Carlyon (2003, Experiment 3), the temporal window was 2 s long. We shortened this temporal window on purpose to favor the simultaneous processing of the tones.

demonstrating good discrimination skills between FM and steady sounds. In both modalities, a training phase composed of 8 trials was administered prior to the test. The order of administration of the two conditions was counterbalanced between participants, as well as the order between the visual and the auditory tasks.

DATA ANALYSIS

Group differences on reading accuracy and speed were assessed by means of independent parametric *t*-tests (or non-parametric *U*-tests when the conditions for carrying out parametric analysis were not assumed) with group (control, dyslexic) as the between-subjects factor. Individual reading performance was compared to age-matched norms from which individual and group average *z*-scores were computed (Bosse and Valdois, 2009). Regarding the cognitive skills of the dyslexic children, individual *z*-scores were computed according to the age-matched corresponding norms for the two phonological tasks (Sprenger-Charolles et al., 2005) and for the VA Span tasks (Bosse and Valdois, 2009).

For the visual and the auditory search task separately, RTs for trials where the target was present and correctly detected, and d' scores were analyzed by means of mixed ANOVAs with group (control, dyslexic) as the between-subjects factor, and condition (O target/Q target; FM target/Steady target) as well as stimulus set size (4, 10, 16) as within subject factors. *Post-hoc* analyses were conducted using Bonferroni tests. In the case of non-homogeneity of variance or non-sphericity of the data, data transformation or Greenhouse-Geisser correction, respectively, were performed.

For partial correlation analyses (controlling for chronological age), we computed an additional search measure corresponding to the average measure of the search performance across the three stimulus set sizes for each modality.

RESULTS

READING SKILLS

As shown in **Table 1**, the performance of control children was significantly higher than the performance of dyslexic children on the three reading lists (for all *t* or *z* values, *ps* < 0.001, **Table 1**). All control children performed well within the norm, with all individual *z*-scores being above -1 on all the reading measures. The severe reading difficulties of the dyslexic children were illustrated by an average performance 2 SD below the norm on all the reading measures. Overall, the dyslexic group of the present study exhibited difficulties on both the global (irregular word reading) and analytic (pseudoword reading) reading procedures.

PHONOLOGICAL SKILLS AND VA SPAN SKILLS IN THE DYSLEXIC GROUP

Table 2 presents the performance of the dyslexic group regarding their phonological and VA Span skills. The dyslexic group was significantly worse at repeating pseudowords compared to the age-matched norm, which illustrated poor phonological short-term memory skills ($z = -1.84, p < 0.05$). In the CCV phonemic deletion task, the dyslexic group tended to exhibit poorer performance compared to the norm ($z = -1.54, p = 0.06$). On the visual control task of single letter identification, no deficit was found at any of the presentation times (33 ms: $z = -0.49$, 50 ms: $z = -0.59$, 67 ms: $z = -0.56$, 84 ms: $z = -0.67$ and 110 ms: $z = -0.67$, all *zs* n.s.), neither on the overall performance (104.4 letters identified out of 150 (±34), $z = -0.56$, n.s.). On the whole report task, the dyslexic group accurately reported 65.6% (±16.3) of the letters on average, indicating a deficit on that task ($z = -1.81, p < 0.05$). On the partial report task, as a group, the dyslexic children did not exhibit any deficit, reporting accurately 78% (±16.3) of the cued letters ($z = -0.88$, n.s.).

SEARCH TASKS

Search performance differences between the control and dyslexic groups

First, in the visual modality (**Figure 2A**), no effect involving the group was found on d' scores (all *Fs* < 1), indicating that there was no group difference on visual target detection sensitivity across all experimental conditions. In the auditory modality (**Figure 2B**), no effect was found on RTs (all *Fs* < 1) indicating that none of the factors (including the group) influenced the time to press the response button after the auditory configuration presentation.

Table 1 | Reading skills of the control group (*n* = 16) and the dyslexic group (*n* = 16).

	Control group		Dyslexic group		Group effect[b]
	M (SD)	*z*-score[a]	M (*SD*)	*z*-score[a]	
REGULAR WORDS					
Accuracy/20	18.8 (1.7)	0.04	13.9 (3.1)	−2.00*	$t_{(30)} = -5.2$***
Speed (s)	16.8 (4.8)	0.24	60.2 (36.5)	−4.70***	$z = 4.5$***
IRREGULAR WORDS					
Accuracy/20	17.6 (2.1)	0.58	7.1 (3.1)	−2.30*	$t_{(30)} = -10.8$***
Speed (s)	19.1 (5.9)	0.24	69.3 (37.6)	−4.50***	$z = 4.5$***
PSEUDOWORDS					
Accuracy/20	17.5 (1.9)	0.310	11.1 (3.9)	−2.40*	$t_{(30)} = -5.6$***
Speed (s)	24.3 (6.0)	0.08	57.3 (25.7)	−3.10**	$z = 4.8$***

[a] *Individual z-scores (one-tailed) computed according to age-matched norms (Bosse and Valdois, 2009).*

[b] *For speed measures, non-parametric Mann-Whitney U-tests were used (z statistics reported).*

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Table 2 | Characteristics of the dyslexic group (*n* = 16).

	M (*SD*)	Range	*Z* score
PHONOLOGY			
Pseudoword repetition (%)[a]	45.5 (20)	19–79	−1.84*
CCV deletion (%)[a]	51.0 (27)	0–100	−1.54, $p = 0.06$
VISUAL ATTENTION SPAN[b]			
Whole report task (%)	65.6 (16.3)	35–91	−1.81*
Partial report task (%)	78.0 (13)	50–92	−0.88 n.s.

[a] *z scores computed from the age-matched norms of Sprenger-Charolles et al. (2005).*

[b] *z scores computed from the age-matched norms of Bosse and Valdois (2009).*

*$p < 0.05$.

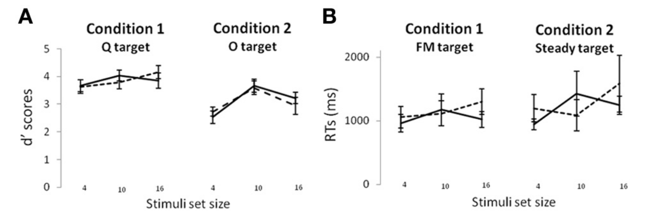

FIGURE 2 | Visual d′ scores (A) and auditory RT scores (B) in the control (solid line) and dyslexic (dotted line) children. Standard error bars are depicted.

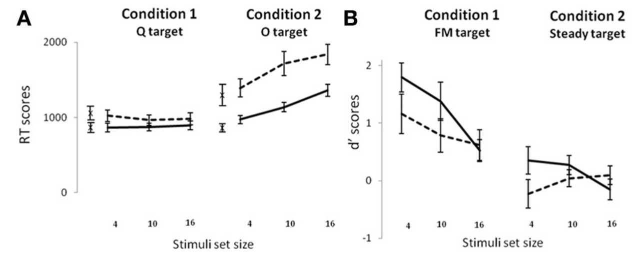

FIGURE 3 | Visual RT scores (A) and auditory d′ scores (B) in the control (solid line) and dyslexic (dotted line) children. Crosses represent the intercept values for the visual task. Standard error bars are depicted.

In the visual task (**Figure 3A**), there was a main effect of group on RTs [$F_{(1,\ 30)} = 4.90$, $p = 0.034$] that was modulated by the condition [$F_{(1,\ 30)} = 5.6$, $p = 0.02$], and that showed that dyslexic children were slower than control children in the O target condition (*post-hoc*: $p = 0.03$ but) but not in the Q target condition (*post-hoc*: $p > 0.9$). There was also a main effect of condition [$F_{(1,\ 30)} = 119.05$, $p < 0.001$] and stimulus set size [$F_{(2,\ 60)} = 22.3$, $p < 0.001$). These two factors interacted with each other [$F_{(2,\ 60)} = 26.2$, $p < 0.001$] indicating that the smaller the number of distracters, the faster the response, but only for the O target condition (*post-hoc*: all *ps* < 0.001; Q target condition, all *ps* > 0.1). RTs differences across stimulus set sizes in the O target condition could be explained by changes in participant's criteria (speed-accuracy tradeoff): Average d' scores and RTs indeed positively correlated in the whole sample ($r = 0.34$, $p < 0.05$) suggesting that the worse target sensitivity the child showed, the faster at responding they were. Importantly, since the two groups showed similar d' scores for all visual experimental conditions (see **Figure 2A**), speed-accuracy tradeoff variations between groups could not explain the aforementioned differences on RTs. As a follow-up of these significant effects on RTs, we computed intercept and slope values of the search functions. The group difference found in the O target condition on RTs was accompanied by a group difference on the search function intercepts (controls: 860 ± 213 ms; dyslexics: 1260 ± 520 ms; $t_{(30)} = -2.7$, $p < 0.05$), but not on the slopes (controls: 32 ± 18 ms/item; dyslexics: 37 ± 32 ms/item; $t < 1$). In the Q target condition, control and dyslexic children presented identical slopes (respectively, 2 ± 8 ms/item and −3 ± 16 ms/item, $t_{(30)} = 1.2, p > 0.05$) and intercepts (respectively, 860 ± 245 and 1037 ± 322 ms, $t_{(30)} = -1.7$, $p > 0.05$).

In the auditory task (**Figure 3B**), no main effect of group was found [$F_{(1,\ 30)} = 2.14$, $p = 0.15$] on d′ measures. There was a main effect of condition [$F_{(1,\ 30)} = 35$, $p < 0.001$] illustrating that participants were better in the FM target condition than in the Steady target condition. There was also an effect of stimulus set size [$F_{(2,\ 60)} = 5.3, p < 0.01$] showing that target detection performance was better for stimulus set size of four than 16 (*post-hoc* test: $p < 0.01$, other *ps* > 0.05). A condition by stimulus set size interaction [$F_{(2,\ 60)} = 4.2, p = 0.02$] revealed that the difference between the set sizes of 4 and 16 was true for the FM target condition (*post-hoc* test: $p < 0.001$), whereas in the Steady target condition, detection was equally hard for all set sizes (*post hoc* tests: all *ps* > 0.10). The condition by set size interaction was similar between groups ($F < 1$). Lastly, there was an interaction between group and stimulus set size [$F_{(2,\ 60)} = 3.4$, $p = 0.04$] showing that control children benefited of being presented with four compared to 16 stimuli (*post-hoc* test: $p < 0.005$) whereas dyslexic children did not, and this was not modulated by the condition ($F < 1$).

Search performance differences between dyslexic subgroups

In order to examine to what extent individual significant VA Span disorders in the dyslexic group were linked to search deficits, we ran subsequent subgroup analyses. We selected all the dyslexic children with a VA Span deficit, i.e., impaired on both the whole and partial report tasks (VASpan subgroup; all individual *z*-scores < -1.65, $n = 6$). We further selected all the dyslexic children with no impairment on any of the two report tasks (noVASpan subgroup: individual *z*-scores > -0.9, $n = 6$). Note that the four remaining dyslexic children exhibited poor performance on only one of the two report tasks and were not included in any of the subgroups. Both of the two subgroups presented the same reading delay compared to the level expected for their age (42 months for the VASpan subgroup and 48 months for noVASpan subgroup), which indicated similar impaired reading level in the two dyslexic subgroups (Mann Whitney *U*-test: $z = 1.26$ $p > 0.05$). Both dyslexic subgroups were impaired on phonological short term memory (VASpan: $z = -2.1$, $p = 0.018$; noVASpan: $z = -1.9$, $p = 0.029$), but only the noVASpan subgroup was significantly impaired on phonemic awareness (noVASpan: $z = -1.7$, $p = 0.045$; VASpan: -1.2, $p = 0.11$ n.s.). Kruskal-Walis tests were conducted with group as a between subject factor (VASpan, $n = 6$; noVASpan, $n = 6$; controls, $n = 16$) on the average performance in the visual O target condition and in the auditory FM target condition. On auditory search, the three groups presented similar performance overall [$H_{(2)} = 0.8$ $p = 0.66$]. On visual search, there was a main effect of group on RTs [$H_{(2)} = 11.1$ $p < 0.005$] that indicated slower target detection for the VASpan subgroup compared to the control group (multiple comparisons on mean ranks: $p < 0.005$, all other *ps* $>$ 0.05). Note that no group effect was found on visual d' scores on the O target condition [$H_{(2)} = 0.59$ $p = 0.77$], suggesting no speed-accuracy tradeoff differences across groups. Although no group effect was found on the slope values [$H_{(2)} = 2.1$ $p = 0.33$], a group effect was found on the intercept values [$H_{(2)} = 6.8$ $p = 0.034$], which revealed higher intercepts for the VASpan group than the control group (multiple comparisons on mean ranks: $p = 0.04$, all other $ps > 0.05$).

PARTIAL CORRELATIONS ANALYSES

Within the whole sample

Following the results reported in section Search Tasks, an average d' obtained on the O target condition was controlled for in the correlations involving RTs for visual search in order to neutralize speed-accuracy tradeoff between participants. None of the reading measures correlated with any of the different search measures neither in the Q target condition for the visual task, nor in the Steady target condition for the auditory task. Therefore, all the subsequent analyses will focus on performance on the O target condition and the FM target condition.

Performance on these critical conditions correlated with each other (-0.33, $p < 0.05$, one-tailed, based on the *a priori* hypothesis of an amodal pool of resources for simultaneous processing, cf. Lallier et al., 2012) suggesting that they tapped into the same pool of amodal resources. As shown in **Table 3**, all reading *z*-scores significantly correlated with visual RTs, illustrating that the better reading (accurate and fast) the faster the search, for all stimulus set sizes. The reading scores also correlated with the intercept measures, but not with the slope measures, suggesting that the greater the intercept the poorer the reading skills. In the auditory modality, search performance (in particular for a set size of 10) significantly correlated with reading speed for all types of items and with real words only (regular and irregular) regarding accuracy, i.e., the higher the d', the faster and better the reading.

Within the dyslexic sample

We further ran partial correlation analyses in the dyslexic group in order to determine whether a low search performance in both modalities would contribute to their reading and/or cognitive deficits (i.e., phonological or VA Span difficulties). As seen in **Table 4**, auditory (d') and visual (RTs) search performance correlated with each other indicating that the higher the RTs in the visual task, the lower the d' score in the auditory task. Moreover, the higher the visual intercepts, the poorer the auditory search performance for a stimulus set size of 10.

Poor search skills of dyslexic children were associated with their poor reading skills. Visual search RTs and intercepts correlated with pseudoword and irregular word reading accuracy and auditory search d′ scores correlated with real word reading accuracy (regular and irregular) and reading speed for all items (**Table 5**). In particular, both visual (i.e., set sizes of 4, 10, and 16, average measure, intercepts) and auditory search performance (set size of 10 in particular) correlated strongly with irregular word accuracy (cf. **Table 5**; **Figure 4**). Visual slope values did not correlate with any of the reading measures.

Table 4 | Partial correlation coefficients visual and auditory search performance in the dyslexic sample ($n = 16$).

	Auditory search (d′) FM target			
	SSS(4)	SSS(10)	SSS(16)	AVG
VISUAL SEARCH O TARGET				
RT—SSS(4)	−0.07	−0.68***	−0.30	−0.35
RT—SSS(10)	−0.05	−0.79***	−0.52*	−0.52*
RT—SSS(16)	−0.22	−0.75***	−0.68***	−0.65**
RT—AVG	−0.06	−0.79***	−0.52*	−0.53*
Slope	−0.37	0.01	−0.43	−0.33
Intercept	0.14	−0.60*	−0.17	−0.24

SSS, stimulus set size; AVG, average measure of the search performance across the three stimuli set sizes.

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.005$, *one-tailed.*

Table 3 | Correlation coefficients between reading *z*-scores and search tasks in the whole sample ($n = 32$).

	REG_Acc	**REG_T**	**IRR_Acc**	**IRR_T**	**PW_Acc**	**PW_T**
VISUAL SEARCH O TARGET						
RT—SSS(4)	−0.43**	−0.51***	−0.57***	−0.48***	−0.63***	−0.32*
RT—SSS(10)	−0.49***	−0.57***	−0.59***	−0.54***	−0.64***	−0.43***
RT—SSS(16)	−0.39*	−0.41*	−0.53***	−0.38*	−0.47**	−0.39*
RT—AVG	−0.46***	−0.53***	−0.60***	−0.50***	−0.61***	−0.40*
Slope	−0.01	0.07	−0.04	0.08	0.14	−0.15
Intercept	−0.40*	−0.49***	−0.52***	−0.47***	−0.62***	−0.27
AUDITORY SEARCH (d′) FM TARGET						
SSS(4)	0.37*	0.30*	0.31*	0.17	0.10	0.36*
SSS(10)	0.34*	0.41*	0.33*	0.35*	0.27	0.36*
SSS(16)	0.29	0.08	0.02	0.04	0.18	0.09
AVG	0.41*	0.35*	0.30	0.25	0.23	0.35*

REG, regular words; IRR, irregular words; PW, pseudowords; Acc, accuracy; T, time; SSS, stimulus set size; AVG, average measure of the search performance across the three stimuli set sizes.

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.005$, *one-tailed based on the a priori hypothesis of a relation between reading deficits and poor search performance.*

Table 5 | Partial correlation coefficients between reading scores and search performance in the dyslexic sample ($n = 16$).

	REG_Acc	**REG_T**	**IRR_Acc**	**IRR_T**	**PW_Acc**	**PW_T**
VISUAL SEARCH O TARGET						
RT— SSS(4)	−0.31	0.24	−0.69***	0.32	−0.56*	0.19
RT—SSS(10)	−0.34	0.34	−0.79***	0.41	−0.48***	0.31
RT—SSS(16)	−0.18	0.11	−0.66**	0.15	−0.28	0.09
RT—AVG	−0.30	0.26	−0.76***	0.33	−0.48*	0.23
Slope	0.21	−0.19	0.14	−0.25	0.42	−0.15
Intercept	−0.32	0.25	−0.64**	0.33	−0.58*	0.20
AUDITORY SEARCH (d′) FM TARGET						
SSS(4)	0.46*	−0.21	0.46*	−0.07	−0.02	−0.26
SSS(10)	0.53*	−0.51*	0.84***	−0.48*	0.32	−0.48*
SSS(16)	0.40	−0.10	0.52*	−0.10	0.24	0.09
AVG	0.57*	−0.33	0.74***	−0.26	0.20	−0.34

REG, regular words; IRR, irregular words; PW, pseudowords; Acc, accuracy; T, time; SSS, stimulus set size; AVG, average measure of the search performance across the three stimuli set sizes.

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.005$, *one-tailed based on the a priori hypothesis of a relation between reading deficits and poor search performance.*

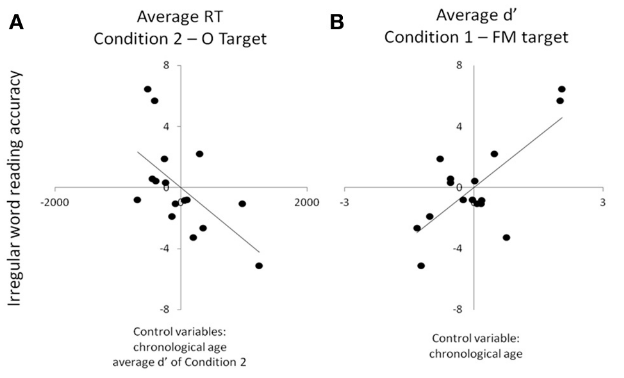

FIGURE 4 | Scatterplots depicting the partial correlations between irregular word reading accuracy (*y* axes) and visual (A) and auditory (B) search performance among the dyslexic children. For each panel, individual residual scores are represented, which stem from the two correlations between the factor(s) controlled for and (i) search performance, as well as (ii) irregular word reading accuracy.

Table 6 | Partial correlation coefficients between cognitive skills and search performance in the dyslexic sample ($n = 16$).

	VA Span		Phonology	
	PARTIAL	**WHOLE**	**PSTM**	**PA**
VISUAL SEARCH O TARGET				
RT—SSS(4)	−0.37	−0.48*	−0.13	0.38
RT—SSS(10)	−0.47*	−0.60*	−0.12	0.34
RT—SSS(16)	−0.52*	−0.31	−0.05	0.26
RT—AVG	−0.48*	−0.51*	−0.11	0.35
Slope	−0.14	0.26	0.12	−0.20
Intercept	−0.30	−0.47*	−0.14	0.38
AUDITORY SEARCH (d′) FM TARGET				
SSS(4)	0.04	0.28	0.33	0.11
SSS(10)	0.48*	0.61*	0.30	−0.20
SSS(16)	0.32	0.15	0.13	0.05
AVG	0.32	0.43	0.32	0.01

PSTM, phonological short term memory; PA, phonological awareness; SSS, stimulus set size; AVG, average measure of the search performance across the three stimuli set sizes. $^{*}p < 0.05$.

Lastly, reduced VA Span skills were found to be associated with both poor visual (RTs and intercepts) and auditory (set size of 10) search performance (**Table 6**; **Figure 5**). No relation was found between search performance and any of the two phonological scores.

DISCUSSION

In the present study, we showed that dyslexic individuals are impaired in visual "serial" search paradigms. Dyslexic children were indeed slower than the control group to detect the letter O among Qs. This deficit was accompanied by a search function characterized by prolonged intercepts for the dyslexic group than the control group in the absence of difference on the search slope. Moreover, auditory search abilities were measured for the first time in children with and without developmental dyslexia. The condition where children had to detect a steady sound among FM sound distracters led to very low performance, suggesting that this task was too difficult for both the controls and the dyslexic groups. In both conditions, the control children's performance was enhanced when few auditory distracters were present, suggesting that stimulus set size influenced their perceptual attentional auditory load. No such modulation was observed in the dyslexic children, which might indicate that their auditory perceptual attention load is already "*at threshold*" for the processing of few stimuli, and might reflect a limitation of attentional resources allocated to auditory simultaneous processing. We will return to this point later. In favor of the amodality of perceptual attention at play in search mechanisms, fast visual "serial" search (O target) correlated significantly with good sensitivity to detect FM targets both in the whole group and within the dyslexic group of children.

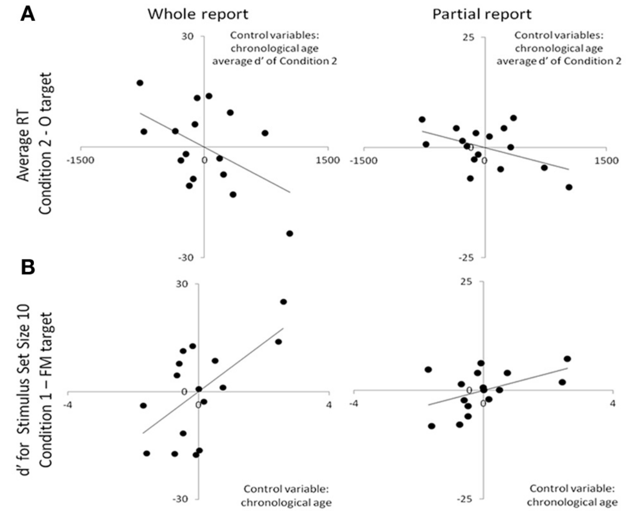

FIGURE 5 | Scatterplots depicting the partial correlations between VA Span skills (whole and partial report, *y* axes) and visual (A) and auditory (B) search performance (*x* axes) among the dyslexic children. For each panel, individual residual scores are represented, which stem from the correlations between the factor(s) controlled for and (i) VA Span skills, as well as (ii) search performance.

Slow visual "serial" search and high intercepts were significantly associated with poor VA Span skills in the dyslexic group. More specific analyses of the individual cognitive profiles of the dyslexic children showed that only the children with a significant VA Span deficit (i.e., impaired on both the whole and the partial report tasks) exhibited slower RTs and higher intercepts on the visual "serial" search compared to controls. This result strongly suggests that the factor at play in both reading and our visual search task is linked to simultaneous visual attention, i.e., the number of visual elements that can be processed in parallel in one fixation. Importantly, we found no correlation between visual search skills and either phonological short term memory or phonemic awareness skills of the dyslexic children. Moreover, the dyslexic group with no VA Span impairment showed no deficit on the visual search task despite of being the only group impaired on phonemic awareness. This dissociation between phonological skills and visual search performance in the dyslexic group suggests that deficits in the "serial" search condition (O target) is unlikely to be driven by serial processing difficulties such as sluggish visual attentional shifting skills previously found to relate to poor phonological skills (Lallier and Valdois, 2012 for a review). This idea finds additional support in both the absence of group effect on the slope values and the absence of correlation between reading, VA Span and these slope values. Indeed, search slope values are thought to relate to serial attentional components of the search (Wolfe and Horowitz, 2008). In our study, the dyslexic children—in particular the subgroup with simultaneous visual processing deficits (VASpan subgroup)—did not exhibit any deficit in the visual sequential processing skills required for an efficient search (i.e., absence of atypically high slope values). This is reminiscent of the results of Lallier et al. (2010a,b,c) which show that simultaneous and sequential visual attentional deficits dissociate in developmental dyslexia. The dyslexic children in our study were rather impaired on components such as those determining the intercept of the search function. Intercept values have been related to factors linked to processes preceding or following search mechanisms *per se* (Woodman et al., 2001). The intercept values of the dyslexic children might therefore have been constrained by visual mechanisms that influenced their response, and that were possibly at play before the start of the attentional serial search (Jolicoeur and Dell'Acqua, 1999; Wolfe and Horowitz, 2008). We will discuss later on how such visual mechanisms could relate to VA Span skills.

In further support for the significant contribution of VA Span disorder to the visual search deficits of dyslexic children, we reported that their visual "serial" search performance (RTs and intercepts) and reading accuracy significantly correlated and especially strongly so for irregular words. In opaque languages like French, it is impossible to correctly read an irregular word using the most frequent grapheme-to-phoneme conversion rules: the only way to be accurate is to retrieve the phonological lexical form automatically from the whole-word visual form whose encoding depends on VA Span skills (Ans et al., 1998; Bosse and Valdois, 2009). Our results in the auditory modality were less clear due to an absence of difference between both the dyslexic and control groups as well as the VASpan and NoVASpan dyslexic subgroups. Still, like in the visual modality, a strong correlation was found between irregular word reading accuracy and auditory search performance (stimulus set size of 10) within the dyslexic group, suggesting that auditory simultaneous attention may also be important for lexical processing in dyslexia. For the irregular word list, dyslexic children had to read each item aloud, hence retrieve its phonological lexical form. Would auditory simultaneous attention mediate the access of auditory whole-word knowledge?

Studies have shown some links between auditory whole-word knowledge and the degree of divided attention engaged in a task. For example, dual-tasking seems to enhance the reliance of lexical knowledge strategies used in speech perception tasks: Mattys and Wiget (2011) showed that the reliance on lexical knowledge was stronger in high cognitive load settings simulating adverse speech perception conditions (dual task, divided attention) than in low cognitive load settings (see also Mattys et al., 2009)[3]. In the present study, the correlation between visual and auditory search performance and irregular word reading accuracy in the dyslexic group indicates that children with better phonological and orthographical whole-word knowledge (and good access to them) were those who could monitor better random increases of the load of perceptual attention for auditory search. According to (Mattys and Wiget, 2011, Experiment 6), the strong lexical knowledge reliance for speech processing in high cognitive load settings might stem from the need to cope with the sensory degradation of *temporal cues* important for phoneme identification. Similarly, Casini et al. (2009) showed that vowel duration was underestimated when participants had to perform a dual task. According to the hypothesis that the estimation of speech units' duration relies on registering the number of "temporal pulses" accumulated during speech unit intervals (e.g., Coull et al., 2004), Casini et al. (2009) proposed that sharing attentional resources between simultaneous tasks (or simultaneous stimuli in the present study) decreases the sampling rate allocated to each task (or stimulus). Such phonemic sampling reduction would thus lead to miss some pulses within phonemic intervals and the underestimation of their temporal features.

In favor of Casini et al. (2009)'s hypothesis and the hypothesis of a permanent "*dual-task-like*" mode of dyslexic individuals, Vandermosten et al. (2010, 2011) showed that dyslexic children exhibit poor phonemic identification skills relying on temporal cues. Lehongre et al. (2011) also showed that dyslexic adults exhibited less oscillatory neural entrainment than skilled readers at the phonemic sampling rate (30 Hz) in the left hemisphere, which further correlated to slow rapid automatized naming skills (phonological whole-word forms retrieval). This last result supports our idea that auditory whole-word knowledge relies on the quality of both phonemic-rate sampling (cf. Poeppel, 2003) and the monitoring of random increases of auditory perceptual attentional load (cf. **Figure 5**). The correlations highlighted between auditory/visual search and VA span skills suggest that dyslexic children with low VA Span skills may suffer from a permanent high perceptual load hindering visual and auditory processing. This should be particularly true when *several* stimuli have to be attended and encoded (like in "serial" search) since we did not report different intercepts between the dyslexic and control children when the attentional focus is automatically directed to *the* relevant target stimulus (such as in "parallel" search). In support of this idea, Woodman et al. (2001) reported an increase of the intercept but not the slope values of the visual "serial" search functions (like the performance of our dyslexic group) when participants had to maintain several visual elements in memory whilst performing the search. A VA Span reduction might therefore have a negative impact on perceptual attentional processing similar to the one generated by a cognitive overload stemming from dual-tasking.

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[3] Even if we did not manipulate the cognitive load in our search tasks, perceptual load was. Perceptual and cognitive loads may further not be that independent in dyslexia since Lallier et al. (2012) showed that dyslexic children's scores on a dichotic listening dual-task (cognitive load) correlated with VA Span skills (perceptual attention load).

Interestingly, the auditory perceptual load generated by the simultaneous presentation of 10 stimuli was found to correlate with VA Span skills, intercept values and reading skills. Why this particular "signal-to-noise ratio" may be relevant for literacy development is an open question, but some studies looking at speech-in-noise deficits in developmental dyslexia could shed light on it (Ziegler et al., 2009; Dole et al., 2012). In particular, we found that auditory search performance was unrelated to phonological awareness (see also Lallier et al., 2012) which is supported by studies that show a relative independence between speech-in-noise deficits and other phonological deficits (Robertson et al., 2009; Ziegler et al., 2009; Messaoud-Galusi et al., 2011; Berent et al., 2012; Dickie et al., 2012). Speech-in-noise skills of dyslexic children also seem to dissociate from slow rate dynamic auditory processing linked to phonological awareness (Poelmans et al., 2011). Weak auditory entrainment to slow auditory frequencies (delta and theta) within speech streams—and critical for rhythm extraction—has been proposed as a cause of phonological awareness deficits in dyslexia (Goswami, 2011; Goswami et al., 2013; Hämäläinen et al., 2012). This weak auditory oscillatory entrainment at slow frequency bands might thus explain sluggish auditory attentional shifting, which appears to be restricted to dyslexia associated with phonological disorders (see Lallier et al., 2013), but is less likely to explain poor simultaneous processing abilities in auditory search. It is noteworthy that in the present study, we did not observe any significant deficit of the dyslexic group on our auditory search task. Although no strong conclusion about the role of auditory search in developmental dyslexia can be drawn at this point, the significant relationships highlighted between auditory search performance and reading skills as well as VA Span skills can still shed light on what this role might be.

Overall, we point out that different auditory perceptual attentional factors might contribute independently[4] to stable sound representations build-up (Hornickel and Kraus, 2013) and reading development. One of them could relate to speech processing in particular in high perceptual load situations (i.e., speech-in-noise, auditory search) and lexical knowledge, and would be linked to the simultaneous dimension of auditory processing (high frequency sampling). Another one would tap into slow modulations which are important for phonological awareness acquisition and that are carried by speech rhythm: this slow frequency sampling would tap into the sequential dimension of auditory processing[5]. We propose that a similar model could *a priori* hold true for the visual modality since perceptual attention deficits on one processing dimension (sequential or simultaneous) generally co-occur in audition and vision in the same dyslexic participants (Lallier et al., 2009, 2010a,c, 2012). We suggest that visual perceptual attention critical for reading acquisition requires both sequential (slow) and simultaneous (fast serial) mechanisms. First, a sequential visual attention mechanism would guide the attentional focus to engage and disengage over orthographic sequences, explaining sluggish visual attentional shifting and phonological disorders in dyslexia (Hari and Renvall, 2001; Facoetti et al., 2008; Lallier et al., 2009, 2010a,b). This visual mechanism would possibly trigger saccades in reading (Belopolsky and Theeuwes, 2009) and tap into parvocellular, hence relatively slow, temporal processing (Vidyasagar, 2004). A second mechanism, engaged in visual "serial" search (O target) would be in charge of screening the orthographic chunks falling under fixation and could be monitored by the magnocellular pathway, hence, characterized by a very high rate serial processing (Vidyasagar, 2004). The present results suggest that this second mechanism might be in part modulated by VA Span skills. Future studies will explore whether and how VA Span skills are monitored by a high frequency oscillatory visual system (gamma band) and whether this system dissociates from or depends on its coupling with a slow frequency oscillatory visual system (delta/theta bands).

CONCLUSION

In the present study, we assessed the search performance of a group of dyslexic children across the visual and the auditory modalities. Dyslexic children were slower than control children on the visual "serial" search condition only, which was accompanied by search function intercepts (but not slopes) that were higher in the dyslexic group than the control group. Despite the absence of deficit of the dyslexic group on the auditory search task, we showed that poor VA Span skills correlated to poor search performance not only in the visual but also in the auditory modalities. These results suggest that dyslexic children with a VA Span disorder may be under a permanent high perceptual load that hinders visual and auditory processing in particular in situations where several elements must be encoded simultaneously. Our results also suggest that limitations in simultaneous perceptual attention may preferentially affect the development of lexical reading (e.g., irregular word reading) and possibly the build-up of some phonological processes (first at the phoneme level, with consequences for auditory whole-word forms access). Finally, we stress the importance of taking into account the heterogeneity of the reading disorders at the cognitive level (e.g., phonological awareness, VA Span), since various time scales of processing might have different and potentially independent roles in literacy acquisition, and lead to different subtypes of developmental dyslexia.

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[4] Since the sampling frequencies characterizing speech streams are coupled and modulate each other, the independence of their respective contribution to reading and dyslexia may be relative and remains to be quantified.

[5] Most of the speech-in-noise deficits assessed in dyslexia reflect problems at lexical, syllabic or phonemic levels. Future studies should examine whether "speech streams"-in-noise perception shares any mechanisms with rhythm perception, phonological awareness and slow rate auditory entrainment.

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The eye-voice lead during oral reading in developmental dyslexia

Maria De Luca[1], **Maria Pontillo**[2], **Silvia Primativo**[1,2], **Donatella Spinelli**[1,3] **and Pierluigi Zoccolotti**[1,2]*

[1] Neuropsychology Unit, IRCCS Fondazione Santa Lucia, Rome, Italy
[2] Department of Psychology, Sapienza University of Rome, Rome, Italy
[3] Department of Human Movement Sciences and Health, University of Rome ≪Foro Italico≫, Rome, Italy

Edited by:
Usha Goswami, University of Cambridge, UK
Andrea Facoetti, Università di Padova, Italy
Marie Lallier, Basque Center on Cognition Brain and Language, Spain
Alan J. Power, University of Cambridge, UK

Reviewed by:
Stefan Hawelka, University of Salzburg, Austria
Matthew H. Schneps, Smithsonian Astrophysical Observatory, USA

***Correspondence:**
Pierluigi Zoccolotti, Department of Psychology, Sapienza University of Rome, Via dei Marsi 78, 00176 Rome, Italy
e-mail: pierluigi.zoccolotti@uniroma1.it

In reading aloud, the eye typically leads over voice position. In the present study, eye movements and voice utterances were simultaneously recorded and tracked during the reading of a meaningful text to evaluate the eye-voice lead in 16 dyslexic and 16 same-age control readers. Dyslexic children were slower than control peers in reading texts. Their slowness was characterized by a great number of silent pauses and sounding-out behaviors and a small lengthening of word articulation times. Regarding eye movements, dyslexic readers made many more eye fixations (and generally smaller rightward saccades) than controls. Eye movements and voice (which were shifted in time because of the eye-voice lead) were synchronized in dyslexic readers as well as controls. As expected, the eye-voice lead was significantly smaller in dyslexic than control readers, confirming early observations by Buswell (1921) and Fairbanks (1937). The eye-voice lead was significantly correlated with several eye movements and voice parameters, particularly number of fixations and silent pauses. The difference in performance between dyslexic and control readers across several eye and voice parameters was expressed by a ratio of about 2. We propose that referring to proportional differences allows for a parsimonious interpretation of the reading deficit in terms of a single deficit in word decoding. The possible source of this deficit may call for visual or phonological mechanisms, including Goswami's temporal sampling framework.

Keywords: reading, eye movements, eye-voice lead, dyslexia, pronunciation time

INTRODUCTION

Reading aloud is a complex task that requires the synchronization of various subtasks or subcomponents which impinge on different ongoing fluxes of information. Thus, for reading to be effective orthographic stimuli have to be visually scanned, individual words have to be decoded and their corresponding entries in the phonological output lexicon have to be activated, a stream of utterances has to be produced and synchronized with the ongoing scanning of visual text and word meaning has to be decoded and maintained in short-term memory to place words in a context and reconstruct the sense of a sentence (or paragraph). By its very nature, scientific research tries to isolate different sub-tasks (using appropriate parameters), because complex behaviors are more difficult to study. This is also true in the study of reading and its disorders. For example, it is widely accepted that word level captures the difficulty of dyslexic children (Coltheart et al., 2001). Therefore, much research has aimed to examine single-word reading performance, often analysing the effects of psycholinguistic variables (such as word frequency or age of acquisition) by means of vocal reaction times (e.g., Ziegler et al., 2003) or lexical decision times (e.g., Martens and de Jong, 2006). As to the visual scanning of texts, research on eye movements has mainly examined the silent reading of lists of words or words embedded in simple sentences, and has avoided the complexities linked to the synchronization of voice outflow and limited the requests for text comprehension (Rayner, 2009).

The complexity of reading, with its multiple interacting subcomponents, represents an intriguing and challenging problem. In a recent study based on reading time measures (Zoccolotti et al., 2012), we contrasted the reading aloud of words presented singly or arranged in multiple arrays in control and dyslexic readers. Skilled readers showed a clear advantage with multiple over single items, indicating that they were able to process the subsequent visual stimulus while uttering the current target. By contrast, dyslexic readers did not show such an advantage and were actually slower in reading multiple than single items. We proposed that difficulty with arrays of words indicates a selective difficulty in integrating the multiple subcomponents of the reading task over and above the basic nuclear deficit in decoding words (Zoccolotti et al., 2012). Other studies (based on the Rapid Automatized Naming paradigm or RAN) also emphasized the particular difficulty of dyslexic children with the sequential nature of the naming task as opposed to the more artificial situation in which single items are presented one at a time and responded to (e.g., Georgiou et al., 2013; for a developmental analysis of this effect see also Protopapas et al., 2013). These observations raise interest in examining dyslexic readers' overall reading behavior, that is, from visual scanning to sentence utterance. Indeed, this might clarify two important aspects of developmental reading deficiencies.

First, the extent to which dyslexic readers are differentially impaired/spared in the different subcomponents that contribute to reading aloud could be evaluated. It could also be determined whether the requirement to integrate these multiple subcomponents causes, or at least contributes to, the reading difficulty. Some evidence concerning the second question has been cited above.

As to the first question, a large literature indicates that dyslexic readers have slower reaction times (RT) to visually presented words (and non-words) than control readers. This finding indicates that they have a basic deficit in decoding visually presented orthographic materials (e.g., Ziegler et al., 2003; Spinelli et al., 2005). By contrast, pronunciation time for words is much less affected (although it is not entirely normal), indicating a much weaker deficit in the production component (Davies et al., 2013; Martelli et al., 2013). Analysis of visual scanning generally indicates that dyslexic children show normal eye movement patterns with non-orthographic visual stimuli and have specific difficulty with orthographic materials in both irregular (e.g., Olson et al., 1983) and regular (e.g., Italian, the language studied here: De Luca et al., 1999) orthographies. There is growing evidence of difficulty also in the acoustic modality (i.e., dyslexia has been found to be associated with reduced perceptual sensitivity to amplitude envelope onset of sounds (e.g., Goswami et al., 2011; Leong et al., 2011). Within the temporal sampling framework (Goswami, 2011), the deficit in rise time sensitivity is associated with impaired low-frequency oscillatory mechanisms involved in parsing and perceiving syllables. Goswami (2011) noted that impairments in auditory entrainment are likely to have consequences for attention and also auditory–visual integration (are likely to affect attention and auditory-visual integration). Indeed, attentional deficits were also reported in dyslexic children (e.g., Hari and Renvall, 2001; Facoetti et al., 2010) and might contribute to the abnormal eye movement pattern shown in reading (see also Hawelka et al., 2010 for a link between word reading and eye movement control).

Even from this sketchy presentation, it is apparent that not all reading sub-components are equally impaired in dyslexic readers and that procedures which allow differentiating the level of involvement within the same general paradigm would be useful to fully describe the profile of reading slowness in these children.

In the present study, we moved in this direction by jointly examining the flow of eye movements and speech production in children with and without developmental dyslexia while they read aloud a short meaningful text. Interest in the inter-play between eye and voice during reading aloud was particularly keen in the first part of the last century (Buswell, 1920, 1921; Fairbanks, 1937; Tiffin and Fairbanks, 1937). These studies were aimed at separating peripheral and central phases of the reading process. By analysing reading errors in good and poor adult readers in relationship to eye movements, Fairbanks (1937) reported evidence that "*faulty eye movements cannot have caused the errors*" and concluded that "*the central processes in reading determine the nature of eye movements*" (Fairbanks, 1937). This position still has a large consensus today (see Rayner, 1998, 2009 for reviews).

Important observations in these studies concern the relationship between visual scanning and voice production during reading. Buswell (1921) effectively synthesized the characteristics of this phenomenon: *"A mature reader tends to maintain a comparatively wide average span between the eye and the voice, which at times may amount to the space occupied by seven or eight words. An immature reader, however, tends to keep the eye and voice very close together, in many cases not moving the eye from a word until the voice has pronounced it. Reading of this type becomes little more than a series of spoken words because there is no opportunity to anticipate the meaning in large units. An eye-voice span of considerable width is necessary in order that the reader may have an intelligent grasp of the material read, and that he may read it with good expression."*

Fairbanks (1937) study of the eye-voice relationship was particularly thorough (although it has been rarely cited). He proposed that eye-voice lead (as compared to eye-voice span) was "*more descriptive of the eye-voice relation as it usually obtains*"; therefore, we will follow Fairbanks's terminology in the present work. Fairbanks (1937) examined the eye-voice lead in relationship to both spatial and linguistic parameters as well as the difficulty of words, defined by word frequency ("scarcity" in Fairbanks's terms) and the effect of stimulus length. The influence of these factors was clear in the pattern of eye movements as well as misreadings. Thus, "*in poor reading the influence of word scarcity is even greater*" than in superior readers, while "*word length has little effect upon good readers, but, to a degree at least, appears to be a measure of difficulty in inferior reading*." Examining mispronunciations in a dynamic context, Fairbanks (1937) gave particular emphasis to multiple utterances, such as hesitations or repetitions with or without self-corrections. He noted that, when good readers repeated a word they did so after a misreading and made a self-correction. By contrast, poor readers often repeated correct words and nearly always failed to correct their errors.

Fairbanks (1937) observed that number of hesitations is also particularly important in discriminating good from poor readers even though they are difficult to measure as "*their determination is essentially qualitative*" and requires "*careful re-checking*." Examining hesitations in association with eye movements, Fairbanks (1937) noted that "*one of the reasons for hesitation in poor reading is the necessity of regressing to words which give difficulty*" and "*…even though the determination of hesitations is a qualitative step, … diagnosis of reading ability by means of describing oral reading should include this measure*."

These observations are particularly revealing because, since the classical work of Marshall and Newcombe (1966, 1973), analysis of misreadings in dyslexia has focused on the cognitive interpretation of errors characterized by the production of a single, isolated response, while multiple utterances "*such as circumlocutions, self-corrections and multiple responses*" did not interest researchers in part because they "*do not occur with great frequency*" (Coltheart, 1980) and in part because they do not easily fit in the cognitive category framework. However, hesitations and repetitions are time-consuming and may be responsible for a large portion of the characteristic slowing reported for dyslexic readers in regular orthographies (Italian: Zoccolotti et al., 1999; German: Wimmer, 1993). Indeed, it has been observed that children learning regular orthographies rarely make "classical" substitution errors and more often produce a slow and fragmented approach to the target word (Bakker, 1992). Hendriks and Kolk (1997) referred to this as "*sounding out behaviour*" to mark reliance on phonologically recoding the target; this is referred to as a reading behavior (rather than error) because, by the end of the process, the child is often able to utter the target correctly. Recently, we confirmed that many of the mispronunciations of Italian children with dyslexia are due to sounding-out behavior, which discriminates them from skilled readers (Trenta et al., 2013). Although Fairbanks is not explicit in his description of hesitations, they seem to resemble the time-consuming errors described by Bakker (1992) or the sounding-out behavior posited by Hendriks and Kolk (1997).

Going back to the eye-voice-lead question, Fairbanks emphasized the role of linguistic factors (such as word scarcity) vs. spatial factors (such as stimulus position). Furthermore, *he* noted that "*since one of the most obvious effects of difficulty in poor oral reading is hesitation of the voice, it appears that this is the cause of increase in eye-voice lead*", and concluded that "*the amount of eye-voice lead is expressive of the combination of important factors involved in reading. It is a measure of the rate of recognition and assimilation.*" In the contrast between single and multiple word processing referred to above, we propose that a comparatively wide eye-voice lead should be taken as indication of the ability to integrate several sub-components of reading.

We have given particular space to the work of Fairbanks (1937) because it represents a very special case of a study in which an explicit attempt was made to cross-analyse the interplay between several sub-components of reading in both good and poor readers. After this pioneering period, interest in the vocal component of reading was seldom shown by eye movement research (for an exception see Morton, 1964), which relied almost completely on silent reading measures. Indeed, interest moved to perceptual or linguistic manipulations of written texts to determine the laws of eye movement control during reading, perceptual span and other topics related to cognitive processing during reading (for a review, see Rayner, 2009).

Consequently, research on eye-voice lead (or span) became rare. Some authors measured eye movements during oral reading by focusing on lexical processes and reading comprehension (Levin, 1979; Levy-Schoen, 1981). Inhoff et al. (2011) investigated the eye-voice span with the aim of refining models of eye movement control involved in reading aloud. Very recently, Pan et al. (2013) extended the study of the eye-voice lead to the multiple naming conditions typical of the RAN paradigm.

In the present study, we extended the early observations of Buswell (1921) and Fairbanks (1937) in measuring the eye-voice lead in Italian dyslexic readers and age-matched controls while they read aloud a meaningful text. By measuring eye movements and voice parameters together, we aimed to decompose the various reading sub-components to investigate which ones are more or less compromised in dyslexic readers. We also aimed to evaluate whether the integration of these multiple subcomponents contributes to generating the slowed reading that is found in children learning to read in regular orthographies (e.g., Wimmer, 1993; Zoccolotti et al., 1999). As a control condition, we also recorded eye movements during the silent reading of a text to evaluate the time advantage of silent over aloud reading.

As to eye movements, based on previous research in Italian children (De Luca et al., 1999, 2002) we expected to find problems associated with the number and duration of fixations. The distribution of fixation durations might be interesting in view of the temporal sampling framework (Goswami, 2011). Transposing Goswami's theory to the visual domain, we explored whether impaired low-frequency oscillatory mechanisms, which are important for mediating syllable perception, also have an effect at the visual level that is, on fixations in the same frequency range, with time durations of approximately 200 ms.

As to the vocal components, previous research indicates that articulation times are minimally affected in single word presentation in children with dyslexia (Davies et al., 2013; Martelli et al., 2013); however, no information is yet available on the articulation times of words immersed in a meaningful text, which was one of the aims of the present study. Finally, we also examined reading accuracy. In view of Fairbanks's (1937) observations, we focussed on sounding out behavior and pauses (which are time-consuming behaviors) in addition to classical substitution errors.

MATERIALS AND METHODS

PARTICIPANTS

Participants included 16 dyslexic readers and 16 chronological age-matched control readers. The school where participants were enrolled collected written informed consent provided by each student's family, as part of an agreement between the school and the Sapienza University of Rome. Groups were comparable for age, gender, and non-verbal IQ level (see **Table 1**). Each of the dyslexic readers scored at least 1.65 *SD* below the norm for either speed or accuracy on a standardized reading test (MT Reading test, Cornoldi and Colpo, 1995). In this test, the child reads a text

Table 1 | Summary statistics for the two groups of participants: mean age (in years, with range in square brackets); number of female and male participants; mean *z*-scores (and *SD* in parentheses) on Raven's Colored Matrices; mean reading times and mean number of errors on the MT Reading test; mean *z*-scores for reading time and accuracy on the same test.

	Dyslexic readers		Control readers		*p*-level
Age	11.9	[11.3–12.9]	11.6	[11.1–13.4]	n.s.
Males/females	9/7		10/6		n.s.
Raven test	−0.7	(0.6)	−0.3	(1.0)	n.s.
Reading time (s/syllable)	0.43	(0.14)	0.22	(0.02)	<0.001
Reading accuracy (number of errors)	22.5	(7.9)	4.7	(2.6)	<0.001
Reading time (*Z* score)	−2.3	(1.6)	0.2	(0.3)	<0.001
Reading accuracy (*Z* score)	−3.4	(1.8)	0.2	(0.5)	<0.001

Probability values for t-tests (except for gender, for which the Chi square test was used) comparisons between the two groups are reported ($p < 0.01$ values are considered significant after Bonferroni correction).

passage aloud with a 4-min time limit; reading time (s/syllable) and accuracy (number of errors, adjusted for the amount of text read) are scored (see **Table 1** for both raw and normalized values). Considering the reading speed raw data, the average reading time of the two groups was 0.22 (typically developing readers) and 0.43 s/syllable (children with dyslexia). This indicates slowing with a factor of 1.95 (below see further comments on this ratio). Non-verbal IQ level was assessed using Raven's Colored Progressive Matrices. All children scored well within the normal limits according to Italian norms (Pruneti et al., 1996). All participants had normal or corrected-to-normal visual acuity.

APPARATUS AND PROCEDURE

Eye movements from the dominant eye were recorded in binocular vision via an SR Research Ltd. Eye Link 1000 eye tracker (SR Research Ltd., Mississauga, Ontario, Canada) sampling at 1000 Hz, with spatial resolution of less than 0.04°. Head movements were avoided by using a headrest, but the chin was left free. The text was displayed on a 17″ CRT monitor at a viewing distance of approximately 57 cm. Screen resolution was 1024 × 768; refresh rate was 85 Hz. The ambient illumination level was kept constant across recordings by artificial lighting. A nine-point calibration procedure was run before the passage was shown. The calibration targets were presented randomly in different positions on the screen. Appearance of the text on the screen was triggered by fixation of a cross in the upper left position corresponding to the blank space adjacent to the initial letter of the passage.

Voice was digitally recorded by a system mounting a Shure microphone, a pre-amplifier, an E-MU sound card, and an ASIO driver, which was interfaced to the eye tracker by Eye Link Experiment Builder software.

Separately for each participant, eye movements and voice utterances were simultaneously recorded and stored in the same PC directory; the output consisted of two parallel recordings: an eye movement dataset and a sound file in wav format. Eye movements and audio recordings were synchronized by the eye-tracking device after eye-movement calibration. The voice-line recording onset and offset was automatically overlaid on the timeline of the eye movements recording output.

MATERIALS

Two text passages were used, one for reading aloud and one for silent reading; both were adapted from Aesop's fables and were appropriate for the age range of the observers. Each text subtended a visual angle of 22 × 13°, displayed at the center of the screen horizontally and at 5° from the top edge of the screen vertically. Passages were written in Times New Roman font (because it is similar to functional reading texts), with black letters on a white background. Average center-to-center letter distance subtended 0.4°. The two texts had the same number of lines (14) and were also matched for number of syllables and characters; finally, the content words of the two passages had comparable mean word frequency. The first line of both texts contained a filler sentence (ending with a full stop), which was not used in the analyses.

Only the three-line sentence, from the second to the fourth line of the text, for reading aloud was used for in-depth analyses of eye and voice parameters and will be described in detail. It contained 31 words (on average 10.3 words per line) and 173 letters (inter-word spaces included). Average word length was 4.6 letters. The mean log frequency of the words was 3.02 (range 0.7–4.9), according to a corpus of the Italian written language of 3,798,275 occurrences (CoLFIS; Bertinetto et al., 2005).

The order of the reading condition was randomized across participants. A cross was displayed in the upper-left quadrant of the screen (2° to the left of the first letter of the first text line) and served as the initial fixation target; the offset of the cross and the simultaneous onset of the display containing the passage was automatically triggered by the eye-tracking device when the participant steadily fixated the cross for at least 150 ms. Participants were asked to read each passage at their normal rate; in the reading aloud condition, the passage remained on the screen until the end of the last word uttered. To reliably assess the last fixation of silent reading, participants had to look at a two-figure number immediately after they finished reading, name the number aloud, and communicate that they had finished reading. The number subtended 0.25° and was displayed in the bottom right corner of the screen. To evaluate general comprehension, at the end of the reading participants were asked to answer questions; there was a yes/no question and an open question for each of the two text passages.

DATA ANALYSIS

Eye movements

Eye movement data were processed using the EyeLink Data Viewer software (SR Research Ltd., Mississauga, Ontario, Canada). Total viewing time (i.e., time needed to visually examine the text, from the beginning of the first fixation until the end of the last fixation) was computed for the whole passage (13 lines) for both oral and silent reading conditions. Only the above-mentioned three-line sentence of the reading aloud text was analyzed in detail: Besides total viewing time, total fixation time (i.e., the sum of all fixation durations), total number of fixations, mean fixation duration, forward saccade mean amplitude (in degrees of visual angle) and percentage of regressions were measured; fixation positions were mapped over the screenshot of the three-line sentence to determine which graphemes in the passage were fixated.

Audio tracks

Audio recordings were processed off-line using Audacity 2.0.2 software. The temporal onsets and offsets of utterances and the silent pauses were marked along the timeline interface of each audio file for the three-line sentence using a mixed criterion of visual inspection of the waveform image and listening to the audio track (the minimum duration for a pause to be reliably detected combining visual and audio information was 40 ms). In fluent readings, between-word pauses were rare; the final and initial phonemes of consecutive word utterances merged due to co-articulation.

Correct utterances, misreadings, and pauses between and within words were identified and labeled along the file timeline.

Total reading aloud time, total pronunciation time (i.e., the sum of utterances excluding pauses and including all kinds of misreadings), total duration of pauses (the sum of the durations of all silent pauses), mean duration of single silent pauses, number of silent pauses, and mean utterance duration for correctly read content words were scored (errors as well as sounding-out were excluded) for the three line sentence. Moreover, total reading aloud time was also computed for the whole text.

Accuracy was scored by considering the following categories of errors: sounding-out behavior (i.e., progressive approximation toward the correct utterance of the whole word made through sounding-out parts of the word; e.g., [ˈta ˈtavolo] instead of [ˈtavolo], "table"), word substitutions, word omissions or insertions and non-word production.

Eye-voice lead

The eye-voice lead was measured by detecting the within-word uttered phoneme for each fixation point in the first three lines of text. The lead was measured as the spatial distance, namely, number of letters, between the fixated grapheme and the simultaneously uttered phoneme. The single letter (grapheme) was chosen as the spatial unit (inter-word spaces counted as one letter). Each letter (and inter-word space) of the three-line sentence was progressively numbered from 1 to 173. Consistently, phoneme positions were progressively numbered along with the printed letters. Because of the transparency of the Italian writing system, there was a 1:1 correspondence between the number of graphemes and phonemes for 27 out of 31 words; three of the remaining four items had a number of phonemes equal to N–1 with respect to the corresponding printed word, and one had N–2 phonemes.

Then, each gaze position (i.e., fixation on a grapheme) was matched with the "voice position," that is, the phoneme uttered at the temporal onset of fixation. This was carried out by identifying the graphemes that were fixated on the eye movement output (see **Figure 1A**) and the phonemes that were simultaneously uttered (at each fixation onset) in the sound file output (see **Figure 1B**). For each of the fixation points, the corresponding grapheme position (number) was computed. Then, the phoneme uttered simultaneously with fixation onset (as determined by the time line of the recording) was "anchored" to the fixated grapheme (see red arrows in **Figure 1**) so that pairs of *grapheme position number* and *phoneme position number* were obtained for all fixations made during reading (N fixations = N pairs).

The eye-voice lead was measured at each fixation point as the difference between phoneme and grapheme positions in space (namely, difference between simultaneous phoneme and grapheme numbers). The individual eye-voice lead (across the three-line sentence) was measured in two ways: first, by averaging the difference values across the grapheme-phoneme pairs; second, by subtraction of the intercept values of the voice from the eye regression lines.

Statistical comparisons

Comparing groups with generally different performances by standard parametric analyses is problematic because groups may show systematic differences in variability (thus, violating the assumption of homogeneity of variance). However, it is generally believed that ANOVAs or Student *t*s are sufficiently robust comparisons for moderate violations of homogeneity. Therefore, *t*-tests for independent samples were run for all group comparisons and the Bonferroni correction was adopted for multiple comparisons.

To evaluate which variables contributed (and how much) to the impaired performance of the dyslexic children, standardized (i.e., Cohen's *d*) and unstandardized (i.e., ratio) effect sizes were computed. The first ones convey the size of an effect relative to the variability in the samples. Reference points for small, medium, and large effects are considered 0.20, 0.50, and 0.80, respectively. However, also unstandardized measures, such as ratios, are of particular interest because they allow comparing performances in proportional terms across conditions (and groups) showing very different variability. To this aim, the mean values of the dyslexic children were divided by the values of the control readers to obtain the ratios (except in the case of forward saccades amplitude, where the inverted ratio was calculated). In all cases, ratios greater than 1 indicate that dyslexic readers performed worse.

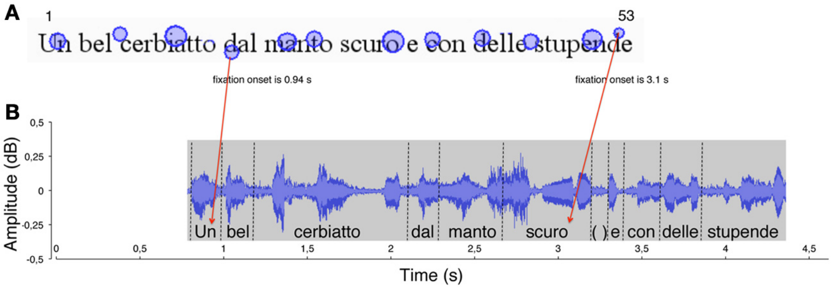

FIGURE 1 | An example of the method used to measure the eye-voice lead is reported for a typically developing reader. (A) In the spatial overlay of the eye movement pattern, the circles represent the localizations of eye fixations over the first line of the sentence. The size of the circles is proportional to fixation duration. The numbers 1 and 53 represent (for example) the first and last labels for letter position number in the line. The onset time of two fixations is indicated. **(B)** The waveform of reading aloud is shown as a function of time. The vertical dotted segments delimit the single word utterances, labeled along the timeline. Red arrows indicate the temporal correspondence between a fixation (the grapheme "d," of the word "dal," letter number 18) and the phoneme that was uttered at the time of fixation (the phoneme/u/, letter number 1). Each fixation (e.g., "d," of the word "stupende," number 52) was linked to the phoneme uttered at the moment of fixation onset (the phoneme /o/ of the word "scuro," number 32). The eye-voice lead was obtained by subtracting the phoneme position number from the grapheme position number for all of the grapheme-phoneme pairs (in the latter example: 52–32 = 20 letters).

Pearson correlations were run between eye-voice lead data and MT Reading Test, eye, and voice parameters for the whole group of children.

RESULTS

READING PERFORMANCE: VOICE DATA

The data based on the audio tracks are presented in **Table 2**. Total reading aloud time was significantly longer for dyslexic than control readers for both the three-line sentence and the total text (with similar ratios of about 2). Total pronunciation time (i.e., time excluding pauses) also distinguished the two groups, but with a lower ratio (1.4). For all these measures, *d* values greatly exceeded the reference for a large effect (0.80).

Utterance duration of single words (for content words correctly pronounced in the three-line sentence) was 119 ms slower in dyslexic with respect to control readers; notably, this effect was highly significant even though it indicated only a quantitatively modest 20% slowing (ratio = 1.2). When we restricted the computation to those words that were correctly pronounced by all children in the two groups, the difference was still present; thus, dyslexic readers needed 655 ms ($SD = 66$ ms) and control readers, 575 ms ($SD = 83$ ms); the 80 ms difference was highly significant ($t = 3.02, p < 0.01$) but again indicated a rather small effect (ratio = 1.1). Note that although the ratio was low, the standardized effect size for this measure was considerably higher and above the cut-off of 0.80 for a large effect size (see **Table 2**).

The children with dyslexia made many more pauses (ratio 4.5) and spent much more time in silence (with a 7.1 ratio for total duration of pauses) than control readers. Mean pause duration was slightly longer in dyslexic readers (this comparison just failed to be significant after Bonferroni correction). The frequency by duration of pauses distribution in the two groups is presented in **Figure 2**. The mode of the distribution was the 350–450 ms interval for control readers; the distribution was more complex for dyslexic readers, with two peaks at 40–150 ms and 450–550 ms (**Figure 2A**) and a third peak at very long intervals (**Figure 2B**; note the different interval scale).

Comments

When overall reading aloud time was considered, there was a remarkable group difference (90% or 1.9 ratio) in the time taken to read the three-line sentence. Notably, the same ratio was obtained in the MT Test reading time measure (1.9; based on data from **Table 1**). A very similar figure was reported by Martelli and co-workers who averaged six different studies (Martelli et al., 2013). Overall, a factor of 2.0 can be considered as a reference point to interpret reading time data as well as other reading parameters.

A quantitatively small (20% or 1.2 ratio), but highly significant, difference was present for pronunciation time of correctly read single words. Notably, all misreadings were excluded from these computations; therefore, the small lengthening in voice

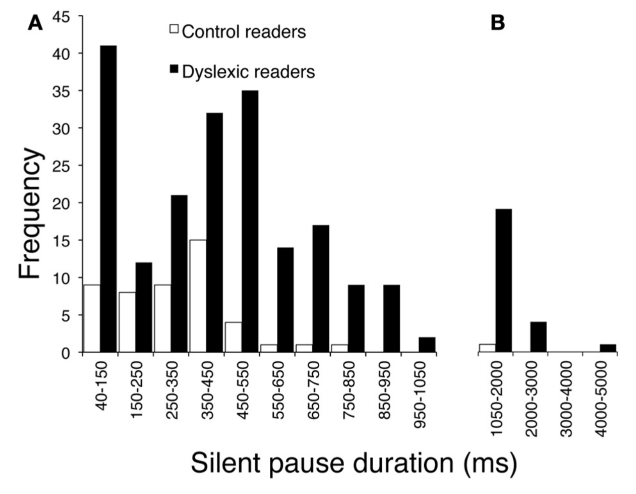

FIGURE 2 | Distribution of frequency for pause durations, separately for children with dyslexia and typically developing readers. (A) Intervals on the abscissa by 100 ms each (except for the first one, which ranges from 40 to 150 ms). **(B)** Intervals by 1000 ms each.

Table 2 | Group results for reading aloud data based on the audio tracks.

	Dyslexic readers		**Control readers**				
	Mean	***SD***	**Mean**	***SD***	***t***	**ratio**	***d***
Total reading aloud time	113.6	31.8	60.2	5.6	6.46	1.9	2.3
Total reading aloud time	22.1	7.4	11.4	1.5	5.67	1.9	2.0
Total pronunciation time	14.6	2.3	10.3	0.9	6.82	1.4	2.5
Mean single word utterance duration	0.608	0.054	0.489	0.046	6.76	1.2	2.4
Total duration of silent pauses	7.5	6.3	1.1	0.8	4.07	7.1	1.4
Mean duration of silent pauses	0.539	0.208	0.363	0.131	2.88*	1.5	1.0
Number of silent pauses	13.5	5.9	3.0	1.9	6.74	4.5	2.4

The first row refers to the full passage (13 lines); the remaining rows to the three-line sentence. Time measures are reported in seconds. Total reading aloud time goes from the beginning of the first utterance to the last pronunciation (pauses and misreadings included). Total pronunciation time is the sum of the duration of all utterances (pauses excluded). The mean pronunciation time was computed for correctly uttered content words. Total duration of silent pauses is the sum of the durations of periods in which no utterance was made. Means and SDs are reported. T and probability values for statistical comparisons between groups ($p < 0.006$ is considered significant after Bonferroni correction) and ratios between the mean values of the two groups are also reported. All p's < 0.001, except $* = 0.007$.

utterance must be taken as genuine. Furthermore, the difference remained when the computation was restricted to the words that were correctly articulated by all children, indicating that the effect on articulation times did not depend on differences in the actual words uttered. Interestingly, individual variability in utterance duration was very low and not different in the two groups of children. This is partially in keeping with the idea that execution times yield smaller individual differences than cognitive times; furthermore, execution times are assumed as a constant in models of decision processing (e.g., *difference engine model* by Myerson et al., 2003). Notably, a considerable difference was detected between unstandardized (ratio) and standardized effect sizes. Thus, the ratio indicated a very small group difference, whereas the standardized measure of effect size (due to the very low variability) indicated a very large group effect for this parameter ($d = 2.4$).

Finally, dyslexic children spent much more time in silent pauses than control readers. This effect was due to a large difference in the number of pauses and a smaller difference in terms of pause length. However, as shown in **Figure 2**, very long pauses were present only in the dyslexic readers. When total pronunciation time without pauses was considered, the ratio between the two groups was considerably smaller (1.40). Thus, frequent and long pauses represent an important characteristic of reading in dyslexia.

READING PERFORMANCE: ACCURACY AND COMPREHENSION

Table 3 reports the percentages of misreadings for the two groups of children. More than half of the inaccurate utterances in both groups indicated sounding-out behaviors. Notably, dyslexic children engaged in this behavior nearly in 10% of cases. They also made few word substitutions (4.4%) and rare omissions or insertions of words (0.8%); in a few instances, their productions resulted in non-words (0.8%). Controls engaged in a much smaller proportion of sounding-out behaviors and made fewer word substitutions and never omitted or inserted a word; furthermore, they never produced a non-word. Effect sizes (whether unstandardized or standardized) were all very large, particularly in the case of sounding-out behavior (i.e., dyslexic readers engaged in this behavior nearly six times more than control readers).

At the end of the reading task, both groups responded correctly to the open and closed questions: 15 out of 16 typically developing children responded well to the open question and 13 to the closed question. The figures were 14 (out of 16) and 15 in the case of dyslexic children. In silent reading, results were quite similar: 14 control readers responded well to the open question and 10 to the closed question. The figures were 14 (out of 16) and 12 in the case of dyslexic readers.

Comments

Misreadings mostly indicated a halting, but effective (i.e., eventually leading to correct pronunciation), approach to the target words (sounding-out behavior). This occurred much more often in dyslexic than control readers (i.e., almost six times more often). These data confirm the predominance of time-consuming errors recently reported in Italian dyslexic children (Trenta et al., 2013). Surprisingly, this ratio is quite similar to the one originally observed by Fairbanks (1937) in English-speaking children; in that study, poor readers made 5.6 more hesitations than good readers (i.e., 8.87 vs. 1.56%).

Word substitution errors also discriminated between the two groups but were relatively few in absolute terms, confirming previous observations in regular orthographies (Wimmer, 1993; Zoccolotti et al., 1999).

Finally, in agreement with previous data collected in silent reading conditions (De Luca et al., 1999), the slow and inaccurate reading of dyslexic children did not prevent adequate text comprehension.

EYE MOVEMENTS DURING READING

Representative eye movement patterns of children with mild and severe dyslexia are presented in **Figures 3B,C**, respectively; the high number of fixations is evident with respect to performance of a typically developing reader (**Figure 3A**).

Table 4 reports eye movement results for dyslexic and control readers.

The first part of the table reports total viewing time for the whole passage read aloud and that read silently. Both groups of children spent less time scanning the text when reading silently than when reading aloud (dyslexic readers: $t = 2.20$, $p < 0.01$; control readers: $t = 4.41$, $p < 0.001$). In absolute values, the

Table 3 | Group results for misreadings.

	Dyslexic readers		Control readers				
	Mean	***SD***	**Mean**	***SD***	***t***	**ratio**	***d***
Sounding-out behaviors (%)	9.5	4.8	1.6	2.0	5.90	5.9	2.15
Word substitutions (%)	4.4	3.7	1.2	2.3	2.95	3.7	1.04
Word omission or insertion (%)	0.8	1.4	0.0	0.0	–	–	–
Non-word production (%)	0.8	1.4	0.0	0.0	–	–	–
Total errors (%)	15.5	7.7	2.8	3.3	6.09	5.5	2.14

Both the percentage of total errors (last row) and the percentages for each category of misreadings (sounding-out behavior, word substitution, word omission or insertion, and non-word production) are presented. The percentages are calculated with respect to the total number of words in the three-line sentence. Means and SDs are reported. T-test comparisons between groups (p < 0.017 is considered significant after Bonferroni correction) and the ratios between values of the two groups are also reported. All p's at least < 0.01.

difference was greater in dyslexic children (22.3 s) than in control readers (10.5 s); however, the ratio between aloud and silent reading was quite similar in the two groups (dyslexic children = 1.24; control readers = 1.21). Also, the ratio between the two groups for viewing time was similar for reading aloud (1.9) and silent reading (1.8). Standardized effects were very large (over 2) and similar for aloud and silent reading.

The second part of **Table 4** reports eye movement results measured in greater depth for reading aloud the three-line sentence. Total viewing time data are consistent with those of the whole passage. Dyslexic readers showed a significantly higher number of fixations and a higher percentage of regressions and smaller forward saccade amplitude with respect to control readers. No significant difference was detected for fixation duration. The distribution of fixation durations for the two groups of children is presented in **Figure 4**: note that the two groups show a very similar number of short fixations (<100 ms), while the number of longer fixations is higher for dyslexic children and highest in the 175–225 ms time interval.

Ratios between the two groups were close to a factor of 2.0 for number of fixations and percentage of regressions and were lower for fixation duration and saccade amplitude. The *d* values were all above the critical value for a large effect, apart from mean fixation duration.

Comments

Both groups of children had longer viewing times when reading aloud than when reading silently. The group differences were quantitatively more marked in the former case but were proportionally constant across the two conditions, i.e., the children with

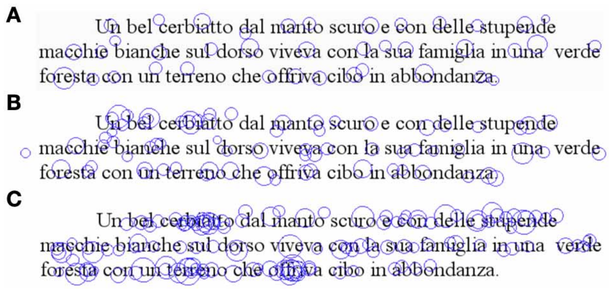

FIGURE 3 | Spatial overlay of the eye movement pattern during reading of the three-line sentence. Fixation points (circles) are indicated for a typically developing reader **(A)**, for a child with mild dyslexia **(B)** and a child with severe dyslexia **(C)**.

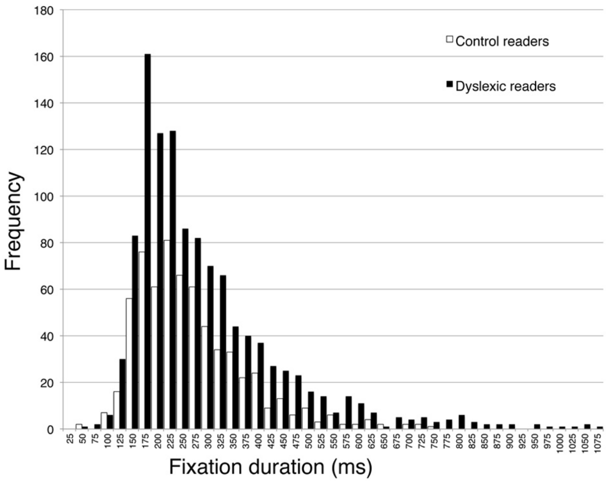

FIGURE 4 | Distribution of frequency for fixation duration, separately for dyslexic and control readers. Intervals on the abscissa by 25 ms each.

Table 4 | Group results for eye movement data.

	Dyslexic readers		Control readers				
	Mean	***SD***	**Mean**	***SD***	***t***	**ratio**	***d***
Total viewing time—aloud	114.1	32.0	60.5	5.5	6.60	1.9	2.3
Total viewing time—silent	91.8	25.1	50.0	7.8	6.34	1.8	2.2
Total viewing time	22.5	7.8	11.5	1.4	5.52	2.0	2.0
Total fixation time	20.7	7.3	10.4	1.2	5.52	2.0	2.0
Number of fixations	72.2	20.9	39.9	5.7	5.95	1.8	2.1
Mean fixation duration	0.29	0.04	0.263	0.026	1.86*	1.1	0.6
Forward saccades mean amplitude	1.68	0.30	2.02	0.24	3.50	1.2	1.2
Percentage of regressions	27.7	5.8	15.1	8.7	4.82	1.8	1.7

*The top part of the table refers to the full passage (13 lines) separately for aloud and silent reading, the bottom to the three-line sentence for reading aloud. Time is reported in seconds, saccade amplitude in degrees. Total viewing time indicates the time starting from the first fixation and ending with the last fixation. Total fixation time was the sum of all discrete fixation durations. Number of fixations includes all fixations (i.e., both first and second pass fixations). Mean fixation duration is the average of all discrete fixations that lasted more than 100 ms. Saccade amplitude is averaged across all rightward saccades, except for small corrective saccades occurring during the return sweeps. Means and SDs are reported. As for between- group comparisons, t-values are reported ($p < 0.007$ is considered significant after Bonferroni correction). The last column reports the ratio between the means of the two groups. The values of children with dyslexia were divided for the values of typically developing readers to obtain the ratios, except in the case of forward saccades amplitude, where the inverted ratio was calculated. In all cases, ratios greater than 1 indicate worse performance of children with dyslexia. All p's < 0.001, except * (n.s.).*

dyslexia were slower than typically developing readers by about a factor of 2 for reading aloud as well as for silent reading. In general, these data confirm well-known observations (e.g., Anderson and Swanson, 1937), but the authors focussed on absolute rather than proportional effects. This indicates a basic problem in analysing reading data. Whenever manipulations of the task (such as, here, reading aloud vs. silent reading) produce an increase in the time necessary to perform the task, group differences also increase; thus, absolute differences in performance change while proportional differences remain stable. Possible interpretations of this pattern of findings will be examined in the Discussion (see below).

As to the pattern of eye movements, children with dyslexia showed a slow and fragmented reading pattern characterized by many fixations, smaller forward saccade amplitude and a higher percentage of regressions with respect to typically developing readers. By contrast, there was a non-significant difference in mean fixation duration between the two groups. Using 200 ms as a standard temporal fixation threshold (Salthouse and Ellis, 1980), **Figure 4** shows that frequency of fixations around this temporal window was particularly high in dyslexic children. Ratios indicate that number of fixations and percentage of regressions were the parameters that distinguished most clearly between the two groups (with values close to the 2-ratio reference), whereas lower ratios emerged for fixation duration and saccade amplitude. Therefore, it seems that the main difference in eye movements between the two groups of children is related to number of movements rather than saccade amplitude or fixation duration.

EYE-VOICE LEAD

Figure 5 illustrates data for a control reader (left) and a child with mild dyslexia (right), respectively. A third example (**Figure 6**) reports data of a particularly severe case of dyslexia.

In the upper plots, the position numbers of the fixated grapheme/uttered phoneme pairs are plotted as a function of time for the three lines of text: filled circles refer to eye fixation data (referred to as "eye") and open triangles to the corresponding utterance data (referred to as "voice"). The ordinate axis reports the spatial position as number of letters. Note that eye data are always above voice data, indicating the leading of the eye.

Two regression lines are drawn separately for the fixation and utterance data; they allow computing the eye-voice lead independent of local variability at specific points of the text. Reading rate is marked by the slopes of the regression lines for both eye and voice data. Slopes are higher for the skilled reader (**Figure 5A**) than the child with mild dyslexia (**Figure 5B**) and the severe case of dyslexia (**Figure 6A**).

In all upper graphs, voice pauses can be detected where consecutive voice data points (triangles) align parallel to the abscissa. This is rare in skilled readers but clearer in dyslexic readers; one very long pause made by the child with severe dyslexia is highlighted in inset of **Figure 6C**. Note the multiple fixations (most of which followed rightward saccades) that characterized the scanning of the word "stupende" ("wonderful") by the child while he silently analyzed the text.

The eye-voice lead measured at each fixation point as the difference between phoneme and grapheme positions in space is

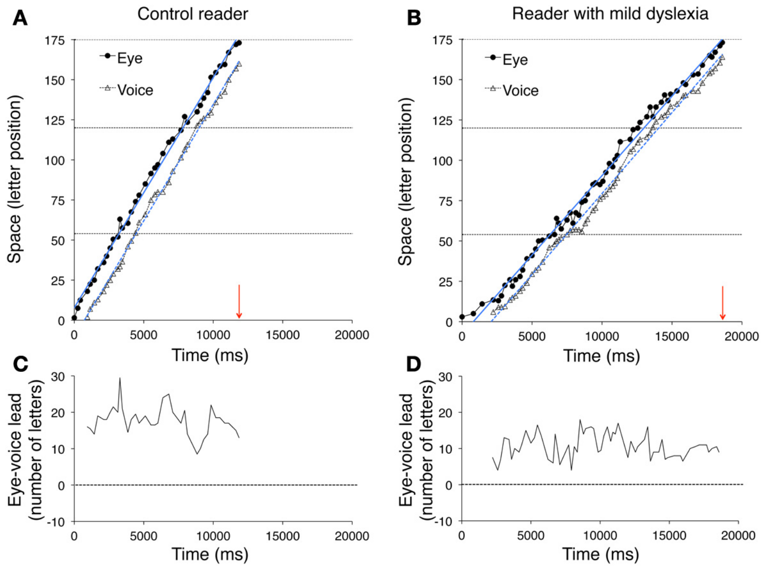

FIGURE 5 | The pairs of fixated grapheme/uttered phoneme positions are plotted as a function of time for a typically developing reader (A) and a child with mild dyslexia (B). The horizontal dashed lines represent the end of the first, second and third line of the sentence, from bottom to top, respectively. The arrows on the abscissa indicate the overall time necessary to read the three lines for each reader. Filled circles and open triangles represent fixations (i.e., eye position data) and utterances (i.e., voice position data), respectively. The ordinate reports the spatial position measured in number of letters (range: 1–173). The vertical space between simultaneous graphemes and phonemes expresses the eye-voice lead as a function of time. Eye and voice positions are fit by regression lines whose slopes indicate the reading rate, separately derived from eye movements and utterances. The intercepts on the ordinate axis (not visible in the figure because the negative part of the axes is not shown) may be used to compute the overall eye-voice lead. In plots **(C,D)**, the eye-voice lead is represented as a function of time as letter difference between pairs of simultaneous grapheme and phoneme positions.

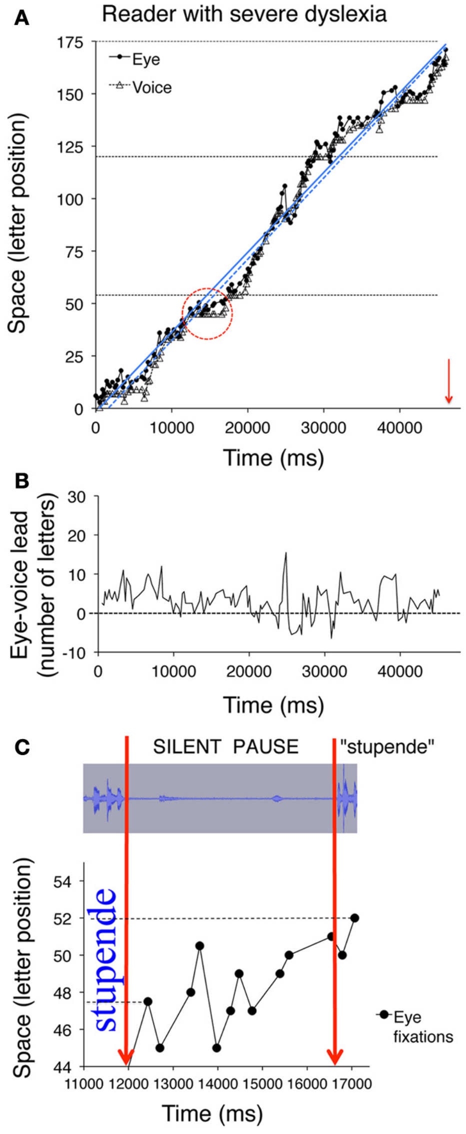

FIGURE 6 | Eye and voice data are presented for a child with severe dyslexia. Similar to **Figures 5A,B**, the pairs of fixated grapheme/uttered phoneme positions are plotted as a function of time in panel **(A)**. Note that the scale on the abscissa of panel **(A)** is twice that of **Figures 5A,B**, therefore the slope indicates a much slower reading rate than that of the child with mild dyslexia represented in **Figure 5B**. In panel **(B)** (as in **Figures 5C,D**) the eye-voice lead is represented as a function of time as letter difference between pairs of simultaneous grapheme and phoneme positions. The **(C)** inset (obtained by zooming on the marked area of plot **A**) represents a long silent pause made by the child, during which eye fixation scanning is characterized by eight rightward saccades and three regressions in the word "stupende" (English translation: "wonderful") before pronouncing it. The top part of the inset represents the spectral image of the audio track corresponding to the time interval represented in the bottom part, which corresponds to the pattern of fixations made on the word. Note that both the second and the fifth fixations (at letter position number 45) follow a regressive eye movement that brings the gaze to the inter-word blank space.

presented as a function of time in the lower graphs of **Figure 5** and the middle graph of **Figure 6**. Note that all values are positive, indicating that pronunciation of a word started after it had been visually inspected. Occasionally, however, in severe cases of dyslexia (including the one presented in **Figure 6**) there are also negative values. This occurred when the reader completed the utterance of a word while his gaze turned backward (second pass reading) to previously fixated portions of text.

Table 5 reports individual and group data for the slopes of eye movements and voice and the eye-voice lead. The eye slope was almost equal to the voice slope in all participants.

The mean eye-voice lead measured by averaging the differences between gaze and voice (as in **Figures 5C,D**, **6B**) was significantly smaller in dyslexic (7.9 letters) than in control (13.8 letters) readers. Computing the eye-voice lead based on the difference between the intercepts of the regression lines produced very similar results: the eye-voice lead was significantly smaller in dyslexic children (8.4 letters) than in control readers (14.0 letters). Note that intra-individual variability (as assessed by the averaged eye-voice position) was similar in the two groups.

Comments

For all individuals in both groups, the values of the slope of the regression lines separately fitting the eye data and the voice data were almost equal (thus, the lines are parallel in all cases). This indicates that, regardless of reading skill, eyes and voice proceeded in synchrony, with a pacing which, despite local variability at specific points of the text (such as in the case of pauses) was kept relatively constant across lines of text. The voice lead showed a ratio between dyslexic and control readers (i.e., 1.7) in line with other key parameters, such as total reading time.

In good readers, the eye and voice regression lines were well spaced (about 14 letters or 5.6° of visual angle on the screen); by contrast, the distance was short in dyslexic children (about 8 letters or 3.2°). Thus, in dyslexic readers, the spatial distance between the uttered phoneme and the fixated grapheme was closer (about half in terms of number of letters or degrees) than in skilled readers. Notably in dyslexic readers the overall processing time of the same three lines (i.e., 22.1 s) was about twice that of control readers (11.4 s). Thus, the time by space product was almost constant in the two groups.

EYE-VOICE LEAD: CORRELATION WITH EYE AND VOICE DATA

Correlations between eye-voice lead and eye and voice parameters as well as performance on the MT reading test are reported in **Table 6** for the whole group of children; after Bonferroni correction, correlations with $p < 0.003$ are considered significant. The eye-voice lead correlated highly with reading time and accuracy in the MT test. As for voice data, the eye-voice lead correlated highly with total reading aloud and total pronunciation time. Correlation with mean word utterance duration was also significant. Furthermore, eye-voice lead correlated highly with the number of pauses and their summed duration but only marginally with the mean duration of a single pause. As for eye data, correlation was high with viewing times, number of fixations, total fixation time and percentage of regressions, but was lower, and non-significant, with mean fixation duration and amplitude of rightward saccades.

Moreover, correlations were calculated considering silent reading of the whole text. The total viewing time for aloud reading was highly correlated with that for silent reading ($r = 0.85$,

Table 5 | Eye-voice lead: mean individual data and group results.

	Reading rate (letters/s)		**Eye-voice lead (number of letters)**		
	Eye slope	**Voice slope**	**Averaged eye-voice position differences**	***SD***	**Intercepts difference**
D1	10.0	10.0	10.7	3.4	11.2
D2	8.2	8.2	9.8	4.7	10.6
D3	9.1	9.1	9.6	4.6	10.2
D4	9.2	9.3	8.9	5.4	9.5
D5	10.3	9.9	11.2	4.7	9.0
D6	11.0	11.0	9.0	4.3	8.8
D7	8.4	8.4	8.0	4.2	8.6
D8	6.2	6.3	7.1	3.0	8.6
D9	10.4	10.4	8.1	5.1	8.3
D10	9.6	9.7	7.5	4.1	8.1
D11	11.6	11.7	6.9	3.6	7.8
D12	9.3	9.3	7.6	4.0	7.6
D13	6.3	6.5	7.1	4.2	9.1
D14	5.7	5.7	7.5	4.1	7.4
D15	6.7	6.7	4.9	2.8	5.1
D16	3.8	3.9	3.0	4.0	4.7
Dyslexic readers mean	**8.5**	**8.5**	**7.9**		**8.4**
SD	**2.2**	**2.1**	**2.1**		**1.7**
C1	17.9	18.4	16.5	4.8	19.3
C2	14.1	14.2	19.1	4.7	19.2
C3	14.4	14.5	17.7	4.0	18.4
C4	18.4	18.4	16.7	4.5	16.8
C5	18.0	17.9	16.9	4.2	16.4
C6	15.8	16.0	13.3	5.5	14.8
C7	18.2	18.1	15.2	5.5	14.4
C8	14.5	14.7	12.2	4.7	14.0
C9	16.5	16.2	15.4	4.5	13.8
C10	17.9	18.2	12.1	4.3	13.6
C11	15.4	15.5	11.3	5.5	12.3
C12	14.3	14.3	12.1	3.8	11.9
C13	13.1	12.8	13.0	3.5	11.6
C14	11.8	11.8	9.7	4.5	9.7
C15	12.6	12.5	9.7	4.1	9.3
C16	12.4	12.4	9.5	2.9	9.3
Control readers mean	**15.3**	**15.4**	**13.8**		**14.0**
SD	**2.3**	**2.3**	**3.1**		**3.3**
t	**8.68**	**8.65**	**6.36**		**6.02**
Control/Dyslexic readers ratio	**1.8**	**1.8**	**1.7**		**1.7**

The first two columns report the reading rate (i.e., the number of letters read per second) as measured by eye and voice slopes, respectively. The mean eye-voice lead, reported in the third column, was obtained by averaging subtraction values of voice position data from eye position data (as in ***Figures 5C,D****,* ***6B****); in the fifth column the lead is reported as the difference between the intercepts of the eye and voice regression lines. T values for statistical comparisons ($p < 0.012$ is considered significant after Bonferroni correction) and ratios between the values of the two groups are also reported. All p's < 0.001.*

Table 6 | Pearson correlations between the eye-voice lead (based on averaged eye-voice position differences) and various parameters of functional reading (MT Reading test), reading aloud, and eye movement data.

		Total sample
MT Reading Test	Reading time	−0.76
	Accuracy	−0.77
Voice data	Total reading aloud time (whole passage)	−0.78
	Total reading aloud time	−0.77
	Total pronunciation time	−0.73
	Mean word utterance duration	−0.61
	Total duration of silent pauses	−0.70
	Mean duration of silent pauses	−0.50*
	Number of silent pauses	−0.83
Eye data	Total viewing time (whole passage)	−0.78
	Total viewing time	−0.76
	Total fixation time	−0.76
	Number of fixations	−0.76
	Mean fixation duration	−0.37°
	Forward saccades mean amplitude	0.40°
	Percentage of regressions	−0.69

*The values of the r coefficient are marked for $p < 0.003$, considered significant after Bonferroni correction. Voice and eye data refer to the first three lines of text unless otherwise specified. All p's < 0.003, except for * $= 0.003$ and ° (n.s.).*

$p < 0.001$). Finally, the eye-voice lead in reading aloud was highly correlated with the total viewing time in silent reading ($r = -0.75, p < 0.001$).

Comments

The pattern of correlation indicated a close relationship between eye-voice lead and several reading parameters associated with speed and accuracy. A large eye-voice lead was closely associated with faster and more accurate reading as well as fewer regressions and nearly absent silent pauses; conversely, a small eye-voice lead was associated with slower and more inaccurate reading, many pauses and regressions. Notably, it is the number of fixations, as well as pauses that carries this relationship, whereas the mean duration of fixations and pauses showed much weaker or non-significant relationships. Finally, utterance duration was also related to the eye-voice lead; this may indicate that, however, small, changes in utterance duration mark individual differences associated with the overall ability to integrate the various sub-components of reading behavior.

Due to limitations in sample sizes, correlations were examined in the whole sample of children. In view of the general differences in performance between the two groups, this might have been expected to inflate the size of the correlations. Examining the pattern of correlation within each of the groups of children yielded quantitatively very similar results; however, it still remains to be verified in larger samples of dyslexic and control readers whether the pattern of correlations found separately holds for these two groups.

DISCUSSION

In this study, we jointly measured several voice and eye movement parameters. Thus, the results allow us to make a comprehensive description of the reading profile of dyslexic and control readers. In reading texts, dyslexic children were slower than control peers. This slowness was expressed in a large number of silent pauses and sounding-out behaviors as well as slightly longer word articulation times. In scanning the text, their eyes were ahead of their voice, but much less so than in skilled readers, indicating that word processing and utterance production were much closer in time than in skilled readers. Errors such as word substitutions and non-word productions were few but considerably more than in control readers, whose accuracy was nearly flawless.

In comparing group differences across different parameters, standard statistical tests were not highly informative. Indeed, as expected, dyslexic children were different from control readers in nearly all parameters. A shortcoming of standard parametric analyses is that they do not easily cope with the over-additivity effect that is present in comparisons across groups, which vary for some general processing ability (Faust et al., 1999); namely, independent of their specific task characteristics, more difficult conditions tend to produce greater group differences. Indeed, previous research on dyslexia has underscored the tendency toward proportional differences between dyslexic and control readers across a large spectrum of conditions and tasks (e.g., Paizi et al., 2011). This has been interpreted as due to a multiplicative interaction between large basic differences in graphemic processing and condition difficulty (De Luca et al., 2010; Zoccolotti et al., 2008). Therefore, the possibility of comparing the reading subcomponents/parameters by using a dimensionless measure such as the ratio, which provides information on the proportional size of the effect, seems more interesting.

RATIOS IN THE COMPARISON OF GROUP PERFORMANCE

Across several eye movement and voice parameters, performance of dyslexic and control readers was expressed by a ratio of about 2. This was the case for total reading aloud time, total viewing time (whether aloud or silent) and number of fixations, as well as reading time on the MT test. Thus, we can consider a factor of 2.0 as a reference value to evaluate the size of group differences in reading parameters. The presence of consistent proportional differences across various different parameters is coherent with the literature, which indicates that dyslexic readers show a consistent deficit across very different stimulus materials (such as short vs. long words or words vs. non-words) when analyzed in ways that allow detecting global components in the data (e.g., Zoccolotti et al., 2008; Van den Broeck and Geudens, 2012).

Thus, within this perspective it is possible to consider unitarily group differences that, if expressed in terms of absolute scores, seem to be different in size. Consider the case of viewing time during silent or aloud reading. In keeping with Anderson and Anderson and Swanson's (1937) early observations, group differences were numerically greater in aloud than in silent reading; but the ratios for these two conditions were very similar, indicating that the increase in group differences can be parsimoniously explained as due to the greater difficulty in the aloud (than the silent) condition, without the need to refer to additional specific effects in the reading aloud condition. Furthermore, the 2-ratio approach allowed us to detect parameters that showed effects which were proportionally smaller or greater than this reference. In particular, pronunciation times showed only a 1.2 ratio or 20% prolongation; by contrast, number of pauses showed a much greater effect with a 4.5 ratio. Thus, the slow reading of dyslexic readers might be characterized as related more to an increase in the frequency of silent pauses and less (although significantly) to slowed articulation times. The data on pronunciation times also underscore the limits of using traditional standardized measures of effect size (such as Cohen's *d*). When *d* values were considered, group differences actually revealed a large group effect because of the very low inter-individual variability in pronunciation times. In this particular case, group differences in inter-individual variability were not merely due to differences in measurement reliability; rather, they reflect the well-known difference between cognitive and motor measures, with the former yielding much greater individual differences than the latter (e.g., Myerson et al., 2003).

However, some limits of the perspective based on ratio comparisons must also be underscored. Compared to models that make explicit predictions to test global components in the data (such as the *rate and amount model*, Faust et al., 1999; the *difference engine model*, Myerson et al., 2003; or the *state trace model*, Van den Broeck and Geudens, 2012), the use of ratios might be considered a rather rough measure for estimating the size of group differences in situations where group differences should be expected to increase multiplicatively due to the interaction of task difficulty and basic group differences in information processing. In particular, by teasing out different components of reaction time measures, models such as the difference engine model (Myerson et al., 2003) allow separating non-decisional from decisional components of the response. A similar outcome is reached with the diffusion model (e.g., Zeguers et al., 2011), which is based on very different assumptions. By contrast, referring to ratios does not allow distinguishing whether (and to what extent) group differences depend on decisional or non-decisional components of the response. At the same time, note that although the quoted models are considerably more powerful by themselves, they are typically used to deal with conditions that have several constraints and are usable only for rather specific predictions.[1] Overall, there

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[1] For example, the rate and amount (Faust et al., 1999) as well as the difference engine (Myerson et al., 2003) model are suited to account for group differences in performance on timed tasks within a relatively short time range (ca. 0–3 s); further, they are based on rather strict linear relationships in the data and cannot deal with closed scale data (such as accuracy measures). Accordingly, although they are convenient for studying RTs, their extension to more natural task conditions, such as reading a meaningful text, is comparatively difficult. A model such as the state trace model (e.g., Van den Broeck and Geudens, 2012) does not have some of these limitations (particularly the requirement of linear predictions or the restriction to closed scales) but still applies best to selected experimental conditions; furthermore, by requiring an overlap in performance between the two groups, it is best suited for experiments with ad-hoc designs, which allow producing such an overlap. Similar considerations apply to the diffusion model. This has the advantage of dealing jointly with accuracy and time data but also requires ad-hoc designs and is difficult to extend to more natural situations, such as those in the present study. Note that in the particular case of reading accuracy may be very high in natural conditions at least in skilled readers, thus violating one requirement of the model.

are clear limitations in examining ratios compared to more formal approaches to modeling group data in cognitive tasks. At the same time, this approach does provide a general profile of the group differences across reading parameters, which would be impossible to tackle using the quoted models.

Some caution should be taken to avoid over-interpreting differences in ratios across conditions/parameters. In particular, we feel this applies to the conditions which greatly deviate from the pattern of variability expected in the case of an over-additivity effect, i.e., appreciably larger SDs for the impaired (dyslexic) group than the control group. For example, the present data indicated very large differences in accuracy between the two groups; namely, dyslexic readers made 5.5 more errors than control readers in reading the text (and, based on data in **Table 1**, a similar 4.8 ratio was present for errors in the case of the MT standard reading test). However, on the basis of these high ratios it seems far-fetched to consider that accuracy is more involved in the dyslexic deficit than speed. Indeed, skilled readers made an extremely small number of errors (or no errors), which is typical in transparent orthographies. We propose that this group difference can be explained in terms of a floor effect, i.e., several children did not actually make any substitution errors or engage in sounding-out behavior. This was clearly more frequent in the control group but spared performance in some parameters was present also in several dyslexic children. Accordingly, the large variability stems from the fact that only some of the children contributed to these measures, while some were flawless. Therefore, values for dyslexic children can easily override control's performance and generate very high ratios that cannot be directly compared with those based on time measures (where all individuals contribute some variability in generating the group average). Overall, it is difficult to directly compare accuracy with measures of eye movements or reading rate. However, in the accuracy measures, ratios may indicate that sounding-out behavior accounted for greater differences than word substitution errors. This finding is in keeping with previous observations in Italian children (Trenta et al., 2013) and indicates the tendency to phonologically recode words when a holistic approach to the target fails. In particular, Trenta et al. (2013) reported that sounding-out behavior was a significant predictor of dyslexic grouping in both text passages and word lists. Within the context of the present study, it is intriguing to observe that the "central" nature of sounding-out (called hesitations) was probably first understood by Fairbanks (1937), although he has not yet been credited for it. Interestingly, he noted that "*substantial positive inter-correlations between errors, hesitations, regressions . . . were obtained, and the coefficients almost always were greater in poor reading . . . Inclusion of hesitations as errors raised the correlation between errors and regressions, suggesting that even though the determination of hesitations is a qualitative step, more central errors were included.*"

EYE-VOICE LEAD

The present study aimed to investigate eye-voice lead. In the 1930s, this phenomenon was the center of attention of a group of studies on eye movements in reading. But when research began to focus on examining silent reading conditions, interest in the eye-voice lead reduced considerably.

The results of the present study confirm a clear difference in eye-voice lead in dyslexic and matched skilled readers. This finding, which was obtained with children who speak a language with regular orthography, is in keeping with the early observations of Buswell (1921) and Fairbanks (1937). At that time, this measure created a considerable technical challenge and investigations could be carried out only in selected laboratories. Contemporary standard eye movement equipment and appropriate audio software have simplified the recording of eye-voice lead; indeed, this measure can now be more easily included in experimental studies on eye movements in dyslexia.

Eye-voice lead is very sensitive to local influences (Fairbanks, 1937; Inhoff et al., 2011) and varies systematically along the line of text and as a function of psycholinguistic parameters of the stimuli, such as high vs. low frequency words. It also decreases when a reader needs to regress to a previous word. At the same time, the present results indicate that the systematic individual tendency can be detected by analyses that cut across these locally determined variations. Some individuals tend to move their eye scanning forward "without waiting" for the execution of voice output, whereas others are so slow in decoding written words that the voice output flow remains nearly simultaneous with decoding. In this sense, eye-voice lead probably represents the idiosyncratic reading style of an individual more than any other parameter. In this view, after years of reading experience the reader develops a systematic tendency to trade-off visual and vocal processing. Within the perspective of the present study, it is interesting that variations in eye-voice lead showed a ratio in the comparison between dyslexic and control readers in line with the reference 2-ratio (i.e., 1.7 for both types of obtained estimates). This indicates that eye-voice lead reflects the proportional differences between the two groups.

Interestingly, the pattern of correlation indicates a widespread relationship between eye-voice lead and critical parameters such as reading aloud time, number (and total duration) of pauses, total viewing time and percentage or regressions. Notably, a significant correlation was present also for utterance duration. Although variations in utterance durations were comparatively small, they contributed quantitatively to participants' setting-up style for integrating voice and eye parameters. Importantly, the eye-voice lead in aloud reading was also highly correlated with total viewing time in silent reading; indeed, the size of this correlation was indistinguishable from those described above. Since eye-voice lead and viewing time in silent reading were evaluated on a different text, this is in line with the idea that eye-voice lead represents a stable individual trait.

The idea that readers develop an idiosyncratic style of reading is in keeping with observations by Carver (1982, 1992). He proposed that through prolonged practice readers develop an optimal reading rate, which is best suited to comprehend the thoughts contained in sentences (which corresponds to ca. 300 words per minute in college students). Carver (1982) referred to this as a "rauding" rate to mark the continuity between reading and listening (or auding). Therefore, in this view the optimal reading rate is that used by an individual to optimize reading comprehension. In keeping with this idea, Carver (1982) observed lower comprehension efficiency when readers were forced to read at a faster or slower rate than their optimal one.

DECOMPOSING DYSLEXICS' READING SLOWNESS

One interesting question is how reading slowness in dyslexic readers expresses in the various sub-components of the reading task.

Dyslexic readers presented a much larger number of silent pauses than control readers. Indeed, in many cases the reading of skilled readers flowed continuously, with effective co-articulation of subsequent sounds regardless of whether or not they were part of the same word. It is clear that during silent pauses eye scanning is occurring through numerous fixations of the as yet unpronounced word, contributing to reading slowness by increasing the number of fixations. Furthermore, dyslexic children engaged much more often in other time- consuming behaviors such as re-sounding the stimulus target before uttering it correctly. Note that some lengthening was also detected in the articulation times of words pronounced without detectable hesitations or silent pauses.

Although the literature on reaction times to single-word presentation is immense, only a handful of studies have examined articulation times to singly presented words (Davies et al., 2013; Martelli et al., 2013). Both of the latter studies found that pronunciation times varied as a function of the lexicality and length of the stimulus (and also frequency in the case of Davies et al., 2013). These findings indicate that coding processes may indeed continue after response onset. Consistent results were also reported by Balota and Abrams (1995). These authors found that when the same arbitrary articulatory response was requested in a lexical decision task the duration of the utterance varied for stimuli of different word frequency. These findings, which indicate a spillover from the decoding phase of processing to the execution phase, point to a continuity between reaction and articulation times and speak against a clear-cut separation between cognitive and motor times. Notably, the effect of variables such as lexicality (Davies et al., 2013; Martelli et al., 2013) or frequency (Davies et al., 2013) on articulation times was very small in the case of singly presented targets; however, it was significant thanks to the extremely small variances present in the case of articulation times. For example, Martelli et al. (2013) found a delay of 6% (or a ratio of 1.06) between the articulation times of dyslexic and control readers across words and non-words. The effect was only 3% (or a ratio of 1.03) in the case of words and 9% (or a ratio of 1.09) in the case of non-words. Compared with these figures, the presence of a 24% delay (or ratio of 1.24) observed here in reading a meaningful text indicates an appreciable increase in the slowing in pronunciation in the case of multiple as opposed to single words (3%), even though the effect (24%) remains quantitatively small. In keeping with the idea that articulation times may indeed capture some of the variance connected with decoding and comprehension processes, it is interesting that they were correlated with a holistic parameter such as the eye-voice lead, that is, individuals with a smaller eye-voice lead showed longer articulation times than individuals with a larger eye-voice lead.

To the best of our knowledge, pronunciation times during reading a text passage have never been reported in dyslexic children; therefore, a comparison with other reading studies is impossible. However, the problem of comparing the predictive value of pauses vs. articulation times has received some attention in research on the RAN paradigm. Several studies have been based on the hypothesis that pause time is responsible for the well-known correlation between RAN tasks and reading speed (Neuhaus et al., 2001; Neuhaus and Swank, 2002; Georgiou et al., 2006). However, when pauses and articulation times were simultaneously recorded, both were highly correlated with reading speed and accuracy, at least for Greek and English observers (Georgiou et al., 2008). Indeed, Georgiou et al. (2008) proposed that the variance which is common to pause and articulation times is most correlated with reading.

Overall, these findings indicate that the slowing of dyslexic readers expresses through a variety of modifications in different parameters even though they occur within very different scales, i.e., producing large, evident differences as in the case of silent pauses (and number of fixations) or small, more difficult to detect, differences as in the case of articulation times.

TOWARD AN INTERPRETATION OF THE DEVELOPMENTAL READING DEFICIT

The present results are in keeping with the general idea that reading requires the efficiency of several cognitive processes, including fast and effective visual scanning, visual selective attention, fast retrieval of lexical entries, short-term memory, and executive functioning. The question is whether it is possible to have a unitary interpretation of the deficit of dyslexic children in dealing with the multiple components of reading or whether separate interpretations are necessary.

Several interpretations have focussed on the efficiency of each of these processes. For example, it has been proposed that dyslexic children show impaired visual scanning (e.g., Vidyasagar and Pammer, 1999). Others studies attributed deficient reading to a reduced visual-attention span (Prado et al., 2007) or to multisensory spatial attention deficits (Facoetti et al., 2010). And other authors have reported that dyslexic readers have low verbal short-term memory (e.g., Wagner and Torgesen, 1987). It has also been reported that developmental dyslexia is associated with poor executive functioning (e.g., Brosnan et al., 2002). This is just a brief list of the complex pattern of impairments which can putatively cause or contribute to causing developmental dyslexia. In this respect, it must be kept in mind that increasing evidence indicates that developmental disorders present a large spectrum of homotopic and heterotopic co-morbidities, which make causal interpretations problematic (for reviews see Pennington, 2006; Pennington and Bishop, 2009). Thus, we think that at least some of the quoted findings represent individual associations, not causal relationships.

An alternative, more parsimonious, interpretation is that dyslexic children have a single predominant deficit; but, given the interwoven nature of the reading task, this deficit spreads to affect all sub-components of reading behavior. Based on previous evidence, the most likely candidate for this nuclear deficit seems to be impaired word decoding. This deficit is very clear in experimentally isolated conditions (e.g., in vocal RTs to singly presented targets). When, in more natural conditions, the child has to couple this impaired decoding with the scanning of visual orthographic stimuli, holding the output phonological traces in memory up to utterance production etc., the impairment increases proportionally simply because of the difficulty in integrating a defective performance into a complex task. In this view, other impairments in relevant processes (such as visual scanning or short-term memory) may co-occur and exacerbate the reading pattern but they do not necessarily account for a severe and selective deficit in dealing with the multiple task requirements intrinsic in the reading task.

Nevertheless, even if one accepts this interpretation, the question is still open concerning the most likely mechanism at the base of the impairment in basic word decoding. Notably, the present results do not offer direct information on this point and only speculative interpretations can be presented. Based on a large body of literature, we feel that the two most likely candidates for this impairment are a deficit in visual or phonological processes. In the first class of mechanisms, one finds deficits in magnocellular functioning (Stein and Walsh, 1997) or visual crowding (Spinelli et al., 2002). For example, in visual crowding word recognition is possible only within an uncrowded window (Pelli et al., 2007), and differences in the size of this window account for the differential efficiency in the reading of dyslexic and control readers (Martelli et al., 2009). In the second class of mechanisms are hypotheses of continuity between acoustic deficits and phonological coding (Goswami et al., 2011). Both children and adults with developmental dyslexia have deficits in perceiving syllable stress in speech (Leong et al., 2011), and dyslexic children have difficulty in discriminating rise times of the speech signal for auditory presented syllables (Goswami et al., 2011). Poor sensitivity to the rhythmic structure of speech produces "*consequences for developing the high-quality phonological representations of spoken words necessary for the acquisition of literacy*" (Goswami, 2011). In particular, according to the temporal sampling framework, children with dyslexia have problems at the temporal integration window, which is typical of the syllable analysis, i.e., around 200 ms, not in the 20–50 ms range, which is typical of phonemes (Goswami, 2011). Although critical experiments on this model have been carried out in the acoustic modality (e.g., Goswami et al., 2011), we thought it would be interesting to compare the predictions of the model concerning the timing of information acquisition in the visual modality. To this aim, the most critical parameter seems to be the duration of individual fixations during reading. In the present study, the peak of fixation duration distribution (time window 175–225 ms) was comparable in young skilled and dyslexic readers; however, the frequency was higher in dyslexic children in the same temporal window than in other time windows, whereas the frequency of very short fixations was nearly comparable. Thus, it seems that there was a visual oversampling at a time window corresponding to the one that is critical for phonological syllable analysis. Based on these preliminary observations, it would be interesting to investigate the temporal sampling framework within the visual modality.

CONCLUSIONS

Overall, the results of the present study allow for a comprehensive description of the reading profile of dyslexic and control readers during the reading of a text, including several eye and voice parameters and accuracy measures. In this context, the eye-voice lead represents a key phenomenon that describes well the complexity of the reading task. Research on the eye-voice lead was at the center of attention in the early part of twentieth century, but then lost impetus; it seems that this measure (which is considerably easier to gather with modern equipment) might provide interesting information about reading efficiency.

Across several parameters, the difference in performance between dyslexic and control readers was expressed by a ratio of about 2. A much lower ratio was measured for pronunciation parameters, indicating that this subcomponent weighed less than other subcomponents in the overall reading time. Referring to proportional differences allows for a more parsimonious interpretation of the reading deficit; in particular, we propose that an impairment in word decoding is the key deficit and that it spreads in such a way as to produce severe difficulty in dealing with the multiple task requirements intrinsic to reading.

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Spatial and temporal attention in developmental dyslexia

Milena Ruffino[1]*, Simone Gori[1,2], Daniela Boccardi[2], Massimo Molteni[1] and Andrea Facoetti[1,2]

[1] Child Psychopathology Unit, Scientific Institute, IRCCS Eugenio Medea, Lecco, Italy
[2] Developmental and Cognitive Neuroscience Lab, Department of General Psychology, University of Padua, Padua, Italy

Edited by:
Alan James Power, University of Cambridge, UK

Reviewed by:
Nicholas Allan Badcock, Macquarie University, Australia
Manon Wyn Jones, Bangor University, UK

***Correspondence:**
Milena Ruffino, Child Psychopathology Unit, Scientific Institute, IRCCS Eugenio Medea, Via Don Luigi Monza, 20, Bosisio Parini, Lecco 23842, Italy
e-mail: milena.ruffino@bp.lnf.it

Although the dominant view posits that developmental dyslexia (DD) arises from a deficit in phonological processing, emerging evidence suggest that DD could result from a more basic cross-modal letter-to-speech sound integration deficit. Letters have to be precisely selected from irrelevant and cluttering letters by rapid orienting of visual attention before the correct letter-to-speech sound integration applies. In the present study the time-course of spatial attention was investigated measuring target detection reaction times (RTs) in a cuing paradigm, while temporal attention was investigated by assessing impaired identification of the first of two sequentially presented masked visual objects. Spatial and temporal attention were slower in dyslexic children with a deficit in pseudoword reading ($N = 14$) compared to chronological age ($N = 43$) and to dyslexics without a deficit in pseudoword reading ($N = 18$), suggesting a direct link between visual attention efficiency and phonological decoding skills. Individual differences in these visual attention mechanisms were specifically related to pseudoword reading accuracy in dyslexics. The role of spatial and temporal attention in the graphemic parsing process might be related to a basic oscillatory "temporal sampling" dysfunction.

Keywords: spatial attention, temporal attention, temporal sampling, phonological decoding, reading disorder

INTRODUCTION

Developmental dyslexia (DD) is a neurodevelopmental disorder identified in about 10% of children which refers to a pattern of learning difficulties characterized by problems with accurate or fluent word recognition, poor decoding and poor spelling abilities, despite normal intelligence, and adequate access to conventional instruction (American Psychiatric Association, 2013).

According to the dual-route model (see Perry et al., 2007 for a review), written words can be processed either by the sub-lexical route, based on grapheme-to-phoneme correspondences, allowing us to read unfamiliar words and pseudowords, or by the lexical route, based on lexical unit correspondences, crucial for reading familiar and irregular words only. Phonological dyslexics show great difficulties in reading unfamiliar words and pseudowords compared to known words, and this is thought to arise from damage to the sub-lexical route. In contrast, surface dyslexia is characterized by impaired reading of irregular words, and this is thought to arise from a damage in the lexical route (e.g., Castles and Coltheart, 1993), potentially linked to an under-stimulation of the visual word recognition system resulting from low experience with literacy. However, in shallow orthographies such as Italian, spelling-sound irregularity is limited to the supra-segmental level (that is, to stress assignment). Thus, in Italian dyslexic children the increased weighting of sub-lexical processing does not permit precise measurement of the efficiency of the lexical-route (see also Gori et al., under revision). It is crucial to note that—regardless of spelling-sound regularity—for a beginning reader all words are at first pseudowords because the lexical-orthographic representations have still to be developed. Accordingly, most longitudinal studies have shown that beginning readers use primarily the sub-lexical route (see Sprenger-Charolles et al., 2003, for a review). Phonological decoding, which is typically measured by examining children's pseudoword reading performance, is one of the most critical skills for successful reading acquisition (e.g., Share, 1995). Interestingly, Ziegler et al. (2003) showed that dyslexics with both regular (German-speaking children) and irregular (English-speaking children) spelling-to-sound correspondences present an extremely slow and serial phonological decoding mechanism. Consequently, an efficient learning to read is crucially mediated by an accurate and fluent use of the sub-lexical route (e.g., Goswami et al., 2000; see Vellutino et al., 2004, for a review).

The underlying neurocognitive mechanisms that lead to the observed reading impairments are still hotly debated (see Vidyasagar and Pammer, 2010; Goswami, 2011). Impaired auditory and speech-sound processing is assumed to characterize the core deficit in DD (e.g., Tallal, 1980; Bradley and Bryant, 1983; Chandrasekaran et al., 2009; Vandermosten et al., 2010; Hornickel et al., 2012; see Wright et al., 2000; Goswami, 2003, 2011; Tallal, 2004; Gabrieli, 2009; Peterson and Pennington, 2012, for reviews). However, the hypothesis that DD arises specifically from a deficit of phonological awareness is still debated because of the circular relationship between reading ability and phonological skills acquisition (e.g., Blau et al., 2009; Dehaene et al., 2010; see Castles and Coltheart, 2004, for a review).

Emerging evidence suggested that DD could arise from a more basic cross-modal letter-to-speech sound integration deficit (e.g., Blau et al., 2009, 2010; Dehaene et al., 2010; see Blomert, 2011, for a recent review). A recent study has also shown that cross-modal binding is impaired at the very early stages of associative learning (Jones et al., 2013). Those authors suggested that dyslexic readers' difficulties in binding may be characterized by inadequate attentional deployment to spatial location. Letters have to be precisely selected from irrelevant and cluttering letters (Bouma, 1970; Bouma and Legein, 1977) by rapid orienting of visual attention (Yeshurun and Rashal, 2010) before the correct letter-to-speech sound integration applies (e.g., Hari and Renvall, 2001; Facoetti et al., 2010a; Vidyasagar and Pammer, 2010; Zorzi et al., 2012). Accordingly, recent studies have shown that visual attention is impaired not only in dyslexic children (e.g., Facoetti et al., 2010a; Lallier et al., 2010), but also in pre-readers at familial risk for DD. These results indicate that visual attention disorders are present before reading acquisition (e.g., Plaza and Cohen, 2007; Facoetti et al., 2010b) and that they are predictors of future reading acquisition skills controlling not only for age, IQ, and phonological processing, but also for non-alphabetic, visual-to-phonological mapping (Franceschini et al., 2012). Moreover, recent findings have shown that attentional training—not involving phonological or orthographic learning—by using action video games can improve reading abilities in children with DD (Franceschini et al., 2013). Visual attention can be oriented in space and time as a spotlight (i.e., attentional shifting; Posner, 1980; Yantis and Jonides, 1984; Jonides and Yantis, 1998). The spotlight of attention (i.e., attentional focus) can also be expanded or contracted in spatial extent to encompass large or small objects, respectively (e.g., Castiello and Umiltà, 1990; LaBerge, 1995; Ronconi et al., 2014). When attention is spatially concentrated in a small portion of the visual field it is called focused attention, while when it is spread across a large part of the visual field it is called distributed attention.

A specific relationship between non-linguistic deficits referred to as attentional shifting has been proposed by Hari and Renvall (2001). According to their multisensory "Sluggish Attentional Shifting" (SAS) framework, when dyslexics deal with rapid stimulus sequences, their automatic attention system cannot disengage fast enough from one item to the next one, yielding slow and degraded processing. SAS is assumed to distort cortical networks, more specifically those which support sub-lexical auditory-phonological (e.g., syllables and/or phonemes) and visual-orthographic (e.g., syllables and/or grapheme) representations. Attentional shifting and rapid processing deficits have been proposed as a more basic problem yielding to the phonological impairment observed in DD (e.g., Breznitz et al., 2013; see Farmer and Klein, 1995; Tallal, 2004, for reviews). This hypothesis is supported by a number of studies showing evidence for temporal processing of brief stimuli within both visual and auditory modalities in dyslexic populations (e.g., Hari and Kiesilä, 1996; Helenius et al., 1999; Hari et al., 1999, 2001; Renvall and Hari, 2002). Consequently, it has been suggested that non-linguistic deficits in dyslexics can be linked to a generally inefficient multi-sensory processing of perceptual stimuli (e.g., perceptual noise exclusion deficit; Sperling et al., 2005; Ziegler et al., 2009; Facoetti et al., 2010a) that impairs the ability to detect relevant stimuli (i.e., signals) when encountering signal interference induced by spatially (Geiger and Lettvin, 1987; Sperling et al., 2005; Geiger et al., 2008; Ruffino et al., 2010) or temporally close noise (Di Lollo et al., 1983; Visser et al., 2004; Montgomery et al., 2005; Facoetti et al., 2008). Notably, attentional deficits in children with DD, with specific language impairment and with autism spectrum disorder (e.g., Ronconi et al., 2012, 2013a) arise from a difficulty in the visual noise exclusion process that specifically requires more time between two stimuli to identify accurately the target as compared to typically developing children (e.g., Ruffino et al., 2010; Dispaldro et al., 2013; Ronconi et al., 2013b).

It is important to highlight that spatial attention is involved in perceptual noise exclusion (e.g., Carrasco et al., 2000, 2002, 2004), by optimizing the perceptual filter so that the signal is further processed and noise is excluded (Dosher and Lu, 2000). The major effect on perceptual functions is that spatial attention appears to enhance the neural representation of stimuli at the attended location (see Reynolds and Chelazzi, 2004, for a review). This signal enhancement manifests itself in a variety of ways, including faster reaction times (RTs) (Posner, 1980), improved sensitivity (lowered thresholds; Carrasco et al., 2002) and reduced interference exerted by flanking stimuli (Carrasco et al., 2000; Facoetti and Molteni, 2000; Boyer and Ro, 2007). An important unresolved issue is whether spatial attention can also speed up the rate at which information is processed. Spatial attention not only improves the spatial resolution, but also accelerates the rate of information processing (Carrasco and McElree, 2001). Moreover, it allows decisions to be based on information at the selected location alone, while disregarding any distracting stimuli (Dosher and Lu, 2000; Braun, 2002). On the basis of these perceptual effects, spatial attention influences all post-sensorial processes, such as the content of short-term memory, perceptual decisions and voluntary responses.

SAS may be a crucial factor behind difficulties in learning to read (Hari and Renvall, 2001; Facoetti et al., 2005) and may be one important factor involved in perceptual difficulties, mostly in tasks requiring an efficient noise exclusion mechanism. Moreover, spatial attention deficits have been repeatedly shown in DD (e.g., Cestnick and Coltheart, 1999; Facoetti et al., 2005, 2006; Bosse et al., 2007; see Hari and Renvall, 2001; Vidyasagar and Pammer, 2010, for reviews) and more specifically in dyslexics with poor pseudoword reading ability (Cestnick and Coltheart, 1999; Buchholz and McKone, 2004; Facoetti et al., 2006, 2008; Roach and Hogben, 2007; Jones et al., 2008; Ruffino et al., 2010). The efficient learning of sub-lexical spelling-sound mappings requires not only accurate representations at the phoneme or syllabic level (Snowling, 2000; Goswami, 2003, respectively), but also an efficient graphemic parsing mechanism (Facoetti et al., 2006, 2010a; Perry et al., 2007; Ruffino et al., 2010; Vidyasagar and Pammer, 2010). These visual attentional processes are hypothesized to be crucially involved in spelling-to-sound conversion mechanisms. Computational models of silent or oral reading assume that graphemic parsing requires the serial engagement of visual attention onto, and its disengagement from, each sub-lexical unit. Among the processes necessary for adequate processing along the sub-lexical route, a graphemic parsing mechanism may be critically linked to the selection mechanism of visual attention (Zorzi, 2005; Perry et al., 2007; Zorzi et al., 2012; Schneps et al., 2013a,b).

Although it has already been demonstrated that visual spatial and temporal attention deficits could contribute independently to the poor reading outcome of dyslexic individuals, as yet, no studies have shown that both spatial and temporal attentional deficits co-occur in the same group of children with DD. These findings indicate that a sluggish shifting of spatial attention is specifically related to a perceptual noise exclusion deficit in DD.

Thus, in the current study, we investigated whether both spatial and temporal attention are impaired in DD with poor phonological decoding, and if they have a specific predictive relationship with phonological decoding skill.

We measured the time-course of visual spatial attention (VSA) and visual temporal attention (VTA) in two groups of dyslexic children, classified on the basis of their phonological decoding (dis)ability, and one group of controls matched for chronological age and IQ.

VSA has been extensively studied by using spatial cuing paradigms (Posner, 1980), in which covert attention (without eye movements) is engaged across two locations of a forthcoming target stimulus by a peripheral, informative spatial cue (i.e., cue location predicts target location) at two variable cue-target intervals (100 and 350 ms). Stimuli presented at the valid location are detected faster than stimuli appearing at the invalid location (the cuing effect reflects facilitation and inhibitory mechanisms of attention; see **Figure 1**). These attentional effects have been interpreted as a consequence of enhanced sensory processing of stimuli appearing at attended locations (Posner, 1980; Carrasco et al., 2000, 2002, 2004), and indicate that VSA has been efficiently engaged. Processing facilitation in VSA is usually found at short cue-target delays only (e.g., 50–150 ms; see Klein, 2000, for a review; see also Facoetti et al., 2010a). Therefore, sluggish VSA might be revealed by a delay in the normal time-course of VSA, i.e., this attentional processing facilitation should be present at longer but not at shorter cue-target delays.

VTA was measured by using an identification task in which the first of two sequentially and centrally presented, forward and backward masked objects had to be recognized (i.e., signal + noise condition; Duncan et al., 1994), and it was compared to the identification of a single displayed object (signal condition). The first visual object (O1) preceded the onset of the second visual object (O2), by a short stimulus-onset-asynchrony (150 ms O1–O2 SOA; Facoetti et al., 2008). However, in order to highlight the O2 perceptual segregation and simplify the task for children, it was displayed in a different color from O1 (see **Figure 2A**). The accuracy to identify O1 allowed us to measure the efficiency of temporal engagement onto a centrally presented visual object.

MATERIALS AND METHODS

PARTICIPANTS

Participants were 32 Italian children with DD recruited at the Child Psychopathology Unit, Scientific Institute, IRCCS Eugenio Medea, Bosisio Parini, Lecco. Chronological age ranged from 8 to 14 (mean = 10, *SD* = 1.85). Reading performance, in terms of accuracy and/or speed, was 2 SDs below the norm on at least one of the age-standardized Italian tests included in the clinical battery (single word and pseudoword reading; Sartori et al., 1995). Dyslexics were selected on the basis of: (i) a full scale IQ greater than 85, as measured by the Wechsler Intelligence Scale for Children-Revised (WISC-R, Wechsler, 1993); (ii) normal or corrected-to-normal vision and hearing; (iii) the absence of neurological and/or psychiatric disorders; and (iv) the absence of attention deficit disorder with or without hyperactivity (because of its high co-morbidity with DD), as evaluated through DSM-IV diagnostic criteria (American Psychiatric Association, 1994). None of the dyslexic children followed an intensive nor a specific training based on well-documented efficacy. Forty-three typically reading children (NR), matched on age and IQ, were also selected. They were aged between 7 and 14 years (mean = 10, *SD* = 2.31) and were recommended as typical readers by their parents, confirmed by individual evaluation in a quiet room in their school. Reading performance was considered typical when accuracy and speed were higher than 1 SD below the norm of the age-standardized Italian tests included in the clinical battery

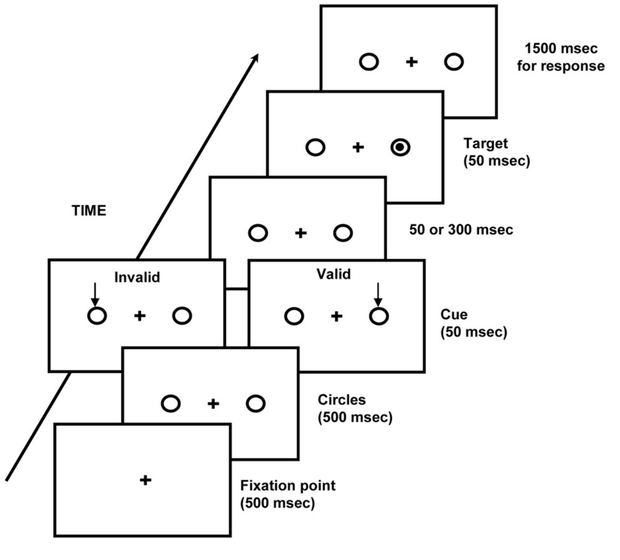

FIGURE 1 | Schematic representation of the display used in the visual spatial attention task.

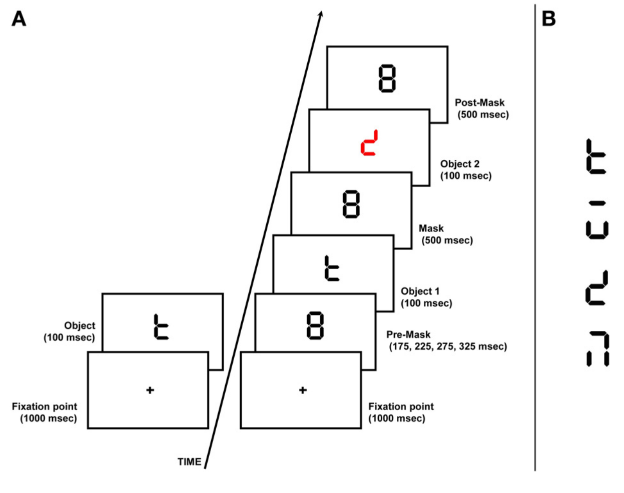

FIGURE 2 | Schematic representation of the display used in the visual temporal attention task (A); Stimuli used in the visual temporal attention task (B).

(single word and pseudoword reading task; Sartori et al., 1995). Informed written consent was obtained from the parents of each child, and the Scientific Institute, IRCCS "Eugenio Medea" ethics committee approved the research protocol. The entire research process was conducted according to the principles expressed in the Declaration of Helsinki. Dyslexic and normally reading children were comparable for chronological age (two-tailed *t*-test, $p = 0.96$) and Performance IQ (Figure Completion subtest, WISC-R, Wechsler, 1993; two-tailed *t*-test, $p = 0.09$), but they were significantly different for both accuracy and speed of word and pseudoword reading (two-tailed *t*-test, all ps < 0.0001).

DYSLEXIA SUB TYPING

In order to study the sub-lexical route efficiency, dyslexic children were divided into two groups on the basis of their accuracy in phonological decoding. In particular, their ability to read aloud was measured on a list of 50 Italian regular and 50 Italian irregular[1] words and 50 pseudowords, in order to assess phonological decoding ability. We measured only accuracy in our study because low accuracy is frequently a problem observed even in Italian dyslexics (e.g., Facoetti et al., 2006, 2010a; Ruffino et al., 2010). Specifically, a dyslexic child was assigned to the DDP− group (where P- indicates severe pseudoword reading) if pseudoword reading accuracy was below the 5th percentile in comparison to normally reading children. We selected this criterion in order to find an inefficient sub-lexical route. All dyslexic children who did not meet the criterion for inclusion in the DDP− group were assigned to the DDP+ group (where P+ indicates less severe pseudoword reading). The percentage mean of pseudoword reading accuracy was 64% ($SD = 10.14$) for the DDP− and 79% ($SD = 14.83$) for the DDP+ group ($p < 0.0001$).

PHONOLOGICAL TASKS

We administered a Pseudowords Phoneme Blending (PPB) task and a Pseudoword Short-Term Memory (PSTM) task to the participants.

In the PPB task, single phonemes were presented, and participants were asked to pronounce the resulting pseudowords from their synthesis (i.e., G-A-S-T-I-B-O = GASTIBO). Performances were calculated on the basis of the number of pseudowords correctly pronounced (the number of words administered were one for familiarization, nine experimental; the number of phonemes included in each pseudoword ranged from 7 to 10). The PSTM task consisted of repeating lists of pseudoword trigrams orally presented (i.e., two items ranging from 2 to 8 trigrams) in the same order as originally presented. Performances were indexed as the number of phonemes correctly repeated in the correct position (the maximum score was 210 phonemes). The number of list items increased with correct responses until participants made an error in both list items administered of the same length. For additional details see Supplementary Material.

VISUAL ATTENTIONAL TASKS

Spatial attention

Testing was carried out in a dimly lit (luminance of 1.5 cd/m^2) and quiet room (approximately 50 dB SPL). Participants were seated in front of a computer screen (background luminance of 0.5 cd/m^2), with their head positioned on a chinrest so that the eye-screen distance was 40 cm. Stimuli were white on a black background and had a luminance of 24 cd/m^2. Each trial started with the onset of the fixation point (1° visual angle; 500 ms). Two circles (2.5°) were displayed peripherally (8° eccentricity, one to the left and one to the right of the fixation point) and 500 ms later the visual cue was shown, consisting of an arrow (1.5° visual angle) displayed for 50 ms above one of the circles. In response trials, a target (dot, 0.5°; duration 50 ms) was presented after one of two cue-target stimulus onset asynchronies (SOA, 100 or 350 ms) in one of the two possible locations. The probability that the cue was presented in the target location was about 80% (i.e., the cue location was predictive of target location). In contrast, in catch trials the target was not presented and participants did not have to respond. Catch trials were intermixed with response trials. Participants were instructed to react as quickly as possible to the onset of the visual targets by pressing the spacebar on the computer keyboard (detection task). Simple RTs and error rates were recorded by the computer. The maximum time allowed to respond was 1500 ms. The inter-trial interval was 1000 ms, after that time the trial started automatically. The experimental session consisted of 128 trials divided into two blocks of 64 trials each, which were distributed as follows: 40 valid trials (20 targets in the right visual field and 20 in the left visual field, 10 for each SOA), 12 invalid trials (6 targets in the right visual field and 6 in the left visual field, 3 for each SOA), and 12 catch trials (6 for each SOA; see **Figure 1**).

Temporal attention

The experimental environment was the same as described above for the spatial attention task. Each trial began with the onset of the fixation mark (0.3° of visual angle; duration 500 ms). Participants were instructed to keep their eyes on the fixation mark throughout the duration of the trial. Two conditions, a "signal alone" (O) and "signal + noise" (O+noise), were randomly presented to each participant. In the O condition a single object (duration 100 ms) was displayed and the aim was to measure the participants' ability to identify the experimental stimuli. In the O+noise condition an 8 digital clock-face font comprising seven line segments was displayed for a variable time exposure (175, 225, 275, or 325 ms) acting as a pre-mask, two successive objects (black O1 and red O2) were presented for 100 ms by removing some of the line segments (see **Figure 2B**, for stimuli used), each followed by a post-mask (8-digital clock-face font) of different duration (i.e., for O1 = 50 and for O2 = 500 ms). This condition was designed to maximize the load of the perceptual noise exclusion mechanism. All visual stimuli displayed had a luminance of 0.6 cd/m^2, the background appeared white and had a luminance of 119 cd/m^2. Participants viewed the sequence of stimuli binocularly and they were instructed to identify, at the end of each trial, O and O1 as accurately as possible, measuring the attentional engagement onto the target (O and O1).

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[1] Italian irregular words are defined as words stressed at third or fourth syllable from last (e.g., rùvido, dòllaro, àbitano, dèlegano).

Before the start of the experimental session, participants viewed each of the four different stimuli one by one with no time constraint (familiarization phase). After each trial all four possible targets were presented on the screen together (two targets per line). Participants responded by pointing on the screen. These responses were registered by the experimenter by pressing the corresponding key on a computer keyboard and no feedback was provided. The experimental session consisted of 40 trials (16 for the O condition and 24 for the O+noise condition; see **Figure 2**).

RESULTS

AGE, IQ, READING, AND PHONOLOGICAL SKILLS: GROUPS ANALYSIS

The differences between the three groups in age, Performance IQ, experimental reading paradigm (the accuracy in regular, irregular word, and pseudoword reading) and phonological tasks (pseudowords and phonemes correctly reported in the PPB and PSTM task, respectively) were analyzed. Results showed no significant differences in age or Performance IQ [$F < 1$ and $F_{(1,\ 72)} = 1.94$, $p > 0.05$, respectively], whereas significant differences were shown in all reading indexes [Regular words: $F_{(1,\ 72)} = 9.77$, $p < 0.0001$; Irregular words: $F_{(1,\ 72)} = 9.86$, $p < 0.0001$; and Pseudowords: $F_{(1,\ 72)} = 54.14$, $p < 0.0001$] and in the two phonological tasks. The NR group demonstrated a significantly higher number of correctly pronounced pseudowords in the PPB task [$F_{(1,\ 72)} = 15.08$, $p < 0.0001$] and correctly pronounced phonemes in the PSTM task [$F_{(1,\ 72)} = 12.31$, $p < 0.0001$] compared to the two groups of dyslexic children. Planned comparisons demonstrated that, although both dyslexic groups were significantly different from NR in all reading and phonological abilities, DDP− and DDP+ were different only in pseudoword reading accuracy (see **Table 1**). Thus, the selective deficit in phonological decoding skills observed in the DDP− group is difficult to explain with respect to differences in their phonological processing, which did not significantly differ between the two dyslexic groups (see **Table 1**).

VISUAL ATTENTIONAL TASKS: GROUPS ANALYSIS

Spatial attention

Mean correct detection RTs were analyzed with a mixed ANOVA that had target condition (valid and invalid) and SOA (100 and 350 ms) as within-subject factors, and group (NR, DDP+, and DDP−) as between-subject factor. The target condition main effect was significant, $F_{(1,\ 72)} = 69.85$, $p < 0.0001$; RTs were slower in the invalid condition (460 ms) than in the valid condition (423 ms; cuing effect = 37 ms). No other main effects were significant. Notably, the critical three-way interaction group × SOA × target condition interaction was significant, $F_{(2,\ 72)} = 3.77$, $p < 0.05$ (see **Figure 3**), indicating a different time-course of attentional orienting in the three groups. At short SOA, both dyslexic groups, in the valid condition, appear to detect targets more slowly in comparison to the normal readers. These results show an apparently reduced facilitation effect in both dyslexic groups. In the invalid condition the DDP− group was similar to the NR group suggesting an unimpaired inhibition mechanism in the DDP− group. The DDP− group was faster than the DDP+ in the invalid cue condition suggesting an abnormal inhibition mechanism in the DDP+ group. All three groups showed a significant cuing effect (i.e., invalid-valid RT differences) at 350 ms SOA [NR = 37 ms ($SD = 39.26$), DDP+ = 32 ms ($SD = 67.74$), and DDP− = 59 ms ($SD = 62.91$); all $ps < 0.005$], demonstrating that they are able to orient spatial attention at the longer time interval. In contrast, only the DDP− group did not show a significant cuing effect at the 100 ms SOA [NR = 37 ms ($SD = 38.15$), DDP+ = 32 ms ($SD = 44.50$), and DDP− = 13 ms ($SD = 44.51$)], demonstrating a sluggish VSA in DDP− in comparison to NR and DDP+ (see **Table 2**). Moreover, the DDP− group showed and amplified cuing effect in comparison to NR and DDP+ grouped together at 350 ms SOA ($p < 0.05$; see **Figure 4**).

In summary, the data highlighted a marked offset of the time-course of visual attention in DDP−, which suggests a sluggish VSA, because differences were selectively present only for the

Table 1 | Mean (M) and standard deviation (SD) of age (months), Performance IQ (Figure Completion, Wechsler, 1993), Reading abilities (Regular, Irregular words, and Pseudowords), pseudowords phoneme blending (number of correct pseudowords), and a pseudoword short-term memory (number of correct phonemes) in normally reading children (NR) and developmental dyslexics without (DDP+) and with (DDP−) phonological decoding deficit.

	NR (*N* = 43)		**DDP+ (*N* = 18)**		**DDP− (*N* = 14)**		**Comparison NR vs. DDP+**			**Comparison NR vs. DDP−**			**Comparison DDP+ vs. DDP−**		
	M	***SD***	***M***	***SD***	***M***	***SD***	$t_{(59)}$	***P***	***C.'s d***	$t_{(55)}$	***P***	***C.'s d***	$t_{(30)}$	***P***	***C.'s d***
Age (months)	122.23	27.87	122.50	20.00	122.57	25.45	−0.04	>0.05	−0.01	−0.04	>0.05	−0.01	0.01	>0.05	−0.003
Performance IQ (ss)	13.65	2.61	12.11	3.41	13.07	2.43	1.17	>0.05	0.51	0.76	>0.05	0.23	−0.93	>0.05	−0.32
Regular words reading (%)	99.67	0.75	90.56	15.76	93.57	3.16	2.45	**<0.05**	0.82	7.17	**<0.001**	2.66	−0.80	>0.05	−0.26
Irregular words reading (%)	98.28	2.64	88.94	16.77	89.00	7.51	2.35	**<0.05**	0.78	4.53	**<0.001**	1.65	−0.01	>0.05	−0.005
Pseudowords reading (%)	93.77	6.02	78.78	14.83	64.43	10.14	4.15	**<0.002**	1.32	10.25	**<0.001**	3.52	−3.24	**<0.001**	1.13
Number of correct pseudowords	5.44	1.76	3.50	2.75	2.18	1.99	2.77	**<0.02**	0.84	5.46	**<0.001**	1.73	−1.57	>0.05	0.55
Number of correct phonemes	56.74	17.20	40.61	15.41	35.86	11.97	3.60	**<0.002**	0.99	5.05	**<0.001**	1.41	−0.98	>0.05	0.34

The effect size (Cohen's d) is reported as C.'s d.

shorter SOA. DDP− group show that for the longer SOA, VSA was abnormally oriented.

Temporal attention

The identification accuracy mean in the O condition was analyzed by a One-Way ANOVA with Group as the between subjects factor. The group main effect was not significant [$F_{(2,\,72)} = 1.34$, $p > 0.05$], highlighting that signal identification in the DDP− group did not differ from either the NR or DDP+ groups. In contrast, the mean O1 accuracy rate[2] ANOVA showed a significant group effect [$F_{(2,\,72)} = 3.23$, $p < 0.05$], demonstrating that signal identification in presence of noise was significantly impaired in DDP− (47%), in comparison to NR (64%) and DDP+ (64%). Planned comparisons showed that the DDP− group, as compared to NR [$t_{(72)} = 5.93$, $p < 0.005$] and DDP+ [$t_{(72)} = 4.84$, $p < 0.05$], was significantly impaired in signal identification when presented with noise (see **Table 3**). In order to test perceptual-noise exclusion mechanism, "intrusion" errors for the identity of the second target were analyzed by a 1-tailed Independent Sample Test, showing a higher incidence of identity intrusions in the DDP− group (mean = 42%, $SD = 11.22$) compared to NR (mean = 36%, $SD = 12.19$), $p < 0.05$ and DDP+ (mean = 34%, $SD = 10.97$), $p < 0.05$ (details are reported in **Table 4**). In summary, our results showed that only dyslexics with phonological decoding deficit present difficulties in their perceptual-noise exclusion mechanism (see **Figure 5**).

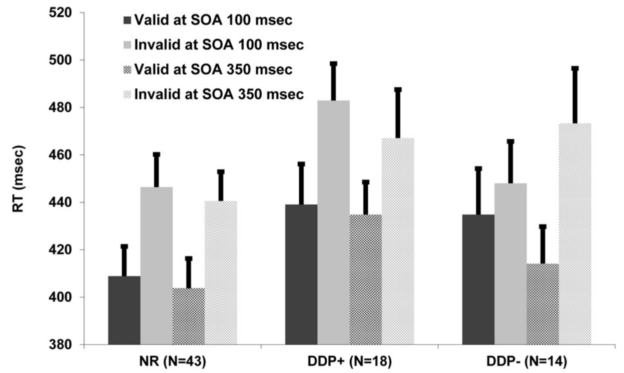

FIGURE 3 | Mean RT and standard error as a function of group (NR, DDP+, and DDP−), target condition (valid vs. invalid cue), and cue-target SOA (100 and 350 ms).

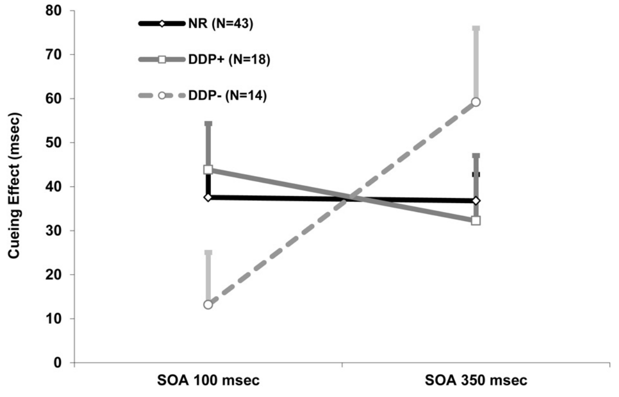

FIGURE 4 | Mean of cuing effect (i.e., invalid – valid RT differences) and standard error as a function of cue-target stimulus onset asynchrony (SOA; 100 and 350 ms) and group (NR, DDP+, and DDP−).

RELATIONSHIP BETWEEN VISUAL ATTENTION AND PHONOLOGICAL DECODING IN DYSLEXIC CHILDREN

Our results demonstrate a specific VSA and VTA deficit in the DDP− group. In order to investigate a possible relationship between individual measures of the cuing effect (VSA) time-course, the perceptual noise exclusion mechanism (VTA), and phonological decoding skill across our entire sample of dyslexic children ($N = 32$), bivariate correlations were computed. Reading abilities were measured on regular words, irregular words and pseudowords. The time-course of VSA was indexed by the difference between the cuing effects at 350 and 100 ms SOA. The efficiency of the VTA corresponded to the identification

Table 3 | Mean (M) and standard deviation (SD) of single object (O) and signal+noise (O+noise).

	NR (*N* = 43)		DDP+ (*N* = 18)		DDP− (*N* = 14)	
	M	***SD***	***M***	***SD***	***M***	***SD***
O	94	8.27	93	10.53	89.50	9.30
O+noise	64	21.89	64	21.66	47	23.83

Table 2 | Mean (M) and standard deviation (SD) of cuing effect at 100 and 350 ms cue-target delay.

	NR (*N* = 43)		DDP+ (*N* = 18)		DDP− (*N* = 14)		Comparison NR vs. DDP+			Comparison NR vs. DDP−			Comparison DDP+ vs. DDP−		
	M	***SD***	***M***	***SD***	***M***	***SD***	$t_{(59)}$	***P***	***C.'s d***	$t_{(55)}$	***P***	***C.'s d***	$t_{(30)}$	***P***	***C.'s d***
100 ms cue-target delay	37.56	38.15	43.83	44.50	12.74	44.51	−0.52	>0.05	−0.01	2.03	**<0.05**	0.88	1.96	**<0.05**	0.96
350 ms cue-target delay	36.79	39.26	32.25	67.74	59.19	62.91	0.27	>0.05	0.08	−1.26	>0.05	−0.43	−1.15	>0.05	−0.41

The Effect Size (Cohen's d) is reported as C.'s d.

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[2] The main effect of the O1 pre-mask variable time exposure (175, 225, 275 or 325 msec) and the interaction effect with the group were not significant ($ps > 0.05$).

Table 4 | Mean (M) and standard deviation (SD) of "intrusion" errors for the identity of the second target in the temporal attention task (O+noise condition).

	NR (*N* = 43)		DDP+ (*N* = 18)		DDP− (*N* = 14)		Comparison NR vs. DDP+					Comparison NR vs. DDP−					Comparison DDP+ vs. DDP				
	M	***SD***	***M***	***SD***	***M***	***SD***	$t_{(59)}$	***P***	***C.'s d***	***l.C.L***	***u.C.L.***	$t_{(55)}$	***P***	***C.'s d***	***l.C.L***	***u.C.L.***	$t_{(30)}$	***P***	***C.'s d***	***l.C.L***	***u.C.L.***
"intrusion" errors (O+noise condition)	35.81	12.19	34.44	10.97	42.14	11.22	0.43	>0.05	0.003	−5.3	8.03	−1.79	**<0.05**	0.051	−13.71	1.05	−1.94	**<0.05**	0.113	−15.76	0.36

The effect size (Cohen's d) is reported as C.'s d. The confidence limits are reported as l.C.L (lower Confidence Limit), u.C.L (upper Confidence Limit).

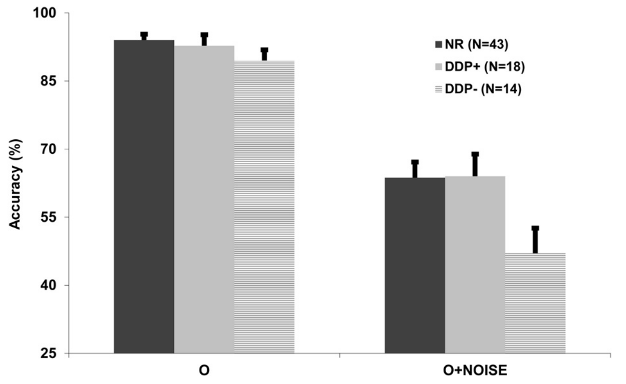

FIGURE 5 | Mean O and standard error as a function of group (NR, DDP+, and DDP−), signal accuracy (O), and signal + noise accuracy (O+noise).

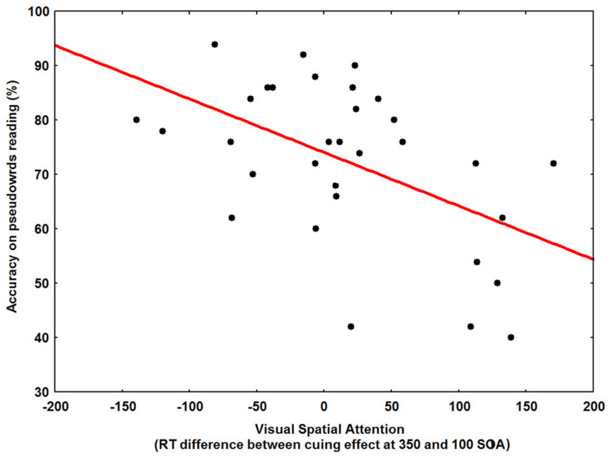

FIGURE 6 | Scatter plot of the relationship between time-course of visual spatial attention (RT difference between cuing effect at 350 and 100 ms SOA) and pseudoword reading accuracy across our entire sample of dyslexic children (*N* = 32).

accuracy mean in the O+noise condition. Phonological abilities were measured by using the efficiency in the PPB and PSTM tasks.

The main results showed that phonological decoding was significantly correlated with both spatial and temporal attention as well as phoneme blending (see **Figures 6**, **7**). In addition, irregular word reading was correlated with both phonological tasks and VSA. Finally, temporal and spatial attention were highly correlated to each other (see **Table 5A**). The same bivariate correlations were computed in our entire sample ($N = 75$), including the NR children, confirming the relationship between visual attention and phonological decoding (see **Table 5B**).

To determine predictive relationships between visual attention and reading (pseudoword and irregular) accuracy, we computed two four-step fixed-entry multiple regression analyses on the individual data of the dyslexic children to control for the effects of age, Performance IQ, attentional mechanisms, and phonological processing.

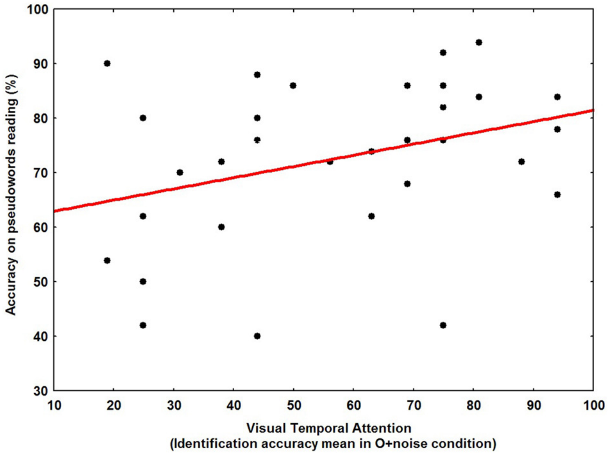

FIGURE 7 | Scatter plot of the relationship between visual temporal attention (identification accuracy mean in O+noise condition) and pseudoword reading accuracy across our entire sample of dyslexic children ($N = 32$).

Descriptive statistics of variables included in the multiple regression analysis are reported in **Table 6**. Because attentional graphemic parsing precedes phonemic blending during the reading process and VSA precedes the perceptual noise exclusion mechanism, we selected the following order of steps. In the first multiple regression analysis the dependent variable was pseudoword reading accuracy and the predictors entered at the four steps were: (i) age and Performance IQ, (ii) VSA, (iii) VTA, and (iv) PPB. Results showed that the time-course of spatial attention accounted for 17% ($p < 0.02$) of unique variance in sub-lexical reading accuracy. Only the PPB entered at the last step accounted for 14% ($p < 0.05$) of unique variance in lexical reading accuracy (see **Table 7**).

In the second multiple regression analysis the dependent variable was irregular word reading accuracy and the predictors entered at the four steps were the same as in the first analysis. Only the PPB entered at the last step accounted for 12% ($p < 0.05$) of unique variance in lexical reading accuracy (see **Table 8**).

DISCUSSION

Our results demonstrate that both spatial and temporal attention were impaired only in dyslexics with a poor phonological decoding (DDP−), confirming the relationship between visual attentional mechanisms and graphemic parsing processes. It is important to note that attentional graphemic parsing precedes the letter-to-speech sound integration.

The attentional cuing effect was present at the shortest cue-target delay (100 ms) in both NR and DDP+, as predicted by automatic capture theories (for a review, see Klein, 2000). In contrast, DDP− children showed a slower visual-spatial attentional orienting, because the cuing effect was not present at the short cue-target delay (distributed attention) whereas it appears at the long cue-target delay, as predicted by the "SAS" theory (Hari and Renvall, 2001; Facoetti et al., 2010a; Lallier et al., 2010; see Facoetti, 2012, for a recent review). We note that in DDP− the cuing effect was stronger than in DDP+ and NR grouped together at the long cue-target delay, suggesting that poor phonological decoders present a more concentrated focus of attention on the cue. These findings could reconcile apparent contradictory results in the literature regarding the different size of the attentional focus in dyslexics. For example, according to some evidence the attentional focus appears more distributed in dyslexics in comparison to normally reading children (e.g., Geiger et al., 1994, 2008; Facoetti et al., 2000). In contrast, other studies have shown more focused attention in dyslexics in comparison to normally reading children (e.g., Bosse et al., 2007). In general, before the cue onset, the attentional focus—controlled by the right frontal eye fields (Ronconi et al., 2014)—is probably distributed across the possible target locations indicated by the two circles. The attentional focus of the poor phonological decoders will be on the cue location for long cue-target delay (cuing effect), whereas their attentional focus will not be there for short cue-target delay (absence of cuing effect), suggesting a sluggish attentional orienting (Facoetti et al., 2010a; see Hari and Renvall, 2001; Facoetti, 2012, for reviews). Once on the cue, the attentional focus appears more focused in comparison to the other two groups. This combination of spatial attention disorders probably impairs the serial letter processing during graphemic parsing.

Moreover, object identification in the object task without noise was not impaired in poor phonological decoders, excluding a possible general visual perception deficit. In contrast, DDP− showed a specific identification deficit in comparison to NR and DDP+ when the object was displayed with noise (i.e., masks and a second object), demonstrating an inefficient perceptual-noise exclusion mechanism. Although the DDP− group showed a larger second object substitution, it would be important for future research to incorporate a baseline measure including O1+mask, but excluding O2, which would better isolate the role of specific O2 interference on O1. This condition could be relevant to even better isolate the pure role of the O2 interference, otherwise it would be difficult to exclude that unknown processing speed differences between the groups may play a role in the results.

According to the phonological hypothesis, it is important to note that poor pseudoword reading accuracy is strongly related to impaired phonological awareness (Frith, 1997; Snowling, 2000; Goswami, 2003, 2011; Vellutino et al., 2004). However, the two samples of dyslexics were not different in general phonological processing (i.e., phoneme blending and short-term memory of pseudowords). Only in DDP− both spatial and temporal attentional tasks were specifically disturbed, consistent with the hypothesis that SAS (Hari and Renvall, 2001) contributes to difficulties in phonological decoding, and it is at least partially independent from phonological skills (Bosse et al., 2007; Facoetti et al., 2010a,b; Franceschini et al., 2012, 2013; Zorzi et al., 2012; see Vidyasagar and Pammer, 2010, for a review).

Our attention indices allowed us to discriminate between dyslexics with poor phonological decoding and dyslexics with unimpaired phonological decoding or normal readers. Our results suggest that visual attention impairments are the core

Table 5 | Bivariate correlations between abilities were measured on Regular and Irregular words and Pseudowords, time-course of visual spatial attention (VSA; RT difference between cuing effect at 350 and 100 ms SOA), time-course of visual temporal attention (VTA; identification accuracy mean in O+noise condition), pseudowords phoneme blending (number of correct pseudowords), and a pseudoword short term memory (number of correct phonemes).

	Regular words reading (%)	Irregular words reading (%)	Pseudowords reading (%)	Number of correct pseudowords	Number of correct phonemes	VTA
(A)						
Irregular words reading (%)	**0.937****	–				
Pseudowords reading (%)	**0.691****	**0.739****	–			
Number of correct pseudowords	0.336	**0.436***	**0.463****	–		
Number of correct phonemes	0.172	**0.350***	0.159	**0.574****	–	
VTA	0.056	0.120	**0.333***	−0.063	0.012	–
VSA	−0.322	**−0.374***	**−0.476****	−0.239	−0.325	**−0.517****
(B)						
Irregular words reading (%)	**0.932****	–				
Pseudowords reading (%)	**0.717****	**0.743****	–			
Number of correct pseudowords	**0.430****	**0.502****	**0.543****	–		
Number of correct phonemes	**0.301****	**0.439****	**0.372****	**0.613****	–	
VTA	0.117	0.206	**0.310****	0.168	0.181	–
VSA	**−0.267****	**−0.347****	**−0.267***	−0.203	**−0.255***	**−0.295***

Bivariate correlations computed in dyslexic children (N = 32) are reported in the ***A****. Bivariate correlations computed in the entire sample (N = 75) are reported in the* ***B****.*

**Correlation is significant at the 0.05 level.*

***Correlation is significant at the 0.01 level.*

Table 6 | Descriptive Statistics of variables included in the multiple regression analysis: age (month), Performance IQ (Figure Completion, Wechsler, 1993), pseudoword reading accuracy, time-course of visual spatial attention (VSA; RT difference between cuing effect at 350 and 100 ms SOA) and time-course of visual temporal attention (VTA; identification accuracy mean in O+noise condition), and pseudowords phoneme blending (PPB; number of correct pseudowords) in dyslexic children (*N* = 32).

	DD (*N* = 32)	
	M	***SD***
Age (months)	122.53	22.16
Performance IQ (ss)	12.53	3.02
Pseudowords reading (%)	72.5	14.70
VSA	13.81	79.50
VTA	56.59	23.84
Number of correct phonemes	38.53	14

deficit in dyslexics characterized by poor (i.e., inaccurate) phonological decoding. This finding was supported by the predictive relationship of reading performance and visual attentional tasks, even after controlling for age and Performance IQ. Attentional graphemic parsing was significantly related to phonological decoding because it represents the first step that precedes not only letter-to-speech sound integration but also phonemic blending (significantly related to pseudoword reading) during the reading process.

It is important to stress that the predictive relationship between attention and reading skills held across the entire sample of dyslexics, independently of any a priori classification or subtyping of the dyslexic children. Thus, regardless of whether children in the DDP+ group constitute a specific subtype in shallow orthographies (Wimmer, 1993) or have partly compensated their reading deficit, rapid and efficient orienting of spatial attention seems to be related to phonological decoding. We suggest that this relationship might be causal because: (i) VSA is impaired in preschoolers at risk of DD (Facoetti et al., 2010b); (ii) it represents a significant predictor of future reading abilities (Franceschini et al., 2012); and (iii) attentional video games training has been proven to increase reading skills (Franceschini et al., 2013).

Our findings are consistent with previous results (e.g., Roach and Hogben, 2007; Facoetti et al., 2010a), and with the predictions of the CDP+ computational model of reading aloud (Perry et al., 2007). Efficient focused attention—indicated by a cuing effect at the short cue-target delay—is necessary for serial letter processing during phonological decoding, limiting the perceptual noise. In the DDP− group the cuing effect was absent at short cue-target delay, increasing the interference produced by perceptual noise during letter processing. Accordingly, several studies suggest that a general disorder in ignoring task-irrelevant information characterizes dyslexia perceptual processing (e.g., Badcock et al., 2008, 2011; Roach and Hogben, 2008). The sluggish attentional orienting index (spatial attention, task 1) is linked to a perceptual noise exclusion mechanism (temporal attention, task 2). The CDP+ assumes that focused attention is specifically involved in the sub-lexical spelling-to-sound mapping process (i.e., the sub-lexical route). Visual attentional tasks

Table 7 | Multiple regression analysis with pseudoword reading accuracy as dependent variable and the following predictors entered at the four steps: (i) age and Performance IQ, (ii) time-course of visual spatial attention (VSA; RT difference between cuing effect at 350 and 100 ms SOA), (iii) time-course of visual temporal attention (VTA; difference between signal accuracy and signal + noise accuracy), and (iv) pseudowords phoneme blending (PPB; number of correct pseudowords) in dyslexic children ($N = 32$).

Predictors	R	R^2	**Change Statistics**				
			R^2 **Change**	F **Change**	*df1*	*df2*	**Sig.** F **Change**
Age and performance IQ	0.283	0.080	0.080	1.265	2	29	>0.05
VSA	0.501	0.251	0.171	6.380	1	28	**<0.02**
VTA	0.506	0.256	0.005	0.187	1	27	>0.05
PPB	0.628	0.394	0.138	5.908	1	26	**<0.05**

Table 8 | Multiple regression analysis with irregular word reading accuracy as the dependent variable and the following predictors entered at the four steps: (i) age and Performance IQ, (ii) time-course of visual spatial attention (VSA; RT difference between cuing effect at 350 and 100 ms SOA), (iii) time-course of visual temporal attention (VTA; difference between signal accuracy and signal + noise accuracy), and (iv) pseudowords phoneme blending (PPB; number of correct pseudowords) in dyslexic children ($N = 32$).

Predictors	R	R^2	**Change Statistics**				
			R^2 **Change**	F **Change**	*df1*	*df2*	**Sig.** F **Change**
Age and performance IQ	0.266	0.071	0.071	1.102	2	29	>0.05
VSA	0.402	0.162	0.072	0.091	1	28	>0.05
VTA	0.438	0.192	0.030	1.006	1	27	>0.05
PPB	0.556	0.309	0.117	4.381	1	26	**<0.05**

accounted almost for 20% of unique variance in phonological decoding, representing an excellent predictor of pseudoword reading. Moreover, irregular word reading accuracy was not significantly predicted by the visual attentional variables, but only by the phonological ones (which accounted for 12%).

Clearly, these results are inconsistent with the hypothesis that DD is an exclusively phonological deficit. The present link between deficits in spatial and temporal attention and impaired phonological decoding is consistent with the hypothesis that visual selection (i.e., the perceptual-noise exclusion mechanism) operates on graphemes as the basic component of the phonological assembly process (Cestnick and Coltheart, 1999; Perry et al., 2007, Gori et al., under revision in the same issue). Both spatial (Geiger and Lettvin, 1987; Sperling et al., 2005; Geiger et al., 2008) and temporal (Di Lollo et al., 1983; Visser et al., 2004; Montgomery et al., 2005; Facoetti et al., 2008) processing windows in which noise interferes with the signal appear to be broader in dyslexics than normally reading children. In this study, we demonstrated that these deficits are specific in poor phonological decoders, and this can be attributed to the perceptual-noise exclusion deficit (Sperling et al., 2005). The link between deficits in VSA and impaired phonological decoding is also consistent with the results of recent studies in dyslexics that used visual search paradigms (e.g., Buchholz and McKone, 2004; Roach and Hogben, 2007; Jones et al., 2008; Facoetti et al., 2010a; Vidyasagar and Pammer, 2010, for a review). Furthermore, our results demonstrate, for the first time, that the relationship between visual attention and phonological decoding skills in dyslexia is explained by a sluggish shifting of spatial attention rather than a general perceptual noise exclusion mechanism. We suggest that inefficient spatial attention could specifically impair the graphemic parsing mechanism in dyslexic children. Although our spatial attention task involves also a temporal component, several studies have shown that the rapid shift of spatial attention modulates the speed of processing and consequentially the temporal aspects of attention (e.g., Carrasco and McElree, 2001; Carrasco et al., 2002, 2004; see Enns and Di Lollo, 2000, for a review). However, further studies are necessary to investigate the specific relationship between spatial and temporal attention. The results of the present study do not speak to the issue of visual vs. auditory and phonological processing deficits in DD. Several authors have argued that the core problem in DD is a deficit in phonological representation (Snowling, 2000; Ramus, 2003). It is important to note that efficient learning of sub-lexical spelling-sound mappings requires not only graphemic parsing but also accurate auditory and speech-sound segmentation mechanisms (see Goswami, 2003, 2011, for reviews). In particular, rise times are crucial events in the speech signal, as they reflect the patterns of amplitude modulation that facilitates the temporal segmentation of the acoustic signal into syllables. Rise time discrimination is impaired in dyslexia in English, French, Hungarian, Spanish, Chinese, and Finnish (Goswami, 2011). Rise time is a significant predictor of phonological awareness. However, efficient acoustic processing and segmentation of the speech signal are likely to require the rapid engagement of auditory attention (Renvall and Hari, 2002; Facoetti et al., 2003, 2005, 2010a). Auditory attention is, indeed, necessary for speech segmentation based on statistical learning (Toro et al., 2005) and for learning phonetic discriminations based on acoustic cues (Gordon et al., 1993; Francis et al., 2008; but see also Seitz et al., 2010). Moreover, auditory spatial attention has been shown to be defective in children with specific language impairment (SLI; Stevens et al., 2006) and reading DD (Asbjørnsen and Bryden, 1998; Renvall and Hari, 2002; Facoetti et al., 2003, 2005, 2010a,b).

Neural coding by brain oscillations is a major focus in neuroscience (e.g., Buzsaki and Draghun, 2004; Schroeder et al., 2008), with important implications for DD research (see Goswami, 2011, for a recent review). The results could be interpreted inside the oscillatory "temporal sampling" framework which is a compelling and robust theoretical framework (Goswami, 2011). Temporal sampling of speech-sound by neuroelectric oscillations that encode incoming information at different frequencies could explain the perceptual and phonological difficulties with syllables, rhymes and phonemes found in individuals with DD. A temporal sampling framework based on oscillations that entrain to sensory input could also have implications for other sensory theories of DD such as the magnocellular-dorsal (M-D) deficit theory (see Stein and Walsh, 1997; Gori and Facoetti, 2013, for a recent review). Thus, we conclude that a temporal sampling disorder of neural oscillations could characterize DD, suggesting innovative training programs not only for treatment but also for the possible prevention of DD at the pre-reading stage.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fnhum.2014.00331/abstract

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Magnocellular-dorsal pathway and sub-lexical route in developmental dyslexia

Simone Gori[1,2] *, Paolo Cecchini[3], Anna Bigoni[3], Massimo Molteni[2] and Andrea Facoetti[1,2]

[1] *Developmental and Cognitive Neuroscience Laboratory, Dipartimento di Psicologia Generale, Università degli Studi di Padova, Padova, Italy*
[2] *Developmental Neuropsychology Unit, Istituto Scientifico "E. Medea" di Bosisio Parini, Lecco, Italy*
[3] *Ophthalmological Unit, Istituto Scientifico "E. Medea" di San Vito al Tagliamento, Pordenone, Italy*

Edited by:
Usha Goswami, University of Cambridge, UK

Reviewed by:
Usha Goswami, University of Cambridge, UK
John Frederick Stein, University of Oxford, UK

****Correspondence:***
Simone Gori, Developmental and Cognitive Neuroscience Laboratory, Dipartimento di Psicologia Generale, Università degli Studi di Padova, Via Venezia, 8 35131 Padova, Italy
e-mail: simone.gori@unipd.it

Although developmental dyslexia (DD) is frequently associate with a phonological deficit, the underlying neurobiological cause remains undetermined. Recently, a new model, called "temporal sampling framework" (TSF), provided an innovative prospect in the DD study. TSF suggests that deficits in syllabic perception at a specific temporal frequencies are the critical basis for the poor reading performance in DD. This approach was presented as a possible neurobiological substrate of the phonological deficit of DD but the TSF can also easily be applied to the visual modality deficits. The deficit in the magnocellular-dorsal (M-D) pathway - often found in individuals with DD - fits well with a temporal oscillatory deficit specifically related to this visual pathway. This study investigated the visual M-D and parvocellular-ventral (P-V) pathways in dyslexic and in chronological age and IQ-matched normally reading children by measuring temporal (frequency doubling illusion) and static stimuli sensitivity, respectively. A specific deficit in M-D temporal oscillation was found. Importantly, the M-D deficit was selectively shown in poor phonological decoders. M-D deficit appears to be frequent because 75% of poor pseudo-word readers were at least 1 SD below the mean of the controls. Finally, a replication study by using a new group of poor phonological decoders and reading level controls suggested a crucial role of M-D deficit in DD. These results showed that a M-D deficit might impair the sub-lexical mechanisms that are critical for reading development. The possible link between these findings and TSF is discussed.

Keywords: transient system, reading acquisition, phonological decoding, reading disability, visual disorder, dorsal stream

INTRODUCTION

Developmental dyslexia (DD) is often defined as a deficit in reading acquisition despite normal intelligence and access to conventional instruction (American Psychiatric Association [APA], 1994). According to the dual-route model (see Perry et al., 2007 for a review), written words can be processed either by the sub-lexical route or by the lexical route. The sub-lexical route is based on grapheme-to-phoneme correspondences and allows reading of unfamiliar words and pseudo-words. The lexical route is based on lexical unit correspondences and is crucial to read familiar and irregular words only. Both acquired and developmental disorders of reading have been generally discussed within this psycholinguistic framework (e.g., Castles and Coltheart, 1993). Phonological dyslexics show great difficulty in reading unfamiliar words and pseudo-words compared to known words, and this is thought to arise from damage to the sub-lexical route. In contrast, surface dyslexia is characterized by impaired reading of irregular words, and this is thought to arise from a damaged lexical route (e.g., Castles and Coltheart, 1993), potentially linked to an under-stimulation of the visual word recognition system resulting from low experience with literacy.

However, in shallow orthographies such as Italian, spelling-sound irregularity is limited to the supra-segmental level (i.e., to stress assignment). Thus, in Italian dyslexic children the increased weight of sub-lexical processing does not permit precise measurement of the efficiency of the lexical-route (see also Ruffino et al., 2014). It is crucial to note that — regardless of spelling-sound regularity – for a beginner reader all words are at first pseudo-words because the lexical-orthographic representations still have to be developed. Accordingly, most longitudinal studies have shown that beginner readers primarily use the sub-lexical route (see Sprenger-Charolles et al., 2003 for a review).

Phonological decoding, which is typically measured by examining children's pseudo-word reading performance, is one of the most critical skills for successful reading acquisition (e.g., Share, 1995). Interestingly, Ziegler et al. (2003) showed that dyslexics with regular (German-speaking children) and irregular (English-speaking children) spelling-to-sound correspondences present an extremely slow and serial phonological decoding mechanism. Thus, in learning to read it is of utmost importance to acquire an accurate and fluent use of the sub-lexical route (e.g., Goswami, 2000; see Vellutino et al., 2004 for a review).

Although there are a number of theories attempting to account for DD, two main views received major support. The first approach proposes that DD arises from deficits in systems that are specifically linguistic in nature. In particular, the phonological deficit theory suggests that DD arises from deficits in phonological processing (e.g., Snowling, 2000). In contrast, many authors suggest that deficits in underlying non-linguistic sensory mechanisms are the real core abnormality in DD (e.g., Stein and Walsh, 1997; Vidyasagar and Pammer, 2010 for visual deficits; Wright et al., 2000; Tallal, 2004 for auditory deficits). This theory, known as the temporal processing hypothesis is the multi-sensory (i.e., visual and auditory) version of the magnocellular dorsal (M-D) theory of DD, suggesting that children with DD have specific deficits in processing rapidly presented or brief sensory stimuli in either the visual or auditory modalities (see Farmer and Klein, 1995; Hari and Renvall, 2001 for reviews). Chiefly, the M-D temporal hypothesis explicitly claims that phonological decoding deficits in dyslexics could arise from impairments in sensory processing of visual and auditory dynamic-stimuli (e.g., Facoetti et al., 2010a,b). The well known M-D theory of DD is often referred specifically to the visual modality, and it is a comprehensive, albeit controversial account (e.g., Amitay et al., 2002; Sperling et al., 2005; Olulade et al., 2013). This theory stems from the observation that some reading disabled children are impaired in the specific visual M-D pathway (see Stein and Walsh, 1997; Boden and Giaschi, 2007; Vidyasagar and Pammer, 2010 for reviews). The M-D pathway originates in the ganglion cells of the retina, passes through the M-layer of the lateral geniculate nucleus (LGN), and finally reaches the occipital and parietal cortices (Maunsell and Newsome, 1987). The M-D stream is considered blind to colors, and responds optimally to contrast differences, low spatial frequencies, and to high temporal frequencies and motion (Livingstone and Hubel, 1987). The M-D stream seems to be impaired in individuals with DD, whereas the other major parallel pathway of the visual system, the parvocellular-ventral (P-V) stream, is intact (see Stein and Walsh, 1997; Boden and Giaschi, 2007; Vidyasagar and Pammer, 2010 for reviews). The P-V pathway is characterized by both lower temporal resolution and superior sensitivity to high spatial frequencies, and it is also sensitive to color changes (Livingstone and Hubel, 1987). Several studies showed the specificity of the M-D pathway deficit in individuals with DD in comparison to P-V processing in the normal range, suggesting the crucial role of the M-D pathway as the dominant visual stream for text reading (e.g., Lovegrove et al., 1986; Chouake et al., 2012). Dyslexics are less sensitive than typically reading controls to luminance patterns and motion displays with high temporal and low spatial frequencies (e.g., Eden et al., 1996), visual features that are primarily associated with the M-D pathway, but they perform normally on tasks primarily associated with the P-V pathway, such as those involving color and form (Merigan and Maunsell, 1993).

Most of the evidence for the visual M-D deficit theory has derived from studies of coherent dot motion perception (see Stein, 2001 for a review), which taps the cortical portion of the M-D pathway.

However, the coherent dot motion deficit is rarely found in all individuals in a dyslexic sample (e.g., Talcott et al., 2013). Children or adult poor readers may be specifically impaired in motion perception only in the presence of high external noise, but not in the presence of low external noise or when the signal is clearly defined (Sperling et al., 2006), weakening the strongest evidence for the more dorsal portion of the M-D pathway deficit in DD. In addition, pure M-D deficits have rarely been documented in dyslexic subjects (e.g., Amitay et al., 2002; Sperling et al., 2005). Disabled readers show impaired performance in non-M-D tasks requiring fine frequency discrimination, and the stimuli used in those tasks were neither modulated in time nor briefly presented (e.g., Amitay et al., 2002). Dyslexic children had difficulties detecting both gratings with high temporal frequency and low spatial frequency (i.e., M-D stimuli) and gratings with low temporal frequency and high spatial frequency (i.e., P-V stimuli) when the grating were embedded in external noise (Sperling et al., 2005). Nevertheless, these results did not falsify the evidence obtained from a large population of studies demonstrating significant and replicable differences between dyslexic and control groups and longitudinal studies in the coherent motion perception task (e.g., Cornelissen et al., 1995; Talcott et al., 2000, 2002, 2013; Boets et al., 2011). In addition, it has been reported that up to 75% of dyslexic individuals show visual temporal processing deficits (Lovegrove et al., 1986). Important literature supports the transient subsystem deficit hypothesis in DD which suggests a dissociation in sensitivity between low spatial, high temporal versus high spatial, low temporal grating stimuli (e.g., Martin and Lovegrove, 1987; Keen and Lovegrove, 2000). These grating stimuli tap into the receptive field characteristics of the M system at a retino-cortical level providing the most relevant support for the lower portion of the M-D theory deficit. Moreover, a post mortem study, in a small sample, showed that in the brain of individuals with DD the M neurons of the LGN were noticeably smaller than those found in normal readers' brains, while the P neurons did not differ (Livingstone et al., 1991).

It should be noted that the M-D pathway terminates mainly in the posterior parietal cortex (Mishkin and Ungerleider, 1982; Merigan and Maunsell, 1993), which is the cortical region controlling selective attention in humans (Facoetti and Molteni, 2000; see Corbetta and Shulman, 2002, 2011 for reviews). Thus, a weakened or abnormal M-D input to the dorsal-stream could result in a spatial and temporal attention deficit in dyslexic children and adults (e.g., Brannan and Williams, 1987; Williams et al., 1987; Valdois et al., 1995; Cestnick and Coltheart, 1999; Hari et al., 1999, 2001; Vidyasagar and Pammer, 1999; Facoetti et al., 2000, 2001, 2005, 2006, 2008, 2010a,b; Iles et al., 2000; Buchholz and McKone, 2004; Bosse et al., 2007; Buchholz and Aimola Davies, 2007; Roach and Hogben, 2007; Ruffino et al., 2010; see Vidyasagar, 1999; Hari and Renvall, 2001; Boden and Giaschi, 2007; Vidyasagar and Pammer, 2010; Gori and Facoetti, 2014 for reviews) and specifically in dyslexics, a more severe poor pseudo-word reading ability in comparison to word reading skills (Buchholz and McKone, 2004; Facoetti et al., 2006, 2010a; Roach and Hogben, 2007; Jones et al., 2008; Ruffino et al., 2010, 2014). Children with autism spectrum disorder have shown attentional zooming-out and dorsal pathway disorders (e.g., Ronconi et al., 2012, 2013a,b, 2014), the visual attentional deficit is now recognized as a core feature of DD (Franceschini et al., 2012, 2013; Zorzi et al., 2012; see Gori and Facoetti, 2014 for a review). The sub-lexical route is crucial for reading pseudo-words or new words during reading acquisition in all alphabetic languages, and it specifically requires serial attentional graphemic parsing (Facoetti et al., 2010a).

Recently, a new model, labeled "temporal sampling framework" (TSF), was proposed by Goswami (2011) providing a new, different and, intriguing prospect in the DD study. TSF integrates the data on the auditory processing deficit with the findings on neural oscillatory mechanisms related to the temporal sampling of speech. In short, the innovative proposal by Goswami (2011) suggests that deficits in syllabic perception at relatively low temporal frequencies (inside of the range of the delta/theta, i.e., <10 Hz) are the critical basis for the reading disability in DD (Power et al., 2013). This hypothesis is supported by the findings that show the role of neuronal oscillations in speech perception (Luo and Poeppel, 2007). Although this approach was presented as a possible neurophysiological substrate of the phonological deficit of DD the TSF it is not only limited to that but also, can easily be applied to all the stages of processing within the visual system (Vidyasagar, 2013). TSF also has the potential to integrate several low level deficits already associated with DD (Vidyasagar, 2013; Pammer, 2014). As suggested by Vidyasagar (2013) the D-stream deficit could also be integrated in the TSF theory because the TSF fits well in describing the attentional feedback within the D-stream. What is expected is a deficit in neural oscillation at higher temporal frequency than in the auditory modality because the M-D visual stream process relatively high temporal frequency (Vidyasagar, 2013).

Assuming that the M-D pathway deficit is the neurobiological basis of visual selective attention disorders in DD, we predict that the M-D deficit should be found mainly in poor phonological decoders. Therefore, the aim of the present study was to investigate the efficiency of the visual M-D pathway inside the TSF approach in dyslexic and typically reading children (age- and reading-matched) using the frequency doubling (FD) illusion. The FD illusion is a visual illusion that was first described by Kelly (1966). Measuring a visual illusion, even if it sounds counterintuitive, can be done in a very accurate way (e.g., Gori et al., 2006, 2008, 2010a, 2011; Yazdanbakhsh and Gori, 2008; Giora and Gori, 2010; Gori and Spillmann, 2010; Ito, 2012). The FD illusion appears to be dependent on the spatial and temporal frequency of a flickering grating. When a grating with a spatial frequency of 0.1–4 c/deg is flickering faster than 15 Hz, the viewer perceives a grating with double the physical spatial frequency. The FD was later explained by Kelly (1981) in terms of the full wave rectification carried out by the visual system. Such rectification is found in M(y)-cells of the primate retina (Benardete et al., 1992) and LGN (Kaplan and Shapley, 1982; Marrocco et al., 1982). It is therefore suggested, that responses from the M(y)-cells underlie perception of the FD illusion (see Maddess et al., 1992 for a detailed discussion regarding the relationship between M(y)-cells and frequency doubling). A previous study (Pammer and Wheatley, 2001) showed that individuals with DD are less sensitive to the FD illusion than normal readers, supporting a low-level deficit in the M-D pathway. Kevan and Pammer (2008) demonstrated that children at risk of DD already show a higher threshold for the FD illusion even at the pre-reading stage. Importantly, the threshold for the FD illusion at the pre-reading stage predicts future reading skills (Kevan and Pammer, 2009). The FD illusion is, therefore, a consolidated M-D index which taps the lower portion of the M-D pathway and can be difficultly described in terms of signal-to-noise exclusion (e.g., Sperling et al., 2005, 2006; Olulade et al., 2013). Interestingly, the FD illusion was never previously tested in children with DD in shallow languages as Italian. More importantly, the FD illusion is a temporal stimulus that fit well with the opportunity to measure the M-D pathway functionality inside the context of the TSF. What is expected, indeed, is that if a neural oscillation deficit is present also in the visual system of children with DD and specifically in their M-D stream (Vidyasagar, 2013), the children with DD will need more contrast to perceive the flickering stimulus at the same oscillation frequency in comparison with the chronological-age control group.

In addition, we studied the efficiency of the P-V pathway in the same children to rule out the alternative explanation that perceptual processing is generally inefficient in dyslexic children (e.g., because of poor perceptual noise exclusion). The task employed was High-Pass Resolution (HPR) perimetry which measures the detection threshold for fixed ring-shaped stimuli of different sizes. HPR perimetry is commonly adopted for selective analysis of the lower portion of the P-V pathway.

A crucial aim of this study was to investigate if a specific subgroup of children with DD, i.e., poor phonological decoders, were affected by the M-D deficit. In the Experiment 1 we selected a poor phonological decoder subgroup and we compared them with the chronological-age control group. In the Experiment 2 we collected a new poor phonological decoder group in order to carry out a replication study. Stringently, we contrast the new group with a reading-level (RL) control group. The RL children (see Goswami, 2003) were never included in previous studies using FD illusion. The inclusion of the RL group is particularly important to address the issue of the causal link between FD illusion perception and poor phonological decoding.

EXPERIMENT 1

METHODS

Participants

Seventeen dyslexic children (mean age 11 years, SD = 2), were selected from a sample of children referred to the Neuropsychiatric Unit of the scientific Hospital "E. Medea" of San Vito al Tagliamento, Pordenone, Italy, because of specific reading disability. These children had been diagnosed as dyslexic based on standard criteria (American Psychiatric Association [APA], 1994). Their performance reading aloud had to be two standard deviations below the norm in one reading subtest or 1 standard deviation below the norm in at least two reading subtests according to the Italian age-standardized tests (Sartori et al., 1995). The ability to read aloud was measured using a clinical standardized Italian test composed of 112 words (separated into four lists; word reading task, Sartori et al., 1995) and phonological decoding ability was measured using three standardized clinical lists of 48 Italian pseudo-words (pseudo-word Reading task, Sartori et al., 1995). Finally, reading fluency and errors in age-standardized prose passages from Italian clinical tests were used to measure ecological-context reading (Sartori et al., 1995).

The children with DD were selected on the basis of:

(1) a full-scale IQ greater than, or equal to, 85, as measured by the Wechsler intelligence scale for children-revised (WISC-R; Wechsler, 1986);

(2) normal or corrected-to-normal vision and hearing;
(3) absence of neurological and/or psychiatric disorders;
(4) absence of specific language impairments (American Psychiatric Association [APA], 1994); and
(5) absence of attention deficit disorders with or without hyperactivity (ADHD and ADD; American Psychiatric Association [APA], 1994). Several recent studies have shown that sustained attention deficits are significant covariates in group studies using dyslexics and controls pointing out the relevance of this exclusion criterion (e.g., Rochelle et al., 2009).

The children with DD were divided into two subgroups (i.e., poor and non-impaired phonological decoders) according to their performance on the pseudo-word reading test (Sartori et al., 1995). Children were considered poor phonological decoders (PPD, $n = 12$ dyslexic children) if their performance, in terms of mean between accuracy and speed of pseudo-word reading, was below two standard deviation from the norm. The remaining children were assigned to the non-impaired phonological decoders subgroup (NPD, $n = 5$ dyslexic children). Note that pseudo-word reading efficiency is the most appropriate measure of phonological decoding skills. A performance well below the normative data implies that the child is a poor phonological decoder (e.g., Facoetti et al., 2006, 2010a; Ruffino et al., 2010, 2014). In dyslexic children with a regular spelling-to-sound correspondence, like Italian, it is practically impossible to apply the classical English sub-typing (i.e., phonological and surface DD; e.g., Castles and Coltheart, 1993; Talcott et al., 2013) because the English language presents an higher number of irregular words. Importantly, the two dyslexic groups did not differ in word reading [$t_{(14)} = 0.68$, $p > 0.05$] nor in text reading [$t_{(14)} = -0.01$, $p > 0.05$] abilities, excluding that our PPDs were simply more severely impaired dyslexic children.

Twenty four chronological, age- and IQ-matched typically reading children (mean age 10 years, SD = 2) were randomly selected from the same primary school. They were of average or above average intelligence on three WISC-R (Wechsler, 1986) sub-tests (i.e., Block Design and Comprehension).

All participants' parents gave informed consent.

Table 1 shows the mean and SD of age, Block Design, Comprehension and text reading tests for the control and dyslexic groups. Controls and dyslexics were comparable to chronological age and IQ. In contrast, controls and dyslexics were significantly different on accuracy and speed of word and text reading. In **Table 2** we showed that PPD and NPD groups differed only for the pseudo-word reading mean (accuracy and speed).

All participants underwent a complete ophthalmological evaluation, consisting of "Early Treatment Diabetic Retinopathy Study" (ETDRS) chart (standardized eye charts and visual acuity test), orthoptic examination, anterior segment slit lamp examination, cycloplegic refraction, and indirect ophthalmoscopy.

Apparatus and stimuli

Frequency doubling perimetry. The FD perimetry relies on the frequency doubling illusion described in the Introduction. The settings resembled the ones adopted, in a previous study, by Pammer and Wheatley (2001). A low spatial frequency grating displayed in counter-phase flicker mode at a high temporal frequency is perceived as if it had twice its actual spatial frequency. The Humphrey Matrix perimeter was the presentation tool used with the program threshold set to 30-2. The threshold is expressed as contrast attenuation in decibels (dB) and it is calculated by a staircase algorithm built into the Humphrey Matrix perimeter tool. Thresholds ranged from 0 to 38 db. The stimulus was presented at 69 locations in the 30 central degrees of the visual field. The background luminance was 100 cd/m^2. The pattern consisted of a sinusoidal grating presented at different contrast levels, arranged in 5° × 5° square stimuli, and a circular macular stimulus of 2.5° radius. The spatial frequency of the bar target was 0.50 cy/deg, the counter-phase flickered at 18 Hz and was presented for 300 ms. The FD provides selective stimulation of the M-retinal ganglion cells and M LGN neurons. Due to the design of the target, no P-cell activity should be stimulated. Visual fields with 20% or less false positive or false negative responses, and 30% or less fixation errors were considered acceptable.

High-pass resolution (ophthimus) perimetry. The Ophthimus system HPR perimetry uses ring-shaped stimuli, consisting of dark borders and a lighter core. Fourteen different sized targets are available (ranged from 1.26 to 17.64 dB). The target contrast was held constant while the size varied in steps of 1.26 dB. The background luminance was 20 cd/m^2. The luminance of the ring borders was 15 cd/m^2 and the luminance of the ring core was 25 cd/m^2. The target was "high-pass spatial frequency filtered". The participants either detected and resolved it, or it was invisible to them. The perimeter assesses resolution thresholds as the smallest stimulus

Table 1 | Mean (M) and standard deviation (SD) of age, Comprehension, Block Design sub-test (WISC-R; Wechsler, 1986), text reading errors and speed in the control and dyslexic groups.

	Controls ($N = 24$)		Dyslexics ($N = 17$)		Comparison	
	M	**SD**	***M***	**SD**	***T*(39)**	***P***
Age (months)	124	21	128	27	−0.46	0.65
Comprehension (standard score)	10.9	2.3	12	2.6	−1.49	0.14
Block design (standard score)	13.8	2.2	12.5	2.9	1.71	0.09
Text reading errors (number) (*Z*-score)	2.1, 0.54	2.5, 0.56	10.7, −1.05	6.7, 1.19	−5.78, −5.66	<0.001, <0.001
Text reading speed (s) (*Z*-score)	33, 0.31	20.7, 0.48	82, −2.58	49.9, 1.5	−4.31, −8.81	<0.001, <0.001

Table 2 | Mean (M) and standard deviation (SD) of Comprehension, Block Design sub-test (WISC-R; Wechsler, 1986), text reading mean (errors and speed), word reading mean (errors and speed), pseudo-word reading mean (errors and speed) in the two dyslexic subgroups: the poor phonological decoders (PPD) and the non-impaired phonological decoders (NPD) groups.

	PPD ($N = 12$)		NPD ($N = 5$)		Comparison	
	M	SD	*M*	SD	*T*(15)	*P*
Comprehension (standard score)	12.5	2.58	11	2.45	1.11	0.28
Block design (standard score)	12.67	2.64	12	2.67	0.42	0.68
Text reading mean (*Z*-score)	−1.66	0.85	−2.15	1.02	−1.02	0.33
Word reading mean (*Z*-score)	−4.03	1.95	−3.33	1.86	0.68	0.51
Pseudoword reading mean (*Z*-score)	−3.26	1.09	−0.92	0.67	4.39	<0.001

size seen in the 50 locations over the central 30° of the visual field. The blindspot is not mapped. The high-pass spatial frequency filter allows for selective analysis of the P-cells of the retina and probably of the LGN. Due to the software characteristics, fixation errors were not tested for the HPR perimetry.

Procedures

All participants performed the FD and the HPR perimetry in random order, beginning with one of the two eyes. On another day, they performed the two visual field tests again, beginning with the other eye, in order to avoid fatigue and any learning effects. The children were verbally instructed on how to perform the two tests and were given the opportunity to practice. Two pauses were given throughout each test, and a 5-min pause was permitted between testing of the first and second eye.

Each child was seated comfortably with their face against the eyepiece. For the FD testing the child was given a description of the display, and instructed to press the response button each time she/he saw a pattern against the homogeneous background. For the HPR task each child had to report whenever they saw a circle in any tested position of the visual field.

RESULTS

FD results

All groups and subgroups were normally distributed as showed by a non-significant Shapiro-Wilk test of normality (all *p*s > .05). The mean FD thresholds (averaged for all positions and the two eyes) for the children with DD ($n = 17$) differed significantly [*t*-test: $t_{(39)} = 2.697$, $p < 0.05$] in comparison to the normal reader age- and IQ-matched controls ($n = 24$), showing that the dyslexic group was less sensitive to the FD illusion at 18 Hz of temporal frequency of (see the **Figure 1** and the plot of the individual data in **Figure 6A**). An univariate ANCOVA (omnibus test) was run in which the independent variable was group (chronological age- and IQ-matched controls, PPDs and NPDs) and the dependent variable was the mean FD threshold, co-varied for the participant's age [$F_{(3,37)} = 11.999$, $p < 0.05$, $\eta^2_p = 0.493$; see **Figure 2** and the plot of the individual data in **Figure 6A**]. A planned comparison (univariate ANCOVA) was then run where the independent variable was group (chronological age- and IQ-matched controls vs. PPDs) and the dependent variable was the mean FD threshold, co-varied for the participants' ages [$F_{(2,33)} = 15.139$, $p < 0.05$, $\eta^2_p = 0.478$]. Finally another planned comparison (univariate ANCOVA), where the independent variable was the group (age- and IQ-matched controls vs. NPDs) and the dependent variable was the mean FD threshold, co-varied for the participants' ages [$F_{(1,26)} = 1.899$, $p > 0.05$, $\eta^2_p = 0.068$]. In summary, only the PPDs were significantly worse than the controls in their mean FD threshold.

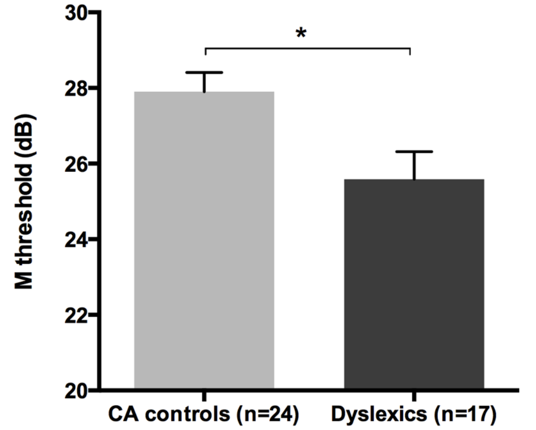

FIGURE 1 | The difference between the chronological age- and IQ-matched (CA) controls and dyslexic children in the FD task measuring the M-D pathway functionality (i.e., M threshold) in the Experiment 1. *$p < 0.05$.

Although PPD children showed a significantly worse performance in the FD task at the group level, in comparison with the controls, it is important to establish how reliable is this abnormal pattern at the individual level. In the PPD group, 75% of them were at least 1 SD below the mean of the controls (**Figure 3**).

Based on these results indicating a specific relationship between M-D pathway and the spelling to sound translation process we concentrate our Experiment 2 only on the PPDs.

HPR results

All groups and subgroups were normally distributed as showed by a non-significant Shapiro-Wilk test of normality (all *p*s > 0.05). The mean HPR thresholds (averaged for all positions and the two

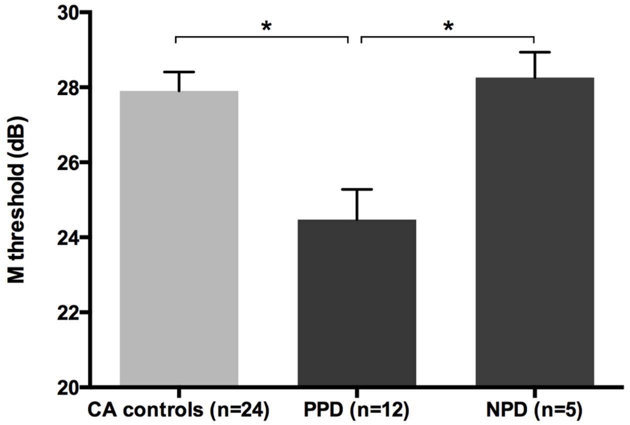

FIGURE 2 | The difference between chronological-age and IQ matched (CA) controls and the subtypes of children with DD (i.e., poor phonological decoders, hereafter PPD and non-impaired phonological decoders, hereafter NPD) in the FD task (Experiment 1). *$p < 0.05$.

eyes) for the children with DD ($n = 17$) and the normal reader age- and IQ-matched controls ($n = 24$) did not differ significantly [t-test: $t_{(39)} = 0.432$, $p > 0.05$] showing that the dyslexic and normal reader groups were similar in their P-V pathway performance (see **Figure 4** and the plot of the individual data in **Figure 6B**).

The relationship between M-D functioning and reading text ability

Partial correlation between M-D pathway functioning (indexed by FD threshold) and the text reading efficiency (the mean between speed and errors z-scores) in the entire sample ($n = 40$; a child with DD score is missing), controlling for chronological age, IQ (block design and similarities), and the P-V functioning, was significant ($r = 0.43$, $p < 0.01$).

To determine the predictive relationships between M-D pathway functioning and ecological reading skills in a more stringent way, we computed a three-step fixed-entry multiple regression analysis in which the dependent variable was text reading efficiency. To control for the effects of chronological age, verbal and nonverbal IQ, and P-V pathway functioning, the predictors entered at the three steps were as follows: (1) age, block design and similarities, (2) P-V pathway threshold, and (3) M-D pathway threshold. The ANOVA regression model was significant [$F_{(5,34)} = 2805$, $p < 0.05$] explaining the 29% of the text reading quote of variance. Only the M-D pathway measure, entered last, accounted for a significant quote of unique variance in text reading efficiency (r^2 change $= 0.16$, $p < 0.01$).

EXPERIMENT 2

METHODS

Participants

In a replication study, we selected a new sample of 8 PPDs (mean age 11 years, SD = 2) and a RL matched control group (10 younger children well matched to the dyslexics for reading ability and IQ, mean age 7 years, SD = 1). In order to find an RL group in Italian speaking language population, it is necessary to search for younger children than would be use in countries with deeper orthographic-to-phonological mapping than in Italian. All the inclusion criteria were the same for the Experiment 1. For details of the new two groups check **Table 3**. All participants' parents gave informed consent.

Apparatus and stimuli

Frequency doubling perimetry. The procedure was exactly the same for the Experiment 1. The HPR perimetry task was not performed because the results were not be discriminative in the Experiment 1.

RESULTS

The mean FD thresholds (averaged for all positions and the two eyes) for PPDs ($n = 8$) and the typical readers IQ- and RL matched

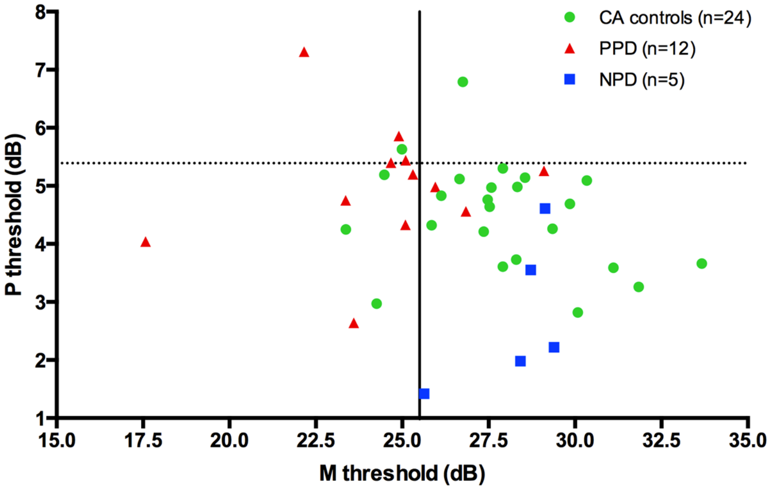

FIGURE 3 | The scatter-plot shows that at individual level the 75% of the PPDs (the red triangle) are at least 1 SD under the mean of the CA controls (the green circle) in the FD task (Experiment 1).

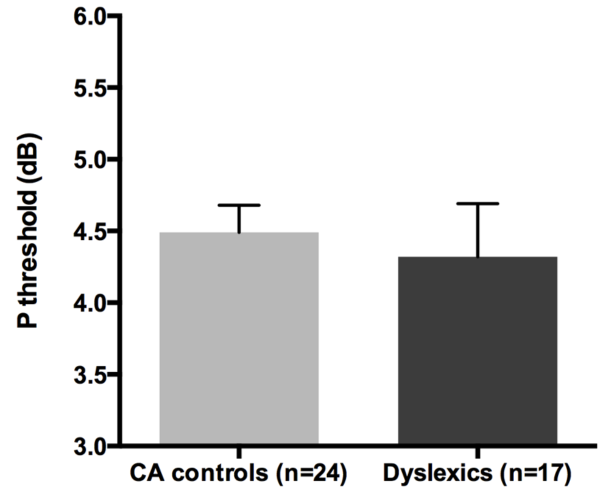

FIGURE 4 | No difference was found between age and IQ matched (CA) controls and the children with DD in the HPR task measuring the P-V pathway functionality (i.e., P threshold) in the Experiment 1.

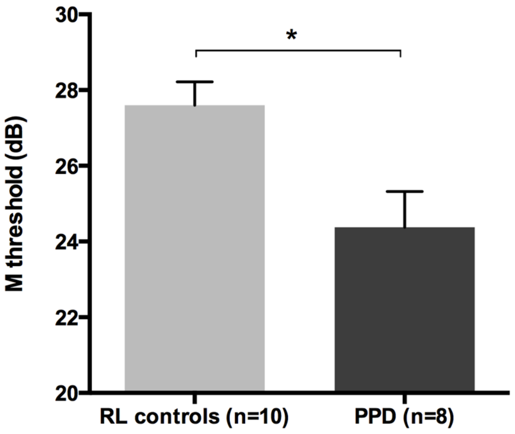

FIGURE 5 | The difference between the new sample of PPDs and reading-level and IQ-matched (RL) controls in the FD task (Experiment 2). $^{*}p < 0.05$.

controls ($n = 10$) differed significantly [t-test: $t_{(16)} = 2.962$, $p < 0.05$] showing that the PPDs were less sensitive to the FD illusion at 18 Hz of temporal frequency even compared to younger normal readers with the same reading abilities (see **Figure 5** and the plot of the individual data in **Figure 6A**). The two control groups (CA and RL) did not differ in the FD illusion threshold ($p > 0.05$). It is not surprising that age did not affect that task because the M-D pathway should be completely operative much before the age of 7 years (e.g., Gori et al., in press).

Although the study was designed as two independent experiments the PPDs of the Experiment 1 and 2 were very similar in age and they did not differ in other relevant variables. Additionally, we found it could be of interest to merge the two groups of PPDs and contrast them with the CA and the RL controls. We applied an univariate ANOVA with the FD threshold as the independent variable and groups (PPD, $n = 25$, CA, $n = 24$ and RL, $n = 10$) as the between subjects factor. The Group main effect was significant [$F_{(2,56)} = 7.33$; $p < 0.05$] and PPD group differed from CA and from RL (Bonferroni multiple comparison with ps < 0.05). This result confirmed the results obtained separately in Experiment 1 and 2.

DISCUSSION

These results provide strong support for an M-D deficit in DD that has its origins at the sub-cortical level of the pathway (i.e., at the LGN). Notably, this deficit characterized only a subgroup of dyslexics, namely the poor phonological decoders.

The absence of differences in the P-V task between groups emphasizes the selectivity of the visual deficit that seems to be associated with the reading disability in the sub-lexical route. It is therefore impossible to attribute the difference found in the FD task to poor testing endurance, as the children with DD performed as well as the typically reading children on the HPR task. The absence of a difference between the two groups in the P-V task cannot be attributed to a ceiling or a floor effect that could mask a poor performance of children with DD as shown by the individual data shown in **Figure 6B**. The graph shows that the data of both groups were not clustered on the limits of the stimulation range. Consequently, even if the M-D and the P-V task could be different in difficulty, both tasks should have enough sensitivity to show a possible difference between groups.

Moreover, the poor phonological decoders with DD not only demonstrated less sensitivity to the FD illusion compared to the typical reading age- and IQ-matched group (supporting Pammer and Wheatley, 2001), but also to a reading-level and IQ-matched

Table 3 | Mean (M) and standard deviation (SD) of chronological age, Block Design sub-test (WISC-R; Wechsler, 1986), phonological decoding speed and errors in the reading-level (RL) controls and poor phonological decoders (PPD) of the Experiment 2.

	RL controls ($N = 10$)		PPD ($N = 8$)		Comparison	
	M	**SD**	***M***	**SD**	***T*(16)**	***P***
Block design (standard score)	11.5	1.43	11	1.51	0.72	0.48
Chronological age (months)	91.5	5.4	126.2	8.67	10.41	0.001
Pseudo-word reading speed (s)	54.5	14.96	64.12	25.38	1.01	0.33
Pseudo-word reading errors (errors)	7.3	2.54	7.9	2.74	0.46	0.65

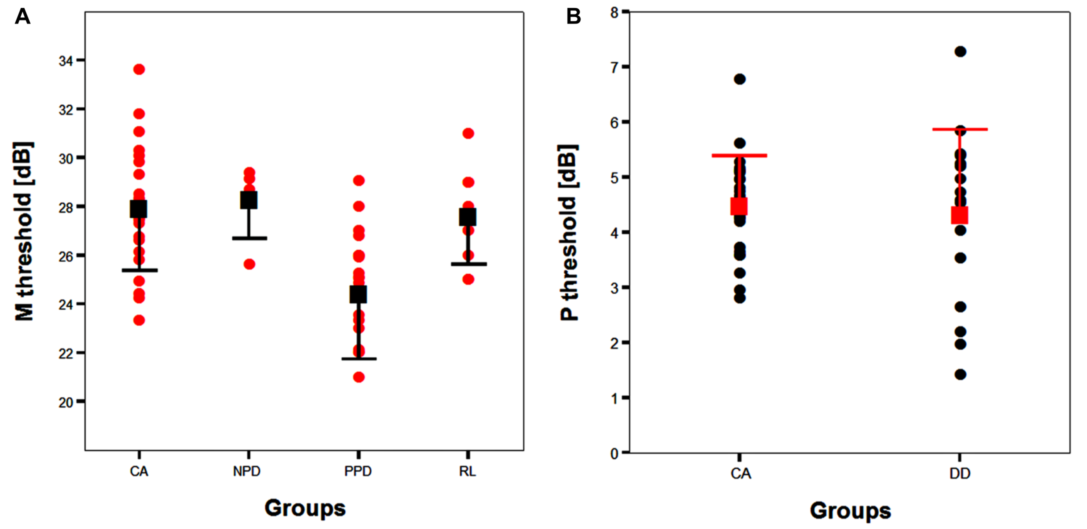

FIGURE 6 | (A) The scatter-plot of the individual data showing the difference between the children without DD (i.e., CA and RL controls) and the subtypes of children with DD (NPD and PPD) in the FD task measuring the M-D pathway functionality (Experiment 1 and 2). The findings did not change running the ANCOVA without the outliers. Error bars represent one standard deviation of the mean. **(B)** The plot of the individual data showing the difference between the children without (i.e., CA controls) and with DD in the HPR task (Experiment 1). Error bars represent one standard deviation of the mean.

control group. The latter result excludes that the M-D deficit is simply an effect of DD.

This is the first study to show that the M-D deficit in children with DD is present also when compared with younger children with the same reading performance, challenging the idea that the M-D deficit is a simple effect of reading deprivation and not a cause, as recently suggested by Olulade et al. (2013). Importantly, the results obtained in the between-group analyses cannot be attributed to the presence of a few (and perhaps peculiar) dyslexic children in the PPD group but were fully confirmed by the analyses at the level of individual cases. M-D deficits were present in a large part of the PPDs (75%) in comparison to CA. Moreover, none of the NPDs presents a deficit in the FD task. Thus, the FD task allowed us to accurately discriminate between poor phonological decoders and CA controls. Regardless of whether children in the NPD group constitute a specific subtype in shallow orthographies (e.g., Wimmer, 1993) or they have partly compensated for their reading deficit, M-D pathway functioning seems to play an important role in phonological decoding. In general, the results from the current study provide evidence for an M-D stream involvement in DD characterized by poor phonological decoding (the most frequent pattern even in Italian individuals with DD; see Facoetti et al., 2006). This conclusion was supported by the finding that individual differences in the M-D pathway were predictive of reading performance even after controlling for age, IQ, and P-V pathway functioning. The FD task allowed us to show an M-D deficit that seems to be in the lower portion of this visual stream (the subcortical component and/or the primary visual cortex) and that cannot be interpreted as a signal-to-noise exclusion deficit (which could be consider the weak point of the coherent dot motion task) or as an effect of reading level (as clearly highlighted by the difference with the RL group). The present results could be interpreted inside the framework of the TSF (Goswami, 2011). A multi-sensory (auditory and visual) temporal sampling disorder of neural oscillations could include the M-D deficit theory as one of several possible causes of DD. While an auditory deficit in low temporal frequency is observed in DD (e.g., Goswami, 2011; Power et al., 2013), in the visual modality a higher temporal frequency processing seems to be damaged in children with DD which is in agreement with the Vidyasagar (2013) prediction of a temporal oscillation deficit in the M-D pathway. However, the spatial and temporal sampling of the orthographic information could also be considered as a proxy deficit for auditory modality deficits in phonological decoding (e.g., Vidyasagar and Pammer, 2010). Moreover, as recently suggested (Vidyasagar, 2013; Pammer, 2014) the TSF seems to be very appropriate to model not only for the auditory deficits of DD but also the visual deficits that appear to be common in DD. Our results, based on temporal illusion sensitivity seem to be the first experimental test of the TSF in visual modality. The fact that children with DD need more contrast to see the FD pattern at 18 hz of temporal frequency, in comparison with both control groups supports the hypothesis of a neural oscillation deficit in the M-D pathway of children with DD. This neural oscillation defict seems to be selective for the M-D stream as theorized by Vidyasagar (2013).

Further research is now necessary to better understand the role of the cortical component of the M-D pathway in DD. In order to pursue that goal a sensitivity task employing specific motion illusions (i.e., Gori and Hamburger, 2006; Gori et al., 2006, 2010b, 2011; Gori and Yazdanbakhsh, 2008; Yazdanbakhsh and Gori, 2008, 2011; Hamburger, 2012) could be devised given the fact that this kind of illusory motion is processed by

V5/MT (Ruzzoli et al., 2011). Potential differences in this task could not be related to a general perceptual noise exclusion deficit.

In conclusion, sensitivity to the FD illusion could provide a simple and powerful diagnostic tool for the evaluation and identification of the risk of DD, even at the pre-reading stage (Kevan and Pammer, 2008, 2009) and the results obtained with the RL group strongly point in the direction of a causal role of a neural oscillatory deficit in the M-D pathway of individuals with DD.

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Executive functions in developmental dyslexia

Pamela Varvara[1,2†], **Cristiana Varuzza**[1†], **Anna C. P. Sorrentino**[1], **Stefano Vicari**[1] and **Deny Menghini**[1]*

[1] Neuroscience Department, Children's Hospital Bambino Gesù, Rome, Italy
[2] Psychology Department, Libera Università Maria Ss. Assunta, Rome, Italy

Edited by:
Alan J. Power, University of Cambridge, UK

Reviewed by:
Laurie E. Cutting, Vanderbilt University, USA
Susan Nittrouer, The Ohio State University, USA

***Correspondence:**
Deny Menghini, Neuroscience Department, Children's Hospital Bambino Gesù, Piazza Sant'Onofrio 4, Rome I-00165, Italy
e-mail: deny.menghini@opbg.net

† These authors have contributed equally to this work.

The present study was aimed at investigating different aspects of Executive Functions (EF) in children with Developmental Dyslexia (DD). A neuropsychological battery tapping verbal fluency, spoonerism, attention, verbal shifting, short-term and working memory was used to assess 60 children with DD and 65 with typical reading (TR) abilities. Compared to their controls, children with DD showed deficits in several EF domains such as verbal categorical and phonological fluency, visual-spatial and auditory attention, spoonerism, verbal and visual short-term memory, and verbal working memory. Moreover, exploring predictive relationships between EF measures and reading, we found that spoonerism abilities better explained word and non-word reading deficits. Although to a lesser extent, auditory and visual-spatial attention also explained the increased percentage of variance related to reading deficit. EF deficits found in DD are interpreted as an expression of a deficient functioning of the Central Executive System and are discussed in the context of the recent temporal sampling theory.

Keywords: developmental disabilities, working memory, central executive system, attention, phonological processing

INTRODUCTION

Executive functions (EF) are a set of high cognitive abilities that control and regulate other functions and behaviors (Welsh et al., 1991). They may involve abilities such as selectively processing information in the environment, retaining task-relevant information in an accessible state over time, making a plan by selecting a sequence of actions to achieve a goal, inhibiting a verbal or motor response, successfully adapting responses to changes in situations and environments, problem solving and self monitoring (Welsh et al., 1991; Pennington and Ozonoff, 1996; Friedman et al., 2006).

EF deficits have been described in several developmental disorders. Attention, working memory, inhibitory control, and flexible thinking deficits have been documented in individuals with attention and hyperactivity disorders (Sergeant et al., 2002; Corbett et al., 2009; Abad-Mas et al., 2011; Pani et al., 2013); inhibition of responses and planning deficits have been described in children with autism (Rinehart et al., 2001; Hill, 2004; Kenworthy et al., 2005; Robinson et al., 2009); planning and memory deficits have been reported in fetal alcohol spectrum disorder (Rasmussen, 2005; Green et al., 2009; Pei et al., 2011). Deficits in a set of EF have also been documented in genetic syndromes associated with intellectual disability (Costanzo et al., 2013). Moreover, a recent meta-analysis (Booth et al., 2010) has highlighted that children with reading disability have difficulties in several EF, including maintaining relevant information in WM, inhibition of irrelevant information, and accessing material in long-term memory.

Indeed, deficits in WM have been mainly investigated using span tasks and are considered one of the major defining characteristics of Developmental Dyslexia (DD) (Willcutt et al., 2005; Swanson et al., 2009, 2010; Bacon et al., 2013). Both verbal and visual-spatial components of WM have been found impaired in children (Poblano et al., 2000; Brosnan et al., 2002; Helland and Asbjørnsen, 2004; Martinussen and Tannock, 2006; Smith-Spark and Fisk, 2007; Menghini et al., 2011) and adults (Smith-Spark et al., 2003; Alloway and Alloway, 2013) with DD. In the light of Baddeley's model, the reduced performance of dyslexics in memory span tasks involving both verbal and visual-spatial modalities may be interpreted as an expression of deficient functioning of the Central Executive component of WM. The tripartite WM model (Baddeley and Hitch, 1974; Baddeley and Logie, 1999; Baddeley, 2000, 2001) includes a Central Executive System (CES) responding to different cognitive functions (e.g., attention, active-inhibition, planning, updating, maintenance and integration of information) and two peripheral slave systems devoted to the temporary storing and rehearsing of information pertaining to a single modality (visual-spatial sketchpad and articulatory loop). The CES coordinates the two slave systems, integrating their storage capacities and making available attentional resources for online processing of incoming information. It has been proposed that the CES may be analogous to the Supervisory Attentional System (SAS) described by Shallice and colleagues (Norman and Shallice, 1986; Shallice and Burgess, 1993). Indeed, the SAS is defined as a conscious control mechanism that resolves interference and allows attentional control over action. CES and SAS not only have a critical control function in WM, but are also involved in several processes requiring higher-order cognitive control. Accordingly, Kane and Engle (2002) define controlled attention as an executive control capability that can effectively maintain stimulus, goal, or context information in an active, easily accessible state in the face of interference, effectively inhibiting goal-irrelevant stimuli or responses (Kane et al., 2001).

Deficits in visual-spatial attention in DD have also been found using tasks which evaluate orientation, focusing, shifting attention and visual search (Helland and Asbjørnsen, 2000; Altemeier et al., 2008; Menghini et al., 2010). Deficits in auditory attention have also been found using discrimination speech tasks (e.g., Casco and Prunetti, 1996; Facoetti et al., 2000; Buchholz and McKone, 2004; Valdois et al., 2004; Dufor et al., 2007). Hari and Renvall (2001) and Laasonen et al. (2012) have suggested that children with DD may suffer from sluggish attentional shifting (i.e., engaging and disengaging attention) as revealed by tasks assessing sustained and divided attention, auditory saltation illusion, auditory pitch streaming sequence, and attentional blink.

Furthermore, studies in DD have documented deficits in categorical fluency, planning, monitoring and revising during problem solving, and response shifting using the flexibility task, the Go/No-go task, and the Tower of London task (e.g., Condor et al., 1995; Mati-Zissi and Zafiropoulou, 2001; Reiter et al., 2005; Swanson et al., 2006). Other authors have demonstrated that DD children were impaired in inhibition tasks such as the Stroop Test (Everatt et al., 1997; Brosnan et al., 2002; Reiter et al., 2005).

With few exceptions (Reiter et al., 2005; Willcutt et al., 2005; Swanson et al., 2006), the above-mentioned studies investigated each EF separately in DD.

However, in the last few years, a multifactorial deficit has been found, supporting the view that neurocognitive developmental dysfunctions in DD may not be limited to the linguistic brain areas, but may also involve a more multifocal cortical system (Pennington, 2006).

Recent functional neuroimaging findings provide evidence of a neurobiological signature for dyslexia, including two crucial posterior systems, one in the occipito-temporal regions and one in the parieto-temporal regions, as well as an anterior system, mainly located in the inferior frontal gyrus (Shaywitz et al., 2008).

The anterior system is implicated in the output of phonological and articulatory aspects, verbal working memory, and the semantic aspects of word reading (Price, 2000; Jobard et al., 2003; Gabrieli, 2009). It was recently suggested (Hoeft et al., 2007; Graves et al., 2010) that in both expert readers and dyslexics the contribution of this system to reading is primarily due to the attention, working memory and executive processes required by reading than to orthographical-phonological mapping *per se*.

The occipito-temporal system has a particularly important role in skilled, fluent reading (i.e., rapid and automatic identification of words) and encompasses the fusiform gyrus (Visual Word Form Area) and the middle and inferior temporal gyrus (Cohen et al., 2000; Vinckier et al., 2007). The parieto-temporal system includes the angular and the supramarginal gyri, and portions of the temporal lobe, such as the left superior temporal gyrus. This system is responsible for cross-modal relation of auditory and visual processes during reading and for the integration of letters and sounds.

To overcome the limitations of previous studies which evaluated each EF separately, the aim of the present study was to simultaneously test different EF domains in the same group of children with DD using numerous tasks.

Children with DD were then compared to children with typical reading (TR) abilities using a neuropsychological battery tapping several EF such as verbal phonological and categorical fluency, spoonerism abilities, visual-spatial and auditory attention, verbal, visual and spatial short-term memory, verbal WM, and visual shifting. To better understand the potential role of EF in reading, the relationships between EF measures and reading abilities were also explored.

MATERIALS AND METHODS

PARTICIPANTS

The study included 60 children and adolescents with DD (27 females) and 65 children with TR abilities (28 females) matched for chronological and mental age.

The chronological age range was 8–17 years for the DD group (mean 11.4 ± 1.9 *SD*) and 8 to 16 years for TR participants (mean 11.9 ± 1.6 *SD*). The diagnosis of DD was made when word or non-word reading speed and/or accuracy level was at least 2 standard deviations below the mean value for the scholar level. In a non-verbal intelligence test Colored Progressive Matrices (CPM; Raven, 1994) all DD participants had a performance level in the normal range (above 10th percentile; mean 29.28 ± 4 *SD*).

The presence of Attention Deficit Hyperactivity Disorder was excluded by means of DSM-IV recommendations (American Psychiatric Association, 2000) and confirmed by behavioral rating scales filled out by parents (Cornoldi et al., 1996; Re and Cornoldi, 2009). Furthermore, none of the children with DD underwent any intensive or specific reading training.

Criteria for inclusion in the TR group were: (i) no reading delay in word and non-word reading tests; (ii) normal or corrected visual acuity; (iii) no Attention Deficit Hyperactivity Disorder diagnosis. In the above-mentioned non-verbal intelligence test (Raven, 1994), TR children had a performance level in the normal range (above 10th percentile; mean 29.83 ± 3.53 *SD*).

DESIGN AND MATERIALS

Children with DD were evaluated in three testing sessions carried out on three different days at the Department of Child and Adolescent Psychiatry of the Bambino Gesù Children's Hospital in Rome. TR children were assessed in three testing sessions in a local primary school. All tasks included a practice phase during which the experimenter explained the task instructions. Tasks were administered in a pseudorandom manner (IQ and reading abilities were always assessed before testing began). All the children's parents gave written informed consent after an extensive description of the research study. The neuropsychological battery involved IQ, reading abilities and EF tasks.

GENERAL INTELLIGENCE

Non-verbal intelligence was measured using the CPM (Raven, 1994), which evaluate the ability to form perceptual relations and to reason by analogy, irrespective of language and formal schooling.

READING ABILITIES

Reading abilities were assessed using two subtests of a battery for the diagnosis of DD (Sartori et al., 1995). Participants were asked to read aloud lists of words and non-words. Speed (in seconds) and errors (each incorrect word or non-word was calculated as one error) were computed for each task. Also, inefficiency reading indexes were considered, calculating the ratio between reading speed and accuracy rate (number of words/non-words correctly read over the total number of words/non-words) for both word and non-word reading tasks.

EF TASKS

Verbal categorical fluency

The Category fluency test (Vicari, 2007) was used to measure verbal fluency. Participants were asked to generate words in a particular category (e.g., animals, clothes, fruits, toys). Deviations from the test rules, including repetitions (perseveration errors) and words not identifiable as an example of the category, were considered errors. All words generated by the participants were recorded by the examiner, and the number of valid responses produced during the time limit (60 s) was calculated (excluding repetitions and errors). The score is calculated as the sum of the number of words generated for each category and the total number of responses.

Verbal phonological fluency

The Phonological Fluency Test (Marotta et al., 2008) was used to evaluate the ability to recall several items using a phonological input. In this task, the child was asked to verbalize as many words as possible beginning with a given phoneme (F, A, and S) within 60 s for each of the three trials. The global score is the sum of the correct responses for the three trials.

Spoonerism

The Spoonerism Task (Marotta et al., 2008) was used to evaluate phonological awareness. The examiner pronounced two words aloud and the participant had to swap the initial phonemes to form two new real words. The child was asked to transpose the beginning sounds of the two words as quickly as possible (time limit to complete a single trial: 60 s; number of trials: 15). The score is the number of correct answers (maximum score: 30) and the time taken to complete the entire test (15 trials).

Visual-spatial attention

Selective visual-spatial attention was evaluated using the Map Mission. In this subtest of the Test of Everyday Attention for Children (Manly et al., 2001), a color-printed A3-laminated city map was presented. Eighty targets representing restaurants (i.e., small knife and fork symbols) were randomly distributed across the map. Distracting symbols of the same size were also present. Participants used a pen to circle as many targets as possible in 60 s. The performance score is the number of target symbols correctly marked by the participants (maximum score: 80).

Auditory attention

Sustained auditory attention was investigated using the Code Transmission task. In this task, which was also a subtest of the Test of Everyday Attention for Children (Manly et al., 2001), participants were asked to monitor a stream of monotonous digits (presented at a rate of one every 2 s) for the occurrence of a particular target sequence (e.g., 5, 5) and then to report the digit that occurred immediately before the target sequence. After a practice sequence to ensure comprehension, 40 targets were presented. The number of targets correctly detected is recorded as the measure of performance accuracy (maximum score: 40).

Verbal short term and working memory

To assess verbal short term memory and WM a verbal span task from an extensive memory battery was used (Vicari, 2007). The task consists of a list of eight, two-syllable low frequency words. In the first block, the examiner read aloud two words at a rate of one item per second. The participants were required to repeat the two words in the same order. Then, four additional strings of two words were presented. If the child was successful in at least three of the five sequences, a sequence one word longer was presented. If the child failed (less than three correct answers in a block), the task was discontinued. The same procedure was used for sequences of increasing length (up to a maximum of seven words). The score is computed by assigning 0.5 to each sequence of items correctly reproduced by the participant (maximum score: 17.5).

Moreover, a non-word repetition task (Vicari, 2007) was used to assess verbal WM. The number of non-words correctly repeated is recorded as a measure of performance accuracy (maximum score: 40).

Spatial short term and working memory

In the visual-spatial span task (Vicari, 2007), the material consisted of a non-verbalizable geometric shape that appears for 2 s in one of seven possible positions on the computer screen. Then, two empty cells were presented in the same spatial positions as before and the child had to indicate the order in which the stimuli appeared. If the child was successful in at least three of five two-position sequences, a sequence one block longer was presented. Also in this case, the same testing procedure was used for sequences of increasing length (up to a maximum of seven spatial positions). The score was computed by assigning 0.5 to each sequence of items correctly reproduced by the participant (maximum score: 17.5).

Visual short term and working memory

A similar procedure was used for the visual span task (Vicari, 2007). In this case, the experimental material consisted of seven complex geometric figures depicted in high contrast colors. Two figures were presented, one at time, for 2 s at the center of the computer screen. After the disappearance of the second figure, the two figures were presented aligned in the center of the screen in a random position and the participant was asked to indicate the order in which they appeared. Also in this case, if the child was successful in at least three of the five trials, a sequence one figure longer was presented and the task continued until a maximum of seven figures have been presented. The score is computed by assigning 0.5 to each sequence of items correctly reproduced by the participant (maximum score: 17.5).

Visual shifting

The Wisconsin Card Sorting Test (WCST; Heaton et al., 1993) is a neuropsychological test of set shifting and also involves cognitive flexibility function. The WCST consists of four stimulus cards and 128 response cards which differ in color (red, green, blue and yellow), shape (circle, star, cross, and star) and number (one, two, three, and four). The stimulus cards are one red triangle, two green stars, three yellow crosses, and four blue circles.

The child was given the response cards and instructed to place each consecutive card under one of the stimulus cards, according to which he/she considered correct. After each sort, the child was informed whether he/she was correct. The first sorting category was color, and after 10 consecutive correct sorts, the category changed to form, without forewarning, and then accordingly to number. Errors in shifting from one category to another and perseveration errors are registered as scores.

STATISTICAL ANALYSIS

Data were analyzed using the Statistical Program for Windows, Version 8.0 (StatSoft, Inc., Tulsa, OK, USA). Participants' performances were transformed into z-scores. Since the assumptions of normality were not met, comparisons between DD and TR children on EF measures were carried out by means of the Kruskal-Wallis non parametric test with Group as independent between-subjects factor. To correct for multiple comparisons, the level of significance was set at $p = 0.005$ using Bonferroni correction (10 comparisons).

Moreover, multiple regression analyses were computed to explore the linear relationship between EF measures (predictor variables) and reading abilities (criterion variable), using the stepwise method.

RESULTS

DD children obtained significantly lower scores (p always ≤ 0.005) than TR children in phonological and categorical fluency, spoonerism abilities, visual-spatial and auditory attention, verbal and visual short-term memory, and verbal WM. For the level of significance adopted ($p = 0.005$), the comparisons of spatial short-term memory and shifting abilities showed no significant results (see **Table 1**).

To determine predictive relationships between EF measures (predictor variables) and inefficiency reading indexes (criterion variables), multiple regression analyses were computed using the stepwise method. Thus, each EF measure was entered in sequence as predictor variable and its value assessed to determine its contribution to the success of the model; variables that did not significantly contribute were automatically removed.

Overall, the first regression model, which included only spoonerism abilities (speed in seconds), accounted for 49.2% of the variance (R^2 change $= 0.492$) in words reading inefficiency index. The inclusion of auditory attention resulted in an additional 4.2% of the variance being explained (R^2 change $= 0.042$). The addition of visual-spatial attention explained a further 2.8% of the variance (R^2 change $= 0.028$).

Similarly to non-words reading inefficiency, the first regression model included only spoonerism abilities, accounting for 49.2% of the variance (R^2 change $= 0.492$). The inclusion of auditory attention explained an additional 3% of the variance (R^2 change $= 0.03$), and the inclusion of visual-spatial attention accounted for a further 2% of the variance (R^2 change $= 0.02$). **Table 2** summarizes multiple regression analyses for words and non-words reading inefficiency index.

DISCUSSION

This study was aimed at testing simultaneously different EF domains in a group of DD children. Deficits in several aspects of EF such as spoonerism, verbal categorical and phonological fluency, visual-spatial and auditory attention, verbal and visual short-term memory, and verbal WM have been found. However, spatial short-term memory and visual shifting abilities were preserved.

Consistent with previous studies, we observed a deficit in verbal phonological fluency (Goswami, 2000; Snowling, 2000; Ramus, 2003; Ramus et al., 2013) and in verbal categorical fluency (Snowling, 2000; Ramus et al., 2003; Reiter et al., 2005). These tasks engage complex cognitive mechanisms, such as WM, self-monitoring, and flexible thinking (Troyer et al., 1998; Schwartz et al., 2003), and in addition require rapid access to words and strategic search through lexical/phonologic and conceptual/semantic memory (Baldo and Dronkers, 2006). Due to the several cognitive mechanisms involved, a large cortical network is required, including the dorsolateral prefrontal cortex and word associative fronto-temporal regions (Frith et al., 1991; Friston et al., 1991; Cilia et al., 2007; Kalbe et al., 2009).

We also found in children with DD a lower performance in the spoonerism task, which is generally used to assess phonological awareness. However, to interpret this result properly it is necessary to focus on the extra task demands and not only on phonological abilities (Wimmer et al., 2000). The child is first asked to segment the word into two parts, the first phoneme (onset) and

Table 1 | Performances of children with developmental dyslexia (DD) and with typical reading (TR) in executive functions tasks (after back-transformation to original measure units).

Measure	DD Mean (*SD*)	TR Mean (*SD*)	X^2	*p*
Phonological fluency (correct responses)	21 (8.26)	25.97 (6.61)	9.03	0.0027
Categorical fluency (correct responses)	43.40 (8.48)	50.97 (7.35)	19.74	<0.0001
Spoonerism (speed in seconds)	413.55 (162.81)	123.69 (76.60)	91.81	<0.0001
Visual-spatial attention (correct responses)	37.15 (10.43)	43.91 (11.69)	7.81	0.005
Auditory attention (correct responses)	34.05 (5.13)	38.22 (2.15)	17.49	<0.0001
Verbal short-term memory (span score)	3.55 (0.62)	4.08 (0.54)	9.76	0.0018
Visual short-term memory (span score)	3.10 (0.48)	3.68 (0.85)	11.20	0.0008
Spatial short-term memory (span score)	4.80 (0.80)	4.94 (0.79)	7.42	0.0064
Verbal working memory (correct responses)	31 (3.54)	37.18 (1.93)	58.09	<0.0001
Non-verbal shifting (errors)	73.18 (13.78)	75.51 (9.28)	0.01	1.0

Table 2 | Multiple regression analysis predicting words and non-words reading inefficiency (only significant relationships are shown).

	Words				Non-words			
Predictor variable	**β**	***t* for β**	***p***	**Adjusted R^2**	**β**	***t* for β**	***p***	**Adjusted R^2**
Spoonerism (speed in seconds)	−0.55	−7.956	<0.001	0.488	−0.575	−8.122	<0.001	0.488
Auditory attention (correct responses)	−0.204	−3.052	0.003	0.527	−0.171	−2.493	0.014	0.514
Visual-spatial attention (speed in seconds)	−0.181	−2.798	0.006	0.552	−0.152	−2.295	0.023	0.53

the remainder of the word (rime), and temporally store the onset and rime of the first word; the child repeats this segmentation for a second word, and then blends the first onset with the second rime, and the second onset with the first rime. Therefore, the spoonerism task requires blending as well as segmentation skills, but also involves short-term and WM abilities, close monitoring of the phonological manipulation, and inhibitory processes. These complex demands could explain the deficits in tasks such as spoonerism usually found in dyslexic children (Jeffries and Everatt, 2004; Berninger et al., 2008; Kibby and Cohen, 2008; Menghini et al., 2011). It is worth noting that the spoonerism task, which involves all of these functions, has an important predictive role for both global and analytic reading skills.

Moreover, our results concerning attention support the hypothesis that both phonological processing and non-verbal processing are impaired in DD. Indeed, significant differences between DD and TR children were found in auditory and visual-spatial attention domains. Although to a lesser extent, our results support the concept that auditory and visual-spatial attention explains an increased percentage of the variance related to reading disorders. A contribution of attention to reading, independent of the sensory modality considered, is then confirmed. Previous studies generally evaluated visual and auditory attention separately. Concerning visual attention, our results are consistent with reports of difficulties in rapidly focusing visual attention observed in individuals with DD (e.g., Brannan and Williams, 1987) as well as deficits in automatic control of visual attention (Facoetti et al., 2000, 2001, 2003; Hari and Renvall, 2001). Moreover, it was found that visual-spatial attention in preschoolers specifically predicts future reading acquisition (Franceschini et al., 2012), suggesting new approaches for early identification and efficient prevention of DD.

With respect to auditory attention, studies have clearly demonstrated auditory attentional deficits in DD (Asbjornsen and Bryden, 1998; Facoetti et al., 2000; Goswami, 2000; Ramus, 2003; Tallal, 2004; Ramus et al., 2013) which have been interpreted not only as a deficit in speech-sound perception (Cunningham et al., 2001) and in processing rapid sound sequences (Helenius et al., 1999), but also as a problem in shifting and focusing auditory attention (Renvall and Hari, 2002). The few studies assessing DD children on both modalities have documented multimodal (i.e., visual and auditory) attention deficits (Facoetti et al., 2000, 2003; Buchholz and McKone, 2004; Valdois et al., 2004; Dufor et al., 2007).

Furthermore, there is some evidence that in TR a visual dorsal pathway provides a mechanism for the early, preattentive visual analysis of words (Vidyasagar, 1999, 2001; Pammer et al., 2006; Vidyasagar and Pammer, 2010). An adequate parsing of a stream of text into grapheme guides the grapheme-phoneme correspondence and the sensory integration of visual signals. For the proper identification of the graphemes and the subsequent matching of graphemes with phonemes, an attentional mechanism is required. The multimodal integration of visual and auditory inputs mediates the synthesis of orthographic and phonological information (Pammer et al., 2006).

In our group of dyslexic children a general multimodal (verbal and visual) deficit in short-term memory and WM has also been found. The results are at variance with the theory that dyslexic children have an isolated verbal short-term deficit, possibly secondary to a deficit of phonological processing or the expression of a dysfunctional articulatory loop (Poblano et al., 2000; Willcutt et al., 2001; Jeffries and Everatt, 2004; Kibby et al., 2004). By contrast, our results concord with data showing deficits in individuals with DD in the temporary storage of visual-spatial as well as verbal material (Poblano et al., 2000; Brosnan et al., 2002; Helland and Asbjørnsen, 2004; Martinussen and Tannock, 2006; Smith-Spark and Fisk, 2007; Menghini et al., 2011). Our findings on WM can be interpreted as a deficient functioning of CES or SAS (Baddeley and Hitch, 1974; Norman and Shallice, 1986; Shallice and Burgess, 1993; Baddeley, 2000, 2001). Indeed, consistent with the model of WM, the failure of the CES to supervise the activity of both peripheral slave systems could fully account for poor performances in tasks involving different modalities as found in our dyslexic children.

Considering the several processes involved in the EF tasks adopted (e.g., attention, active-inhibition, temporary storage, maintenance, update and integration of information from several domain-specific codes) and their cross-modalities nature, deficits found in our dyslexic children could be the expression of a deficient functioning of CES/SAS. Therefore, we propose that a more global deficit in higher-order cognitive mechanisms might be a crucial feature of DD.

Additional support to this hypothesis is given by our findings which show that some EF tasks, primarily spoonerism but also auditory and visual-spatial attention, are strictly related to reading deficits in DD children. These data could confirm the contribution of the executive attention and domain-general attention control abilities (e.g., CES/SAS) to reading, irrespective of the sensory modality.

However, an additional hypothesis cannot be excluded. During recent years it has been proposed that DD arises from an abnormal auditory sampling (Goswami, 2011). Since cortical oscillations have been implicated in several aspects of human cognition, it has been assumed that the abnormal phonological processing observed in DD reflects a deficit in temporal sampling of speech by neuroelectric oscillation that encodes incoming information at different frequencies (Goswami, 2011). Indeed, temporal coding via the synchronous activity of oscillating networks of neurons at different frequency bands is crucial in the perceptual processing of speech (Luo and Poeppel, 2007). In dyslexics the auditory sampling might be altered, yielding phonemic representations of an unusual temporal format, with specific consequences for phonological processing and phoneme/grapheme associations (Lehongre et al., 2011).

Similarly, studying high-frequency auditory oscillations associated with verbal WM, Lehongre et al. (2011) found that dyslexics exhibited a supranormal entrainment of bilateral planum temporal to fast temporal modulations in the 50–70 Hz range. It has been hypothesized (Lehongre et al., 2011) that in dyslexics too fast low-gamma oscillations might flood the auditory system with overdetailed spectrotemporal information, thereby saturating theta-based auditory buffer capacity and verbal WM. However, the relationship between neuronal oscillations and non-verbal WM correlates is still an open issue in DD.

Finally, the cellular synchronization of oscillatory responses might be responsible for the above mentioned multimodal integration of visual and auditory inputs which mediates the synthesis of orthographic and phonological information (Gray et al., 1989). Indeed, changes in gamma-band signals have been implicated in cognitive integration of stimuli (Pulvermüller et al., 1997; Ward, 2003; Hermann et al., 2004) and alpha-band activity contributes to specific attentional processes such as attentional selection and filter. Moreover, alpha power is larger over visual cortices when attention is focused on the auditory part of a multimodal auditory-visual stimulus (Klimesch, 2012). So, different frequency domains might interact in terms of cross-frequency coupling of oscillations, with cross-modal knock-on effects. One possibility is that atypical cross-frequency coupling in DD might interfere with the attentional mechanism for the multimodal integration of visual and auditory inputs.

In conclusion, our findings support the hypothesis that DD is a multiple neurocognitive deficit and not solely related to a phonological system dysfunction. The relation of brain oscillation to EF networks remains to be explored and could be useful for the further development of current neurophysiological models of DD.

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Why do adults with dyslexia have poor global motion sensitivity?

Elizabeth G. Conlon*, Gry Lilleskaret, Craig M. Wright and Anne Stuksrud

Griffith Health Institute, School of Applied Psychology, Griffith University, Gold Coast, QLD, Australia

Edited by:
Alan James Power, University of Cambridge, UK
Usha Goswami, University of Cambridge, UK
Andrea Facoetti, Università di Padova, Italy
Marie Lallier, Basque Center on Cognition Brain and Language, Spain

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Elisabet Service, McMaster University, Canada
Gerd Schulte-Körne, Ludwig-Maximilians-Universität München, Germany

***Correspondence:**
Elizabeth G. Conlon, Griffith Health Institute, School of Applied Psychology, Griffith University, PMB 50 Gold Coast Mail Centre, Gold Coast, QLD 9726, Australia
e-mail: e.conlon@griffith.edu.au

Two experiments aimed to determine why adults with dyslexia have higher global motion thresholds than typically reading controls. In Experiment 1, the dot density and number of animation frames presented in the dot stimulus were manipulated because of findings that use of a high dot density can normalize coherence thresholds in individuals with dyslexia. Dot densities were 14.15 and 3.54 dots/deg^2. These were presented for five (84 ms) or eight (134 ms) frames. The dyslexia group had higher coherence thresholds in all conditions than controls. However, in the high dot density, long duration condition, both reader groups had the lowest thresholds indicating normal temporal recruitment. These results indicated that the dyslexia group could sample the additional signals dots over space and then integrate these with the same efficiency as controls. In Experiment 2, we determined whether briefly presenting a fully coherent prime moving in either the same or opposite direction of motion to a partially coherent test stimulus would systematically increase and decrease global motion thresholds in the reader groups. When the direction of motion in the prime and test was the same, global motion thresholds increased for both reader groups. The increase in coherence thresholds was significantly greater for the dyslexia group. When the motion of the prime and test were presented in opposite directions, coherence thresholds were reduced in both groups. No group threshold differences were found. We concluded that the global motion processing deficit found in adults with dyslexia can be explained by undersampling of the target motion signals. This might occur because of difficulties directing attention to the relevant motion signals in the random dot pattern, and not a specific difficulty integrating global motion signals. These effects are most likely to occur in the group with dyslexia when more complex computational processes are required to process global motion.

Keywords: coherent motion, dyslexia, temporal recruitment, perceptual contrast effect, attention

INTRODUCTION

Dyslexia is a neurobiological disorder that can affect multiple brain areas (Stein, 2001; Shaywitz et al., 2003; Vidyasagar and Pammer, 2010). Adults with dyslexia show evidence of poor phonological awareness (Wilson and Lesaux, 2001), slower processing speed (Laasonen et al., 2001; Conlon et al., 2011; Stenneken et al., 2011), poor spelling (Bruck, 1990) and reduced comprehension (Conlon and Sanders, 2011). Although researchers agree on the characteristics that distinguish adults with good and poor reading skills, there is less agreement found concerning the visual processes that are impaired in this group.

Evidence that some individuals with dyslexia have a sensory processing deficit isolated to the magnocellular (M) and/or dorsal visual streams has been reported over many years (Lovegrove, 1993; Habib, 2000; Stein, 2001). Groups with dyslexia have poorer temporal contrast sensitivity than controls but do not have poorer spatial contrast sensitivity, measured in the parvocellular visual stream (Lovegrove et al., 1986). Difficulties replicating these findings (Amitay et al., 2002; Williams et al., 2003) and evidence that poorer sensitivity is found only with use of methodologies that require either sequential processing (Ben-Yehudah et al., 2001) or prior adaptation to a stimulus (Johnston et al., 2008), indicates that groups with dyslexia have a visual sensory processing deficit only when performing tasks that use complex computational processes. The evidence indicates that these processes are particularly impaired in the medial temporal area (MT) of the dorsal stream (Cornelissen et al., 1995; Talcott et al., 2000; Hansen et al., 2001; Conlon et al., 2004, 2009, 2012; Wilmer et al., 2004; Roach and Hogben, 2007; Benassi et al., 2010).

Evidence supporting the hypothesis of poorer performance of groups with dyslexia on computationally complex tasks is obtained from studies that have used methodologies that require discrimination of speed or the direction of global motion at MT. Reduced sensitivity is found in groups with dyslexia than in typically reading controls on these tasks (Cornelissen et al., 1995; Demb et al., 1998a; Raymond and Sorensen, 1998; Talcott et al., 2000; Hansen et al., 2001; Conlon et al., 2004, 2009; Wilmer et al., 2004; Wright and Conlon, 2009; Benassi et al., 2010). Convergent evidence of poorer performance in groups with dyslexia on speed, contrast and direction discrimination tasks has been obtained using electrophysiological (Schulte-Körne et al., 2004; Schulte-Körne and Bruder, 2010; Jednoróg et al., 2011) and functional MRI technology in which reduced neural activation has been found in these groups compared to controls (Eden et al., 1996; Demb et al., 1998b; Ben-Shachar et al., 2007).

Although there is compelling evidence for reduced efficiency when processing these complex stimuli in individuals with dyslexia, there have also been failures to replicate the effects found (Amitay et al., 2002; Hill and Raymond, 2002; Ramus et al., 2003; Reid et al., 2007). One explanation of these inconsistent findings concerns the extent that individuals with dyslexia can capture or sample the relevant motion signals for further processing. Using the global motion task, the aim of the experiments conducted was to determine whether coherent motion thresholds in groups with dyslexia would systematically change with presentation of stimuli that either increase or decrease the probability that coherent motion will be detected in the stimulus used.

The perception of global motion is commonly assessed using an apparent motion task generated with a random dot kinematogram (RDK) containing signal and noise dots (Newsome and Paré, 1988). This process occurs in the MT area of the dorsal stream (Thakral and Slotnick, 2011). The signal dots move in a single direction while noise dots move randomly. The RDK contains a series of single animation frames in which apparent motion is generated by presenting the dots in different locations in the RDK, and then presenting the series of stimuli rapidly and sequentially. Signal dots must be extracted from the noise dots and then integrated to form a global perception of motion (Raymond, 2000). The minimum percentage of signal dots needed for accurate perception of global motion is defined as the "motion coherence threshold." The lower the proportion of signal dots needed to reach coherence threshold, the greater the sensitivity of the visual system to global motion.

Experimenters can systematically increase or decrease coherence thresholds by manipulating the stimulus parameters used to generate global motion. For example, increasing the number of animation frames presented on a single trial reduces coherence thresholds (McKee and Welch, 1985). This effect is known as temporal recruitment (Raymond and Isaak, 1998) and occurs because cell groups in the dorsal visual stream that are sensitive to direction of motion have increased opportunity to detect and integrate the signal dots across time with presentation of more animation frames. This allows for greater co-operation between stimulated motion analysers (Raymond and Isaak, 1998; Snowden and Braddick, 1989), which increases the probability that global motion will be detected.

Although there is evidence for temporal recruitment in good readers, the evidence for its influence on coherence thresholds in groups with dyslexia is limited. In one study, coherence thresholds were significantly lower in a group with dyslexia with presentation of ten animation frames (duration of 333 ms) when compared to four (duration of 133 ms; Hill and Raymond, 2002). However, in a second study, temporal recruitment had no influence on coherence thresholds in a group with dyslexia (Raymond and Sorensen, 1998). One important difference between the two studies was the dot density used to generate the RDK.

Dot density is the number of dots presented per degree of visual angle (dots/deg^2). This parameter has little influence on coherence thresholds in typical readers (Barlow and Tripathy, 1997). However, increasing the dot density can reduce coherence thresholds in groups with dyslexia (Talcott et al., 2000). In a previous study that manipulated the dot density in a RDK, Talcott et al. (2000) found that coherence thresholds were higher in a group with dyslexia than in controls when the dot density was 9 dots/deg^2 or less. No group differences in coherence thresholds were found when the dot density was 12.2 dots/deg^2. Increasing the dot density increases the number of motion signals that can be sampled in a limited area in space. Previous research has concluded that directionally selective cells in the dorsal stream are fewer and more sparsely distributed in individuals with dyslexia (Galaburda and Livingstone, 1993; Stein and Walsh, 1997; Talcott et al., 2000). In addition, visual evoked potentials (VEP) are attenuated with presentation of coherent motion, but not by presentation of noise only (Schulte-Körne et al., 2004). On this basis increasing the dot density in a RDK might increase the probability that these sparsely distributed cell groups can capture and integrate motion signals (Talcott et al., 2000). This might explain the reported findings of no reader group differences on global motion tasks that have used high dot densities (Hill and Raymond, 2002; Edwards et al., 2004).

In most studies that have investigated global motion processing in dyslexia, a single task has been conducted to determine whether the groups with and without dyslexia differ on coherence thresholds. Investigation of the influence of the stimulus parameters used has been limited. Experiment 1 aims to systematically manipulate the number of animation frames presented and the dot density in the RDK, thereby determining the influence of these parameters on coherence thresholds in groups with dyslexia and controls.

Additional parameters found to systematically influence global motion thresholds in groups with dyslexia are the contrast or color of the signal and noise dots presented in the RDK, and the use of a pre-cue as an attention aid. When the signal and noise dots are the same color and contrast, groups with dyslexia have higher coherence thresholds than controls (Cornelissen et al., 1995; Talcott et al., 1998, 2000). When the signal dots are of either a higher contrast or presented in a different color to the noise dots, no group differences in coherence thresholds are found (Sperling et al., 2006; Conlon et al., 2012). Using this methodology, the influence of the noise dots is reduced, therefore allowing more efficient sampling of the signal dots in the global stimulus. One explanation of this effect is that presentation of stimuli of higher contrast produce increased excitation in the cell groups stimulated, allowing automatic exclusion of the noise dots in the RDK (Edwards et al., 1996; Croner and Albright, 1997; Martinez-Trujillo and Treue, 2002). When the stimuli of higher contrast are the target motion signals, there is a greater probability that these stimuli will be sampled by the visual system, particularly when competing with lower contrast, lower energy stimuli for sampling.

Relative to conditions in which the signal and noise dots in the RDK are of equal contrast, individuals with dyslexia have higher coherence thresholds than controls when the signal dots are presented at a lower contrast than the noise dots (Conlon et al., 2012). This occurs because the high contrast, high energy noise dots mask the lower contrast, lower energy signal dots, reducing the capacity of the group with dyslexia to sample the available signal dots. However, if the signal dots are of a lower contrast than the noise dots and a pre-cue is presented alerting participants that the low contrast dots contain the coherent motion signals, no reader group differences in coherence thresholds are found. This occurred because the pre-cue resulted in lower coherence thresholds for the group with dyslexia but had no influence on the control group (Conlon et al., 2012). These findings are consistent with studies that have reported that the use of a pre-cue can also increase accuracy in visual search tasks that contain multiple stimuli in groups with dyslexia (Hawelka and Wimmer, 2008; Moores et al., 2011). One explanation of these findings is obtained from physiological data. Sensitivity to motion at MT in single cell recordings can be influenced by the attentional state of the receptive field (Treue and Maunsell, 1996; Treue and Trujillo, 1999). Using functional MRI technology, these findings have been extended to demonstrate an increased level of activation at MT in the human visual system on the basis of manipulations of attention to specific stimulus attributes (O'Craven et al., 1997; Buchel et al., 1998), for example, the speed changes in a motion stimulus. Behaviourally, directing attention in this way increases the length of the motion aftereffect, relative to passive viewing conditions (Buchel et al., 1998). The increased activity at MT occurs because of a top-down feedback loop from the posterior parietal cortex (PPC). This feedback loop acts to modulate sensory performance. In groups with dyslexia there is now substantial evidence of impairment in attention processing at the level (Vidyasagar, 1999; Lallier et al., 2010; Vidyasagar and Pammer, 2010).

A problem with the studies that have manipulated contrast or color or used a pre-cue is that the signal dots differed from noise in terms of motion, color and contrast. It may therefore have been the influence of contrast or color, rather than the availability of the target signal dots that led to systematic increases and decreases in coherence thresholds in groups with dyslexia.

The impact of stimulus parameters that can systematically influence coherence thresholds, while allowing the signal and noise dots to differ only on the direction of motion requires further investigation. One task that has been found to produce systematic changes in coherence thresholds by using motion alone is the perceptual contrast effect (Raymond and Isaak, 1998). Relative to a baseline condition in which coherence thresholds are obtained using a static prime, coherence thresholds are increased (i.e., sensitivity is reduced) in typical readers when a briefly presented, fully coherent motion prime is presented before a partially coherent test stimulus. This effect occurs provided the prime and test stimulus have the same direction of motion. When motion detectors responsive to the same direction of motion are stimulated by both the prime and test stimuli, the highly salient fully coherent prime reduces the visibility of the signal dots presented in the test stimulus because of the dramatic change in coherence of the prime and test. In fact, if presentation of the final two frames in a sequence of fully coherent motion is presented as partially coherent, these frames are not detected by participants (Raymond and Isaak, 1998). In contrast, coherence thresholds are reduced relative to the baseline condition when the prime and test have opposite directions of motion (Raymond and Isaak, 1998). The latter result might have occurred because the visibility of noise dots that matched the direction of motion in the prime was reduced, so decreasing the proportion of effective noise dots available for processing in the test RDK.

In explanation of their results, Raymond and Isaak (1998) argued that the prime was viewed as an object, so could disrupt processing of subsequently presented stimuli by reducing the efficiency of visual selection processes, if the prime and test had the same motion characteristics. These results cannot be explained by adaptation because the duration of the prime was less than 100 ms and the interstimulus interval (ISI) between the prime and test stimuli had no influence on thresholds (Raymond and Isaak, 1998; Glasser et al., 2011). Importantly, the only difference between the stimuli presented were the motion attributes of the prime. Experiment 2 will use the perceptual contrast effect to determine whether coherence thresholds can be systematically increased or decreased in individuals with dyslexia.

The overall aim of the experiments conducted in this study was to determine if using different methodologies can vary the strength of the motion signals used in a RDK, thus leading to subsequent systematic changes in coherence thresholds in groups with and without dyslexia. In the first experiment, the dot density and number of animation frames presented in a RDK were manipulated. In Experiment 2, coherence thresholds were obtained after brief exposure to a fully coherent prime moving in either the same or opposite direction of motion to the partially coherent test stimulus.

EXPERIMENT 1

The effect of dot density and temporal recruitment on coherence thresholds in groups of adults with or without dyslexia was investigated. Two dot densities, high (14.15 dots/deg^2) and low (3.54 dots/deg^2) were used. These dot densities were selected based on findings that no reader group differences in coherence thresholds are found at dot densities of 12.2 dot/deg^2 or greater (Talcott et al., 2000; Hill and Raymond, 2002). Temporal recruitment was manipulated by presenting each dot density condition for five (total duration, 83 ms) or eight (total duration, 133 ms) animation frames. These parameters were selected because Hill and Raymond (2002) found no reader group difference on a global motion processing task when dot density was high (45 dots/deg^2) and four animation frames (total duration, 133 ms) were presented.

If increasing dot density alone provides a sufficient increase in the capacity of the group with dyslexia when sampling the signal dots, no group difference in coherence thresholds were expected with presentation of a RDK with high dot density. This was expected to occur regardless of the number of animation frames presented. The group with dyslexia were expected to have higher coherence thresholds than the control group when dot density was low. If temporal recruitment effects are only found in the group with dyslexia in the high dot density condition, lower coherence thresholds were expected with presentation of the high dot density condition in which eight animation frames were presented. In the low dot density condition, no influence of the number of animation frames presented was expected.

MATERIALS AND METHODS

PARTICIPANTS

There were 21 individuals with dyslexia ($M_{\text{age}} = 23.64$ years; $SD = 6.4$) and 22 typically reading controls ($M_{\text{age}} = 18.64$ years; $SD = 3.33$). All participants had English as a first language and normal or corrected to normal visual acuity. Due to associations found in previous studies between visual discomfort and global motion processing, participants with a high score on the Visual Discomfort Scale were excluded (Conlon et al., 1999, 2009). Individuals with dyslexia were recruited from the University disability office, the laboratory register and from advertising. Typical readers were obtained from the student participant pool. All procedures were conducted in accordance with the University human research ethics committee that approved this project.

The criteria used to define adults with dyslexia were based on those used previously (Conlon et al., 2004, 2009, 2011, 2012; Conlon and Sanders, 2011). Individuals with dyslexia reported a history of reading difficulties and had standard word reading scores below average on the Wide Range Achievement Test – 3rd Edition (WRAT-3; Wilkinson, 1993). This test consists of 42 words of increasing difficulty and has internal consistencies of 0.90–0.95 for the age groups used in this study. A further criterion was that scores on the test of word reading efficiency (TOWRE; Torgesen et al., 1999) were below a standard score of 90.

Individuals with dyslexia also had scores at least two standard deviations (SD) below the mean of the control group on non-word and exception word reading tests. The non-word and exception word tests each had 25 items matched for word length. The internal consistencies for the non-word and exception word tests are .77 and .84 respectively. At least average ability as measured by the Block Design subtest from the WAIS-3 (Wechsler, 1998) was the final criterion.

Criteria for inclusion in the control group were word reading scores on the WRAT-3 and reading fluency scores on the TOWRE of at least a standard score of 105. Nonword and exception word reading test scores were at least 75%. At least average ability as measured by the Block Design subtest from the WAIS-3 (Wechsler, 1998) was the final criterion.

The group with dyslexia was significantly poorer than the control group on word reading, $t(41) = 13.24$, $p < 0.001$, non-word reading, $t(41) = 10.61$, $p < 0.001$, exception word reading, $t(41) = 11.23$, $p < 0.001$, and word reading fluency, $t(41) = 12.24$, $p < 0.001$ tests. No significant difference was found between groups on the measure of non-verbal ability used, $t(41) = 0.238$, $p = 0.81$. Both groups performed in the average range (see **Table 1**).

Table 1 | Performance of the control ($n = 22$) and dyslexia ($n = 21$) groups on the reading and ability measures. Experiment 1.

	Control	Dyslexia
	Mean (SD)	**Mean (SD)**
WRAT reading (standard)	110.82 (4.35)	91.67 (5.12)
Non-words/25	22.32 (1.8)	14.43 (2.9)
Exception words/25	19.5 (1.8)	10.57 (3.2)
TOWRE total (standard score)	112.4 (6.8)	83.48 (8.6)
Non-verbal ability (scaled)	12.54(3.0)	12.52(2.8)

STIMULI

Stimuli for the global motion task were generated using the Cambridge Research Systems hardware and Operating System Software, VSG Version 2/5. Stimuli were displayed on a 21 inch Hitachi HM-4721-D monitor with a resolution of 800 × 600 pixels, and a vertical screen refresh rate of 120 HZ.

The RDK contained either 100 (low dot density: 3.54 dots/deg^2) or 400 (high dot density: 14.15 dots/deg^2) white dots (luminance: 20 cd/m^2) presented on a black background (luminance: 0.54 cd/m^2) displayed within a borderless area subtending 6° × 6° presented in the middle of the computer screen. The display size was chosen to avoid pursuit eye movements (Hill and Raymond, 2002). The velocity of the stimuli was 10.5°/s and the dots had a diameter of one pixel (0.35 mm). The duration of a single animation was 16.67 ms, with a dot lifetime of two animation frames (33.34 ms), after which the signal dots disappeared before being regenerated at a randomly selected stimulus location within the panel. A standard wrap around technique was used for the signal dots as they reached the side of the screen. The noise dots randomly changed position in a Brownian fashion. Stimuli were presented for either five (84 ms) or eight animation frames (133 ms).

For each of the experimental conditions there were two blocks of trials. Separate coherence thresholds were obtained for each block. The adaptive psychophysical procedure used to estimate coherence thresholds was a three-down, one-up staircase with eight reversals. After three correct responses, coherence was halved, and after each incorrect response coherence was doubled. This allowed for an estimation of the coherence value needed to obtain a correct response on 79% of the trials (Kaernbach, 1991). Participants selected the direction of motion, left or right at the completion of each trial. Geometric mean thresholds were combined across both blocks of trials to obtain an overall estimate of coherence thresholds. The starting coherency was 50% in each condition.

Response bias was determined by presenting trials at 1% coherence at least once every five trials. Participants were expected to respond randomly to these trials, with about half the responses being to the left and half to the right. Response bias was evaluated by obtaining a percentage score for the proportion of left responses to these trials. No significant group differences in response bias were found (dyslexia, $M = 46\%$, $SD = 12.36$; control, $M = 44\%$, $SD = 11.07$), $t(42) = 0.676$, $p = 0.503$.

PROCEDURE

Each participant was assessed for reading ability. This assessment was followed by a separate session in a darkened laboratory in which coherence thresholds were obtained. Viewing was binocular with natural pupils and the viewing distance of 57 cm was controlled with a chin rest. A block of 20 practice trials was presented prior to each of the four conditions. Each trial began with presentation of a fixation cross which was replaced after 150 ms with the RDK. Participants responded to the direction of motion by depressing either the left or right button on the Cambridge

Research Systems CB-2 response box at the end of each trial. A new trial was automatically triggered after each response. The order of presentation of the experimental conditions was counterbalanced between and within groups.

RESULTS

The influence of dot density and the number of animation frames presented on coherence thresholds for the reader groups is shown in **Figure 1**. These data were analyzed using a 2 (group: dyslexia or control) × 2 (dot density: low or high) × 2 (animation frames: five or eight) mixed factorial ANOVA. The assumptions of the analysis were met. A significant main effects was found for reader group, $F(1, 41) = 15.80$, $p < 0.001$; $\eta_p^2 = 28$. Regardless of the condition, the group with dyslexia ($M = 47.09$; *95% CI* = 41.87–52.03) had higher coherence thresholds than controls ($M = 32.74$; *95% CI* = 27.65–37.84). Significant main effects were also found for dot density, $F(1, 41) = 18.81$, $p < 0.001$; $\eta_p^2 = 0.31$, and the number of animation frames presented, $F(1, 41) = 10.66$, $p = 0.002$; $\eta_p^2 = 0.21$. These were modified by a significant interaction between dot density and the number of animation frames presented, $F(1, 41) = 8.68$, $p = 0.005$, $\eta_p^2 = 0.17$. There were no other significant interactions found.

The influence of dot density and the number of animation frames presented on coherence thresholds was investigated with simple effects analysis. In the five-animation frame condition, dot density, high or low had no influence on coherence thresholds, $F(1, 41) = 3.97$, $p = 0.069$, $\eta_p^2 = 0.08$. Significantly lower coherence thresholds were found with presentation of the high compared to the low dot density stimuli for the eight animation frame condition, $F(1, 41) = 32.29$, $p < 0.001$, $\eta_p^2 = 0.44$. When dot density was low there was no evidence of temporal recruitment found, $F(1, 41) = 0.73$, $p = 0.396$, $\eta_p^2 = 0.02$. However, when dot density was high, coherence thresholds were significantly lower with presentation of eight than five animation frames, $F(1, 41) = 28.8$, $p < 0.001$, $\eta_p^2 = 0.41$, showing the influence of temporal recruitment. The percentage reduction in coherence thresholds in the high dot density condition with presentation of the higher number of animation frames was 7.5% for the group with dyslexia and 6.1% for the control group, indicating similar effects of temporal recruitment in each reader group.

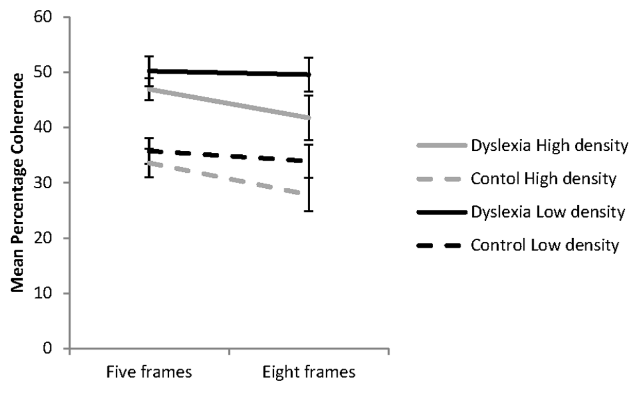

FIGURE 1 | Coherent motion thresholds for the effects of dot density and the number of animation frames presented for the groups with ($n = 21$) and without dyslexia ($n = 22$) in each of the four experimental conditions. Error bars represent ±1 standard error.

DISCUSSION

It was expected that manipulating the dot density and the number of animation frames presented in a single trial of the global motion task would systematically increase or decrease the capacity of the reader groups to efficiently sample the motion signals present in the RDK. The findings from the study were partially consistent with our hypotheses. Regardless of reader group, lower coherence thresholds were found with presentation of the high dot density condition when presented for eight animation frames, showing temporal recruitment effects. In the low dot density condition, temporal recruitment effects were not found. Across all conditions presented, the group with dyslexia had higher coherence thresholds than the control group. These findings are partially consistent with our hypotheses for the group with dyslexia only.

Previous studies have found that presentation of a RDK with a high dot density promotes increased processing efficiency in the group with dyslexia (Hill and Raymond, 2002; Edwards et al., 2004) because of the increased capacity to sample the signal dots presented within a limited area in space (Talcott et al., 2000). The findings of the current experiment indicate that the combination of high dot density and eight-animation frames used was not sufficient to normalize coherence thresholds in the group with dyslexia. The previous study that found no reader group differences in coherence thresholds when four animation frames (133 ms) were presented used a higher dot density (45 dots/deg^2; Hill and Raymond, 2002) than that used in the current study. In addition, when using a dot density of 12.2 dot/deg^2 one previous study found no reader group differences on the global motion task when stimulus durations of 900 ms were used (Talcott et al., 2000). These results indicate that dot density alone, unless very high, cannot normalize coherence thresholds in the group with dyslexia.

Lower coherence thresholds were found in the group with dyslexia in the high dot density condition and when the RDK was presented for eight animation frames. These results indicate that given sufficient signal dots captured when the higher dot density was used, normal temporal recruitment is found in the group with dyslexia. This result is consistent with the findings of Hill and Raymond (2002). The group with dyslexia can integrate motion signals over time, given sufficient motion samples from the high dot density condition. Findings that temporal recruitment did not occur in the low dot density condition support this conclusion, a result consistent with a previous study (Raymond and Sorensen, 1998).

Together these findings indicate that integration of the signal dots over time in the global motion task relies on the observer's capacity to extract sufficient signal dots from noise. A minimum level of energy in the motion signals may be required. This could be obtained with presentation of a high dot density, a greater number of animation frames or a combination of both. These findings might indicate that with sufficient signal energy to stimulate adequate neural activity in the less efficient dorsal stream of the group with dyslexia, the computation of the direction of global motion becomes more efficient.

There was no evidence of temporal recruitment in the low dot density condition for either reader group. Although these results were expected for the group with dyslexia, temporal recruitment effects were expected in the control group in this condition (Raymond and Sorensen, 1998; Talcott et al., 2000). These results indicate that presentation of the five frame stimulus in which the total stimulus duration was 84ms increased the perceptual difficulty of the stimulus beyond a level that even a well-functioning system could utilize when the dot density was low (Braddick, 1995). In addition, the duration of a single animation frame was short. Although the dot life-time of 33 ms was consistent with that used in previous studies (Raymond and Sorensen, 1998; Hill and Raymond, 2002), the frame duration was below 20 ms. In this case, a greater number of animation frames might have been needed to reach asymptotic motion thresholds (Snowden and Braddick, 1989).

The critical findings obtained from Experiment 1 are that coherent motion thresholds can be reduced in groups with and without dyslexia by increasing both dot density and the number of animation frames in a RDK. However, none of the experimental manipulations led to coherent motion thresholds being normalized in the group with dyslexia who had higher thresholds than controls in all conditions.

EXPERIMENT 2

Coherent motion thresholds in groups with dyslexia can be systematically increased by presenting signal dots at a lower contrast than the noise dots, and decreased by presenting signal dots at a higher contrast or different color to the noise dots (Sperling et al., 2006; Conlon et al., 2012). These effects are found because the higher contrast signals are the most salient so are preferentially processed in the human visual system (Edwards et al., 1996; Croner and Albright, 1997). In Experiment 2, manipulating motion only, we aimed to determine if coherence thresholds could be systematically increased and decreased in a group with dyslexia using a fully coherent prime presented in either the same or opposite direction of motion to the test stimulus.

It was expected that presentation of a fully coherent prime before the test stimulus would reduce the visibility of the signal dots in the partially coherence test stimulus in a similar way to that found when noise dots are presented at a higher contrast to the signal dots in the RDK. This would occur because of the reduced salience of the coherent motion in the partially coherent test, relative to the highly salient fully coherent prime. We expected that the threshold elevation found in a group with dyslexia would be greater than that found in the control group. However, if presenting a fully coherent prime in the opposite direction to the partially coherent test stimulus facilitates global motion processing in a group with dyslexia in a similar way to that found when presenting signal dots at a higher contrast to the noise dots, it was expected that no group difference in coherence thresholds would be found. In the baseline condition in which a stationary test stimulus was presented, higher coherence thresholds were expected in the group with dyslexia than for controls.

MATERIALS AND METHODS

PARTICIPANTS

There were 20 participants, 10 with dyslexia ($M_{\text{age}} = 22.11$ years, $SD = 3.49$) and 10 normally reading controls ($M_{\text{age}} = 21.9$ years; $SD = 4.12$). They were obtained using the same procedures as Experiment 1. No participant took part in both studies. All participants had a history of dyslexia, English as a first language and normal or corrected to normal visual acuity. The study had approval from the Human Research Ethics Committee. Group classification procedures were the same as Experiment 1 (see **Table 2**).

STIMULI AND APPARATUS

The apparatus and adaptive psychophysical procedure used were the same as those used in Experiment 1. In the global motion task, the RDK used as both the prime and the test had 300 white dots (luminance: 20 cd/m^2) presented on a dark background (luminance: 0.54 cd/m^2). The stimulus was displayed within a borderless area subtending 13.35° × 13.35° presented in the middle of the computer screen. Dot density was 3.83 dots/deg^2 and dot life time was three animation frames (50 ms). The dot life time was increased from Experiment 1 from the results of pilot testing. The motion primes were presented at 100% coherence, with one moving to the left and the other moving to the right. The baseline control stimulus was a stationary RDK with no dot displacement. Each of these stimuli was presented for 96 ms. When extinguished these were replaced with a blank low luminance field (0.54 cd/m^2) for 32 ms. This field was replaced with the partially coherent test stimulus, which was presented for 10 animation frames (160 ms). The method used is shown in **Figure 2**.

In each condition, the task was to determine whether the direction of coherent motion was to the left or to the right. Beginning coherence in all conditions was 25%. Two blocks of trials were presented for each condition. Threshold estimates were based on six threshold reversals for each block of trials.

Table 2 | Performance of the control ($n = 10$) and dyslexia ($n = 10$) groups on the reading measures. Experiment 2.

	Control	Dyslexia	
	Mean (SD)	**Mean (SD)**	***t*-test**
WRAT reading (standard)	115.6 (4.35)	94.1 (5.4)	$t(18) = 10.88$, $p < 0.001$
Non-words/25	24.0 (0.89)	15.5 (3.4)	$t(18) = 6.85$, $p < 0.001$
Exception words/25	21.9 (0.78)	11.4 (2.9)	$t(18) = 10.36$, $p < 0.001$
Non-verbal ability (scaled)	12.1 (0.87)	11.4(1.90)	$t(18) = 1.06$, $p = 0.303$

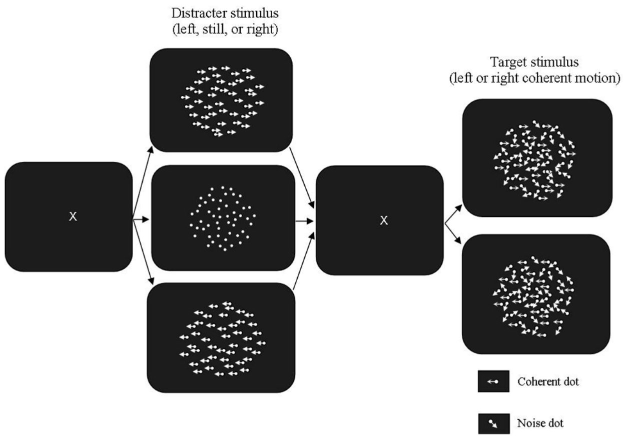

FIGURE 2 | Motion Segmentation Task used in Experiment 2. The fully coherent prime was presented in either the same or opposite direction to the partially coherent test. The stationary prime was used as a control condition. The blank stimulus between the prime and test was presented for 96 ms and the test stimulus was presented for 160 ms (10 animation frames).

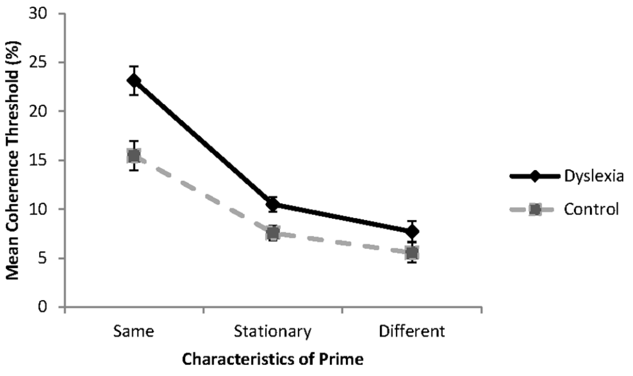

FIGURE 3 | Global motion coherence thresholds for group with dyslexia ($n = 10$) and controls ($n = 10$) when the probe and prime are presented in the same direction (same), in opposite directions (different) or when the prime is a stationary control stimulus. Standard error bars represent ±1 standard error.

The geometric mean coherence thresholds were obtained for each block of trials. These were averaged to determine coherence thresholds for each condition.

PROCEDURE

The global motion task was conducted in a separate session after assessment of reading ability. Testing took place in a darkened laboratory. Viewing distance of 57 cm was controlled with a chin rest. Viewing was binocular with natural pupils. Participants were instructed to judge whether the dots presented on the screen were moving to the left or the right. A block of 20 practice trials was followed by the experimental trials. Participants registered the direction of coherent motion by depressing the left or right keys on the response box at the end of each trial. A new trial began automatically after a response.

RESULTS

The results of the experiment are shown in **Figure 3**. The impact of the prime on threshold performance was analyzed using a 3 (condition: same, different, baseline) × 2 (group: dyslexia or control) mixed factorial ANOVA. All the assumptions of the analysis were met. Significant main effects were found for condition, $F(2, 36) = 113.8$, $p < 0.001$, $\eta_p^2 = 0.86$, and reader group, $F(1, 18) = 11.80$, $p = 0.003$, $\eta_p^2 = 0.40$. These effects were modified with a significant reader group by condition interaction, $F(2, 36) = 5.61$, $p = 0.008$, $\eta_p^2 = 0.24$.

Inspection of **Figure 3** shows that as expected, highest coherence thresholds were found when the prime and test were presented in the same direction of motion, and lowest coherence thresholds were found when the prime and test were presented in opposite directions of motion. Simple effects analysis revealed that the group with dyslexia had significantly higher coherence thresholds than the control group when the prime and test were presented in the same direction of motion, $F(1, 18) = 13.34$, $p = 0.002$, $\eta_p^2 = 0.43$, and in the baseline condition, when the prime was a stationary stimulus, $F(1, 18) = 7.69$, $p = 0.013$, $\eta_p^2 = 0.30$. No significant differences were found between reader groups when the prime and test were presented in opposite directions of motion, $F(1, 18) = 2.07$, $p = 0.167$, $\eta_p^2 = 0.10$. These results are consistent with the hypotheses of the study.

To determine to what extent the prime influenced coherence thresholds in each of the groups relative to the baseline condition, difference scores were obtained for each of the primed thresholds. Coherence thresholds were elevated by 12.63% ($SD = 3.81\%$) for the group with dyslexia and 7.87% ($SD = 3.60\%$) for the control group when the motion of the prime and the test was presented in the same direction. The increase in threshold was significantly greater for the group with dyslexia than for the control group, $t(18) = 2.86$, $p = 0.010$. When the prime and test were presented in opposite directions of motion, thresholds were enhanced by 2.76% ($SD = 1.74\%$) for the group with dyslexia, and by 2.03% ($SD = 1.48\%$) for the control group. The degree to which coherence thresholds were reduced, did not differ between the reader groups, $t(18) = 0.68$, $p = 0.513$, failing to support the hypothesis of greater facilitation in processing for the group with dyslexia. Although this change was sufficient for findings of a statistically significant threshold enhancement when compared to the baseline condition for the group with dyslexia, $t(18) = 4.78$, $p < 0.001$, the change was not sufficient to reveal reader group differences.

DISCUSSION

It was expected that presentation of a prime in the same or opposite direction of motion to the test would systematically increase or decrease the capacity of the group with dyslexia when sampling the signal dots in the partially coherent test stimulus. The results of the study are consistent with our hypotheses. Relative to the baseline condition, for both reader groups, higher coherence thresholds were found when the prime and test were presented with the same direction of motion and lower coherence thresholds were found when the prime and test were presented with opposite directions of motion. These results replicate the original findings of Raymond and Isaak (1998).

The significantly greater increase in coherence thresholds found in both reader groups when the prime and test were presented in the same direction of motion is consistent with our hypothesis that exposure to the highly salient fully coherent prime would reduce the visibility of the coherent motion signals in the test stimulus. This effect could have occurred because the visibility of the coherent motion signals was reduced, temporarily reducing their salience relative to the noise dots. This effect would have reduced the capacity of each reader group when excluding the noise dots in the test RDK. In this condition, the group with dyslexia had greater difficulty than the control group sampling the signal dots presented in the partially coherent test, producing a greater processing disadvantage. These findings are similar to those obtained in a previous study in which the signal dots were presented at a lower contrast than the noise dots in a RDK (Conlon et al., 2012). One explanation of these results is the capacity of the group with dyslexia to sample the available motion signals was reduced more than that found in the control group because of undersampling of the signal dots presented.

No significant reader group differences in coherence thresholds were found when the prime and test were presented in opposite directions of motion. These results are similar to those obtained when the signal dots presented in the RDK were a higher contrast or different color to the noise dots (Sperling et al., 2006; Conlon et al., 2012). This result occurred because of the higher energy in the target signal dots (Croner and Albright, 1997; Martinez-Trujillo and Treue, 2002) allowing greater sampling of these stimuli over the lower contrast noise dots. When the prime and test were presented in opposite directions of motion, similar facilitation of coherence thresholds was found. When the direction of motion in the test was in the opposite direction to the prime, the salience of a proportion of the noise dots would have been reduced, which might have increased the probability that signal dots would have been sampled. Evidence supporting this conclusion is obtained from the influence of presentation of a prime containing noise dots only. Higher coherence thresholds were found in the test because some of the directions of motion in the prime also masked the motion signals in the test stimulus (Raymond and Isaak, 1998).

The last important finding from the experiment was that the group with dyslexia had higher coherence thresholds than controls in the baseline control condition when the prime was a stationary stimulus. This result is consistent with many studies that have shown evidence of a global motion processing deficit in groups with dyslexia (Cornelissen et al., 1995; Raymond and Sorensen, 1998; Talcott et al., 2000; Conlon et al., 2004). Overall the findings from the experiment indicate that presentation of a fully coherent prime can influence the size of coherence thresholds, by increasing or decreasing the proportion of signal dots that can be easily sampled by individuals with dyslexia. While the perceptual processing explanation presented here can explain the systematic changes in coherence thresholds found, and provides a sensory explanation of the effects for the group with dyslexia, attention mechanisms might also be implicated. These will be discussed in the following section.

GENERAL DISCUSSION

The results of these experiments indicate that motion coherence thresholds in groups with dyslexia can be systematically increased or decreased when the capacity of these individuals to sample the signal dots in the RDK is manipulated. Increasing the dot density and number of animation frames used or presenting the prime and test stimulus in opposite directions of motion results in lower coherence thresholds for each reader group. Conversely, reducing the dot density and the number of animation used or presenting the prime and test in the same direction of motion produces higher coherence thresholds for each reader group. The efficiency of the computational processes needed when undertaking a global motion task in individuals with dyslexia will be discussed. The viability of explanations which include sensory processes only and those that include attention mechanisms will each be addressed.

When processing global motion two important computational processes are required, that of extracting signal from noise and integration of the extracted motion signals over space and time (Raymond, 2000). The results of the current study demonstrate that the efficiency with which individuals with dyslexia can sample the signal dots in the RDK and therefore efficiently perform these processes depends on the stimulus parameters and methodology used. The latent variable manipulated in both experiments was the strength or energy of the motion signals presented in the RDK. In Experiment 1, higher signal strength was produced by increasing the dot density and the number of animation frames over which the RDK was presented. In Experiment 2 signal strength in the test stimulus was manipulated by the direction of motion in the prime. In both experiments, lower coherence thresholds were obtained in the reader groups when stimuli producing the strongest motion signals were presented. Highest coherence thresholds were found in both experiments, when the strength of the signal dots in the RDK was weakest. In Experiment 1, this was presentation of stimuli with a low dot density, or presentation of stimuli presented for five animation frames and in Experiment 2, this was the condition in which the prime and test stimuli were presented in the same direction of motion.

Although the group with dyslexia had higher coherence thresholds than typical readers in all conditions of Experiment 1, evidence of normal temporal recruitment was found in the high dot density condition. Coherence thresholds for both reader groups were reduced by over 6% with presentation of the eight compared to the five frame condition. These results indicate normal temporal recruitment in the group with dyslexia when these individuals are able to sample sufficient motion signals. In a previous study that used a higher dot density than that used in the current study, normal temporal recruitment was found in the group with dyslexia. In addition, no significant reader group differences in coherence thresholds were found (Hill and Raymond, 2002). Together these results indicate two things. First, if dot density is sufficiently high, normal temporal recruitment occurs in the group with dyslexia because these individuals are able to sample sufficient motion signals to perform the integration process. Second, either a very high dot density or a combination of a high dot density and longer stimulus durations is needed to enable normal global motion processing in the group with dyslexia. In low dot density conditions, problems with temporal recruitment were found. This might occur because of the poorer capacity of individuals with dyslexia when sampling more motion signals presented more sparsely in space (Talcott et al., 2000; Stein, 2001, 2003). Electrophysiological studies in which lower activation was found with exposure to coherent motion but not to noise dots alone provides support for this explanation (Schulte-Körne et al., 2004; Jednoróg et al., 2011), indicating that the strength of the motion signals alone might be insufficient to promote efficient integration in the group with dyslexia.

Evidence that increased signal strength can normalize coherent motion processing in the group with dyslexia was also obtained in Experiment 2, where there were no significant group differences found when the prime and test stimuli were presented in opposite directions of motion. In this condition, the reduced salience of a proportion of the noise dots increased the efficiency of the signal extraction process, which in turn resulted in efficient integration of the extracted signals. These results are consistent with previous studies that have presented stimuli in which the noise dots were automatically excluded (Sperling et al., 2006; Conlon et al., 2012). It would be tempting to conclude that purely sensory processes are sufficient to potentially normalize coherent motion thresholds in groups with dyslexia, by facilitating noise exclusion. However, the impact of attention must also be considered.

Evidence that presentation of a fully coherent prime activates spatial attention has been found in an experiment similar to that conducted in Experiment 2, in which a transparent motion stimulus was used as the prime (Raymond et al., 1998). In a transparent motion task two fully coherent sheets of dots appear to move independently, each with orthogonal directions, for example motion moving leftward and upward. Prior to presentation of the prime a pre-cue alerted participants to the direction of motion in the transparent prime (horizontal or vertical) for which a judgment of motion direction was made. Presentation of the prime was followed by the partially coherent test stimulus, for which coherence thresholds were obtained. The results of the study found that for typical readers, if the attended direction of motion in the prime matched the direction of motion in the test, higher coherence thresholds were obtained. If the non-attended direction of motion of the prime matched the direction of motion of the test, lower coherence thresholds were found. These results were obtained only when the prime contained fully coherent motion, and not when arrows indicating the directions of motion were presented. These results indicate that selective attention is activated by the motion prime which influences coherence thresholds in the test, dependent on the allocation of attention to the prime (Raymond et al., 1998). These results are consistent with physiological data that has shown attention modulates activity in MT (O'Craven et al., 1997; Buchel et al., 1998). These results suggest that presentation of a single direction fully coherent prime also activated spatial attention when using the current methodology. Spatial attention may have modulated the response to the partially coherent test stimulus, dependent on the direction of motion in the prime. The time course of this activity might have been different for the group with dyslexia and the control group because of impaired attentional mechanisms in the group with dyslexia.

There is a growing body of research that has found groups with dyslexia have difficulties directing attention to rapidly presented stimuli (Vidyasagar and Pammer, 2010), shifting attention between stimulus sequences that are rapidly and sequentially presented (Hari and Renvall, 2001; Visser et al., 2004; Lallier et al., 2010) or orientating spatial attention (Facoetti et al., 2010). In the motion segmentation task (Experiment 2), two distinct stimulus events occurred rapidly and sequentially. First, the fully coherent prime was separated from the partially coherent test by an ISI of 32 ms. Spatial attention would have been automatically captured by the fully coherent prime, stimulating cell groups responsive to that direction of motion at MT (Martinez-Trujillo and Treue, 2002). With the rapid presentation of the test stimulus, attention had to be rapidly disengaged from the prime and directed at the test stimulus. If the group with dyslexia have difficulty rapidly disengaging attention from the prime and re-engaging attention on the test as suggested by Hari and Renvall (2001), the influence of the prime might be greater for the group with dyslexia than for the control group. When the prime and test were presented in the same direction of motion, difficulties disengaging attention from the prime might have added to the poor salience of the target motion signals in the test. This would have produced the much higher coherence thresholds found in this condition for the group with dyslexia than those found for the control group. Conversely, difficulties disengaging attention from the opposite direction prime might have increased the salience of the target motion signals in the test more for the group with dyslexia than for the control group, resulting in no significant group differences in coherence thresholds. This explanation raises the possibility that difficulties shifting attention are most apparent when stimuli to be processed stimulate cells groups in the same cortical area, so are task relevant. As no condition was presented using a blank prime, it is unknown if presentation of the stationary baseline condition also influenced thresholds. However, if difficulties shifting attention between the prime and test stimuli, partially account for the results obtained, presentation of longer ISIs between the prime and test, should reduce the processing disadvantage found when the prime and test are presented in the same direction. When the prime and test are presented in opposite directions, the amount of facilitation found should also be reduced. For a control group, presentation of ISIs up to 600 ms has no influence on coherence thresholds obtained (Raymond and Isaak, 1998).

Although difficulties shifting attention between the different objects (prime and test) presented in Experiment 2, could contribute to the results obtained, it is difficult to use this attentional process to explain the findings of Experiment 1 in which regardless of the stimulus parameters used, the group with dyslexia had higher coherence thresholds. However, when dot density was increased and longer stimulus duration used, normal temporal recruitment was found. These longer presentation times and high dot density might have allowed the group with dyslexia to orientate attention to the signal dots in the RDK more efficiently than in the conditions in which a low dot density and shorter stimulus duration was used. This would have allowed normal temporal recruitment. Findings of a larger effect size in between groups analysis when a low dot density is used in a global motion task provides some support for this conclusion (Benassi et al., 2010).

In addition, presentation of stimuli of a higher contrast or different color to the noise dots might also have captured attention, allowing normal processing of coherent motion (Sperling et al., 2006; Conlon et al., 2012). The use of a pre-cue to direct attention either to low contrast motion signals in the RDK or to direct attention to specific features in a visual search task (Moores et al., 2011) has also provided evidence that directing attention can normalize coherence thresholds and improve visual search in groups with dyslexia. Although speculative, these results do indicate that attentional processes at PPC might influence coherent motion sensitivity, particularly when the computational complexity of the task is high.

The presence of a sensory processing deficit in the M or dorsal streams in groups with dyslexia is controversial (Ramus et al., 2003), with many studies presenting evidence that supports the presence of such a deficit (e.g., Cornelissen et al., 1995; Talcott et al., 2000). There are also studies that have found no evidence that a deficit is present (Ramus et al., 2003; Edwards et al., 2004; White et al., 2006) or have reported that about 30% of the group with dyslexia have this type of deficit (Amitay et al., 2002; Conlon et al., 2009). Alternative explanations such as difficulties with noise exclusion (Sperling et al., 2006), inattention (Williams et al., 2003) or temporal integration (Raymond and Sorensen, 1998) have also been presented. The results of the current study could be explained within the controversial sensory processing framework of dyslexia. The findings are supported by physiological evidence that neurons in the M and dorsal stream of groups with dyslexia are fewer in number, presented more sparsely and in a more disorganized manner than those found in normal readers (Galaburda and Livingstone, 1993; Stein and Walsh, 1997; Talcott et al., 2000) and that reduced neural activation at MT is found when VEP activity is measured during exposure to coherent motion (Schulte-Körne et al., 2004; Jednoróg et al., 2011). These findings are consistent with problems sampling the available motion signals present in the RDK, particularly when the perceptual difficulty of the task is high. However, these results might also indicate that directing and shifting attention between the feature specific components of these complex stimuli also contributes. Further research should directly investigate the extent that groups with dyslexia can optimize the perceptual filters needed to process complex stimuli and exclude noise, processes that can be evaluated within the perceptual template model of attention (Lu and Dosher, 2008).

Reading is also a computationally complex process which requires the use of a combination of visual, auditory and linguistic processes. Some researchers have suggested that the attentional consequences of impaired processing in the M and dorsal streams, causes difficulties with attention processing at PPC (Hari and Renvall, 2001; Vidyasagar and Pammer, 2010). Attentional difficulties have been linked to the way that children and adults with dyslexia process the sequentially presented letters on pages of text (Vidyasagar, 1999). Due to the sample sizes used in the current experiments, particularly Experiment 2, the associations between the sub-skills of reading and coherence thresholds were not evaluated. The systematic increases and decreases in coherence thresholds found in the group with dyslexia when different methodologies are used indicates that the processes need to efficiently perform a coherent motion task in adults with dyslexia can be normalized under specific circumstances. The challenge for future research is to determine whether the motion processing deficit found in dyslexia occurs in some individuals because of a vulnerability that is independent of their reading difficulties, or whether the deficit found is associated with the development or maintenance of word reading difficulties in this group. To make causal associations prospective longitudinal studies are needed, which measure temporal processing prior to the development of reading skills.

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Temporal sampling in vision and the implications for dyslexia

Kristen Pammer*

The Research School of Psychology, The Australian National University, Canberra, ACT, Australia

Edited by:
Usha Goswami, University of Cambridge, UK
Andrea Facoetti, Università di Padova, Italy
Marie Lallier, Basque Center on Cognition Brain and Language, Spain
Alan J. Power, University of Cambridge, UK

Reviewed by:
Jarmo Hamalainen, University of Jyvaskyla, Finland
John F. Stein, University of Oxford, UK

****Correspondence:***
Kristen Pammer, The Research School of Psychology, The Australian National University, Canberra,
ACT 0200, Australia
e-mail: kristen.pammer@anu.edu.au

It has recently been suggested that dyslexia may manifest as a deficit in the neural synchrony underlying language-based codes (Goswami, 2011), such that the phonological deficits apparent in dyslexia occur as a consequence of poor synchronisation of oscillatory brain signals to the sounds of language. There is compelling evidence to support this suggestion, and it provides an intriguing new development in understanding the aetiology of dyslexia. It is undeniable that dyslexia is associated with poor phonological coding, however, reading is also a visual task, and dyslexia has also been associated with poor visual coding, particularly visuo-spatial sensitivity. It has been hypothesized for some time that specific frequency oscillations underlie visual perception. Although little research has been done looking specifically at dyslexia and cortical frequency oscillations, it is possible to draw on converging evidence from visual tasks to speculate that similar deficits could occur in temporal frequency oscillations in the visual domain in dyslexia. Thus, here the plausibility of a visual correlate of the Temporal Sampling Framework is considered, leading to specific hypotheses and predictions for future research. A common underlying neural mechanism in dyslexia, may subsume qualitatively different manifestations of reading difficulty, which is consistent with the heterogeneity of the disorder, and may open the door for a new generation of exciting research.

Keywords: reading, dyslexia, vision, temporal coding, oscillation, synchronisation, review

Developmental Dyslexia is a cognitive learning difficulty where a child demonstrates a specific problem in reading, with no obvious cause. A "definition by exclusion," it refers to a child that has experienced normal teaching and learning environments, has had normal social experiences, has no other comorbidities, and has a normal IQ, yet still demonstrates a specific reading difficulty (Scanlon, 2012). In reality, a dyslexic child quite often demonstrates comorbidities, or experiences impoverished social environments for example, and a child with a low (or high) IQ can still present as dyslexic. However, the definition by exclusion is important for researchers when trying to isolate biological bases for dyslexia, as it allows them to be more confident that the cognitive disorder the child is presenting with, is in fact likely to be dyslexia. Moreover, dyslexia is not just a childhood problem. Many adults who have suffered from developmental dyslexia as children never develop good reading skills (Hatcher et al., 2002). Those who do compensate for their reading difficulty and become good readers, invariably suffer from residual difficulties such as poor spelling and poor phonological coding (Lindgren and Laine, 2011).

The majority of children presenting with dyslexia demonstrate problems with phonics, where "phonics" is generally characterized as sensitivity to the subtle sounds of language. Tests of phonological awareness tend to be tests of how well an individual can understand, segment and manipulate speech and language sounds. Poor phonological coding precedes subsequent poor reading: most dyslexic children demonstrate some kind of difficulty in phonological coding, poor phonological coding remains when children grow into adulthood and develop compensated reading skills, and explicit training in phonics is the best strategy available with regard to a treatment for dyslexia (refer to Snowling, 2000 for a review). However, in regards to the latter point, phonics training is the best form of remediation as indicated by current evidence, but this could also be because research looking at other types of training such as visual training (e.g., Franceschini et al., 2013) or training grapheme-phoneme correspondences based on grain size (e.g., Kyle et al., 2013) is in its infancy. Thus dyslexia is often considered a form of language disorder as its basic aetiology may be in the form of deficits in auditory coding that make it difficult to develop stable phonological-graphemic relationships.

In addition to phonological coding, a large amount of research over the last 40 years has also demonstrated that many dyslexic readers have subtle visual deficits. Historically, dyslexia was considered a visual deficit, in the form of congenital word blindness; however, that dyslexic readers consistently demonstrated normal visual acuity, challenged the old "visual deficit" hypothesis in favor of deficits in phonological coding. Nevertheless, subsequent evidence suggests that many dyslexic readers appear to suffer from a deficit in coding visual information that is specific to the dorsal (or magnocellular) visual pathway (e.g., refer Stein, 2001; Pammer and Vidyasagar, 2005 for reviews).

THE MAGNOCELLULAR DEFICIT THEORY OF DYSLEXIA

At the subcortical level, the visual system consists of at least two pathways, magnocellular and parvocellular pathways, which carry visual information from the retina, through separate layers of the lateral geniculate nucleus (LGN) and project to distinct layers of primary visual cortex (V1). The two pathways run parallel to each other and consist of neurons which differ not only anatomically but also physiologically (Galaburda and Livingstone, 1993; Merigan and Maunsell, 1993; Zeki, 1993), suggesting that the they are specialized for processing different kinds of visual information. The magnocellular pathway demonstrates a high degree of sensitivity to low contrast, low spatial frequency, high temporal frequency, and achromatic visual information (Merigan and Maunsell, 1993). Consisting of large heavily myelinated neurons with fast conduction velocity, the magnocellular pathway responds maximally to rapid temporal changes, with magnocells responding at stimulus onset/offset rather than throughout the entire stimulus presentation. Conversely, the parvocellular pathway consists of small neurons that are sensitive to high spatial frequency, low temporal frequency, and color information, demonstrating sustained response activation throughout the entire duration of the stimulus (Goodale and Milner, 1992; Merigan and Maunsell, 1993).

From V1 the anatomical and functional dissociation of the magnocellular and parvocellular pathways becomes less clear, with visual information from the two streams interacting considerably as they project to extrastriate visual areas (Ferrera et al., 1992; Merigan and Maunsell, 1993; Nealey and Maunsell, 1994; Vidyasagar et al., 2002). Anatomical data indicates that the magnocellular and parvocellular systems may converge as early as layer 4 of V1 (Yabuta and Callaway, 1998), suggesting that higher order dorsal processing may not be entirely indicative of lower level magno functioning. Nevertheless two distinct cortical streams, the dorsal and ventral streams respectively, exist (Benardete et al., 1992; Zeki, 1993). The ventral (or "what") stream receives both magnocellular and parvocellular inputs as it projects to the inferotemporal cortex, an area specialized in extracting details relating to an object's shape and color (Zeki, 1993). This is in contrast to the magnocellular dominated dorsal (or "where") stream, which passes through V5 before projecting to the posterior parietal cortex, a selective spatial attention area specialized for processing the location of objects in space. Thus the dorsal pathway is considered to be responsible for visual qualities such as spatial awareness and movement, while the ventral pathway is considered to be responsible for qualities such as color processing and visual detail.

It is thought that dyslexic readers demonstrate difficulties transmitting visual information that is carried by the dorsal/magnocellular pathway. Here "dorsal" and "magnocellular" are somewhat different in that "magnocellular" refers to the cells that make up the dorsal visual pathway, and the dorsal pathway actually contains a small proportion of both parvocells and koniocells. However in the literature this distinction has frequently been blurred, and for the sake of brevity I will use "dorsal/magnocellular" to refer to theories and research that refer to both or either terminology. This Theory has become known as the "magnocellular deficit" hypothesis (Stein, 2001). Why the dorsal pathway is impaired in dyslexia, remains open to speculation, but may lie in the possibility that developmentally, the dorsal pathway is more vulnerable than the ventral pathway (Braddick et al., 2003). Numerous behavioral studies have demonstrated that; dyslexic readers are less sensitive to visual information that is carried by the dorsal/magnocellular pathway (e.g., Martin and Lovegrove, 1987; Pammer and Wheatley, 2001; Wright and Conlon, 2009), that sensitivity to dorsal/magnocellular tasks exist in children at risk for reading difficulties before they learn to read (Kevan and Pammer, 2008), that dorsal /magnocellular deficits predict subsequent reading ability in pre readers at risk for reading impairment (Boets et al., 2008; Kevan and Pammer, 2009), and that dorsal/magocellular sensitivity is correlated with reading ability (Witton et al., 1998; Pammer and Kevan, 2007). There is also good neurophysiological evidence to support a deficit in the dorsal/magnocellular pathways in dyslexic readers (Eden et al., 1996; Demb et al., 1998; Jednorog et al., 2011). Yet despite deficits in the dorsal pathway, visual coding in the ventral/parvocellular pathway in dyslexic readers remains normal. There is also substantial evidence to suggest that dyslexic readers have deficits in other sensory domains, such as auditory (refer to Hämäläinen et al., 2013 for a recent review) and motor processes (e.g., Thomson et al., 2006; Thomson and Goswami, 2008), prompting the suggesting that dyslexia might be a disorder that encompasses sensory systems more globally (Stein and Walsh, 1997).

However the view that dyslexic children demonstrate sensory coding deficits is not universal. For example, auditory processing deficits have not been found in all dyslexic children (Hill et al., 1999; Edwards et al., 2004; White et al., 2006). Halliday and Bishop (2006) compared dyslexic, normal readers and children with sensory hearing loss on auditory frequency modulation thresholds, they demonstrated that an amplitude modulated signal disrupted both low and high frequency coding, but only the children with sensorineural hearing loss differed from the normal readers, with no difference found between normal and dyslexic readers. Similarly, in some cases no differences have been found between dyslexic and non-dyslexic readers in the perception of speech signals (Messaoud-Galusi et al., 2011). Similar discrepant results have been found for visual processing (Ben-Yehudah et al., 2001; Stuart et al., 2001; Amitay et al., 2002; Olson and Datta, 2002; Ramus et al., 2003; White et al., 2006), where dyslexic readers have not been found to be different from normal readers. Refer to Skottun for comprehensive, alternative reviews of the magnocellular literature (e.g., Skottun, 2005; Skottun and Skoyles, 2007, 2008). Ramus et al. (2003) has suggested that sensory deficits may be characteristic of specific groups of dyslexic readers, such that deficits in different domains may be characteristic of different behavioral manifestations. This notion will be revisited in the "questions and hypotheses" section of this paper.

One important question regarding visual coding and dyslexia is to understand the link between dorsal/magnocellular processing, reading, and dyslexia. Because dorsal/magnocellular processing is not intuitively a natural candidate to support reading skill (its area of expertise is in coding spatial information, movement, and contrast), this link is not obvious. Some of the specific visual tasks that dyslexic readers have difficulties with, include: orienting attention (Facoetti et al., 2001, 2006), focusing attention (Facoetti et al., 2000, 2003), scanning cluttered environments

(Williams et al., 1987; Vidyasagar and Pammer, 1999; Sireteanu et al., 2008), and coding the locations of letters within words (Cornelissen et al., 1998). One interpretation of this evidence is that the dorsal/magnocellular pathway is important in the reading process by virtue of its role in attention (Hari et al., 1999; Iles et al., 2000; Vidyasagar and Pammer, 2010; Moores et al., 2011), specifically in the spatial coding and binding of letter and word features, letters within words, and directing saccadic movements across the page (Vidyasagar, 1999, 2004; Vidyasagar and Pammer, 1999). Problems with these processes would make it difficult for a young reader to generate stable visual representations of words, and move the eyes in a way to access the important visual qualities of text.

The notion that visual deficits in dyslexia may occur as a consequence of difficulties in binding the visual components of letters and words is consistent with what is known about the cortical processing of other visual objects. Object recognition is dependent on different parts of the cortex "binding" or synchronizing information to provide a coherent whole. For example, identifying a red bird flying from a tree requires at its very basic level, identifying the color of the bird, and the color of the leaves, identifying the bird-features and the tree-features, extracting the bird-object from the tree-object, and the movement of the bird, as distinct from the movement of the tree. This simple percept requires highly sophisticated cortical binding. For example, color needs to be bound to the locations of the various objects in space, which needs to be bound with the movement information. Moreover, all of this occurs within tens of milliseconds, and the visual system is extremely good at it; we would rarely—in the above example—perceive a green bird and red tree, suggesting that there are highly accurate and robust neural networks that communicate their information across time and space. Reading may be seen as an extension of this sophisticated cortical binding. Natural reading requires binding similar temporal and spatial information; letter features are to be bound into coherent letters, which are then placed within the correct locations within words, such that they can be identified, and the eye guided to the next location. Because the eye is moving very quickly across a page—fixations and saccades are in the order of 20 and 200 ms respectively—the spatio-temporal synchrony necessary to extract the letter, word, and sentence objects is really astounding.

However, like natural object recognition, these bottom-up processes do not occur in a linear, isolated fashion, but rather, are supported and sustained by top-down influences that facilitate recognition. For example, we demonstrated that "higher-level" cognitive functions in the reading network, such as language processing, are active within a few hundred milliseconds of the start of visual coding in the visual cortex. This was followed by both visual and language processing occurring in a dynamic, cascaded way, featuring feed-forward and feedback information flow (Pammer et al., 2004). This supports the notion that reading skills are dependent on a dynamic synthesis of both bottom-up and top-down information flow.

Thus, like other forms of object recognition, visual coding of text requires large populations of neurons to be synchronizing and synthesizing information extremely quickly, over disparate cortical areas to form coherent percepts.

TEMPORAL SAMPLING

Neuronal firing has a stochastic element, showing in their discharge, a large amount of variability and seemingly random firing patterns (e.g., Wang, 2010). However, behavior is not dependent on single cells firing at random, but rather on the coordinated, synchronous firing of thousands of cells in a neuronal population. That the brain demonstrates rhythmic discharge variations within neuronal populations has been known since the 20's with the first recordings of the alpha rhythm (Berger, 1929) and has resulted in hundreds of papers dedicated to understanding how and why such cortical rhythms occur. Indeed it is likely that unlocking the secrets of cortical rhythms will unlock many of the secrets of the brain.

In the current context, I will consider only rhythmic neural oscillations at the macroscopic level. Although oscillations have been observed for many years at the single-cell level (e.g., Hodgkin and Huxley, 1952; Llinas et al., 1991; Llinas and Steriade, 2006), the rhythmic cortical activity observable using EEG or MEG occurs when large populations of neurons synchronize to produce oscillations with a common frequency, amplitude and phase (Hämäläinen et al., 1993). In some cases, populations of neurons decouple from a common oscillation to synchronize at a different frequency or amplitude. This is referred to as Event Related Desynchronisation (ERD), and Event Related Synchronisation (ERS) occurs when local cell populations synchronize to form a coherently oscillating population (Pfurtscheller and Lopes da Silva, 1999). Moreover, populations of neurons in different areas of the brain can synchronize their oscillatory activity, which has been hypothesized to reflect cortical communication (Singer, 1999, 2009; Wang, 2010; Thut et al., 2012). It is this synchronisation of oscillatory behavior that is believed to underlie cortical binding, perception, cognition and behavior (Singer, 1999; Engel and Singer, 2001; Wang, 2010; refer to Siegel et al., 2012; Thut et al., 2012 for recent reviews).

Although it is assumed that cortical rhythms are causally related to behavior, it is possible that such cortical rhythms are simply epiphenomenal to information processing and behavior. However, there are a number of brain rhythms that have been associated with different cognitive or behavioral states, although there is a great deal of fluidity around the notion that particular cortical rhythms = cognitive function, and all the oscillatory rhythms that are generated by the brain have been demonstrated in one way or another with most cognitive functioning. Nevertheless, there is some broad consistency in the literature regarding some frequency ranges and cognitive/perceptual functioning. For example, theta rhythms (4–8 Hz) have been associated with maze navigation (Caplan et al., 2003; Kahana et al., 1999), episodic memory (Lega et al., 2012; Burke et al., 2013) and working memory (Sauseng et al., 2009; Moran et al., 2010). The alpha rhythm is one of the primary brain rhythms and frequently associated with various aspects of perception and cognition (e.g., Pfurtscheller and Klimesch, 1991). Beta rhythms (15–30 Hz) have been associated with motor preparation (Alegre et al., 2006; Cheyne et al., 2012) and control (e.g., Salmelin et al., 1995; Stancák and Pfurtscheller, 1996), and gamma rhythms (30–80 Hz) appear to be an index of attention (Jensen et al., 2007), feature binding (Tallon-Baudry et al., 1997) and object recognition (Tallon-Baudry and Bertrand, 1999; Martinovic et al., 2008; Friese et al., 2012). Some frequencies have been directly associated with changes in perception, for example, Fries et al. (2001) demonstrated that a gamma response in the visual cortex increases in response to attending to a behaviorally relevant stimulus. Connectivity at specific frequencies has also been demonstrated to reflect behavior. We demonstrated (Kujala et al., 2007) that unique areas of the brain synchronized at 8–12 Hz (alpha range) in response to different reading requirements. In this study, participants were presented with continuous text presented at rates that made comprehension easy, effortful, very difficult (only the general gist of the story was apparent), or impossible (random text). Left hemisphere cortical activations consistent with a reading network were activated at 8–12 Hz in a dynamic way that reflected the cognitive requirements of the reading task. Similarly, Hummel and Gerloff (2005) required participants to perform a visuo-tactile integration task, where a braille-like pattern was to be matched to a visual pattern on a computer screen. Long-range coherence between visual and motor areas, at the alpha frequency increased with better performance on the visuo-spatial integration task.

There are many examples of changes in oscillatory power or frequency in response to changes in information processing (refer Siegel et al., 2012 for a recent review), supporting the proposal that cortical oscillations, and the synchronisation of oscillations may represent a biological mechanisms for perception and cognition (e.g., Neuper and Pfurtscheller, 2001).

AUDITORY TEMPORAL SAMPLING IN DYSLEXIA

It has recently been suggested that poor phase-locking at low frequency theta and delta bands, (approximately 2–10 Hz), could be the proximal cause of dyslexia (Goswami, 2011). Phase-locking, also referred to as phase-synchrony (Lachaux et al., 1999), is the synchronisation of a brain signal at a specific frequency, reflecting the fact that the phase of the neural oscillation synchronizes with other neural oscillations, typically as fast evoked response to an external signal. Unstable auditory phase-locking at 2–10 Hz is believed to underlie the specific phonological impairments characteristic of dyslexia, and it has been suggested that such impairments may reflect a broader multi-sensory deficit, explaining some of the visual deficits also apparent in dyslexia (Goswami, 2011).

However, abnormal cortical oscillations in the auditory domain in dyslexia are not unique to theta or delta oscillations. For example, Lehongre et al. (2011) demonstrated abnormal auditory frequency dynamics in dyslexic readers in the gamma (25–35 Hz) frequency range. They presented dyslexic and normal readers with an auditory stimulus that was modulated linearly from 10 to 80 Hz. The associated auditory entrainment in the gamma range in normal readers was lateralized to the left hemisphere, specifically the superior temporal sulcus and planum temporale. They suggested that this neural signal is necessary for the fast formant transitions that occur in phonemic segregation. In dyslexic readers, however this gamma signal to the same stimulus was significantly reduced—providing a potential neurophysiological correlate of the common observation that dyslexic readers are impaired in phonological processing (Snowling, 2000). Moreover, dyslexic readers showed increased entrainment at 30 Hz in the right hemisphere—both compared to their left hemisphere, and compared to normal readers. This is also consistent with the evidence that dyslexic readers may develop compensatory right hemisphere reading networks, compared to normal readers (Leonard and Eckert, 2008), particularly for phonological output measures such as rapid automatized naming which requires left and right hemisphere integration (Eden et al., 2004). In addition, dyslexic readers show abnormally strong entrainment in the high gamma range (50–70 Hz) in the planum temporale of both hemispheres compared to controls.

Using sentences presented auditorily, Han et al. (2012) demonstrated that normal readers synchronize (normalized phase locking) high frequency gamma band (30–45 Hz) information bilaterally in the left and right auditory cortex, such that phonologically similar target words resulted in increased phase-locking, while phonologically dissimilar words resulted in decreased phase locking. Dyslexic readers however showed the opposite pattern of synchronisation. Since phonologically similar words require a more sophisticated analysis of phonemic information in order to distinguish between a "sensible" word, and a phonemically similar foil, the findings suggest better phonemic segmentation for heard words in normal readers compared to the dyslexic readers.

Clearly then cortical oscillatory activity in the auditory domain differs in dyslexia compared to normal reading. According to the temporal sampling hypothesis proposed by Goswami (2011), abnormal neural oscillatory activity may be responsible for dyslexia as a consequence of poor theta synchronisation to the sounds of language. There is also evidence for abnormal oscillatory activity in higher frequencies for dyslexic readers in response to auditory processing, which may also contribute to poor auditory temporal coding of language signals, making it difficult to develop good reading skills. However, reading is foremost a visual process, and dyslexia has also been associated behaviorally and physiologically with deficits in the dorsal visual pathway. Therefore, is there evidence for a visual correlate of the auditory temporal sampling hypothesis?

PHASE LOCKING OF SPEECH AND READING SIGNALS

Entrainment refers to oscillatory activity of neurons becoming synchronized with a repeated signal or perturbation (Pikovsky et al., 2003). External entrainment can occur by providing constant rhythmic stimuli such that neural assemblies phase-lock to the stimuli, synchronize their phase, and thus increase the neural signal (Thut et al., 2011). In this case, synchronizing and entrainment refer more-or-less to the same result—neural populations that have phase-locked to a signal and now oscillate at the same (or its harmonic Price and Ibbotson, 2001) frequency (refer to **Figure 1A**). One of the proposals of the temporal sampling hypothesis, is that auditory coding entrains to the temporal sampling of the speech signal—specifically its syllabic structure, and that this entrainment occurs at approximately the theta rhythm reflecting the temporal rhythm of syllabic structure (refer to **Figure 1B**). Dyslexia occurs when this phase-locking, entrainment and synchronisation are impaired, resulting in poor coding of speech, and thus a difficulty in generating

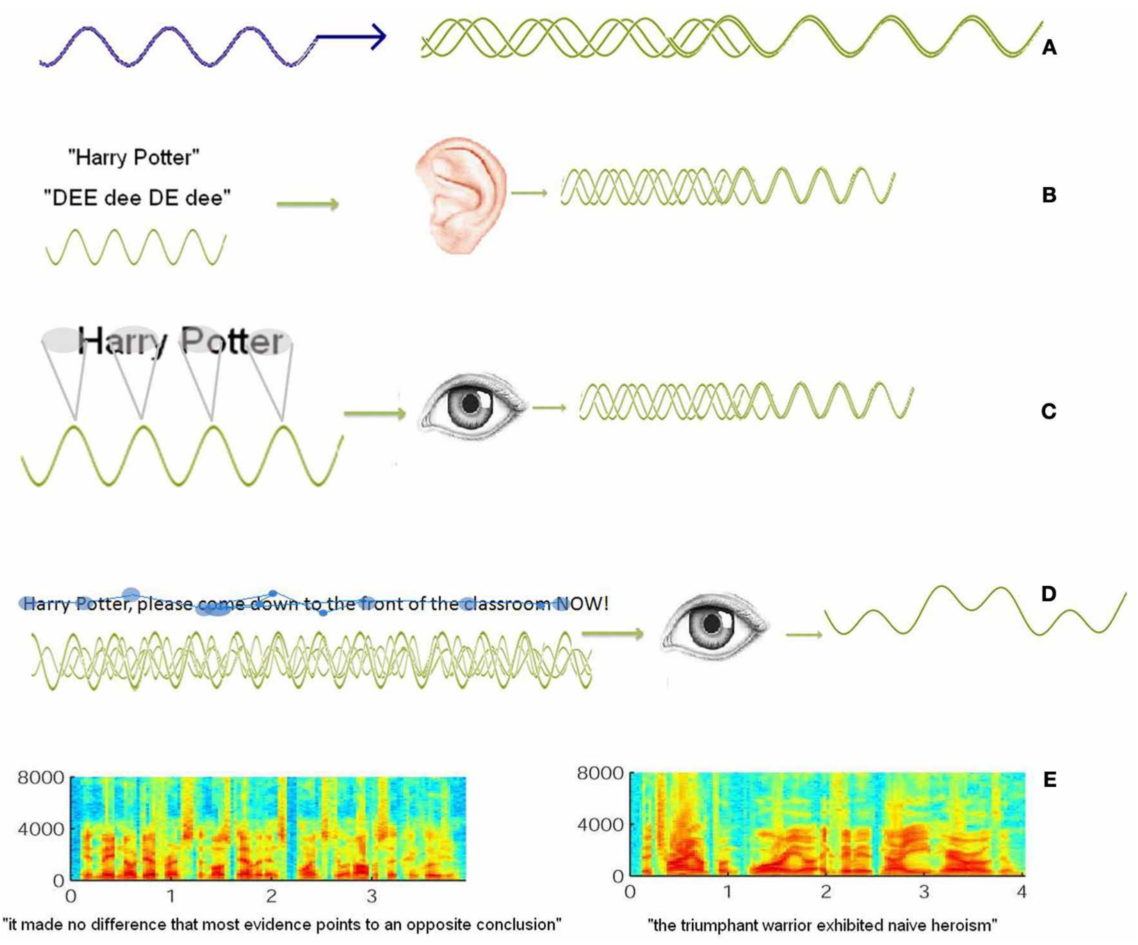

FIGURE 1 | (A) Is an illustration of how oscillatory signals—either external, or internal, can entrain a cortical oscillation, such that networks of neurons synchronize to oscillate at a critical frequency. It has also been suggested that the rhythmic nature of spoken language, such as "Harry Potter" in "dee's" (Goswami, 2011) can entrain an oscillatory cortical signal **(B)**. Moreover, the sequential spatial coding of words when reading lends itself to temporal sampling at much the same frequencies **(C)**. However, **(D)** is an example of how when reading, the unpredictable nature of fixations, saccades and regression might make it difficult to generate a single stable oscillatory signal, which in turn might make it difficult to entrain an associated oscillatory signal in the visual cortex. Here, the blue dots represent fixations of varying length and regressions. Similarly, when listening to speech, sentences have different spectral energy, **(E)** the sentence on the left has a spectral signature that is much more regular than that on the right. Nevertheless, Luo and Poeppel (2007) demonstrated entraining in the auditory cortex to both sentences (reproduced with permission from Luo and Poeppel (2007), supplementary material. Elsevier).

stable language-graphemic representations. Using the same arguments, it should also be possible for the visual system to entrain a visual signal that is phase-locked into the visual sampling of text.

Like the auditory coding of the speech stream, visual coding of text requires sequential sampling of words and text (refer to **Figure 1C**), and this sampling rate is consistent with the sampling rate of speech, i.e., approximately 2–10 Hz. In reading, fixations occur approximately every 200 ms (Rayner, 1998), and understanding the text requires the very fast sampling and concatenation of information from fixations to form a continuous, understandable percept—much like understanding speech. Moreover, it has been suggested that the temporal-spatial sampling of text is controlled by the magnocellular/dorsal stream, which then gates sampled information to the ventral pathways and other higher order cognitive mechanisms (Vidyasagar, 1998, 1999). If then, similar temporal mechanisms exist in both speech perception, and reading, it is possible that a common mechanism underlies both, and this would predict that dyslexic readers would be less sensitive to some of the visual equivalents of auditory signal processing.

It has been demonstrated that dyslexic readers are less sensitive to visual stimuli of low *spatial* frequency (Lovegrove et al., 1980; Badcock and Lovegrove, 1981; Slaghuis and Ryan, 1999), but the above hypothesis would predict that dyslexic readers would be less sensitive to visual signals that are presented at a regular temporal frequency, in much the same way they are impaired at processing auditory signals presented at a regular temporal frequency (refer to Goswami, 2011 for a review). However, "temporal coding" in vision in dyslexia can mean quite different things, and the research findings are highly variable. One interpretation of temporal coding is the speed at which the visual system can code visual information, another is the ability for the visual system to detect rapidly changing temporal events (e.g., refer to Farmer and

Klein, 1995; McLean et al., 2011), and the research literature rarely distinguishes between the two.

There is evidence to suggest that dyslexic children have difficulties in sequencing the temporal order of quickly presented stimuli (e.g., di Lollo et al., 1983; Brannan and Williams, 1988; Hari et al., 2001; Jaskowski and Rusiak, 2008; Liddle et al., 2009). These are typical Temporal Order Judgment (TOJ) tasks in which the participant is presented with a number of items (usually 2 or 3) in fast succession, and required to indicate their temporal order. The problem with TOJ tasks is that they can be quite difficult, and have quite a high memory load, so any differences between dyslexic and non-dyslexic readers could manifest from a number of different perceptual or cognitive causes. Similarly, the length of time it takes for a neural signal to decay in order to identify two discrete events, is Visible Persistence (VP). Dyslexic readers have been shown to require longer delays between signals (Badcock and Lovegrove, 1981; Slaghuis and Lovegrove, 1985; Lovegrove et al., 1986; Slaghuis and Ryan, 1999; Conlon et al., 2004), suggesting a longer period of neural persistence, although other studies have failed to find such a difference (e.g., Schulte-Körne et al., 2004). Temporal coding can also mean how quickly the visual system can deal with visual information i.e., processing speed. McLean et al. (2011) measured the temporal integration thresholds of the magnocellular and parvocellular pathways respectively. Here two isoluminant colored patches are alternated to "flicker." The temporal resolution of the flicker increases until the color merges, but the flicker is still noticeable—this is the parvocellular resolution limit. If the temporal frequency is increased further, then the colors not only merge, but the perceptual flicker goes away—this is the magnocellular resolution frequency. In this study, dyslexic children showed lower resolution thresholds compared to normal readers in their magnocellular, but not parvocellular thresholds.

If temporal coding in a language framework is predicated on the rhythmic frequency modulation of speech, and if temporal coding in reading is the rhythmic saccadic sequencing of visual information, then Attentional Blink (AB) may be a useful candidate to conceptualize visual temporal coding, and has the added bonus of at least one theoretical framework that is based on rhythmic pulses of neural signals. AB is a task that involves an RSVP stream of distractor stimuli (such as letters) in which are imbedded two targets (such as numbers); T1 and T2. Perception of T2 decreases when the delay between T1 and T2 is between 200–400 ms. The Boost and Bounce theory of AB (refer to Olivers and Meeter, 2008 for a comprehensive discussion of this theory) suggests that AB reflects a continuous, rhythmic sequence of visual signals. In dyslexia then if this fast temporal signaling is impaired (slower, or longer, less defined for example), then it might predict a number of outcomes: dyslexic readers should show less T1-sparing and lower detection of T1 because of a more prolonged signal from the distractor the precedes it. Although the research findings are mixed in AB and dyslexia, this is in fact one common finding (e.g., Hari et al., 1999; Visser et al., 2004; Facoetti et al., 2008). The dip in the "blink" might also be prolonged, and/or shifted to the right in dyslexic readers because the signal from T1 also lasts longer, which is consistent with some findings (Hari et al., 1999; Visser et al., 2004; Facoetti et al., 2008), although others have failed to find this effect (e.g., Lallier et al., 2010). Others have found no differences between dyslexic and normal readers (Badcock et al., 2008; McLean et al., 2010). One of the problems about AB is that there are multiple ways in which the dip can be analyzed and reported, which makes it difficult to compare results.

For the purposes of this paper, "temporal coding" is probably best conceptualized as both processing speed and the ability of the visual system to deal with information presented quickly, such as at the rate of saccadic and fixation sequences, or even faster. As in the auditory domain, temporal coding here really refers to the ability of the visual system to effectively process quickly presented information. Here "quickly presented information" comes about either because stimuli is presented quickly in sequence, such as in an RSVP (IB) task, or the visual system engages in a sequential temporal sampling process such as when reading. Thus, as an RSVP task presents the visual system with fast discrete visual percepts, so does reading when the bottom-up data acquisition during a fixation is separated by a "dwell time" caused by the saccade. The differences between the temporal processing tasks above and reading, is that the temporal component in the above tasks is procedural, caused by the stimuli itself and the eyes are static, compared to reading, where the temporal component is mechanical, caused by the fixations, saccades and eye movements, while the stimuli is static. A summary of some of the research regarding temporal coding in dyslexia is in **Table 1**. However, an important distinction here is that this is behavioral research, where "temporal coding" refers to the ability to process quickly presented information. It is still unclear the degree to which these studies inform the neural process of temporal coding which refers to the synchronisation of neural signals.

Conceptualizing visual temporal processing in this mechanical way also allows us to consider visual search and change detection. Here, like reading, the stimulus is static and the temporal information flow through to the visual system is mediated by fixations, saccades, and eye movements. There is a theoretical argument that links visual search to magnocellular/dorsal processing (Vidyasagar, 1998, 1999; Vidyasagar and Pammer, 1999, 2010), and studies have shown that dyslexic readers are worse than control readers at detecting a target in serial search and change detection (e.g., Vidyasagar and Pammer, 1999; Rutkowski et al., 2003; Jones et al., 2008; de Boer-Schellekens and Vroomen, 2012), and serial search predicts later reading ability in prereaders (Franceschini et al., 2012).

Thus, many visual temporal coding tasks also draw on quite significant cognitive abilities, such as sequencing, judgment and memory, and although such mechanisms are also required in reading, it makes it difficult to use tasks such as these to explicitly isolate the neural components of visual coding in the temporal sampling process. Studies looking directly at the neural correlates of simple visual synchronisation and entrainment have not been done for normal or dyslexic readers, but would provide a good test of a visual example of the temporal coding hypothesis as has been developed in the auditory domain.

One potential confound for the proposal that visual oscillatory activity may be able to entrain to the temporal sampling rate when reading, is that entrainment or synchronisation is most

Table 1 | A summary of some of the behavioral evidence regarding visual temporal coding in dyslexia.

Study		Task details			Outcome	
Attentional blink		**Distracters**	**Targets**	**Timings**	**Magnitude of dip**	**Location of dip**
	Hari et al., 1999	Black letters	White letter	106 ms, no ISI	Dyslexics generally poorer at detecting the target	Shifted to longer durations for dyslexics
	Visser et al., 2004	Random dots	A shape (square, cross etc.)	40 + 60 ms ISI	Dyslexic generally poorer than controls, similar pattern as for reading matched controls	Shifted to longer durations for dyslexics compared to controls, same patters as for reading matched controls
	Facoetti et al., 2008	None. Only T1 and T2 were presented at varying intervals and each were masked	Letters, each had a pre and post-mask	T1 and T2 were each 100 ms	Shallower and longer for Dyslexic's	Shifted to longer durations
	Badcock et al., 2008	Black letters	T1 = white letter T2 = black X	100 ms	No difference between dyslexic and non-dyslexic adults after correcting for baseline sensitivity	No difference between dyslexic and non-dyslexic adults
	Lallier et al., 2010	Black digits	T1 = Red digit (1 or 5) T2 = black "0"	50 + 66 ms ISI	Lower detection for dyslexics at lag 4. However, no difference between dyslexic and controls. When using technique by Cousineau et al. (2006) Participants had to achieve a performance criteria	No difference between dyslexic and controls.
	McLean et al., 2010	1 of 4 arrows	A shape (square, cross, plus, diamond, circle, triangle)	26 + 80 ms ISI	Demonstrated an overall deficit for dyslexic children compared to controls that was not specific to any of the AB parameters	
Visible persistence		**Task**	**Details**		**Results**	
	di Lollo et al., 1983	Gap-detection	Line stimulus-gap-line stimulus. Duration of line = 20 ms Gap ISI = staircase threshold. Participants compared this to a "no-gap" stimulus. The task was to indicate which stimulus contained the gap		Dyslexic readers required longer ISI's to make accurate judgements to detect the gap between line stimuli	
		Pattern integration	Participants were to detect the presence of a missing dot over successively presented dots that form a matrix pattern		No difference between dyslexic and non-dyslexic participants	
	Badcock and Lovegrove, 1981; Slaghuis and Lovegrove, 1985	VP	grating-blank-grating sequence. Duration of gratings = 300 or 75 ms ISI blank period = staircase threshold. Participants to indicate if they had seen the blank period		Duration of VP was the duration at which the blank field was just visible. Dyslexic readers required longer durations to detect the blank period	

(Continued)

Table 1 | Continued

Visible persistence		**Task**	**Details**	**Results**
	Slaghuis and Ryan, 1999	Ternus apparent motion	3 squares in a row where the outermost square jumps from the left to the right side. Perception reflects the square jumping (element motion), or all 3 squares moving from left to right (group motion) 40 ms stimulus duration, 10-70 ms ISI. Participants were to indicate whether they saw "group" or "element" movement.	Dyslexic participants were less likely to perceive "group" movement. Suggesting that Dyslexic children demonstrated longer visible persistence
			120 ms stimulus duration	No differences between groups on the perception of group or element movement
	Conlon et al., 2004	Temporal counting	Adult dyslexic were required to count the count square targets presented as a RSVP	Dyslexic participants were significantly less accurate in counting rapidly presented stimuli compared to normal adults readers
	Schulte-Körne et al., 2004	VP	grating-blank-grating sequence. Duration of gratings = 300 ms ISI blank period = staircase threshold. Participants to indicate if they had seen the blank period	Duration of VP was the duration at which the blank field was just visible. Dyslexic readers were no different from dyslexic readers (indeed normal readers required longer durations to detect the blank period)
	Jones et al., 2008	Ternus apparent motion	3 squares in a row where the outermost square jumps from the left to the right side. Perception reflects the square jumping (element motion), or all 3 squares moving from left to right (group motion) 40 ms stimulus duration, 10-70 ms ISI. Participants were to indicate whether they saw "group" or "element" movement.	No difference between dyslexic and non-dyslexic children
Temporal order judgement		**Task details**		**Results**
	Brannan and Williams, 1988	3-letter words, or a symbol (and or #) were presented to the left or right of fixation. Stimuli = 900 ms ISI = variable staircase to achieve 75% threshold		Dyslexic readers required a significantly longer ISI to make accurate judgements regarding which order the stimuli appeared.
	Hari et al., 2001	Stimuli were presented in the left and right hemifield, participants were to indicate which stimulus appeared first. The ISI between stimuli was varied		Dyslexic participants required longer durations to determine which stimulus appeared first. However, results were asymmetric such that they showed a right visual field (left hemisphere) advantage
	Jaskowski and Rusiak, 2008	Pairs of rectangles where each were presented above/below or left/right of fixation. Participants had to indicate which rectangle appeared first—the left or the right, the top or the bottom. The ISI was varied between the stimuli presentations.		Dyslexic participants generally required a longer interval to make accurate judgements. However contra to Hari et al, there was no left/right asymmetry
	Liddle et al., 2009	Stimuli were presented in the left and right hemifield, participants were to indicate which stimulus appeared first. The ISI between stimuli was varied. Participants had to indicate whether the left or right stimuli appeared first. In Exp2 Participants had to indicate the shape of the stimuli that appeared first.		d' for accuracy showed significantly lower sensitivity for temporal order judgements for dyslexic adults compared to non-dyslexic adults. There was no left/right asymmetry
Visual search and change detection[a]		**Task**	**Details**	**Results**
	Vidyasagar and Pammer, 1999	Visual Search	Conjunction search using shape and color.	Dyslexic children became progressively less accurate compared to normal reading children, in more cluttered arrays

(Continued)

Table 1 | Continued

Visual search and change detection[a]		Task	Details	Results
	Rutkowski et al., 2003	Change detection	4 letters arranged in a square array around the fixation point. Followed by a blank period (250 ms), followed by another 4-letter stimuli arrangement. The stimuli alternated until a response was made.	Dyslexic children required longer presentation times compared to normal readers to determine whether the two 4-letter target stimuli were the same or different.
	Jones et al., 2008	Visual search	gratings in a circle around a fixation. 1 target + (2, 4, 8, or 16) distractors. Presentation = 100 ms. Target was an off-vertical grating. Distractors = vertical grating	Dyslexic children were less accurate over all set sizes except 2 items
	Franceschini et al., 2012	Visual search	Children scan left-to-right across lines of stimuli to circle specific targets. Children were young, identified as "at risk" at grade year 1.	Poor readers made significantly more errors. Search performance predicted later (1 year) pseudoword reading, text reading and letter naming.
	de Boer-Schellekens and Vroomen, 2012	Visual search	Distractors = Line segments (24 or 48 items) Target = horizontal or vertical line The target and distractors changed color dynamically red through green.	Dyslexic readers took significantly longer than normal readers to detect the target, particularly at the larger set size
	Tulloch and Pammer, submitted	Visual Search	Stimuli presented on a computer tablet were "game-like" bugs. Participants had to find the target bug always present on the screen (no memory component)	Search results significantly predicted reading rate for a group of children with a large range of reading ability.

[a] *Not typically considered a temporal task, but here I am considering the possibility of a static display, where the visual temporal quality occurs because of the "shutter-like" extraction of information at fixations as the eye scans across the page.*

easily studied in the context of a regular periodicy in the signal stream (refer to **Figure 1A**). An input signal that does not have a regular periodicy will not generate stable oscillations, because there simply is not a stable oscillatory signal to entrain to (refer to **Figure 1D**). Reading (like speech perception), is in fact highly variable. Smooth, effortless reading does involve spatial sampling at approximately the theta range, but the crucial word here is "approximately." Fixations vary considerably: they are longer and more frequent for more difficult words, or unexpected words, regressions are common, and saccade length can also determine the speed at which the text is sampled (refer to Rayner, 1998 for a review), and there are also cognitive confounds such as attention, anticipation, and decision making that could generate their own entrained signals (Thut et al., 2011) which could make it difficult for the system to entrain to the visual input signal. Similarly, in natural language the rhythmicity of the language itself can be quite variable (refer **Figure 1E**). Despite these reservations, entraining of theta signals to speech *has* been demonstrated (e.g., Luo and Poeppel, 2007), and the theta synchronisation was correlated with speech intelligibility. Furthermore, it is certainly possible that different oscillatory networks may entrain to different frequency components of the speech signal, and poor reading and/or language processing could result from differential impairments in specific frequencies in the overall spectral network, or the interaction of these networks.

If reading *can* be demonstrated to entrain a low-frequency oscillation in the visual domain as a consequence of temporal sampling in the reading process (refer to **Figure 1C**), then this may have enormous implications for dyslexia. Dyslexic readers' eye movements when reading, are dramatically different from those of normal readers (e.g., refer to Rayner et al., 2001 for a review), with more frequent fixations that are longer and less stable, as well as shorter saccades and more frequent regressions. Moreover it has been suggested that dyslexic readers also have problems in achieving stable binocular control (Stein et al., 2000). Therefore, consistent with Goswami (2011), if normal reading can entrain the visual system, then the highly unstable and variable eye movement behavior in dyslexic readers could very well result in a poor oscillatory coding, because of an inability to generate a systematic, rhythmic saccadic rhythm.

AN ARGUMENT FOR A TEMPORAL SAMPLING HYPOTHESIS IN VISION IN DYSLEXIA

Cortical frequency oscillations have long been considered to underlie visual perception (e.g., refer to Pfurtscheller and Lopes da Silva, 1999; Sewards and Sewards, 1999; Singer, 1999, 2009; Tallon-Baudry and Bertrand, 1999; Engel and Singer, 2001, for reviews). However the question of interest here is the role of cortical frequency oscillations in visual processing in the context of dyslexia. Specifically, do dyslexic readers differ from normal readers in oscillatory phase-locking in visual tasks related to reading. The most direct test of whether dyslexic children demonstrate temporal coding deficits in the visual domain, that are consistent with those found in the auditory domain, is to measure cortical frequency dynamics in dyslexic children for visual stimuli, and/or to evaluate cortical frequency dynamics in dyslexic children in the visuo-spatial areas of the brain. No studies have done this in the context of entrainment to a visual stimulus. Almost all research into cortical frequency dynamics in dyslexic readers, has used auditory stimuli, such as tones (Nagarajan et al., 1999; Ucles et al., 2009; Heim et al., 2011), sounds—such as white noise (Lehongre et al., 2011; Hämäläinen et al., 2012), phonological tasks (Rippon and Brunswick, 2000), or sentences (Han et al., 2012). One EEG study looking at visuo-spatial cuing in dyslexic adults found reduced coherence in the parietal cortex in dyslexic compared to normal readers (Dhar et al., 2010), however the results were only presented in the 8.5 Hz (alpha) range, and it is not known if differential impairments exist in other frequency ranges.

Some studies of linguistic processing in dyslexic readers have used visually presented words, which might allow the extraction of some vision-specific coding. Milne et al. (2003) found an increase in beta power in the posterior brain regions for dyseidetic dyslexic adults, and the reverse pattern, with an increase in beta signals anteriorly for dysphonetic dyslexic adults in a visual lexical decision task. However, only broad-spectrum beta (12–30 Hz) was analyzed, and the lack of spatial specificity inherent in EEG allowed only "posterior" or "anterior" descriptions of the results. Similarly, using EEG and visually presented words, letters or pseudowords, power changes have been demonstrated in theta (Klimesch et al., 2001a,b), as well as alpha and beta oscillations (Klimesch et al., 2001a,b) in dyslexic children. In the first study, differences in theta activity between dyslexics and controls were interpreted to result from difficulties in working memory encoding in dyslexic readers, and potentially more effortful coding for words in occipital sites. In the second study, changes in the patterns of alpha and beta activation were interpreted to reflect differential allocation of sustained attention in dyslexic compared to normal readers. However, in both studies the analysis period consisted of 5 sec after the presentation of a stimulus, making it unlikely that vision-specific coding of the stimuli could be specifically extracted. Other researchers have also presented word, or word-like stimuli visually, but their analyses have been in terms of the linguistic and not the visual coding of the stimuli such that ROI's are language-related areas rather than visual areas (e.g., Spironelli et al., 2008).

To summarize, while a number of studies have specifically looked at oscillatory activity in the auditory cortex of dyslexic readers, none has looked at oscillatory activity to visual temporal coding in the visual cortex of dyslexic readers. This provides two areas to explore: First, in the normal reading population, what is known about cortical oscillatory responses in vision and reading? Second, what is known about cortical responses in some of the visual tasks underlying reading? From these two explorations, a reasonable theoretical framework might be constructed of a role for temporal visual coding deficits in dyslexia.

The visual aspects of reading involve a number of complex and interrelated components, such as object recognition, visual search, extracting information from a cluttered array, guiding eye movements, feature binding, attentional shifting, and preattentive visual coding. Such tasks have been hypothesized to be mediated by the dorsal/magnocellular visual pathway (Vidyasagar, 1998, 1999, 2004), and many of these tasks involve synchronous gamma oscillations (refer to Sauve, 1999; Tallon-Baudry and Bertrand, 1999; Engel and Singer, 2001; Singer, 2009; Tallon-Baudry, 2009; Merker, 2013). Thus it is not at all unreasonable to predict that oscillatory gamma signals are apparent in reading in the way that they are in the perception of speech, and it remains to be seen whether differences in gamma oscillations also characterize dyslexia in the visual domain, like in the auditory domain.

TEMPORAL SAMPLING AND THE MAGNOCELLULAR PATHWAY

Given that a deficit in the magnocellular pathway appears to be found in many dyslexic readers, it would seem logical to ascertain whether the magnocellular pathway is selectively responsive to particular cortical frequencies.

Sewards and Sewards (1999) speculated that low frequency oscillations are characteristic of the parvocellular pathway, and high frequency gamma oscillations of the magnocellular pathway. They reached this conclusion from the following evidence: alpha signals are characteristic of stimuli that are static, and where the eyes are also static, whereas gamma *and* alpha oscillations occur when the stimulus itself moves or, with static stimuli when the eyes move. This is consistent with the observation that the magnocellular pathway is responsive to motion. Similarly, cell layers in the LGN that oscillate in the gamma range were found in the layers innervated primarily by retinal magnocellular cells (Livingston, 1996). However, Sewards and Sewards, also point out that Livingstone only measured gamma oscillations, making it difficult to assess the nature of other frequency oscillations in the LGN layers[1]. Sewards and Sewards also suggest that the physiological responses of the magnocells and parvocells are consistent with differential oscillatory activity, in that the fast magno cells are sensitive to temporal frequencies up to 50 Hz, but the slower-transmitting parvo cells have specific modulation frequencies of <10 Hz (Wiesel and Hubel, 1966). More recently, Fründ et al. (2007) demonstrated that low spatial frequency visual stimuli (1 cpd)—which would be transmitted primarily by the magnocellular pathway—generated an evoked gamma signal, whereas high spatial frequency stimuli (10 cpd)—which would be transmitted primarily by the parvocellular pathway—generated an evoked alpha signal.

Pammer et al. (2006) conducted an MEG study in which participants were to perform a lexical decision task that used words presented normally, and words in which the internal letters were shifted up or down relative to each other. The aim was to selectively activate the magno/dorsal pathway in reading, by manipulating the spatial configuration of the internal letters of the words. In this study we demonstrated strong gamma and

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[1] It has also recently been demonstrated that low frequency rythms (<10 Hz) are characteristic of cells in the koniocellular layers of the LGN, not the magnocellular or parvocellular layers (Cheong et al., 2011).

alpha signals for the "shifted-words" condition, in the posterior parietal cortex—where we would expect magnocellular/dorsal activity. In addition, the time course of these signals was interesting, in that the first signal at approximately 150 ms was a gamma (35–40 Hz) signal, the second, at approximately 200 ms, an alpha signal, and the next signal at about 300 ms, again a gamma signal. It was argued that the initial gamma signal reflected a transient evoked signal—perhaps reflecting initial attentional mechanisms for spatial selection (Moran and Desimone, 1985; Motter, 1993; Vidyasagar, 1998, 1999; Martinez et al., 1999) and that the later gamma signal could be consistent with feature binding (Galambos, 1992; Başar-Eroglu et al., 1996; Pulvermüller et al., 1997; Tallon-Baudry and Bertrand, 1999; Hermann et al., 2004). The alpha signal that occurred between the early and late gamma signals was also associated with activation in a number of different cortical areas, possibly reflecting the recruitment of other cortical areas to support a relatively complex cognitive task.

Although projections of magnocellular and parvocellular neurons through the dorsal and ventral pathways respectively are not completely discrete, making it more difficult to isolate the two pathways, the evidence nevertheless suggests that high frequency neural oscillations could be a mechanism for binding the visual qualities of text, carried by the magnocellular/dorsal pathway. Thus a story is emerging that both high and low frequency signals may be important in visual coding in reading.

TEMPORAL CODING, VISION, AND READING

Very little research has been done to measure frequency oscillations specifically targeting the visual cortex in reading, and there is a tension between evidence for a theta deficit in dyslexia, and evidence that the magnocellular pathway is associated with gamma oscillations. However a few studies have found vision-specific coding to visually presented words and sentences, in the context of whole-cortex language networks. The results appear to be mixed, but suggest an interesting relationship between gamma and theta oscillations. In one study, Goto et al. (2011) conducted a time × frequency analysis for the reading network. In this study, participants engaged in a silent reading task, and the data was analyzed in five frequency bands (theta, alpha, beta, low gamma, and high gamma), using a 200 ms moving window technique up to 1550 ms post stimulus onset (see also Pammer et al., 2004 for a description of the methodology and an example of the reading network). **Figure 2A**, is adapted from Goto et al. (2011) and shows two spectrograms of interest. The first (a) is isolated in that part of the visual cortex responsible for the fast coding of the visual components of text. The associated spectrogram suggests that there is an early, transient increase in power (ERS) in the theta range, followed by a sustained decrease in power (ERD) in the beta and low-gamma range. If we map this to a similar spectrogram but in the auditory cortex (in fact the location of "c" in **Figure 2** is slightly below the auditory cortex), there is a similar theta ERS approximately 100 ms after the signal in the visual cortex, and then a similar sustained beta/low gamma ERD. It is possible that these signals may be functionally coupled, but this remains to be seen. Moreover, this visual theta signal is also transient, and may reflect quite different functionality to the sustained theta signals described in the auditory temporal coding hypothesis. For example, Bosman et al. (2010) using a visual search and detection task, found that a transient increase in visual theta was locked to stimulus onset when the stimuli was present, but sustained when the target was not present. It was suggested that the sustained response might reflect a sustained search, while the transient response might reflect a stimulus-locked, motor preparation. Thus it will be important to differentiate between transient and sustained signals in terms of functional consequence.

Similarly, we presented participants with nine-word sentences as a rapid serial visual presentation (RSVP) (*Pammer and Holliday, unpublished data*) and found a sustained theta signal. In this study we isolated two visual signals: one in the primary visual cortex, and the other in the posterior parietal cortex (**Figure 2C**). The former we considered to represent early visual coding, while the latter should involve the dorsal visual pathway and early attentional allocation (e.g., Shomstein and Behrmann, 2006). Like Goto et al., the activation in the primary visual cortex reflects ERS and occurs in the theta/alpha range, start very early, but in this case is sustained. It is likely that this sustained signal reflects the fact that the RSVP were word strings forming sentences, rather than single words as presented in Goto et al. However, whether this signal reflects a "higher-order" cognitive component such as memory, or is a simple visual entrained signal, remains to be seen. With respect to the activity in the posterior parietal cortex, again there was a fast, early theta/alpha signal, but there was also a high frequency gamma signal peaking at approximately 200 ms and then sustained for approximately 500 ms. These results are also consistent with Fitzgibbon et al. (2004), who found both theta and gamma signals in a naturalistic silent reading task. The increase in power relative to a control condition is in red (**Figure 2B**), and although this was an EEG study and thus lacks some temporal and spatial specificity, the signals are clearly concentrated in the occipital cortex. Other reading studies that have focused on particular frequency bands have also found significant gamma and theta signals (e.g., Bastiaansen et al., 2010) in visual areas in the context of the larger reading network.

In summary, an important and interesting consistency between these studies and the studies in the auditory domain is the presence of oscillatory signals in the theta and gamma range. Thus a coherent framework is beginning to develop that may link poor reading to both theta and gamma synchrony, and thus may start to provide a resolution of the conflict between a temporal coding deficit in dyslexia which is believed to be characterized by deficits in the theta range, and deficits in the magnocellular pathway, where the magnocellular pathway has been implicated in gamma oscillations.

PHYSIOLOGICAL MECHANISMS

The cortical networks involved in reading are highly complex, requiring a sophisticated interplay of temporally and spatially dynamic interactions. Thus, a common mechanism such as temporal sampling for normal reading, and by extension—abnormal reading, could be explained in two possible ways. On the one hand, auditory and visual signals—both necessary for successful reading—may involve unique and discrete phase-locking at the local level, such that deficits within one or

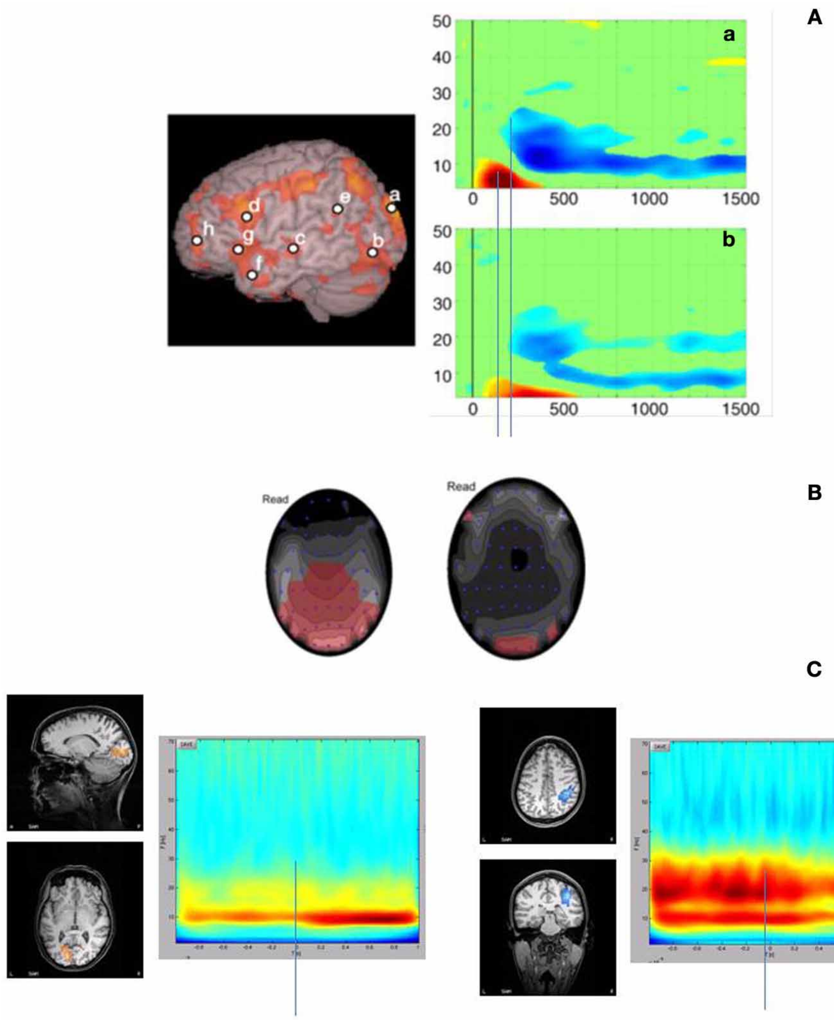

FIGURE 2 | Some illustrations of the potential relationship between low frequency and high frequency synchronisation in reading. (A) is adapted from Goto et al. (2011) demonstrating similar ERS and ERD interactions in the theta and gamma ranges in the visual and auditory cortices, refer to text for more detail **(A)** is partially reproduced with permission from Goto et al. (2011, p566, Elsevier). Similarly, Fitzgibbon et al. (2004) also demonstrate increases in gamma power (left) as well as theta (right) **(B)**. **(B)** is partially reproduced with permission from Fitzgibbon et al. (2004, p1806, Elsevier). The findings in **(A)** and **(B)** are consistent with results from our lab in which we demonstrate both gamma and theta/alpha signals to a RSVP reading task **(C)**. In this task, the stimuli were 8–9 word sentences presented RSVP at a rate of 102 ms per word, with a 16 ms ISI. Data was analyzed individually using SAM statistical mapping. SAM is a linear beamforming technique in which the MEG signal is passed through each channel, modified as a weighted linear function of the remaining channels (Vrba, 2002). SAM generates a statistical map by comparing and "active" period with a "control" period. In the current study, the reference control period for all comparisons was 1000 ms prior to the sentence onset. Montages were created for 5–40 Hz frequency bands, and the time × frequency spectrograms were created for two regions of interest that were apparent in all 10 subjects: the right PPc and the visual cortex. In the spectrograms, time includes the 1 sec pre-stimulus interval, and 1 sec sentence duration. Sentence onset is at 0 ms.

both modalities may manifest as a reading difficulty. Another possibility is the importance of long distance cross modal entrainment.

CROSS-MODAL MODULATION OF OSCILLATORY SIGNALS

One way in which cross modal modulation may manifest, is that the gamma and theta signals that are characteristic of language processing in dyslexia and implicated in visual coding in reading, are functionally coupled. One possibility is that the amplitude and/or phase of gamma oscillations are modulated or controlled by the phase of a theta oscillation (Siegel et al., 2012). The implications then are that a theta signal may provide a common regulatory mechanism for higher frequency signals in large-scale cortical networks. This makes intuitive sense in that any large scale neural network such as language perception, memory or reading requires a complex interplay of brain signals from disparate areas in the brain; communicating dynamically by various feed-forward and feedback interactions, with local networks synchronizing at different frequencies both within the network and between individual networks. That a lower-frequency signal may couple to these higher-frequency interactions provides a putative regulatory mechanism that would assist in guiding and adjusting phase and/or amplitude oscillations (e.g., Jensen and Colgin, 2007; Sauseng et al., 2008) between and within local neural networks.

Using direct sub-dural recordings during a number of different perceptual and cognitive tasks, Canolty et al. (2006) demonstrated that the power of very high frequency gamma oscillations (>75 Hz) as modulated by theta signals. Similarly, Doesburg et al. (2012) in an auditory cue task demonstrated significant increases in gamma synchronisation between the auditory and parietal cortex that were modulated by the phase of a concomitant theta signal. However, in both cases, these results could be the result of either within-modality, or within-site coupling. On the other hand, Demiralp et al. (2007) found theta/gamma coupling in a visual perception task, where the amplitude of an occipital gamma synchronisation was associated with a theta occipital as well as a frontal signal, suggesting the existence of more long range theta-to-gamma modulation.

There is also evidence for cross modal oscillatory phase setting such that an auditory signal entrains an oscillatory signal in the visual cortex, and importantly, increases perception for a visual signal (Romei et al., 2012). Although this was only demonstrated for alpha oscillations, it provides a principle to support the possibility that sensory stimuli, for example in the auditory domain, can entrain signals in the visual domain. This is important when considering reading, because the reading process is multi-modal. Behaviorally, reading and word recognition invariably generate a verbal code, and often an internal dialogue, and neuroimaging models of the reading network are consistent in involving visual, auditory and higher order language areas (Pammer et al., 2004).

If theta oscillations assist in coalescing discrete gamma oscillations into large-scale neuronal networks (Siegel et al., 2012), then the abnormal theta oscillations observed in language processing in dyslexia, may have an additional impact in the modulation of gamma synchronisation in the visual domain. Moreover, the abnormal theta oscillations observed may not be functionally important *per se* for the auditory coding of speech, or the visual processing of text, but instead modulate the higher frequency signals required in both the visual and auditory domains. For example, in reading and/or language, a gamma signal may be important for the fast sampling and coding of sensory events at the local level—in the visual domain such sensory coding may be controlled by the magnocellular pathway, while low frequency oscillations like theta may be responsible for more cognitive functions that are ubiquitous across modalities, such as working memory and/or attention, reflecting longer range interactions that mediate cognitive functions.

Lisman and Idiart (1995) were the first to propose that an interaction between low frequency brain waves such as theta oscillations and high frequency gamma oscillations may support short-term or working memory. Sensory—specific information may be coded at high frequencies, in spatially discrete networks (the visual or auditory cortex for example); then bound together in a short-term working memory mechanism coded through low frequency theta waves and via more long range networks, possibly via frontal and/or thalamic networks (refer to Jutras and Buffalo, 2010 for a review). For example, theta-gamma coupling is associated with working memory capacity (Moran et al., 2010), may be particularly important in maintaining temporal rather than spatial relationships (Roberts et al., 2013) and may specifically reflect retention in STM rather than encoding or recognition (Mizuhara and Yamaguchi, 2011).

Another candidate for a top-down theta mechanism, is attention, because both listening to a speech signal and reading require significant attentional input. However the evidence thus far suggests that gamma-theta coupling is specific to working memory, rather than sustained attention (Park et al., 2013). Moreover, attentional modulation of sensory signals appears to be characteristic of gamma and beta signals (refer to Siegel et al., 2012, for a recent review), rather than theta oscillations. Thus, both sensory coding and attentional modulation may be associated with oscillatory activity in the gamma range. It will be important in subsequent research to attempt to isolate attention from sensory coding, before making inferences about functionality. This will be particularly important in attention-intensive tasks like reading.

CONCLUSIONS, QUESTIONS, HYPOTHESES, AND PREDICTIONS

A substantial amount of research has been devoted to understanding coherent oscillatory activity in dyslexia, but most of this research has focused on the auditory domain. Similar research involving visual processing in dyslexia is virtually non-existent. Thus although I started out with the ambitious aim of describing a visual correlate of the auditory temporal coding hypothesis in dyslexia, this review has in the end attempted to weave together different strands of evidence to support the possibility of a common mechanism for both visual and language deficits in dyslexia. A targeted research program will be necessary to systematically analyse visual coding deficits in dyslexia in the context of temporal coding. Speculations here, suggest a number of hypotheses with clear predictions.

One question reflects the nature of hypothesized visual entrainment to reading. In language, the auditory entrainment occurs via amplitude modulation, but what is the physical visual signal that might entrain a theta rhythm? The first and simplest possibility is that the "shutter-like" quality of the saccade—fixation rhythm projects a rhythmic sequence of patterns at a frequency that will entrain a cortical response. If this was the case, then one should also be able to achieve the same cortical response using a simple RSVP task with patterns, letters or words. However, if cortical entrainment is coupled to the oculomotor behavior of the saccade-fixation rhythm, then maximum entrainment would be dependent on natural, contextual reading. Moreover, if this is the case, then the same signal should be able to be elicited by eye movements that simulate natural reading. Finally, if the cortical signal is in fact dependent on a memory code intrinsic to lexical access and the concatenation of current with previous lexical context when reading, rather than the actual saccade-fixation rhythm, then entrainment should occur in natural reading, but not simulated reading-like eye movements.

The temporal coding hypothesis as applied to auditory processing draws on a large amount of research which has investigated basic auditory coding, and suggests that dyslexic readers are less sensitive to some of the temporal coding aspects of speech, for example amplitude and frequency modulation at low frequencies.

A reasonable theoretical framework exists to implicate visual coding in much the same way; the temporal coding of reading mirrors in many ways the temporal coding of speech processing. Therefore, if poor phase locking and entrainment to an external signal forms part of the basis for dyslexia, then we should be able to show responses in the visual domain in dyslexic participants, which mirror those in the auditory domain. For example, if theta synchronisation is pervasive in visual and auditory processing, dyslexic readers should demonstrate reduced sensitivity also in visual tasks that modulate the input frequency in the theta range. For completeness, similar frequency modulations could be done at a range of frequencies in order to explore the possibility of differential sensitivities to different oscillations. Moreover, any sensitivity should also be correlated with reduced auditory sensitivity in the same theta frequency ranges.

Furthermore, exploring a temporal coding framework in other sensory domains from auditory coding, my give us some insight into the discrepancies that exist in the literature, where sensory deficits are not ubiquitous. While discrepant finding are well documented, once again we have little insight into why this might be the case. Thus, as I alluded to above, a temporal coding deficit in dyslexia may in fact be multi-modal, involving auditory, visual, and even motor kinaesthetic (e.g., Thomson and Goswami, 2008) elements. This is consistent with the behavioral literature, and theories suggesting that different manifestations of dyslexia, or different categories of dyslexia may reflect modality-specific differences in sensitivity (e.g., Hogben, 1996; Witton et al., 1998; Stein, 2001; Ramus et al., 2003). Moreover, there is no biological reason why this should not be the case, as multi-modal manifestations of temporal coding are well known, as described above. In the context of dyslexia then, it may be the case that temporal coding deficits may be weighted more heavily toward one or another modality in any individual. Here then, most dyslexic readers may show auditory temporal coding problems of varying degrees, consistent with the relatively stable findings of phonological deficits in dyslexia. However, individuals may also demonstrate visual temporal coding deficits which may manifest as dorsal coding deficits. If this were the case, then we should be able to show that the relative visual, auditory, and even kinaesthetic deficits in temporal coding are directly proportional to the behavioral manifestation of dorsal, auditory, and motor deficits in dyslexia.

Over 20 years of research suggests that there is a deficit in visual coding in dyslexia, and this deficit occurs as a consequence of abnormal visual coding in the magnocellular/dorsal pathway. The evidence reviewed here suggests that the magnocellular visual pathway generates high frequency gamma oscillations. Hence, dyslexic readers may have specific deficits in gamma synchronisation for tasks mediated by the magnocellular pathway, compared to normal readers.

One hypothesis that can be derived from the above discussion is that reading involves binding visual and spatial information in much the same way that occurs for general object recognition. Much of the research on object feature binding implicates gamma frequencies as an important cortical mechanism. Therefore, if dyslexic readers have problems in the binding of visual feature information in a way that is reflected in less stable synchronisation at gamma frequencies, then this should be reflected not only in word recognition, but also in other visual tasks that require feature binding.

The notion that high frequency cortical oscillations are the domain of the magnocellular visual pathway is still relatively speculative. Although good evidence attests to this suggestion, studies are still required to determine the exact spatio-temporal make-up of contrast sensitivity. A logical step here would be a replication of Fründ et al. (2007) but using MEG instead of EEG to allow better spatial mapping of the signals. Like Fründ et al., we would predict sensitivity to stimuli of a low spatial frequency to be associated with signals in the parietal cortex, and brain signals sensitive to higher spatial frequencies to be observed in the inferior temporal areas.

Studies using spatio-temporal mapping such as MEG would allow researchers to attribute oscillatory activity in different areas of the visual cortex to different functional components of the reading network. Such mapping is required at the very least in normal readers, and can then form a framework from which the causes of abnormal reading can be derived.

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