



Behavioral and ERP evidence for amodal sluggish attentional shifting in developmental dyslexia

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ARTICLE INFO

Article history:

Received 6 May 2010

Received in revised form 19 June 2010

Accepted 23 September 2010

Available online 8 October 2010

Keywords:

Developmental dyslexia

Automatic attentional shifting

Stream segregation

ERP

Amodal processing

Phonology

ABSTRACT

The goal of this study was to examine the claim that amodal deficits in attentional shifting may be the source of reading acquisition disorders in phonological developmental dyslexia (sluggish attentional shifting, SAS, theory, Hari & Renvall, 2001). We investigated automatic attentional shifting in the auditory and visual modalities in 13 dyslexic young adults with a phonological awareness deficit and 13 control participants, matched for cognitive abilities, using both behavioral and ERP measures. We tested automatic attentional shifting using a stream segregation task (perception of rapid succession of visual and auditory stimuli as one or two streams). Results of Experiment 1 (behavioral) suggested that in order to process two successive stimuli separately dyslexic participants required a significantly longer inter-stimulus interval than controls regardless of sensory modality. In Experiment 2 (ERPs), the same participants were tested by means of an auditory and a visual oddball tasks involving variations in the tempo of the same alternating stimuli as Experiment 1. P3b amplitudes elicited by deviant tempos were differently modulated between groups, supporting predictions made on the basis of observations in Experiment 1. Overall, these results support the hypothesis that SAS in dyslexic participants might be responsible for their atypical perception of rapid sequential stimulus sequences in both the auditory and the visual modalities. Furthermore, these results bring new evidence supporting the link between amodal SAS and the phonological impairment in developmental dyslexia.

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1. Introduction

Developmental dyslexia is a specific deficit in written language acquisition that occurs despite normal intelligence and learning opportunities and in the absence of sensory or psychiatric disorders (Shaywitz & Shaywitz, 2005). Amongst many hypotheses regarding the possible origins of dyslexia, the phonological deficit hypothesis remains the most accepted and documented (Snowling, 2000; Vellutino, Fletcher, Snowling, & Scanlon, 2004 for a review). In this framework, a dysfunction in the build up of phonemic and phonological representations, necessary for adequate decoding skills (e.g., Hulme & Snowling, 1992), would lead to difficulties in acquiring automatic fluent reading (Share, 1995).

Several hypotheses have been put forward to explain the source of the phonological deficit itself. Focusing on the auditory component of phonological perception, a number of studies have suggested central auditory deficits in developmental dyslexia (Banai & Ahissar, 2006; Bailey & Snowling, 2002; Tallal, 1980). For instance, rapid auditory temporal processing deficits have been repeatedly reported in relation to phonological difficulties in dyslexic adults (Helenius, Uutela, & Hari, 1999; Lallier et al., 2009) and children (Boets, Wouters, van Wieringen, De Smedt, & Ghesquiere, 2008; Meng et al., 2005). In addition, research focusing on amodal temporal deficits in dyslexia (Farmer & Klein, 1995) has brought to light a possible involvement of both the visual transient magnocellular system and its auditory counterpart (Stein & Talcott, 1999; Van Ingelghem et al., 2001; Witton et al., 1998). However, the evidence for a role of magnocellular temporal processing in reading (Au & Lovegrove, 2008; Hulslander et al., 2004) and phonological processing (Boets et al., 2008; Heim et al., 2008; Kronbichler, Hutzler, & Wimmer, 2002; Ramus et al., 2003) remains inconsistent.

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Moving away from perceptual-level explanations but still compatible with a magnocellular deficit, Hari and Renvall (2001) acknowledge the proposition made by Stein and Walsh (1997) that a failure of attention subtended by a parietal lobe deficit could explain temporal impairments in developmental dyslexia. The magnocellular theory offers an attractive neurophysiological framework to explain developmental dyslexia, but a dorsal stream function (e.g., temporal perceptual processing) may not reliably reflect a magnocellular deficit since the dorsal pathway also receives parvocellular and koniocellular inputs (Skottun & Skoyles, 2006). Therefore, the temporal processing impaired in developmental dyslexia may not only be characterized by magnocells' functional properties, but also by that of the cerebral structure most affected by the magnocellular dysfunction, e.g., the parietal lobe (Vidyasagar & Pammer, 2010). With these considerations in mind, Hari and Renvall (2001) put forward the amodal sluggish attentional shifting (SAS) as the origin of rapid temporal processing deficits in dyslexia.

According to the SAS theory, when dyslexic individuals are faced with rapid stimulus sequences, their automatic attention system cannot disengage fast enough from one item to move to the next. The SAS theory is supported by studies conducted separately in the auditory (e.g., Hari, 1995; Hari & Kiesilä, 1996; Helenius et al., 1999) or the visual (e.g., Hari, Renvall, & Tanskanen, 2001; Hari, Valta, & Uutela, 1999) modality in different groups of dyslexic participants. However, few studies have examined an attentional deficit in both visual and auditory rapid serial presentation tasks in the same dyslexic participants. Using a spatial cueing paradigm, Facioetti, Lorusso, Cattaneo, Galli, and Molteni (2005) and Facioetti et al. (2010) have found that dyslexic children exhibit slower covert attentional orienting skills in both modalities. In addition, Lallier, Berger, Donnadieu, and Valdois (2010) showed that a dyslexic adult presenting with phonological problems was impaired in both visual and auditory attentional blink tasks similarly designed. Finally, Lallier et al. (2009) reported that dyslexic adults had higher thresholds in both auditory and visual stream segregation tasks whereas dyslexic children were impaired on the auditory task only.

Interestingly, stimulus stream integration/segregation deficits have been consistently found in relation to reading impairments in both children (Lallier et al., 2009; Ouimet & Balaban, 2010) and adults (Helenius et al., 1999; Lallier et al., 2009). Processing correctly acoustic cues at fast tempo in speech streams is crucial with respect to reading acquisition, and to language acquisition more generally (e.g., Pasquini, Corriveau, & Goswami, 2007; Schulte-Körne, Deimel, Bartling, & Remschmidt, 1999a). Thus, the phonological disorder which is a common source of literacy difficulties in developmental dyslexia may itself derive from an atypical perception of rapid auditory sequences in the dyslexic brain. The role of rapid visual processing in phonological skills development is less clear although it may relate to sequential visual attention processes required to analyze and segment the orthographic input before its conversion into a phonological code (Pammer & Vidyasagar, 2005).

So far, the possible role of SAS in developmental dyslexia has only been studied using behavioral measures, although Neville, Coffey, Holcomb, and Tallal (1993) have provided both behavioral and neurophysiological evidence for visual and auditory attentional deficits in language-impaired children. The goal of the present study was to strengthen and extend the current evidence for an amodal SAS deficit, by examining rapid stimulus stream perception using both behavioral measures and event-related potentials (ERPs) in the same participants. ERPs are particularly adapted to the study of fine temporal processing differences because of their high temporal resolution (data points every millisecond over a number of scalp sensors). Moreover, ERP data may reflect the perceptual experience elicited by rapid stimulus streams more directly

than behavioral measures which are more susceptible to strategic response biases or may lack sensitivity. As an illustration of this general point, Stoodley, Hill, Stein, and Bishop (2006) showed that dyslexic adults had normal auditory psychophysical thresholds but reduced ERP amplitudes as compared to controls, even though the same testing materials were used in the two methodologies. According to Stoodley et al. (2006) the fact that their participants were high-functioning dyslexic adults may explain why they did not exhibit deficits in behavioral tasks while still showing anomalies using more sensitive electrophysiological measures. Note that this study did not test the SAS theory (Hari & Renvall, 2001) since the frequency modulation detection task used did not involve rapid sequences of stimuli. Indeed, the SAS theory proposes that the temporal deficit in developmental dyslexia exclusively affects sequential processing by increasing the processing time between stimuli. Importantly, the SAS theory remains compatible with the magnocellular hypothesis of developmental dyslexia that hypothesizes temporal deficits to be both *transient*, i.e., affecting the processing of temporal variations within a single stimulus, and *sequential*.

The aim of the present study was to establish a link between behavioral (Experiment 1) and electrophysiological (Experiment 2) evidence for a sequential SAS deficit in dyslexic adults matched for cognitive abilities with control adults. The SAS deficit will be measured using stream segregation tasks (tested in adaptive and oddball paradigm contexts, respectively) in both the visual and the auditory modalities (Helenius et al., 1999; Lallier et al., 2009). Our hypothesis is that an amodal SAS deficit (Experiment 1) will be accompanied by an atypical perception of rapid stimulus sequences in both modalities (Experiment 2).

In both experiments, participants were presented with streams of alternating tones (high/low pitch) or alternating dots (above/below fixation). In Experiment 1, participants engaged in a stream segregation task as used in Lallier et al. (2009). This task measures the speed at which participants automatically disengage their attention from a given stimulus and reengage with the next. This is done by varying gradually the tempo of stimulus alternation according to whether participants report perceiving one or two streams, which allows us to establish individual SOA-driven segregation thresholds. According to the SAS theory, dyslexic participants should show higher visual and auditory segregation thresholds. Namely, they should require a longer time interval between stimuli in order to start perceiving successive auditory/visual stimuli as independent from one another.

In Experiment 2, the same participants performed visual and auditory oddball tasks involving stimulus sequences varying in SOA. Based on the segregation thresholds determined in Experiment 1, we measured P3b ERP responses elicited by the detection of deviant SOA targets (fast tempo and ambiguous tempo) embedded in standard SOA stimulus series (slow tempo). For both groups, the slow tempo (SOA 340 ms) allowed full disengagement/reengagement of attention with each stimulus and the fast tempo deviant prevented shifting attention back and forth between stimuli (SOA 90 ms). The ambiguous tempo deviant was intermediate (SOA 175 ms) and likely to allow disengagement for control participants only. Thus, differences between fast and ambiguous deviant tempos on amplitude in the P3b range were expected to arise between participants groups.

2. Methodological aspects common to Experiments 1 and 2

2.1. Participants

Twenty-six adult volunteers (13 dyslexics: 5 males, 1 left-handed, 20.4 ± 1.0 years old; 13 controls: 4 males, 1 left-handed,

Table 1
Mean scores for dyslexic ($N = 13$) and control ($N = 13$) participants in diagnostic tasks.

	Control group Mean (SD)	Dyslexic group Mean (SD)	p^a
WAIS matrices standard score	13.2 (2.4)	11.7 (2.5)	.12 n.s.
WAIS vocabulary standard score	12.1 (1.5)	10.9 (1.7)	.07 n.s.
DAST reading and spelling raw score	73 (6.1)	60 (1.8)	<.001
DAST reading and spelling normed score ^b	0.1 (0.5)	-1.4 (0.7)	<.001

^a Non-verbal IQ and vocabulary: two-tailed t -test; literacy measure: one-tailed t -test.

^b The DAST provides an indicative score relative to age norms ranging from -3 to +1 (where: -3 = 1st–4th percentile; -2 = 5th–11th percentile; -1 = 12th–22nd percentile; 0 = 23rd–77th percentile; +1 = 78th–100th percentile).

19.4 ± 0.6 years old) were recruited via the Bangor University's student participant panel and the Bangor Dyslexia Unit. The study has been approved by Bangor University ethics committee and has therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All dyslexics were high-functioning young adults with well compensated dyslexia. Participants received course and printer credits or financial payment. They were all native speakers of English, had normal or corrected-to-normal vision, normal hearing, and no history of neurological or psychiatric disorders. The assignment to one of the two groups was based on two criteria: (1) the presence or absence of a previous diagnosis of dyslexia, and (2) the average performance on the one-minute reading and the two-minute spelling tasks of the Dyslexia Adult Screening Test (Fawcett & Nicholson, 1998). Participants with no diagnosis of dyslexia who obtained an average reading and spelling DAST score above the 23rd percentile were assigned to the control group. Participants with a previous diagnosis of dyslexia and with a DAST score below the 23rd percentile were assigned to the dyslexic group. Thus, the literacy performance of the two groups differed significantly ($t(24) = 3.62$, $p < .001$). Characteristics of the two groups are provided in Table 1. To ensure that the two groups had similar cognitive abilities, their performance was matched on the matrix reasoning and the vocabulary subtests of the Wechsler Adult Intelligence Scale 3rd UK (WAIS-IIIUK). On these two tasks, participants needed a minimum standardized score of 7 for inclusion in the study. The two groups showed comparable performance on these tests, although dyslexic participants tended to exhibit poorer vocabulary skills than control participants.

2.2. Further language screening

The 26 participants were administered three reading tasks, two spelling tasks, and two phonological tasks.

2.2.1. Reading skills

Nonsense passage reading: This task consisted of two short passages with interspersed pseudowords taken from the York Adult Assessment (Hulme et al., 2002). Participants were required to read aloud the two passages one after the other and the number of errors and time needed to complete the task were measured.

Pseudoword and irregular word reading tasks: The 20 monosyllabic pseudowords and the 44 irregular words were taken from Manis, Seidenberg, Doi, McBride-Chang, and Petersen (1996). Participants were asked to read the items aloud as quickly and accurately as possible. For both reading lists, the number of errors and time needed to complete the task were recorded.

2.2.2. Spelling skills

Pseudoword and irregular word spelling: Twenty irregular words were selected from the list of 44 words of Manis et al. (1996) and twenty matched pseudowords were derived from this selection and presented in a spelling to dictation task. For pseudowords, participants were asked to repeat each stimulus before writing it down to ensure correct perception. If needed, the stimuli were repeated.

For both spelling lists, the time needed to complete the task (cumulative time required to write all words) and the number of errors was recorded.

2.2.3. Phonological skills

Spoonerisms task (York Battery, $N = 12$): Participants were required to swap around the initial sounds of people's names to form new pseudowords (for example Sue Lawley to Loo Sawley). The main task was preceded by three practice trials. Accuracy (Max = 24) and a measure of time (correct items total time divided by 24) were recorded.

Phonemic segmentation and spoonerism (DAST, $N = 15$): The task included 12 segmentation items and 3 spoonerism items. In the segmentation items participants were required to divide words into constituent parts by deleting a syllable or a consonant [for example saying "rainbow" without "bow" (i.e., /rain/) or saying the first sound of the word "dog" (i.e., /d/)]. For the spoonerisms, the instructions were the same as for the York task. Accuracy was measured.

2.2.4. Results

As shown in Table 2, dyslexic participants performed worse than the controls in both reading and spelling. Their reading performance was poor on all types of items although not significantly different as regards spelling speed of irregular items ($p = .17$). Dyslexic participants further exhibited poor performance in the phonological spoonerism and phonemic segmentation tasks ($ps < .05$). Overall, the dyslexic group exhibited a phonological dis-

Table 2
Reading, spelling and phonological performance in the control ($N = 13$) and the dyslexic ($N = 13$) groups.

	Controls Mean (SD)	Dyslexics Mean (SD)	p
<i>Reading skills</i>			
Nonsense passages reading			
Errors	1.4 (1.3)	8.0 (7.2)	<.001 ^b
Speed (s)	45.3 (10.2)	60.8 (15.6)	<.01 ^a
Pseudoword list ($N = 60$)			
Errors	4.0 (3.0)	12.8 (10.0)	<.001 ^b
Speed (s)	50.6 (25.1)	96.9 (56.6)	<.05 ^a
Irregular word list ($N = 44$)			
Errors	1.3 (1.2)	3.4 (3.3)	<.05 ^a
Speed (s)	28.9 (6.2)	37.0 (13.0)	<.05 ^a
<i>Spelling skills</i>			
Pseudoword list ($N = 20$)			
Errors	5.5 (2.2)	8.3 (3.7)	<.05 ^a
Speed (s)	116.4 (24.8)	162.5 (48.9)	<.01 ^b
Irregular word list ($N = 20$)			
Errors	4.6 (2.9)	12.1 (3.1)	<.001 ^a
Speed (s)	98.2 (34.7)	113.2 (39.4)	17 n.s. ^b
<i>Phonological skills</i>			
Phonemic segmentation ($N = 15$)			
Accuracy	14.5 (1.3)	10.9 (2.8)	<.001 ^b
Spoonerisms ($N = 24$)			
Accuracy	23.5 (0.6)	20.9 (2.9)	<.05 ^a
Speed (s/item)	1.2 (0.6)	3.4 (2.0)	<.01 ^a

^a One-tailed t tests.

^b Non-parametric U -test.

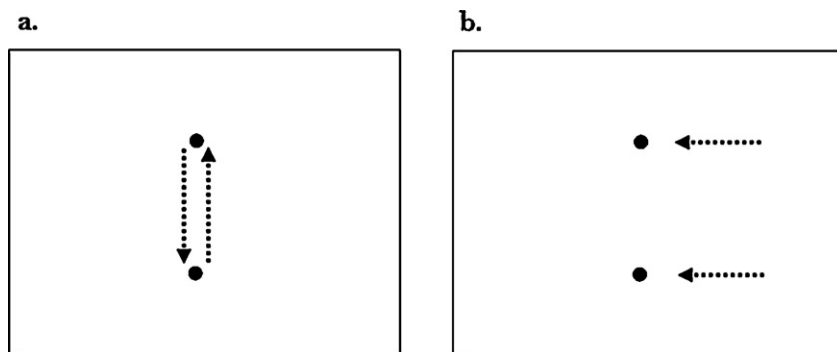


Fig. 1. Schematic representation of the stream segregation procedure. The dotted arrows symbolise the one-stream (a; longer SOAs) or two-streams (b; shorter SOAs) conditions. Note that the figures refer to perceived patterns, not to stimuli.

order, both in terms of reading and spelling decoding procedures and in terms of phonological awareness. Note that it was important to show a phonological deficit in our dyslexic group since temporal processing deficits may cause phonological processing difficulties (Hari & Renvall, 2001; Stein & Talcott, 1999; Tallal, 1980).

3. Experiment 1: measuring attentional shifting speed with segregation thresholds

3.1. Material and methods

3.1.1. Stimuli

As in the study by Lallier et al. (2009), the auditory sequences were composed of high (1000 Hz) and low (400 Hz) pitch pure tones presented in alternance. Each auditory sequence lasted 5 s. Sounds were digitally converted to 16-bit resolution at a sampling rate of 44.1 kHz using *Sound Forge 8.0* (Sony Creative Software, Inc.). Tones lasted 40 ms (including 5 ms linear onset/offset amplitude ramps in order to prevent onset and offset clicks). Stimuli were presented using *E-prime 2.0* (Psychology software Tools, Inc.) on a PC computer running the rapid serial auditory sequences binaurally through headphones (Earthquake, TS 800) at approximately 65 dB sound pressure level.

Visual sequences were composed of black dots subtending $0.1^\circ \times 0.1^\circ$ of visual angle, displayed on a white background. The dots were displayed in alternance 2° above and below a fixation cross along the vertical median line of the screen (see Fig. 1). The participants were asked to fixate the central cross at all times. The dots were thus foveally presented, and could be perceived accurately without eye movements.

3.1.2. Procedure

Participants sat 60 cm from a computer screen in a moderately lit room. Within each trial, a fixation cross, subtending $0.5^\circ \times 0.5^\circ$ of visual angle appeared at the centre of the screen followed by the auditory or visual sequence after 500 ms. Participants were asked to fixate the cross throughout the session. After each sequence, they reported whether they had perceived one stream or two streams in a forced-choice paradigm. Before the testing phase, a short training phase was administered to provide example stimuli featuring one or two streams, both for the visual and auditory tasks. During practice, an unambiguous one-stream stimulus (SOA = 400 ms) and an unambiguous two-streams stimulus (SOA = 50 ms) were presented and associated with corresponding schematic drawings (see Fig. 1). After each sequence, participants answered by pointing at the drawing corresponding to the pattern they had perceived. When unsure, they were instructed to guess. The order of the auditory and visual tasks was counterbalanced between participants.

In order to determine individual auditory and visual segregation thresholds, a simple 'one-up, one-down' adaptive method was used to estimate the 50% chance level in a two forced-choice paradigm context (Levitt, 1971). As long as the answer was "one stream", the program automatically decreased the SOA. Conversely, as long as the answer was "two streams" the SOA was automatically increased. Each session included 30 sequences of auditory or visual stimuli. The experiment started with a 300 ms SOA in both modalities, which unambiguously yielded the "one stream" answer, whatever the modality, providing the same initial perceptual context for all participants. The SOA was decreased or increased initially by steps of 40 ms and by steps of 20 ms after the first categorical change, then by steps of 10 ms after the second categorical change, and, finally, by steps of 5 ms after the third categorical change. The stream segregation threshold was defined as the mean SOA over the last 10 trials. This measure corresponded to the SOA at which participants could no longer dissociate the one-stream from the two-streams percepts and was taken as an

index of the highest speed at which participants were able to shift their attentional focus automatically.

3.1.3. Data analysis

The SOA thresholds were compared by means of an analysis of variance (ANOVA) with group (dyslexic, control) as the between-subject factor and modality (auditory, visual) as the within-subject factor.

3.2. Results

As expected, a significant main effect of group was found ($F(1,24) = 4.33$; $p < .05$), with no main effect of modality or modality by group interaction ($F_s < 1$). Thus, segregation thresholds were higher in the dyslexic group irrespective of modality (controls: $130 \text{ ms} \pm 30$; dyslexics: 163 ± 46). As shown in Fig. 2, thresholds were higher in both the auditory (controls: $131 \text{ ms} \pm 49$; dyslexics: $161 \text{ ms} \pm 31$) and the visual modality (controls: $129 \text{ ms} \pm 54$; dyslexics: $166 \text{ ms} \pm 57$). Moreover, the correlation between the visual and the auditory segregation thresholds within the whole sample approached significance ($r = .36$, $p = .07$) suggesting that a high (or a low) threshold in the auditory modality tended to be associated with a high (or low) threshold in the visual modality.

4. Experiment 2: Studying rapid stimulus sequences perception with ERPs

The goal of this ERP experiment was to determine whether the amodal sluggish attentional shifting skills of dyslexic participants evidenced in Experiment 1 led them to perceive auditory and visual rapid sequences differently from skilled reader participants.

4.1. Material and methods

4.1.1. Stimuli

The visual dots and auditory sounds presented in Experiment 2 had the same physical characteristics as in Experiment 1. Stimuli consisted of one-second long sequences of alternating dots or tones belonging to three different tempo conditions: slow tempo (standard stimulus, SOA = 340 ms), fast tempo (fast deviant stimulus, SOA = 90 ms), and intermediate tempo (ambiguous deviant stimulus, SOA = 175 ms; see Fig. 3a and b). SOAs were selected based on the results of Experiment 1 and of previous stream segregation studies (Fisher et al., 2006; Helenius et al., 1999; Lallier et al., 2009). The ambiguous SOA was likely to yield different stream percepts in the two participant groups. More specifically, it was more likely to be perceived as an unambiguous one-stream sequence by control participants than by dyslexic participants who have higher segregation thresholds. Each block started with six standard slow tempo stimuli to induce perception of a rhythmic baseline. In a given block, 66% of the stimuli were standards, making up a slow tempo baseline. Fast deviant tempos and ambiguous deviant tempos were presented pseudorandomly with a probability of 17% each, always preceded and followed by a standard tempo stimulus (Fig. 3a).

4.1.2. Procedure

All participants were tested in a dimly lit, sound-attenuated room. They sat 60 cm away from a 19 in. computer screen. After giving written consent and filling

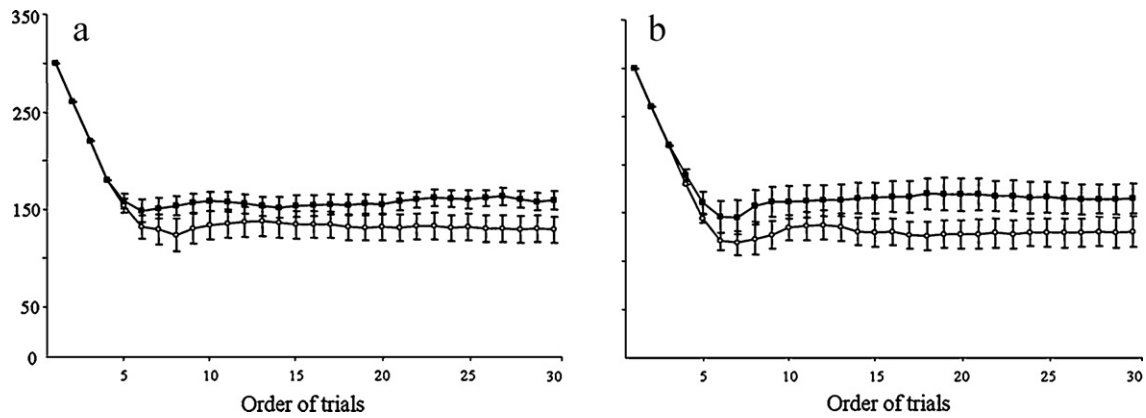


Fig. 2. Mean auditory (a) and visual (b) stream segregation thresholds (and standard error bars) for the dyslexic (black squares; $N=13$) and control (white dots; $N=13$) groups; statistical analyses were performed on the average of the last 10 trials.

in handedness and biographical questionnaires, participants were fitted with a 64 channel Ag/AgCl electroencephalographic cap. Then, they were told that their task would be to detect tempo changes (both tempo increases and decreases) within two blocks of alternating tones and two blocks of alternating dots by pressing the space bar of a computer keyboard. In the visual task, participants were asked to look at the fixation cross throughout each block. In the auditory task, sound level was adjusted to a comfortable level, the monitor was turned off and participants were asked to stare at a round sticker set at the bottom of the monitor. Each block lasted 4 min and participants were given a break between blocks. Block order was counterbalanced across participants. At the end of the session, participants were fully debriefed, compensated, and thanked for their participation. The entire session lasted a maximum of two hours, 45–50 min for the experimental tasks themselves.

4.1.3. Behavioral data analysis

Accuracy (percentage correct detection) and reaction times (RTs) were computed only for baseline-to-fast or baseline-to-ambiguous tempo transitions since

only these were relevant to deviancy detection and P3b elicitation. RTs were computed from correct responses only and RTs exceeding the mean RT by more than 2.5 standard deviations within in each condition and group were replaced by the corresponding mean RT (13% RTs replaced overall). Accuracy and corrected RTs were analyzed by means of an ANOVA with group (dyslexic, control) as a between-subject factor and modality (auditory, visual) and type of deviancy (fast, ambiguous) as within-subject factors.

4.1.4. ERP recording

Electrophysiological data were recorded in reference to electrode Cz at a rate of 1 kHz from 64 Ag/AgCl electrodes placed according to the 10–20 convention. Impedances were kept below 7 kOhm. EEG activity was filtered on-line band pass between 0.1 Hz and 200 Hz and re-filtered off-line with a 25 Hz low pass zero phase shift digital filter. Eye blink artifacts were mathematically corrected based on a model artifact computed from a minimum of 50 individual artifacts in each participant using the procedure implemented in Scan 4.3 (Neuroscan, Inc., El Paso, TX, USA) and remaining artifacts were manually

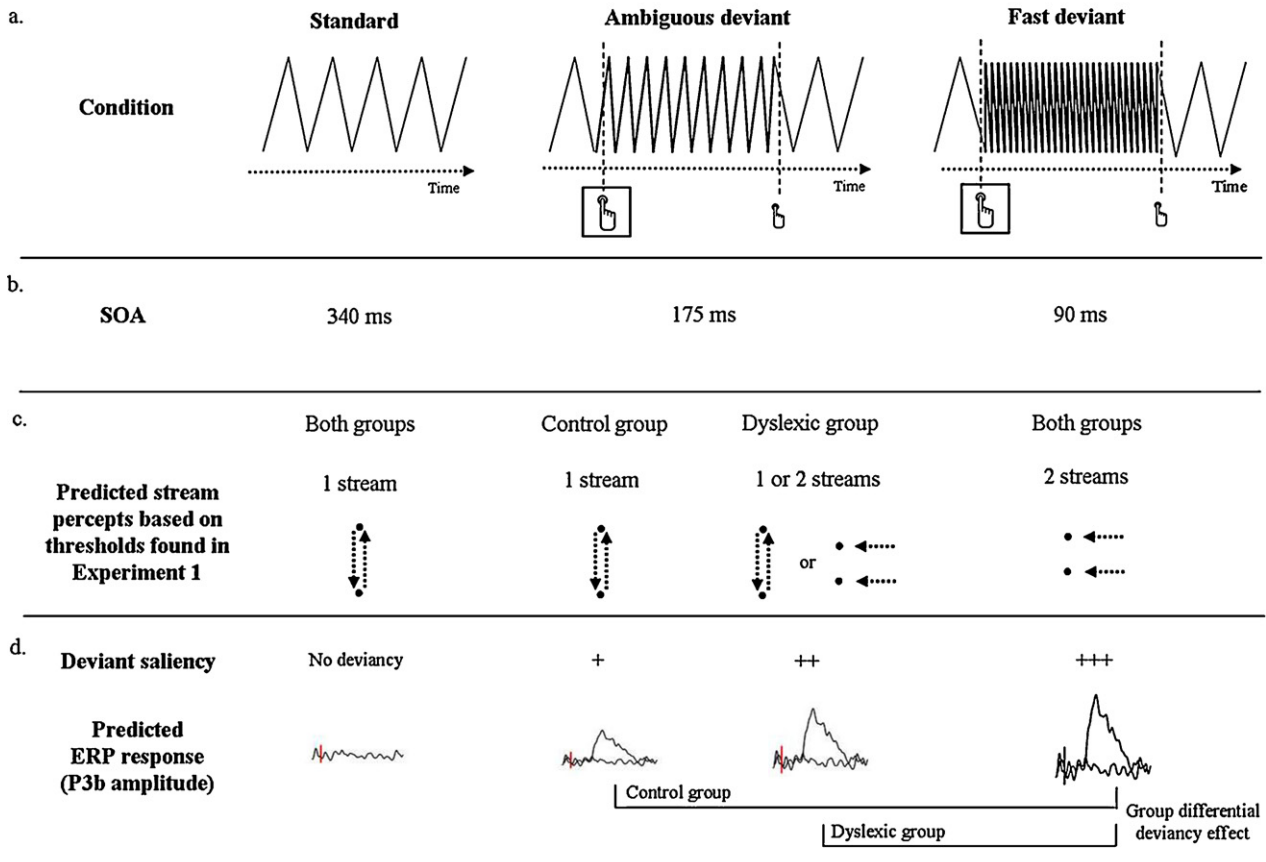


Fig. 3. Illustration of the procedure, expected stream perception and ERP patterns in response to each stimulus condition in the visual and auditory oddball tasks.

dismissed. Epochs ranged from –100 to 1000 ms after the onset of target presentation.

4.1.5. ERP analysis

Grand-average ERPs were derived from all trials uncontaminated by movement artifacts, i.e., both hits and omission trials were included in the ERP analysis. Two main reasons motivated this choice: (1) the accuracy of the dyslexic and control groups was comparable in all conditions of the two oddball tasks (see Section 4.2), and (2) we were primarily interested in perception rather than decision making regarding tempo deviancy (note that such decision making processes were studied independently in Experiment 1 with the adaptive procedure which relied on the response given by participants). Baseline correction was performed in reference to pre-stimulus activity and individual averages were digitally re-referenced to a global field power reference which summarizes the contribution of all electrodes in the form of a single vector norm (Picton et al., 2000). ERP peaks were identified based on the mean global field power measured across the scalp, which allowed automatic peak detection in the following intervals: 250–400 ms for the P3b in the auditory modality, and 370–750 ms in visual modality. Mean P3b peak amplitudes were computed at electrodes selected *a priori* because they were expected to display maximal P3b amplitude (Luck, 2005), namely at midline centroparietal, parietal and parietooccipital sites (CPz, Pz, POz) in both the auditory and the visual modalities. Note that Ji, Porjesz, Begleiter, and Chorlian (1999) showed that P3b peaks elicited in similar auditory and visual oddball tasks correlate in amplitude over these regions. An ANOVA was conducted on mean P3b latency (in reference to Pz where amplitude was maximal) with group (control, dyslexic) as the between-subject factor, and modality (auditory, visual), and type of deviancy (fast, ambiguous) as within-subject factors. A second ANOVA was conducted on differential mean P3b amplitudes (i.e., the difference in amplitude elicited by fast or ambiguous deviants vs. standard stimuli) with group (control, dyslexic) as the between-subject factor, and modality (auditory, visual), type of deviancy (fast, moderate) and electrodes (centroparietal, parietal, parietooccipital) as within-subject factors. Greenhouse–Geisser correction was implemented when applicable.

4.1.6. Predictions

First of all, no specific group differences were expected on behavioral data in the oddball tasks (both accuracy and RTs in both modalities). Indeed, participants were not asked to report the stream patterns perceived as in Experiment 1, but to detect changes in tempo which should be salient enough for all participants.

However, we expected the ERP measures to uncover fine group differences regarding how the brain processes these rapid stimulus sequences. Based upon the stream segregation thresholds measured in Experiment 1, we predicted that the two participant groups would exhibit differential deviancy effect on P3b amplitude (see Fig. 3). Whereas the fast deviant stimulus condition should elicit a two-stream percept in both groups (because this tempo is well below threshold for both groups), the ambiguous deviant stimulus condition should elicit different stream percepts, i.e., one stream in the control group, since they should be able to shift their attention back and forth between stimuli at this intermediate SOA, and one or two streams in the dyslexic group, depending on whether participants managed to shift back and forth between the stimuli in that condition (Fig. 3c). In other words, deviant stimuli were expected to be equally salient for the fast deviant condition in the two groups, because it unambiguously corresponded to a transition from one to two streams. In the case of ambiguous deviant detection, control participants were expected to perceive a change in tempo between standard and ambiguous stimuli, i.e., change from SOA of 360 ms to SOA of 175 ms, but *no change* regarding the number of streams perceived, i.e., one stream for both standard SOAs and ambiguous SOAs (Fig. 3c). In contrast, when detecting ambiguous deviants, dyslexic participants were likely to perceive a change in tempo, i.e., change from SOA of 360 ms to SOA of 175 ms, *together with* a change in the number of streams perceived, i.e., a change from the perception of one stream to the perception of two streams, respectively. Therefore, for dyslexic participants as compared to control participants, the transition between standards and ambiguous deviants resulting in a change regarding both the tempo and the number of stream was expected to add saliency to ambiguous deviants thus becoming perceptually closer to fast deviants (Fig. 3d). Predictions regarding the P3b were directly derived from these considerations (Fig. 3d), since P3b has been shown to index a combination of deviant stimuli saliency and task difficulty (e.g., Azizian, Freitas, Watson, & Squires, 2006; Sawaki & Katayama, 2007). We were therefore expecting that ambiguous deviants should elicit smaller P3b, together with possible delayed latencies (Polich, 1987), than fast deviants. We expected that this deviancy effect on amplitude should be greater in the control group while the P3b in the two deviancy conditions would be of closer magnitude for dyslexic participants (Fig. 3).

4.2. Results

4.2.1. Behavioral performance (see Fig. 4)

4.2.1.1. Accuracy. There was a significant main effect of deviancy type on accuracy ($F(1, 24) = 63, p < .001$) showing that the ambiguous deviant was more difficult to detect (0.47 ± 0.29) than the fast deviant (0.71 ± 0.33). There was no main effect of group ($F < 1$),

suggesting that the overall performance of the two groups was similar. No group by deviancy interaction was revealed ($F(1, 24) = 1.9, p = .18$), suggesting that the ambiguous deviant was harder to detect than the fast deviant to the same extent in both groups when the two modalities were considered. A trend for a modality main effect was observed ($F(1, 24) = 4.2, p = .052$) suggesting that the task tended to be more difficult in the visual (0.56 ± 0.34) than in the auditory (0.62 ± 0.33) modality. Moreover, the significant deviancy by modality interaction ($F(1, 24) = 55.5, p < .001$) showed that the difficulty in detecting ambiguous deviants was greater in the visual than in the auditory modality. Lastly, a trend was found for the group by modality by deviant interaction ($F(1, 24) = 4, p = .057$) but follow up planned comparisons did not reveal any critical deviancy by group interaction either in the auditory ($F < 1$) or in the visual modality ($F(1, 24) = 3.0, p = .1$) suggesting that the deviancy effect on accuracy was similar for both groups in each modality. Visual and auditory accuracy scores correlated within the whole sample for both fast ($r = .89, p < .001$) and ambiguous deviant detection ($r = .67, p < .001$) suggesting that high (or low) detection performance in the auditory modality was associated with high (or low) detection performance in the visual modality. These correlations persisted after nonverbal IQ was partialled out ($r_{\text{partial}} = .89$ and $r_{\text{partial}} = .75, p < .001$, respectively).

4.2.1.2. RTs. A main effect of modality was observed ($F(1, 24) = 9.6, p < .01$) reflecting longer RTs to detect visual ($629 \text{ ms} \pm 113$) than auditory ($574 \text{ ms} \pm 84$) deviants. A main deviancy effect was also revealed ($F(1, 24) = 30, p < .001$) showing that ambiguous deviants were detected more slowly ($624 \text{ ms} \pm 86$) than fast deviants ($579 \text{ ms} \pm 78$). A main effect of group was also observed ($F(1, 24) = 6.8, p < .01$), suggesting that dyslexic participants were generally slower ($625 \text{ ms} \pm 63$) at detecting deviants than control participants ($578 \text{ ms} \pm 101$), although this was not modulated by the other factors neither in single- nor in second-order interactions ($F_s < 1$). Lastly, auditory and visual RTs did not correlate ($p_s > .05$).

In summary, the behavioral results confirm our predictions that the dyslexic group should not show a deficit in tempo detection or a differential pattern of responses for fast vs. ambiguous tempo deviants. Accuracy levels were comparable across groups, and although dyslexic participants were slower overall, they were similarly affected by variations in tempo deviancy as the control group.

4.2.2. ERPs data

Grand averaged ERPs obtained for the auditory and the visual tasks are presented in Fig. 5, and both amplitude and latency characteristics are presented in Table 3

4.2.2.1. P3b amplitude. First of all, note that no interaction between electrode and any other factor survived Greenhouse–Geisser correction or vector normalisation (McCarthy & Wood, 1985). As expected, we found a significant effect of deviancy type on P3b amplitude ($F(1, 24) = 73, p < .001$), such that fast deviants elicited larger P3bs ($4.2 \mu\text{V} \pm 3$) than ambiguous deviants ($2.7 \mu\text{V} \pm 3$; Table 3 and Fig. 5). This deviancy effect was greater in the visual modality ($2.3 \mu\text{V} \pm 2.4$) than in the auditory modality ($0.8 \mu\text{V} \pm 2.3$), as reflected by the modality by deviancy interaction ($F(1, 24) = 10.2, p < .005$).

As predicted (cf. Fig. 3d), a group by deviancy interaction was found ($F(1, 24) = 8.7, p < .01$) reflecting that the deviancy effect was greater in the control group ($2.1 \mu\text{V} \pm 2.8$; Newman–Keuls post hoc test, $p < .001$) than in the dyslexic group ($1.0 \mu\text{V} \pm 2.0$; Newman–Keuls post hoc test, $p < .01$); this interaction was not modulated by modality ($F < 1$; Fig. 6). In addition, visual and auditory amplitude measures for ambiguous deviants correlated significantly within the whole sample ($r = .41, p < .05$) even after controlling for nonverbal IQ ($r_{\text{partial}} = .41, p < .05$).

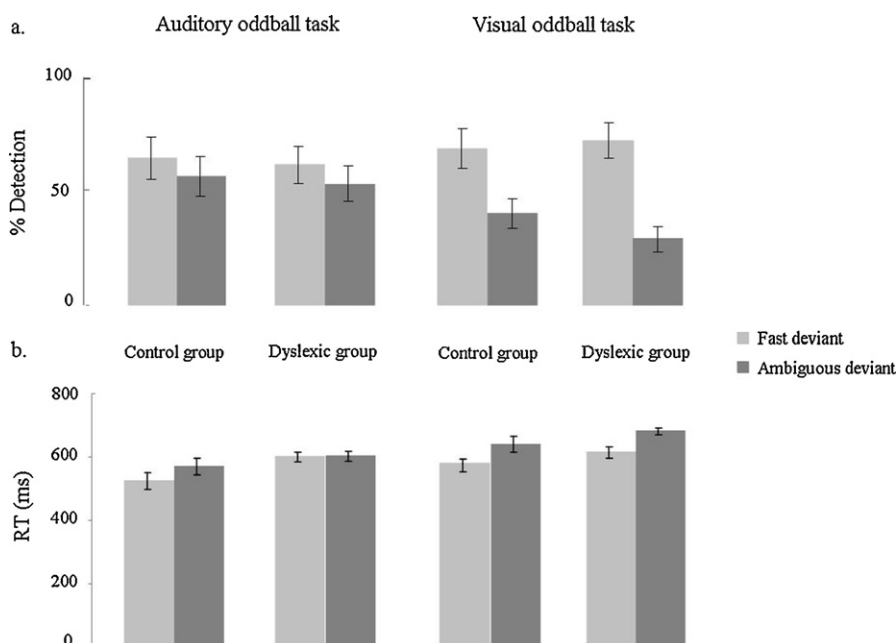


Fig. 4. Percentage of deviant detection (a) and reaction times (b) in Experiment 2 (bars depict standard error of the mean).

Table 3

Mean P3b latency at Pz (in ms) and mean differential P3b amplitude between standard and deviant stimuli over each electrode site (in μV) in the oddball tasks.

	Auditory oddball task		Visual oddball task	
	Controls Mean (SD)	Dyslexics Mean (SD)	Controls Mean (SD)	Dyslexics Mean (SD)
<i>P3b amplitude difference (μV)</i>				
Fast deviant				
CPz	5.0 (2.2)	3.7 (2.2)	5.5 (2.9)	4.9 (2.9)
Pz	3.8 (2.5)	4.6 (2.5)	4.5 (2.9)	5.2 (2.8)
POz	2.9 (2.5)	3.9 (2.5)	3.2 (3.3)	3.6 (3.3)
Moderate deviant				
CPz	3.8 (2.2)	3.2 (2.2)	2.4 (2.3)	2.7 (2.3)
Pz	2.6 (2.3)	4.3 (2.3)	1.1 (2.9)	3.2 (2.9)
POz	1.8 (2.4)	3.6 (2.4)	0.6 (3.5)	2.7 (3.5)
<i>P3b latency (ms)</i>				
Fast deviant	359 (28)	352 (45)	572 (92)	606 (100)
Moderate deviant	358 (36)	344 (45)	648 (91)	648 (56)

4.2.2.2. *P3b latency.* A main effect of modality was observed ($F(1, 24) = 312, p < .001$) consistent with the different temporal windows determined for ERP amplitude analyses, reflecting a longer latency for the P3b elicited by visual ($618 \text{ ms} \pm 92$) than auditory ($353 \text{ ms} \pm 39$) deviants. As expected, a main type of deviancy effect was also revealed ($F(1, 24) = 4.5, p < .05$) showing that the P3b elicited by ambiguous deviants peaked later ($500 \text{ ms} \pm 160$) than the P3b elicited by fast deviants ($472 \text{ ms} \pm 138$). However this deviancy effect on P3b latency was only present in the visual modality (modality by deviancy interaction: $F(1, 24) = 6.4, p < .05$) as showed by Newman–Keuls post hoc comparisons (visual: $p < .01$; auditory: $p = .8$). No main effect or interactions involving the group factor was observed (all $F_s < 1$), suggesting that P3b latencies elicited by visual and auditory fast and ambiguous deviants were similar between groups. Lastly, there was no correlation between visual and auditory P3b latencies ($p_s > .05$).

5. Discussion

This study evaluated the amodal SAS theory of developmental dyslexia (Hari & Renvall, 2001) using combined behavioral and electrophysiological measures in the same groups of participants and in two different sensory modalities. In Experiment 1, we replicated

the behavioral evidence for amodal SAS in dyslexic adults (Lallier et al., 2009) by showing that dyslexic participants displayed significantly higher stream segregation thresholds, in both the visual and the auditory modalities (see also Facoetti et al., 2005, 2010; King, Wood, & Faulkner, 2007; Lallier et al., 2010). The stream segregation thresholds measured in Experiment 1 allowed us to estimate the speed of automatic attentional shifting in each group, and to formulate specific hypotheses regarding the stream perception that would be elicited by variations in stimulus tempo in the oddball ERP Experiment 2 (see Fig. 3). As expected, the amplitude difference between the P3b elicited in response to ambiguous vs. fast deviants was larger in the control group than the dyslexic group in both modalities, although this group by deviancy interaction did not appear on the behavioral measure of change of tempo detection. Such a group difference in ERP responses was attributed to a lesser perceptual saliency of ambiguous than fast deviants in control participants compared with dyslexic participants. Indeed, the change in tempo (i.e., from SOA 340 ms to SOA 175 ms) would be accompanied by a change in the number of stream perceived in dyslexic participants only (i.e., from one to two streams), due to their sluggish attentional shifting. Thus, group differences in the P3b range dependent upon the presentation speed of stimuli indicate that dyslexic participants perceive auditory and visual

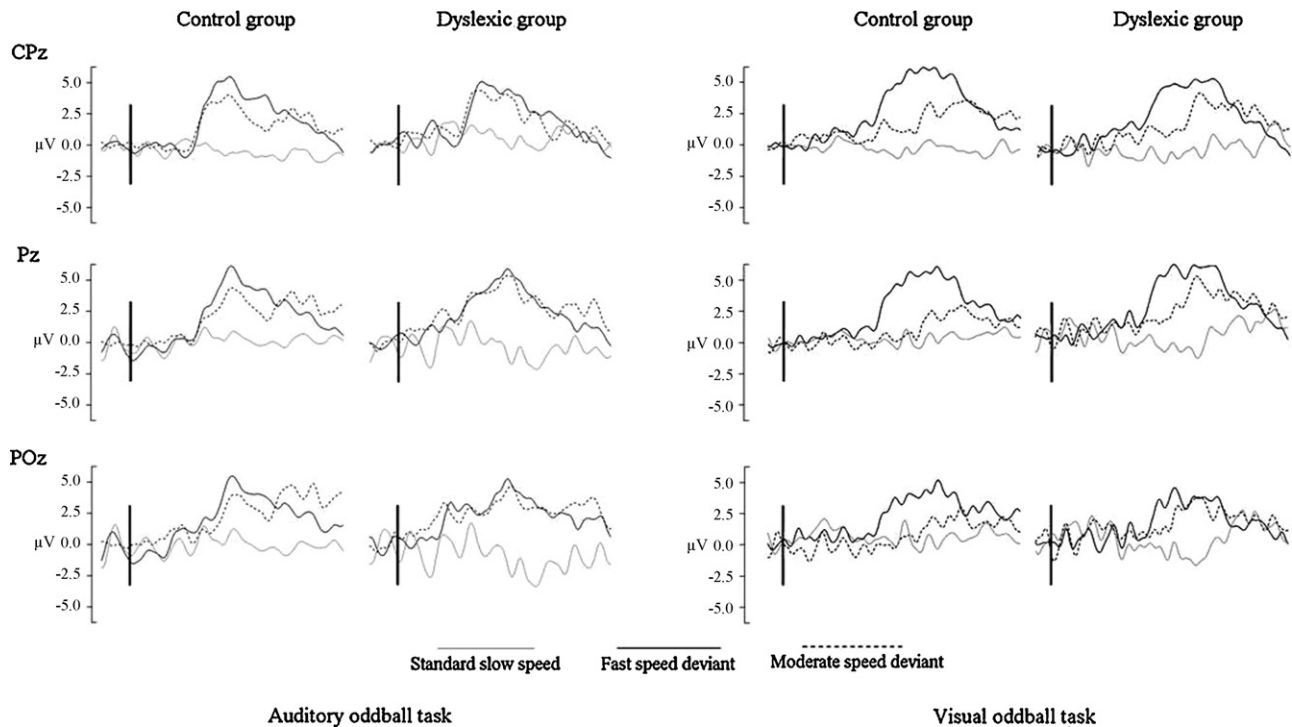


Fig. 5. Grand averaged ERPs in the oddball tasks.

rapid stimulus sequences in an atypical fashion, consistent with an amodal sluggish automatic attentional shifting. Although segregation thresholds could have been biased by behavioral strategies, the ERP data directly reflects the different perceptual experience of dyslexic and control participants when presented with rapid sequential stimuli. As stated in the introduction, Stoodley et al. (2006) failed to provide evidence for a *transient* temporal auditory behavioral deficit associated with dorsal stream processing (i.e., frequency modulation detection), but found evidence for an ERP deficit in the same high functioning dyslexic group. Our results with comparable participants suggest that the outcome of Stoodley et al.'s experiment might have been different if their task had tapped into *sequential* magnocellular processes rather than *transient* magnocellular processes as suggested by the SAS theory, since we demonstrated a deficit affecting the sequential nature of stimulus presentation.

One important finding is that auditory and visual measures correlated in (i) stream segregation thresholds—although the correlation only approached significance, (ii) detection performance in the oddball tasks, and (iii) P3b amplitude elicited by the ambiguous deviant. This suggests that the perception of rapid stimulus sequences in developmental dyslexia is affected by limitations in amodal attentional resources allocated to *sequential* processing.

Our results can be related to a study of language impaired (LI) children (Neville et al., 1993) showing atypical auditory ERPs for a short SOA (250 ms) compared with longer SOAs (1050 ms and 2050 ms) in a sub-group of LI children. Their visual ERPs were also atypical, but not specifically for the short SOA (see however Scheuerpflug et al., 2004 and Schulte-Körne, Bartling, Deimel, & Renschmidt, 2004 for ERP deficits on visual rapid temporal processing in dyslexic participants). Since dyslexic and LI individuals are thought to have phonological processing difficulties in common (Bishop & Snowling, 2004), both groups are indeed likely to exhibit amodal SAS symptoms (Hari & Renvall, 2001).

The visual-auditory correlations found in the present study support the idea that attentional shifting speed has to be synchronized between modalities in order to acquire fluent reading (Breznitz, 2003; Breznitz & Meyler, 2003; Breznitz & Misra, 2003). Whilst reading, synchronization between integration of rapid sequential graphemic/visual scanning and phonemic/auditory mapping may be necessary for the build-up of stable graphemic and phonemic representations. Along these lines, it has been suggested that auditory phonological awareness acquisition might at least in part be constrained by the visual processing entailed in grapheme-to-phoneme mapping (Pammer & Vidyasagar, 2005; Vidyasagar and Pammer, 2010). In the same vein, studies have shown that learn-

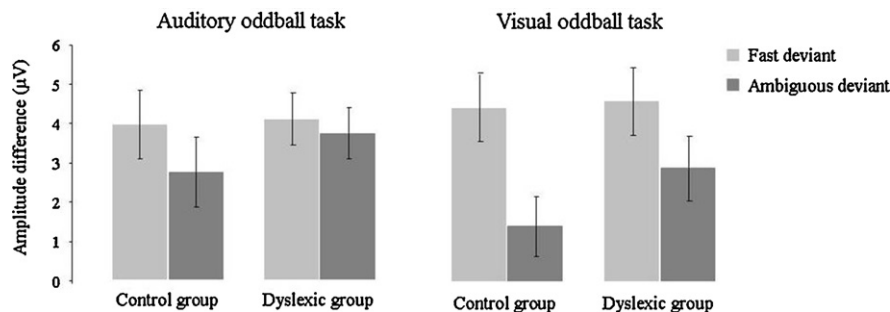


Fig. 6. Amplitude difference between standards and deviants over CPz, Pz and POz (bars depict standard error of the mean).

ing to read in an alphabetic system enhances the development of phonological awareness (e.g., Morais, Alegria, & Content, 1987). Moreover, phonological awareness would depend on the integration of auditory information extracted from both (visual) reading and (auditory) speech perception (Cheung, Chen, Lai, Wong, & Hills, 2001).

Although the present study is the first to have used ERPs to illustrate the atypical tempo perception of dyslexic individuals, some studies focusing on specific components reflecting automatic orienting, i.e., the mismatch negativity (MMN) and the P3a, bring further support to the results of Experiment 2. Indeed, the MMN, generated in response to perceptible changes in the context of an oddball paradigm (e.g., Näätänen & Winkler, 1999), is a reliable index of automatic sound discrimination and has been used extensively in the study of developmental dyslexia (see Bishop, 2007 for a review). In the context of a temporal deficit hypothesis, one would expect that the MMN elicited by a change of tempo in a rapid standard rhythmic structure should be atypical in dyslexic participants because of sluggish automatic temporal processing preventing them from efficiently shifting between successive stimuli. Accordingly, MMN amplitude differences between dyslexic and control participants have already been reported for tempo deviancy (Fisher et al., 2006; Kujala et al., 2000; Meng et al., 2005), tone order reversals (Kujala, Belitz, Tervaniemi, & Näätänen, 2003; Schulte-Körne, Deimel, Bartling, & Remschmidt, 1999b), or tone duration deviancy (Corbera, Escera, & Artigas, 2006; Kujala, Lovio, Lepisto, Laasonen, & Näätänen, 2006). Although the MMN evidence for a temporal deficit in dyslexia is substantial, it should be noted that stimulus presentation speed varied considerably between studies. Consistent with the predictions of the SAS theory, most studies have shown processing difficulties in the context of fast tempo presentation in dyslexic participants, i.e., using SOAs varying between 50 and 250 ms (Fisher et al., 2006; Kujala et al., 2000, 2003; Meng et al., 2005; Nagarajan et al., 1999). However, other studies have reported atypical MMN responses with slower stimulus presentation tempos, i.e., SOAs > 250 ms (Corbera et al., 2006; Kujala et al., 2006; Renvall & Hari, 2003; Schulte-Körne et al., 1999b).

In addition to the assessment of the MMN, a few studies have focussed on the P3a as an index of automatic orientation of auditory attention to nonverbal stimuli in developmental dyslexia (see Escera, Alho, Schröger, & Winkler, 2000 for a review on the functional significance P3a). Even though Hämäläinen, Leppänen, Guttorm, and Lyytinen (2008) failed to find an MMN reduction in dyslexic participants processing deviant pitch in tone pairs for short (110 ms) and long (355 ms) SOAs, they found a significant modulation of P3a amplitude at the short SOA. Also, Corbera et al. (2006) found a reduced and delayed P3a in dyslexic children in response to deviant tone durations presented with a SOA of 300 ms. Lastly, two studies showed atypical P3a elicited by various types of tone deviants presented at a slow tempo (SOAs > 600 ms; Kujala et al., 2006; Rüsseler, Kowalczyk, Johannes, Wieringa, & Münte, 2002).

Overall, although the aforementioned ERP studies support an automatic orientation deficit indexed by the auditory MMN and the P3a in dyslexic participants, it is unclear whether the deficit was due to sluggish automatic attentional shifting for fast presentation speeds (Hari & Renvall, 2001) or to general impairment of attentional shifting *regardless of* presentation speed. The P3b peak amplitude results of Experiment 2 clarify this question, as the anomaly of dyslexic participants was restricted to rapid tempos (ambiguous deviant tempo, SOA < 200 ms). Moreover, contrary to MMN or P3a cases, it is unlikely that the elicitation of the P3b, that we chose as the ERP peak to test our hypotheses, is affected in developmental dyslexia, both in the visual and the auditory modalities (e.g., Breznitz & Misra, 2003). Since we showed here that the fast deviant elicited a P3b of similar amplitude in both groups and within each modality, our results are a priori inconsistent with the

hypothesis of a general P3b elicitation deficit in developmental dyslexia, i.e., a deficit of endogenous attentional orientation (see Facchetti et al., 2003 for the same conclusion from behavioral tasks). Along the same lines, Dhar, Been, Minderaa, and Althaus (2008) showed that developmental dyslexic participants exhibited greater difficulty on automatic (MMN) than endogenous attentional (P3b) orientation, contrary to ADHD participants (see also Duncan et al., 1994).

Lastly, the present study focused on P3b amplitudes, and while delayed P3b latencies were observed for ambiguous compared with fast deviants in the visual modality, it is noteworthy that dyslexic and control participants showed similar P3b latency effects in all experimental conditions. Interestingly, this seems to go against the claim of Breznitz (2003) that ERP latencies would be the critical measure when investigating the neural basis of developmental dyslexia. This claim has been based on several studies showing that auditory and visual ERP latencies in response to nonverbal visual and auditory stimuli were prolonged in dyslexic individuals as compared to controls (Breznitz, 2003; Breznitz & Meyler, 2003; Breznitz & Misra, 2003; Duncan et al., 1994; Neville et al., 1993), supporting the idea that a general slow processing speed may hamper reading acquisition by desynchronizing graphemic and phonemic cue integration whilst reading (Breznitz, 2003; Breznitz & Meyler, 2003; Breznitz & Misra, 2003). In the present study, RTs to detect deviants were indeed slower in the dyslexic group. Even if this may reflect a motor processing speed deficit in these participants (e.g., Stoodley & Stein, 2006), it did not affect the time-course of cerebral activity linked to exogenous attentional orienting (i.e., P3b). Note that electrophysiological studies showing delayed ERP latencies in dyslexic participants generally used *slow* serial presentation tasks (SOAs > 1000 ms; e.g., Breznitz & Meyler, 2003; Breznitz & Misra, 2003; Duncan et al., 1994) in addition to focusing on different ERP components. The relationship between the amodal ERP latency deficit of dyslexic participants on slow tempo tasks and the amodal SAS demonstrated in this study remains unclear at present.

6. Conclusion

This study shows that, tested on similar designs in the auditory and the visual modalities, dyslexic participants impaired in phonological processing exhibit amodal behavioral and neurophysiological SAS symptoms which specifically affect rapid (<200 ms) temporal processing. As argued by Hari and Renvall (2001), SAS may lead to disorders in reading acquisition because the distortion of rapid speech stream perception would affect the development of phonological representations. Although it has been suggested that phonological developmental dyslexia may be caused by auditory sequential attentional dysfunction, our results show that visual processing difficulties are also present and correlated to auditory ones. Future studies will aim at determining to what extent visual sequential attentional impairments impact on reading acquisition. Lastly, the present results validate the stream segregation task as a tool to assess SAS in dyslexic adults.

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