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Research Report

Auditory event-related potentials differ in dyslexics even when auditory psychophysical performance is normal

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ABSTRACT

Developmental dyslexia is characterized by a phonological processing deficit and impaired low-level auditory processing may contribute to this problem. However, this remains controversial because not all dyslexic individuals show psychophysical deficits on auditory processing tasks; hence it has been argued that auditory processing deficits are not a causal factor in dyslexia. Because behavioral psychophysical tasks include both bottom-up processing and top-down strategies, dyslexics' successful coping strategies may positively influence their performance on auditory behavioral measures. Therefore we have studied whether dyslexics who perform adequately on auditory psychophysical tasks nevertheless show electrophysiological evidence of impaired auditory processing. We compared auditory event-related mismatch negativity (MMN) potentials to frequency modulated (FM) tones at 5, 20 and 240 Hz between dyslexic adults and controls. Groups were matched for age, cognitive ability and psychophysical FM detection thresholds. The dyslexic group showed significantly smaller MMNs in the 20 Hz FM condition in both the early (150–300 ms, $P = 0.010$) and late (300–500 ms, $P = 0.049$) time frames. A 2-way ANOVA showed a significant group by FM rate interaction ($P = 0.012$). There were no significant differences between the groups in the 5 Hz or 240 Hz conditions. The magnitude of the 20 Hz FM MMN correlated with the degree of discrepancy between cognitive and literacy skills (0.66, $P = 0.003$) in the entire group. Thus, even among compensated dyslexics with above-average cognitive abilities and adequate performance on auditory psychophysical tasks, the MMN responses of some dyslexic adults were found to be abnormal.

1. Introduction

Developmental dyslexia affects 5–15% of the population and is diagnosed when literacy skills are much lower than would be expected given a person's cognitive ability and education. One of the greatest difficulties that dyslexic readers have is to efficiently translate letters into the sounds they represent. It has been shown that difficulties in performing this task are related to problems in identifying speech sound segments, i.e., poor phonological awareness (see Snowling, 2000). One suggestion is that these phonological processing deficits are due to impaired low-level auditory processing (see Tallal, 1980; Farmer and Klein, 1995; Klein and Dick, 2002; Talcott and Witton, 2002; Stein, 2001). Some dyslexic readers have elevated thresholds for discriminating frequency modulated (FM) tones at low frequencies (e.g., 2 Hz), and performance on

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FM tasks has been found in some studies to correlate with reading ability and phonological awareness in both dyslexic and control adults and children (Witton et al., 1998; Talcott et al., 2003; Boets et al., 2006). However, not all dyslexic participants fall into the 'impaired' range on tasks requiring the detection of FM tones (Ramus et al., 2003); furthermore, even in the studies where significant group differences were found, the thresholds between the control and dyslexic groups overlapped. These data are often used to contest the idea that dyslexics have deficient low-level auditory processing, and to dismiss theories that propose that auditory dysfunction may underlie phonological deficits in dyslexia (Ramus et al., 2003; Ramus, 2003).

However, the validity of measuring the sensitivity of the auditory system in dyslexia using behavioral psychophysical tasks has been called into question. Some have argued that dyslexics are less able to perform these tasks because the task demands rather than any auditory deficits may be the cause of their higher detection thresholds (Banai and Ahissar, 2004, in press; Stuart et al., 2001; Roach et al., 2004). On the other hand, Marriage et al. (2001) highlight the need for auditory tests to be sensitive enough to identify 'compensated' participants. They define these as individuals who have developed strategies to overcome their weakness in real-life situations, but who continue to have subtle deficits. This population of compensated individuals is of particular interest as it is likely to include many of the college-educated dyslexics included in experimental samples. Thus psychophysical tasks may allow room for high-functioning dyslexics to successfully compensate for low-level deficits by using 'top-down' strategies; in particular, there is time to consider responses. This could lead to some dyslexics scoring in the normal range, overlapping with control participants, despite potential differences in neural processing.

To address the question of whether or not dyslexics who seem behaviorally 'normal' may have undetected auditory processing differences, we used an auditory event-related potential (ERP) mismatch negativity (MMN) paradigm to provide a more objective measure of early auditory processing of FM tones. ERP components reflect the perception and encoding of stimuli, and represent neural activity in response to stimuli in real time. During the MMN measurement, participants do not need to attend to the stimuli, nor do they have to make any type of response; this eliminates possible poor performance due to inability to stay on task or properly attend to the stimuli. Naatanen suggests that the MMN is a fairly objective measure of auditory discrimination and sensory memory, and that it can be used to study clinical populations (Naatanen, 2003; Naatanen et al., 1978, 1992; Naatanen and Escera, 2000). A decreased MMN amplitude may reflect a reduced duration of auditory sensory memory or a decreased automatic response in detecting a difference in stimuli.

The frequency modulations for both the behavioral and the ERP aspects of this study were chosen to reflect the results of past studies: dyslexics have been shown to have elevated thresholds to relatively slow frequency modulations (2 Hz and 40 Hz FM), but not to 240 Hz FM (Witton et al., 1998, 2002). We anticipated that if there were differences between our groups in the size or latency of the MMN measures, we would see these differences only in response to the slower frequency modulations.

In most previous studies investigating auditory ERPs in dyslexic participants, there has been a difference in auditory behavioral performance between the dyslexic and control groups, yet data from psychophysical studies have been inconclusive with regard to deficits at the behavioral level. We wanted to determine whether the ERP paradigm could detect group differences even when there were none at the psychophysical level. As discrimination of modulated and non-modulated tones is a higher-level cognitive process than the ERP task, we hypothesized that if a low-level processing deficit exists in dyslexia, we may be better able to detect it in compensated dyslexics using an ERP rather than a behavioral paradigm.

2. Results

Nine control and 10 dyslexic adults participated in the study. As expected the dyslexic group performed significantly worse on tests of reading, spelling and component literacy skills (literacy mean, $P=0.003$; orthographic choice task, $P=0.026$; phonological choice task, $P=0.05$—see Table 1). The dyslexic participants also had significantly worse short-term verbal memory ($P=0.048$) than the controls. Even though the dyslexics' standardized reading scores were in the normal range, these scores were well below the level expected for university students with high cognitive ability.

There were no significant differences between our dyslexic and control groups on the auditory FM tasks at any of the frequency modulations measured ($P>0.05$; Table 2).

The dyslexic group showed significantly smaller MMNs in the 20 Hz FM condition, in both the early (150–300 ms, $P=0.010$) and late (300–500 ms, $P=0.049$) time frames (Fig. 1b, Table 3). A two-way ANOVA for the MMN mean amplitudes showed a significant interaction between group and FM rate ($P=0.012$). There were no significant differences between the groups in the 5 Hz or 240 Hz conditions (Figs. 1a, 1c, Table 3). There were no differences between the standard waveforms for the groups in any of the three conditions.

We then investigated the relationship between the cognitive and literacy variables and the size of the MMNs measured for 5, 20 and 240 Hz FM. There were significant relationships between the early 20 Hz MMN and reading (−0.56, $P=0.012$), literacy (−0.48, $P=0.037$) and the size of the discrepancy between cognitive ability and literacy scores (0.66, $P=0.003$; a smaller MMN was related to a larger discrepancy between cognitive ability and literacy achievement) (Fig. 2). The late component of the 20 Hz MMN also correlated with the size of the cognitive-literacy discrepancy (0.52, $P=0.028$).

3. Discussion

Even though our dyslexic participants were unimpaired on the psychophysical FM discrimination tasks, they showed significant attenuation of the MMN amplitude to 20 Hz FM stimuli compared to the control group. This suggests that a difference in auditory processing may exist between good readers and

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Table 1 – Cognitive and literacy scores

Measure	Control, $N=9$	Range	Dyslexic, $N=10$	Range	P-value	Cohen's d
Age (years)	27.6 ± 7.4	19.75–36.1	23.6 ± 3.0	19.5–27.0	n.s.	0.54
Digit span	12.3 ± 3.3	7.0–18.0	9.2 ± 2.8	5.0–15.0	0.048	0.94
Similarities	12.9 ± 2.5	9.0–17.0	15.2 ± 2.8	11.0–18.0	n.s.	0.82
Vocabulary	15.0 ± 2.0	13.0–18.0	14.6 ± 3.9	7.0–19.0	n.s.	0.10
Block design	14.2 ± 3.6	9.0–19.0	13.7 ± 3.1	8.0–18.0	n.s.	0.14
Digit symbol	12.2 ± 2.5	9.0–16.0	9.2 ± 2.8	4.0–16.0	n.s.	1.07
Cog	14.0 ± 2.3	11.0–17.7	14.5 ± 2.0	12.0–17.7	n.s.	0.22
Reading	114.2 ± 6.0	105.0–122.0	101.5 ± 13.4	78.0–123.0	0.021	2.12
Spelling	113.8 ± 4.5	105.0–118.0	95.2 ± 18.8	51.0–112.0	0.010	4.13
Literacy	114.0 ± 5.0	106.5–119.0	98.3 ± 12.9	79.0–117.5	0.003	3.14
Orth %	98.2 ± 1.7	95.0–100.0	93.5 ± 5.5	83.8–100.0	0.026	2.76
Orth RT	857.0 ± 179.5	627.1–1115.6	1115.4 ± 387.7	624.1–1848.6	n.s.	1.44
Phon %	92.1 ± 5.2	86.7–100.0	84.8 ± 9.0	66.8–95.0	0.053	1.40
Phon RT	2824.0 ± 812.1	1045.7–3604.8	3289.8 ± 1253.0	1984.5–6289.5	n.s.	0.57

Key: Scores are presented as mean ± standard deviation. Cog = mean scores of the similarities, vocabulary, block design and digit symbol subtests of the WAIS-III. Digit span and Cog scores are based on a mean of 10 with a standard deviation of 3. Reading, spelling and literacy scores are from the WRAT-3. Scores are based on a mean of 100 and standard deviation of 15. Orth = orthographic choice task; phon = phonological choice task. RT = reaction time in ms. % = percent correct. P-values are the result of independent t-tests. n.s. = $P > 0.05$.

high-functioning dyslexics even when FM behavioral performance falls in the normal range.

Our results may illuminate the long-standing debate as to whether or not low-level auditory temporal processing deficits contribute to the phonological problems seen in developmental dyslexia. The behavioral results from psychophysical studies have been inconsistent. Our data suggest that, in high-functioning dyslexic participants, psychophysical paradigms may not be sensitive enough to detect subtle auditory processing impairments, whereas more objective electrophysiological recordings may be able to do so. Furthermore, our results suggest that those dyslexics with larger continuing discrepancies between their cognitive ability and their literacy skills show more abnormal auditory responses than those who have compensated more successfully for their literacy difficulties. Finally, while differences between dyslexic and control subjects seem to be restricted to the frequency modulation ranges important in speech processing, these differences are detectable even with non-speech stimuli.

Other groups who have measured event-related potentials to study the differences between neural processing in dyslexic and control participants have found that dyslexics' ERPs can differ in latency, amplitude and topography (for a review, see Kujala and Naatanen, 2001). Previous studies also have shown attenuated MMN responses to basic auditory stimuli in dyslexics (Baldeweg et al., 1999; Kujala et al., 2002, 2003), although there has been some debate as to whether dyslexics' auditory processing as measured by ERPs differs in response to basic auditory tones and frequency modulations, or if only speech stimuli, such as syllables or phonemes, discriminate dyslexic from control participants. For example, Baldeweg et al. (1999) found differences in MMN responses to deviants in tone frequency (but not tone duration) in dyslexic individuals as compared to normally reading controls. Maurer et al. (2003) showed that kindergarten children with a familial dyslexia risk showed an attenuated late MMN to frequency deviants. Csepe et al. (2001) demonstrated that dyslexics have diminished MMNs to tone, vowel and consonant changes, though the effect was most pronounced for consonant changes. Using magnetoencephalography (MEG), Parviainen et al. (2005) found that in dyslexic adults the interhemispheric balance and timing of MEG signals were altered for speech sounds, non-speech sounds and sine-wave tones, supporting the idea that general auditory processing is affected in dyslexic populations. While Lachmann et al. (2005) found only children with irregular word reading difficulties showed altered MMNs in response to syllable and tone changes, in the current study there was not a sufficient number of dyslexic participants that could be classified as having purely irregular word or nonword reading problems to evaluate this pattern.

However, work from Schulte-Korne et al. (1998, 2001) suggests that dyslexics' ERP responses differ from controls only during speech stimuli (syllables, phonemes) rather than to simple tones. Differing results are likely due to the wide range of stimuli used to elicit the MMN in these studies, as well as the different age groups of the participants, ranging from

Table 2 – Psychophysical thresholds on auditory tasks

Measure	Control, $N=9$	Range	Dyslexic, $N=10$	Range	P-value	Cohen's d
2 Hz FM	1.50 ± 0.68	0.77–2.94	1.50 ± 0.60	0.79–2.78	n.s.	0
20 Hz FM	0.32 ± 0.17	0.18–0.73	0.31 ± 0.14	0.14–0.58	n.s.	0.06
240 Hz FM	0.0048 ± 0.0030	0.0010–0.0099	0.0045 ± 0.0023	0.0010–0.0085	n.s.	0.01

Key: Auditory threshold scores are presented as mean ± standard deviation of the modulation depth (Hz). FM = frequency modulated. P-values are the result of independent t-tests. n.s. = $P > 0.05$.

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at-risk infants to adults. Some have suggested that, particularly in older dyslexics, only electrophysiological responses to stimuli specifically employed in speech are affected (Schulte-Korne et al., 1998). Schulte-Korne et al. (2004) investigated male adolescents with and without dyslexia on a recognition paradigm using previously learned pseudowords and graphic symbols. The dyslexic participants showed an attenuation of the positivity around 600 ms, which was thought to represent the recognition of the previously learned pseudowords, but the same attenuation was not seen with the graphic symbols. The authors take this as evidence that only speech-specific components of the ERP will be impaired in adult dyslexics. Further support for this comes from the lack of differences found when dyslexic and control adults' P3a and P3b waveforms in response to tones of different (but not modulated) frequencies are compared. Rüsseler et al. (2002) showed that, in a passive listening condition, there were no differences in dyslexics' responses to novel, non-speech stimuli (1500 Hz tones as compared to 1000 Hz standard tones). While the fact that we found group differences only to 20 Hz FM may reflect the importance of this frequency in language processing (McBridge-Chang, 1996), our data indicate that differences can be found in non-speech stimuli provided the stimuli are within certain parameters.

Why did we find differences only to 20 Hz FM and not to 5 Hz or 240 Hz FM? Differences between dyslexic and control participants have not been shown at high (240 Hz) frequency or amplitude modulations (Witton et al., 1998, 2002), and

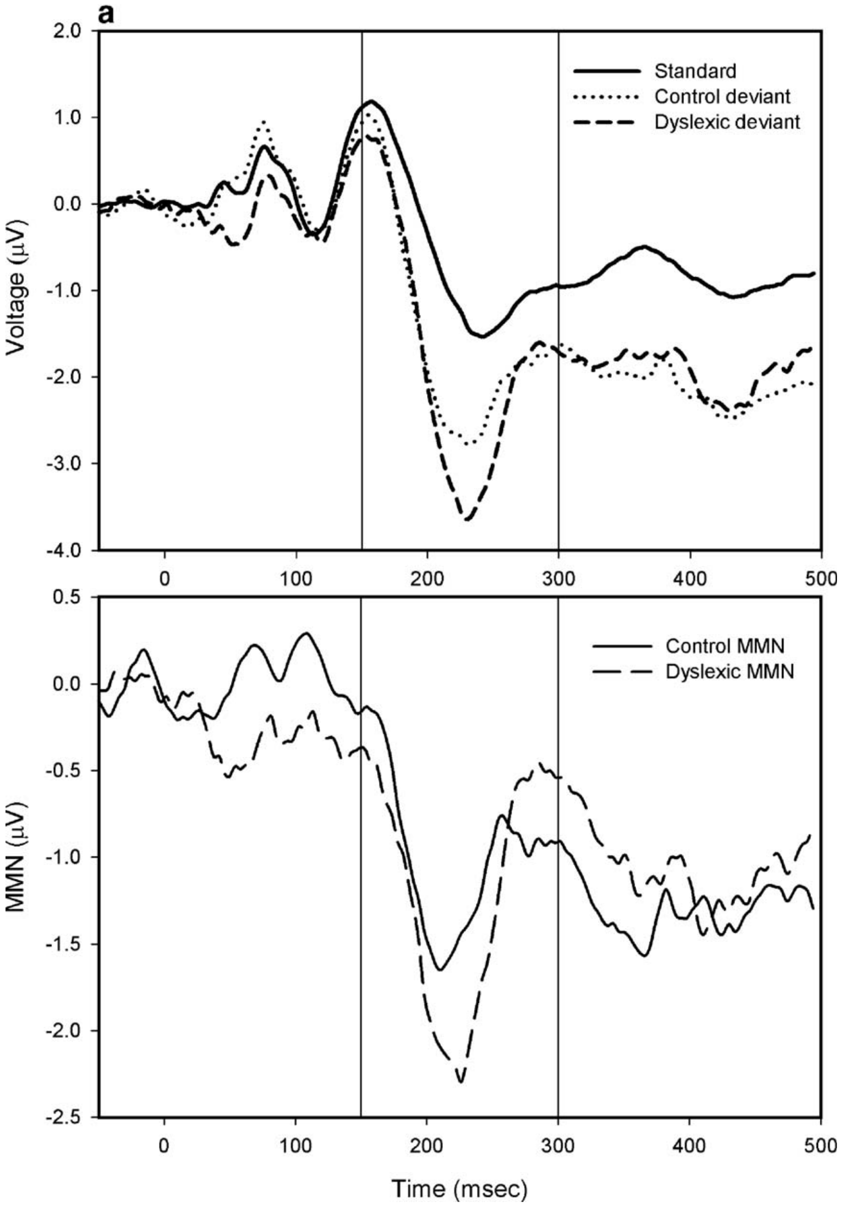

Fig. 1 – Grand average waveforms to the standard and deviant stimuli (top) and the MMN differential waveforms (bottom) for 5 (a), 20 (b) and 240 (c) Hz FM. Top: Standard stimuli (solid black) did not significantly differ between groups. Bottom: Control (solid black) and dyslexic (dashed line) MMN responses differed in the 20 Hz FM condition (b). Vertical lines indicate the early MMN range (150–300 ms) and late MMN range (300–500 ms).

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therefore we were not surprised that 240 Hz FM did not discriminate between the groups, either behaviorally or electrophysiologically. However, differences have been seen at lower frequencies (2 Hz) (Witton et al., 1998, 2002; Talcott et al., 2003), so we did expect to see differences between the groups at the lower rates of modulation (5 Hz, 20 Hz). However, we did not see any effects at 5 Hz FM. Further research will be necessary to determine why the effect is specific to the 20 Hz FM condition.

Several studies have found differences in the response to tones and more complex phonemic stimuli in infants and children at familial risk for dyslexia (Guttorm et al., 2003, 2005) or language-learning impairments (Benasich and Tallal, 2002; Benasich et al., 2006). ERP responses to syllables can discriminate infants with and without genetic risk of dyslexia, and this predicts their later language and verbal memory skills (Guttorm et al., 2005). At a more basic auditory processing level, Maurer et al. (2003) studied MMN paradigms with frequency and phoneme deviants in kindergarteners with and without familial risk of dyslexia. They found that the at-risk group had significantly attenuated responses to frequency deviants and the responses to phoneme deviance were less left-lateralized in the late MMN segment (in this case 300–600 ms). Our data also suggest that there are differences between control and dyslexic groups in the later MMN component in response to 20 Hz FM, even in high-functioning adult dyslexics. Also investigating responses to non-speech stimuli, a recent study by Benasich and colleagues (2006) investigated infants at risk for language-learning impairments. The at-risk infants showed a smaller mismatched response than the control infants, suggesting that at this early age non-speech stimuli can discriminate infants with and without a risk of language difficulties. In a previous study by the same group, 7.5-month-old infants from at-risk families

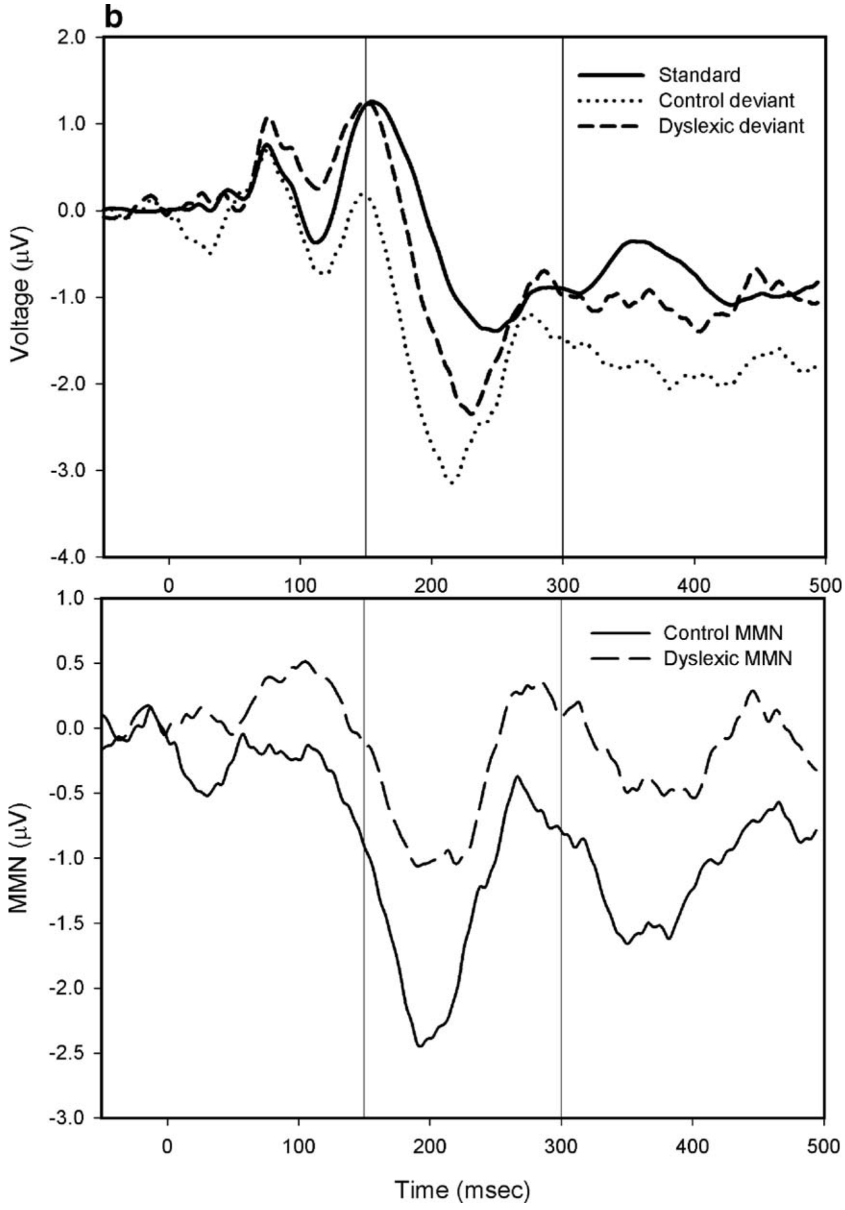

Fig. 1 (***continued***).

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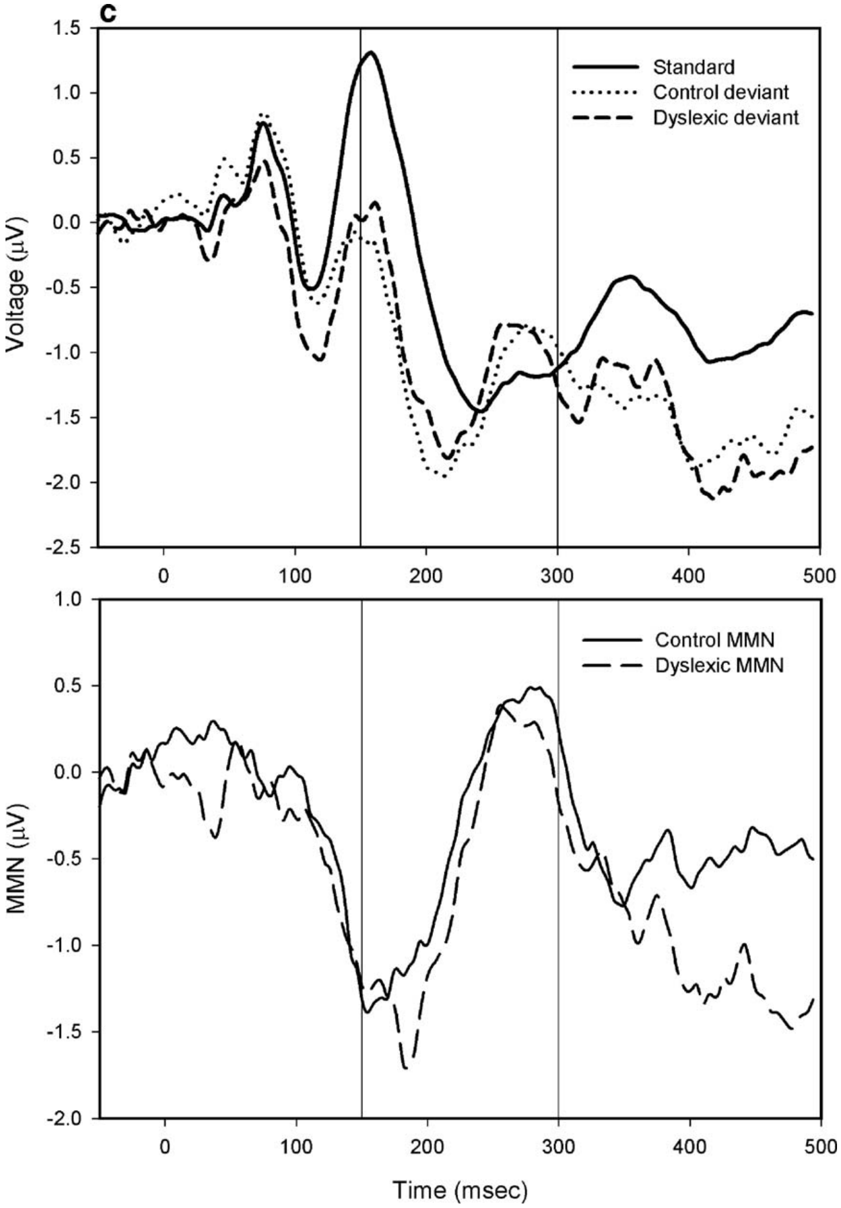

Fig. 1 (*continued*).

had worse thresholds on a rapid auditory processing task, and these thresholds were the single best predictor of language development at 2 years of age, and (along with gender) predicted 40% of the variance in language outcome at 3 years of age (Benasich and Tallal, 2002). The authors suggest that the auditory processing deficits both predict and precede language impairments, suggesting a causal relationship between low-level auditory processing and later language

Table 3 – MMN mean amplitude

Measure	Control, *N* = 9	Range	Dyslexic, *N* = 10	Range	*P*-value	Cohen's *d*
Early 5 Hz	−1.13 ± 1.07	−3.14–0.51	−1.18 ± 0.78	−1.97–0.09	n.s.	0.05
Late 5 Hz	−1.36 ± 1.33	−3.9–0.57	−1.05 ± 0.97	−1.93–0.94	n.s.	0.23
Early 20 Hz	−1.38 ± 0.72	−2.96–0.38	−0.46 ± 0.67	−1.72–0.25	0.010	1.28
Late 20 Hz	−1.09 ± 1.13	−2.57–0.61	−0.19 ± 0.66	−1.43–0.87	0.049	0.80
Early 240 Hz	−0.49 ± 0.54	−1.26–0.51	−0.58 ± 0.77	−1.56–0.70	n.s.	0.17
Late 240 Hz	−0.50 ± 0.62	−1.39–0.75	−1.02 ± 0.55	−1.84–0.48	n.s.	0.84

Key: MMN scores are presented as mean ± standard deviation (µV). *P*-values are the result of independent *t*-tests. n.s. = *P* > 0.05.

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skills. The evoked potential studies in infants at-risk for developmental dyslexia described above also indicate that differences in responses to both speech and non-speech stimuli exist very early in life. Unfortunately, the results of the follow-up of these children are not yet available; while they are 'at risk' for reading or language deficits, it is not clear yet whether or not they will develop the clinical conditions.

The fact that there are continua of both performance thresholds and electrophysiological responses that correlate with early language development suggests that children who are ultimately classified as having developmental dyslexia may be on the tail end of a continuum of perceptual ability. This is supported by data suggesting that even in normal school populations low-level sensory thresholds correlate with reading and spelling abilities (Talcott et al., 2002). All these data indicate that basic neurophysiological processing can constrain much higher-level processes such as phonological processing and ultimately reading and spelling. Importantly, the degree to which the neurophysiological processing deviates from normal may determine the degree of literacy difficulties; in this sample, there was a strong relationship between the size of the MMN response to 20 Hz FM and the size of the discrepancy between the participants' cognitive and literacy skills.

Differences in ERPs between dyslexic and control participants could result from two possible, but not mutually exclusive, effects: first, auditory ERPs may pick up functional differences between groups that are not evident at the

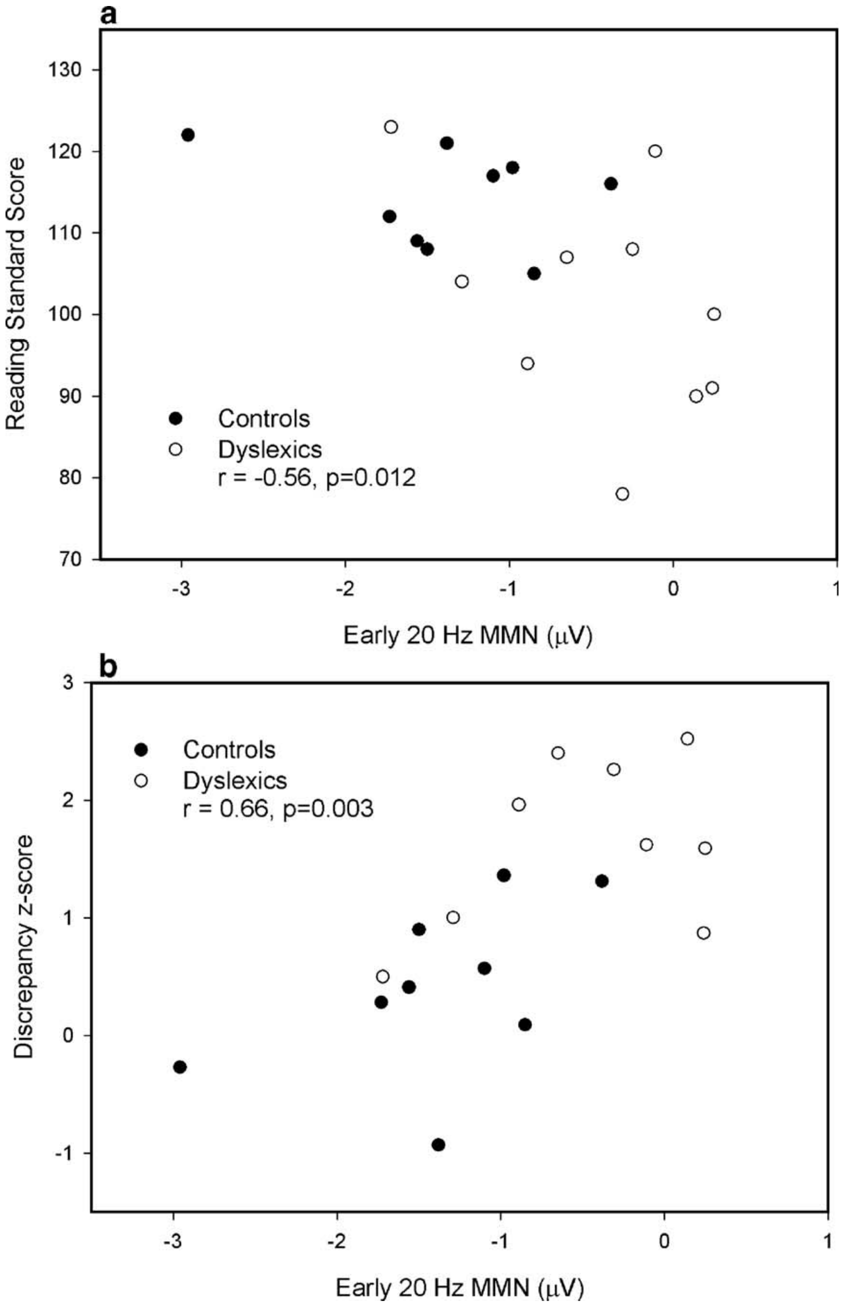

Fig. 2 – Correlations between the early 20 Hz FM MMN and literacy (a) and discrepancy (cognitive-literacy scores) measures (b).

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behavioral psychophysical level; and, second, auditory ERPs may be more sensitive to differences in the underlying brain morphology of their generators, which may differ between dyslexics and controls (Eckert et al., 2003). These may also reflect the anatomical and functional left-hemisphere differences seen in dyslexia (Galaburda et al., 1994; Heim and Keil, 2004; Leonard et al., 2001, 2002; Chiarello et al., 2006). Functionally, a reduction in the size of the MMN response may reflect either poorer detection of the difference in stimuli (both early and late components) or a reduced auditory memory span (late MMN component), both of which were reduced in response to 20 Hz FM in the dyslexic group as compared to the control group (Naatanen, 2003; Naatanen et al., 1978, 1992; Naatanen and Escera, 2000).

This study investigated a group of dyslexic university students and graduates in their early 20's with cognitive scores over a standard deviation above the norm. Indeed, even some of the reading scores in the dyslexic group were comparable to the control group; this was because these particular students had superior cognitive ability and discrepant, albeit good, reading scores. Given recent research suggesting that only a subgroup of dyslexics with lower cognitive ability and poor working memory show poor performance on auditory processing tasks (Banai and Ahissar, 2004), perhaps it is not surprising that this group of dyslexic participants was well-matched with our control group on the behavioral measures. What was most interesting was the fact that even though their performance on psychophysical tasks was within the range of the control group, they still showed neurophysiological differences in response to the same frequency-modulated stimuli. Our results may explain why there is such inconsistency of results when studying adult dyslexics who fall into the above-average range for cognitive ability (e.g., Ramus et al., 2003). Furthermore, psychophysical procedures using 1-up, 1-down staircases to estimate sensitivity thresholds may not be sensitive enough to pick up subtle processing differences between groups (see Klein, 2001 for a review). This points to the importance of taking into account age, cognitive ability and the sensitivity of the measures employed when investigating low-level sensory deficits in developmental disorders. Deficits that are evident in the electrophysiological studies of at-risk infants and young children may carry through to adulthood, but may not be easily detected using behavioral paradigms due to confounding factors such as working memory load and task difficulty (Banai and Ahissar, 2004, in press).

Thus, in high-functioning dyslexic populations, such as university students, even though it may not be possible to find behavioral differences on auditory psychophysical tasks, processing differences at the electrophysiological level may nevertheless be demonstrable (see also Rüsseler et al., 2002). The 20 Hz modulations used in this study represent frequency modulations that are in the same time frame as those that are important for distinguishing stop consonants (see Clark and Yallop, 1995); hence dyslexics' abnormal auditory processing may underlie their poor acquisition of phonological skills. These data suggest that neurophysiological responses to frequency modulated tones may be a more sensitive indicator of auditory processing than psychophysical measures. Even in adult university students with high cognitive scores and no psychophysical deficits, discrepancies between their literacy and cognitive skills may be associated with low-level auditory processing. Given the strong correlation between the size of the MMN and the size of the discrepancy between cognitive and literacy scores in the group as a whole, the MMN could serve as a physiological marker to differentiate dyslexics that one would expect to achieve good literacy skills and those that will not. It may be that the degree of neurophysiological impairment ultimately will affect the child's ability to respond to remediation.

4. Experimental procedures

Our participants were 10 dyslexic (4 male, 6 female) and 9 control (3 male, 6 female) adults matched on age and cognitive ability. The majority of participants taking part were either students or staff of the University of Oxford or Oxford Brookes University. The controls had no previous nor current literacy or neurological problems. The dyslexic participants had a history of reading problems from childhood and an independent diagnosis by an Educational Psychologist, based on a discrepancy between their cognitive scores and literacy skills.

The participants all completed the similarities, vocabulary, block design, digit span and digit symbol subtests of the Wechsler Adult Intelligence Scales version III (WAIS-III; Wechsler, 1981). These subtests sampled non-verbal (digit symbol, block design) and verbal (similarities, vocabulary) cognitive ability and verbal short-term memory (digit span). The single word reading and spelling subtests of the Wide Range Achievement Test version 3 (WRAT-3; Jastak and Wilkinson, 1984) were also administered.

The participants also completed component literacy tasks to assess orthographic and phonological ability. Both tasks were computerized, and the participant was asked to respond as quickly and accurately as possible. The Olson orthographic test is a word-pseudohomophone discrimination task programmed using SuperlabPro (version 1.04, Cedrus) (Olson et al., 1994). A two-alternative forced-choice paradigm presents two letter strings side by side: one is a correctly spelled real word (e.g., 'rain') and the other is a pseudohomophone of the word (e.g., 'rane'). The subjects had to decide which was the 'real' word. Feedback ('Correct' or 'Incorrect') was given during the task. The participants started with an 8-item practice session followed by 80 experimental items. This task is strongly orthographic, since the visual form of the word must be known to solve it; sounding out the letters cannot yield the correct answer. Percent correct for the 80 test items and mean response time (RT) were calculated offline. The phonological choice task was administered using the same software and procedure as the orthographic task. Three nonwords were presented in a three-alternative forced-choice paradigm. The participant was asked which of the three (e.g., *nite dite hote*) sounded like a real word, and worked as quickly and accurately as possible. Feedback ('Correct' or 'Incorrect') was given as the participant completed the 5 practice and 60 experimental trials. Percent correct and the mean response time were calculated offline.

The participants' thresholds for discriminating FM tones from pure tones were measured psychophysically using a 1-

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up, 1-down staircase; this task has been shown to discriminate some dyslexic from control participants (Witton et al., 1998, 2002; Talcott et al., 2003). Psychophysical thresholds were obtained for auditory frequency modulated (FM) detection tasks at 2, 20 and 240 Hz. Tones of 1000 ms duration, one standard 1 kHz tone and one frequency modulated tone, were presented as singing birds with a 500 ms inter-stimulus interval (ISI). Participants were asked to select which bird 'sang' the frequency modulated tone. The task was self-paced by the subjects using the computer mouse to make their responses; trials were initiated by a button-click. Feedback was given in the form of colored eggs for correct responses, and a blue 'X' for incorrect responses. The sounds were presented through headphones in a quiet room at 70 dBSPL. A 1-up, 1-down adaptive staircase was used to adjust target stimuli to obtain threshold measurements, and the thresholds represent the mean of 16 reversals (the final 8 of 10 reversals obtained during two separate runs of the staircase).

Event-related potentials were recorded using Neuroscan software (version 4.3). A 32-electrode 10/20 array with Ag/AgCl electrodes was used with a chloride-free abrasive electrolyte gel. Ocular potentials were recorded from outer canthi of both eyes and above and below the left eye. The recording reference was the left mastoid. The data were sampled at 250 Hz and band pass filtered (0.1–30 Hz).

Three blocks (one for each modulation rate) of 750 trials (127 deviant trials, 17%) were run. In each block, a separate deviant tone was used—as for the behavioral task, slow, medium and fast rates of modulation were used. In order to have a stimulus that changed detectably within a few hundred milliseconds of stimulus onset, the slow rate was 5 Hz rather than 2 Hz modulation. The medium and fast modulation rates were 20 Hz and 240 Hz, as in the behavioral study. These stimuli had previously been shown to generate a significant MMN in typical adults (Bishop et al., 2005). The order that the blocks were administered was counterbalanced between subjects. The standard tones (200 ms) were interleaved with modulated tones; the modulated tones had a 500-Hz carrier frequency that was varied sinusoidally at a rate of 5, 20 or 240 Hz with a modulation depth of 20 Hz. The stimulus-onset asynchronies were jittered (mean 1200 ms, SD 93 ms). The stimuli had 10-ms rise/fall ramps and were presented dichotically at 80 dBSPL via calibrated Sennheiser headphones in a soundproof booth while the subject watched a muted nature film.

The data processing included ocular artifact correction and re-referencing to the average of all electrodes. The participants were asked to avoid excessive eye movements, and the silent video was shown on a television screen that was positioned such that the entire screen could be viewed without eye movements. The ocular artifact reduction used an algorithm of an average blink that was calculated from greater than or equal to 20 oculogram epochs triggered by a 10% increase in activity (Semlitsch et al., 1986). The data were divided into 550 ms epochs (−50 ms before onset of stimulus to 500 ms after the stimulus occurred). The standards (1 kHz tones) and deviants (modulated tones) were averaged into separate files for each participant. The MMNs quoted here were recorded from Fz (mid frontal) and reflect the mean amplitude response difference between the deviant and standard trials during the 150–300 ms (early MMN) and 300–500 ms (late MMN) time windows.

Data analysis was performed using SPSS version 12.0. All data were normally distributed (one-sample Komolgorov–Smirnov tests, all $P > 0.05$) so parametric tests were used for data analyses.

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