Dyslexics are impaired on implicit higher-order sequence learning, but not on implicit spatial context learning

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Abstract

Developmental dyslexia is characterized by poor reading ability and impairments on a range of tasks including phonological processing and processing of sensory information. Some recent studies have found deficits in implicit sequence learning using the serial reaction time task, but others have not. Other skills, such as global visuo-spatial processing may even be enhanced in dyslexics, although deficits have also been noted. The present study compared dyslexic and non-dyslexic college students on two implicit learning tasks, an alternating serial response time task in which sequential dependencies exist across non-adjacent elements and a spatial context learning task in which the global configuration of a display cues the location of a search target. Previous evidence indicates that these implicit learning tasks are based on different underlying brain systems, fronto-striatal-cerebellar circuits for sequence learning and medial temporal lobe for spatial context learning. Results revealed a double dissociation: dyslexics showed impaired sequence learning, but superior spatial context learning. Consistent with this group difference, there was a significant positive correlation between reading ability (single real and non-word reading) and sequence learning, but a significant negative correlation between these measures and spatial context learning. Tests of explicit knowledge confirmed that learning was implicit for both groups on both tasks. These findings indicate that dyslexic college students are impaired on some kinds of implicit learning, but not on others. The specific nature of their learning deficit is consistent with reports of physiological and anatomical differences for individuals with dyslexia in frontal and cerebellar structures.
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Fluent reading is achieved in a series of stages or phases over a protracted period in childhood via regular instruction and practice (for reviews, see Ehri, 1999) and is accompanied by brain-based changes (Simos et al., 2001; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003). However, even with adequate educational opportunity, some children do not become fluent readers; 5–12% of school-aged children are identified with developmental dyslexia (Lyon, 1995; Vellutino, Fletcher, Snowling, & Scanlon, 2004). The most prominent weaknesses of developmental dyslexia are found in word identification, phonological (letter-sound) decoding and spelling. Although adults

with developmental dyslexia may compensate in some areas of reading, the cardinal markers observed in childhood, such as poor phonological awareness skills (Bradley & Bryant, 1981), frequently persist into adulthood (Ransby & Swanson, 2003; Shaywitz et al., 1999).

Behavioral studies conducted in children and adults with dyslexia have focused on a diverse set of language and non-language skills. In addition to faulty phonological processing, developmental dyslexia has been described as a reading disorder attributable to other deficits, including impaired temporal processing, magnocellular processing or rapid naming, as well as a lack of automatization or a combination of the above (for reviews, see Eden & Zeffiro, 1998; Rayner, Foorman, Perfetti, Pesetsky, & Seidenberg, 2001; Stein & Walsh, 1997; Vellutino et al., 2004; Wolff & Lundberg, 2002). The result is an ongoing

discussion on the contribution of these observed language and sensorimotor deficits and their potential role in the etiology of dyslexia. Anatomical (Eckert & Leonard, 2000; Eckert et al., 2003; Galaburda, Sherman, Rosen, Aboitiz, & Geschwind, 1985) and functional studies in individuals with dyslexia have revealed differences in regions of occipital–temporal, temporo-parietal and frontal regions of the left hemisphere when compared to typical readers. These variations in brain function have been demonstrated while participants engage in cognitive linguistic (Brunswick, McCrory, Price, Frith, & Frith, 1999; Eden et al., 2004; Flowers, Wood, & Naylor, 1991; Rumsey et al., 1992; Shaywitz et al., 1998) as well as sensorimotor tasks (Demb, Boynton, & Heeger, 1998; Eden & Zeffiro, 1998). Taken together, both behavioral and brain-based research indicates that the manifestations observed in dyslexia are complex, making it difficult to provide a unitary account of the etiology of this common and heritable learning disability (Eden & Zeffiro, 1998).

Despite the apparent discrepancies in the field, it is widely accepted that children with dyslexia have impaired phonological awareness. Phonological awareness is the ability to isolate and manipulate the constituent sounds of oral language, and proficiency in phonological awareness is crucial in learning to map alphabetic symbols to sound, leading to successful phonological decoding of text (Vellutino et al., 2004). Further, there is strong evidence of beneficial effects of intervention using phonological awareness training, suggesting a direct causal relationship between phonological awareness skills and learning to read (Alexander & Slinger-Constant, 2004; Torgesen et al., 2001). Yet, little is known about why dyslexic children struggle to learn the code which links graphemes with phonemes, and whether their inability to learn the mapping of alphabetic symbols to sounds is evident in non-linguistic domains of learning. Dyslexia is rarely studied in the framework of the contemporary learning literature. The present research does so via a focus on implicit learning.

Unlike the deliberate and conscious processes that occur in explicit (declarative) learning, implicit learning occurs automatically without the intention to learn or the resulting explicit knowledge of what was learned (e.g., Reber, 1989). Learning to read involves both explicit and implicit processes; children initially learn grapheme–phoneme mappings explicitly after which they apply and continue to learn them implicitly (Gombert, 2003). They also learn the orthography–meaning correspondence explicitly through picture–word matching and implicitly through context.

One could contemplate several mechanisms by which a deficit in implicit learning contributes to difficulties associated with dyslexia, but the small literature on implicit learning and dyslexia has yielded mixed results. Five studies have used the serial reaction time task (SRTT) introduced by Nissen and Bullemer (1987) in which people respond to each of a series of stimuli by pressing a corresponding key. Sequence learning is revealed by a decline in performance when the predictable repeating pattern is replaced by a random sequence. Three of these studies reported an implicit learning deficit in poor readers (Stoodley, Harrison, & Stein, 2006; Vicari et al., 2005; Vicari, Marotta, Menghini, Molinari, & Petrosini, 2003), whereas the

other two did not (Kelly, Griffiths, & Frith, 2002; Waber et al., 2003). Two additional studies have used other implicit learning tasks, again with mixed results. Pothos and Kirk (2004) found no reading-related deficits in one version of an artificial-grammar learning task and a significant advantage for dyslexic people on the other version. Yet another study found a relationship between implicit categorical learning and reading ability such that poor readers were impaired in implicit learning, but not explicit learning (Sperling, Lu, & Manis, 2004). And finally, in contrast to most earlier studies that focused on only one kind of implicit learning, Vicari et al. (2005) examined two implicit learning tasks that engage different cognitive skills, serial reaction time and mirror drawing. They found that dyslexic children did more poorly than controls on both tasks, leading them to conclude that dyslexia is characterized by a general deficit in implicit learning.

These findings suggest that it is not enough to compare implicit versus explicit learning or to investigate a single implicit learning task. Thus, in the present study we used two implicit learning tasks that we expect to be differentially affected by dyslexia. The first is an alternating SRTT in which sequential dependences exist across non-adjacent elements (Howard & Howard, 1997; Howard, Howard, Japikse et al., 2004). The second is a spatial context learning task in which the global configuration of a display cues the location of a search target (Chun & Jiang, 1998). These two implicit learning tasks appear to rely on different cognitive skills and different brain regions (Howard, Howard, Dennis, Yankovich, & Vaidya, 2004). Learning of non-adjacent, higher-order, sequential regularities calls on fronto-striatal-cerebellar circuitry whereas spatial contextual learning depends on medial temporal lobe structures (Chun & Phelps, 1999; Prull, Gabrieli, & Bunge, 2000). Cerebellar (Nicolson, Fawcett, & Dean, 2001b) as well as striatal (Vicari et al., 2005) deficits have been associated with dyslexia, but there is no evidence to suggest medial temporal lobe dysfunction in developmental dyslexia. We therefore predicted that poor readers would be impaired on implicit sequence learning, but not implicit spatial context learning. Furthermore, a dissociation between the two types of implicit learning tasks would help to establish that the deficits shown on one implicit learning task are unlikely due to general attention deficits which would presumably influence both tasks.

Both of the implicit learning tasks used in the present study are structured so that predictable and unpredictable trials occur in every block, making it possible to measure pattern learning continuously throughout training. This approach is an improvement over the studies described above in which learning is not measured until a single random block occurs near the end of training. Hence, the present design should be more sensitive to any group differences in the rate of implicit learning. In addition, both tasks have been shown to result in relatively pure implicit learning: subjects are unable to consciously recognize or produce the regularities they have learned at above chance levels (Howard & Howard, 2001; Howard, Howard, Dennis et al., 2004; Howard, Howard, Japikse et al., 2004).

Another new aspect of the present study is that the sequence learning task used here requires that people learn higher-order structure. Unlike the simple repeating sequences in the previous

studies with dyslexics, the predictive relationships to be learned span at least three events (i.e., the stimulus on trial *n* predicts the stimulus on trial *n* + 2). This is important because the level of sequential structure influences the cognitive and neural systems engaged. For example, healthy aging is characterized by deficits in learning higher-order, but not lower-order repeating sequences (Curran, 1997a; Howard & Howard, 1997; Howard, Howard, Japikse et al., 2004). Therefore, it is likely that sequences containing only higher-order structure will be more sensitive to sequence learning deficits.

In the present study, we tested college students with and without a history of dyslexia consistent with previous research (e.g., Kelly et al., 2002; Pothos & Kirk, 2004). We compared their performance on two implicit learning tasks. On the basis of the known dissociable functional correlates underlying these two tasks and the well-documented weakness in learning reading-related skills, we predicted that students with a history of poor reading skill would show impaired implicit learning on the higher-order sequence learning task, but unimpaired implicit learning on the spatial contextual cueing task.

1. Method

1.1. General procedure

Participants were scheduled for either 2 (13 people) or 3 (10 people) testing sessions on separate days. On the first day, participants signed an informed consent approved by the Institutional Review Boards of both Georgetown and Catholic Universities. They then completed the contextual cueing task (SCCT described below). The alternating serial reaction time task (ASRTT) was completed either in two sessions on the second day or in individual sessions on two separate days. A rest break of at least 15 min was given between sessions for those tested on a single day. Several standardized neuropsychological tests (see below) were administered following the experimental tasks over the two or three days of the study.

1.2. Participants

Twenty-three college student volunteers (11 dyslexic and 12 non-dyslexic) participated in the experiment. Eight of the dyslexic participants responded to an e-mail solicitation sent to dyslexic students by the Catholic University Disability Support Services Office. These individuals had a documented history of dyslexia as required to receive disability support. The remaining dyslexics and the typical controls responded to flyers placed on campus. Documentation was not obtained for the three additional dyslexics; however, they did not differ from the documented dyslexics on a statistical comparison of scores on the standardized tests associated with reading ability (see below). None of the participants had been in a similar study and each was paid for participating.

Participants underwent behavioral testing in order to characterize their handedness, single word reading, verbal working memory, spelling, phonemic awareness, rapid naming and vocabulary (described below). As may be seen in Table 1, the two groups did not differ in age or digit span, but as expected the dyslexic group scored more poorly on tests of single real and non-word reading (word identification and word attack) as well as skills related to reading, such as rapid automatized naming (RAN), phonological awareness, spelling and vocabulary. Four of the dyslexic subjects and none of the controls reported a prior diagnosis of attention deficit hyperactivity disorder (ADHD). All participants were right-handed, as determined by the Edinburgh Handedness Inventory (Oldfield, 1971) and were native speakers of English.

Single real word reading and pseudoword (phonetically regular non-word) decoding skills were assessed using subtests from the Woodcock–Johnson Psycho-Educational Battery: letter–word identification and word attack (Woodcock & Johnson, 1990). Auditory working memory was tested by asking

Table 1
Participant characteristics

	Control	Dyslexic
Gender	8 F, 4 M	5 F, 6 M
Age	20.25 (1.14)	20.59 (1.46)
Handedness[*]	93.82 (11.80)	61.34 (52.25)
Word identification (W–J WI)[***]	133.00 (17.04)	102.09 (14.61)
Word attack (W–J WA)[**]	116.67 (15.23)	98.54 (8.85)
Digit span combined (WAIS-III)	108.33 (14.82)	99.09 (10.44)
Spelling (TWS)[***]	119.58 (10.41)	99.18 (9.68)
Phoneme awareness[a] (TAAS)[*]	12.75 (.45)	11.73 (1.42)
Rapid automatized naming[*]	102.00 (10.32)	88.00 (16.05)
WASI vocabulary[*]	70.00 (8.15)	59.18 (10.84)

[a] Raw score, others standard scores.
[*] $p < .05$.
[**] $p < .01$.
[***] $p < .001$.

subjects to repeat increasingly longer lists of numbers in sequences of increasing length (from 2 to 9 numbers), forwards and backwards (Wechsler Adult Intelligence Scale, WAIS-III; Wechsler, 1997). The Test of Written Spelling test was employed to measure encoding of predictable (phonetically regular) and unpredictable (irregular) words (Larsen & Hammill, 1986). Subjects' ability to segment spoken words was assessed via the Test of Auditory Analysis Skill (Rosner & Simon, 1971) and the Rapid Automatized Naming Test (Denckla & Rudel, 1976) was used to assess naming fluency (for objects, colors, letters and numbers combined). The vocabulary portion of the Wechsler Abbreviated Scale of Intelligence (WASI) required subjects to orally define words and was used to assess word knowledge (Wechsler, 1999). Published norms were used when available, with the exception of the Rosner Test of Auditory Analysis Skills and the Rapid Automatized Naming Test. For the former, we present raw scores and for the latter norms were based on the distribution of scores from a large sample of adult subjects in whom developmental reading disability had been ruled out by childhood testing (Felton, Naylor, &Wood, 1990; Flowers, 1995). All standardized scores have a mean of 100 and a standard deviation of 15, except the WASI vocabulary that has a mean of 50 and standard deviation of 10.

1.3. Alternating serial reaction time task

1.3.1. Design
The design was a 2 × 2 × 8 (Group × Trial Type × Epoch) mixed factorial, with Group (dyslexic versus control) as a between-subjects variable and Trial Type (pattern versus random) and Epoch (1–8) as within-subjects variables.

1.3.2. Stimuli and apparatus
Four open circles (.5° each) were displayed horizontally on the iMac computer screen. The top part of Fig. 1 shows a schematic of the display. The entire display subtended 12° of visual angle at the 56 cm viewing distance. An event occurred when one of the open circles became solid black. Four labeled keys were used for responding with the middle and index finger of each hand (*z*, *x* and "," "/"). Target locations were determined by a repeating eight-element structure in which fixed and random locations alternated. Participants were assigned one of the six unique permutations of the fixed sequence locations (i.e., ArBrCrDr, ArBrDrCr, ArCrBrDr, ArCrDrBr, ArDrBrCr, ArDrCrBr, in which A–D represent spatial positions ordered from left to right). Each permutation was used twice for the control group, whereas five of the permutations occurred twice and one only once for the dyslexic group. On random trials, the events were sampled from a uniform distribution such that the four locations were equally likely. Hence, unlike many previous sequence learning studies, in this study the same event could repeat on immediately successive trials.

1.3.3. Procedure
Participants were told that they were to press the key under the target circle as quickly as possible while maintaining approximately 92% accuracy. The sequence regularity was not mentioned. Participants completed two 20-block
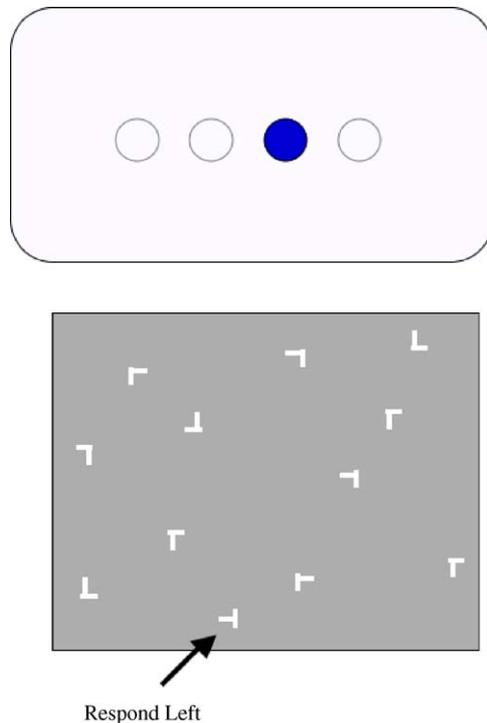
Respond Left

Fig. 1. Schematic of computer display for the sequence learning (upper part) and contextual cueing (lower part) tasks.

sessions. Each block began with 10 random trials followed by 80 learning trials, i.e., 10 repetitions of the 8-element long pattern. On each trial one of the circles filled in and remained so until a correct response occurred. Reaction time was measured from target onset to the first response. The next stimulus followed the correct response after a fixed 120 ms delay. Feedback was presented on the computer screen after each block asking people to focus more on either speed or accuracy to encourage responding at about 92% accuracy. In all, each person responded to 3200 trials or 400 repetitions of the pattern.

After completing these 40 blocks, participants completed several tasks designed to assess their explicit knowledge. In the first, they responded to a single *recognition block* in which they observed a sequence of 16 events on each of 20 trials. After observing the sequence they were asked to evaluate if it had occurred during the response trials using a scale of 1 (certain it did not) to 4 (certain it did). On half the trials the events consisted of two passes through the alternating sequence that was used on the response trials (e.g., BrCrArDr, beginning at a random starting point). On the remaining trials the events were produced by a foil sequence made up of either the alternating response sequence in reverse (i.e., DrArCrBr, again from a random starting point) or a randomly generated sequence. The reverse sequence ensured that the first- and second-order statistics of the target and foil sequences were identical whereas these differed for the random foils.

Following recognition, people undertook a *sorting task*. They were given a deck of 64 cards each of which portrayed 3 successive trials as 3 rows of 4 circles each, with 1 circle darkened on each trial (the event). There was one card for each of the 64 possible three-trial sequences or triplets. Participants were asked to examine each card carefully and sort it into one of three categories reflecting the frequency with which that triplet occurred during the experiment ("most frequent," "somewhat frequent" or "least frequent"). In previous research, we have shown this sorting task to be a sensitive indicator of explicit knowledge in the ASRT task (Japikse, Howard, & Howard, 2001).

The experiment concluded with an *interview* to probe declarative knowledge of the sequence. People were asked a series of increasingly specific questions, ranging from "Do you have anything to report regarding the task?" to "did you notice any regularity in the way the stimulus was moving on the screen?" Finally, they were told that there was in fact a regularity that occurred on every other trial and they were asked again to identify it.

1.4. Spatial contextual cueing task (SCCT)

1.4.1. Design
The design was a $2 \times 2 \times 6$ (Group $\times$ Configuration $\times$ Epoch) mixed factorial, with Group (dyslexic versus control) as a between-subjects variable and Configuration (repeated versus new) and Epoch (1–6) as within-subjects variables.

1.4.2. Stimuli and apparatus
The stimuli consisted of 12-element arrays of 11 distractors and a single target shown on an Apple iMac 15 in (38 cm) monitor as white characters on a gray background. As shown in the lower half of Fig. 1, the target was a horizontal T with the tail pointing either left or right and the distractors were L's randomly rotated by $0°, 90°, 180°$ or $270°$. Following Chun and Phelps (1999) Experiment 2, the L leg was offset by three pixels to increase similarity with the target. Each element subtended approximately $1.1°$ of visual angle at a viewing distance of 56 cm. Arrays were generated by randomly placing the 12 items into cells of an invisible 6×8 (rows $\times$ columns) grid. Across arrays, target location was balanced for eccentricity with respect to the center of the screen as well as for left and right screen half. Targets never appeared in the four center cells or at the extreme corners of the display grid. Every element was randomly repositioned within its cell by ± 2 pixels along each axis to avoid co-linearity with other elements. A set of 12 arrays was constructed for repeated presentation across the experiment (details below). Individuals within each group received a different set of new and repeated configurations, but the same sets were used across groups with their presentation order randomized.

1.4.3. Procedure
The experimental task was the same as that used by Chun and Jiang (1998). Subjects completed a 24-trial *practice block* after receiving instructions. Trials began with a white fixation dot (approximately $.5°$) centered on the screen. After 1 s the dot was replaced by a search array and participants had to press a key indicating the target orientation ("z" for left and "/" for right pointing). They were told to "... locate the "T" on the screen, determine which way it is facing and press the key that corresponds to that direction as quickly and as accurately as possible. An occasional error is acceptable (e.g., one error per block of 24 trials)." Auditory feedback was provided after every response (a beep or tone to signal correct or error responses, respectively). A different search array was presented on each trial in the practice block.

After further questions, participants completed 30 blocks of 24 trials. These blocks were similar to the practice block except that only 12 of the search arrays in each block were new configurations. The remaining 12 arrays (repeated configurations) were repeated across blocks, appearing once in each block. The repeated configurations predicted the location of the target element, but not its orientation. Presentation order was randomized within blocks, and people were encouraged to take a short break between blocks. As in previous studies (Chun & Phelps, 1999; Manns & Squire, 2001), trials on which a response did not occur within a 6-s time-out interval were aborted—a tone sounded and the next trial began.

After completing these 30 blocks, participants were asked a series of progressively more focused questions to obtain insights into their strategy and their declarative knowledge of the task. Next, subjects were given a single 24-trial recognition test, consisting of the 12 repeated configurations and 12 others not presented during learning, in random order. On each recognition trial subjects judged whether they had seen "... a display with items in the same screen positions as this earlier in the experiment." They responded by pressing either a key labeled "yes" or one labeled "no." They were urged to guess if they were unsure. No feedback was provided.

2. Results

2.1. Alternating serial reaction time task

In this analysis, we test the hypothesis that dyslexic college students will show impaired higher-order implicit sequence learning compared to age-matched controls. This
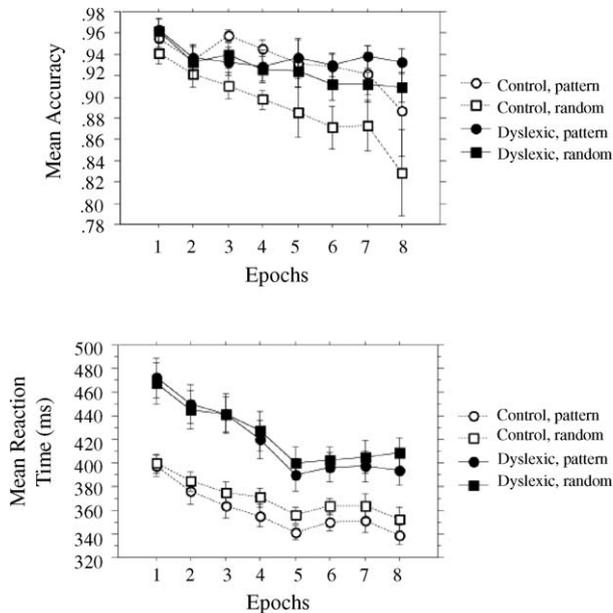
Fig. 2. Mean accuracy (upper graph) and mean of median RT (lower graph) on predictable (pattern) and unpredictable (random) trials as a function of epoch for both groups on the serial reaction time task.

was accomplished by comparing the accuracy and speed of responding on the repeating "pattern" trials to the unpredictable "random" trials (see Howard & Howard, 1997). Median reaction times were first determined separately for correct pattern and random trials on each block for each person. Following the convention established in previous work, these medians were then averaged across successive blocks to obtain a value on each of 8 five-block (400-trial) epochs for each individual and Trial Type (pattern or random). A similar data reduction was performed on accuracy. A statistical criterion of .05 was used in all significance tests.

2.1.1. Trial Type effects on accuracy and speed

Fig. 2 plots the mean accuracy (upper graph) and mean of median RT (lower graph) data for both groups. These data were submitted to Group (dyslexic versus control) × Trial Type (pattern versus random) × Epoch (1–8) mixed design ANOVAs with repeated measures on the Trial Type and Epoch factors. Although the dyslexic group responded significantly more slowly than the control group (422 ms versus 365 ms overall), $F(1,21) = 13.50$, MSE = 22379, they did not differ from the controls in overall accuracy (93 and 91%, respectively). Hence, the feedback provided to equate the two groups at 92% accuracy was effective. There were also significant main effects of Epoch on both measures reflecting overall motor skill learning, $F(7,147) = 5.16$, MSE = .003 and $F(7,147) = 53.89$, MSE = 427, for accuracy and reaction time, respectively.

More importantly, however, there is evidence of higher-order sequence learning in that the pattern and random trials diverge in both accuracy and speed with practice. This was demonstrated by significant main effects of Trial Type for both accuracy, $F(1,21) = 69.85$, MSE = .001, and speed, $F(1,21) = 25.77$, MSE = 227, as well as Trial Type × Epoch interactions for

both accuracy, $F(7,147) = 4.76$, MSE = 4.09E−4, and speed, $F(7,147) = 6.03$, MSE = 55.37. This indicates that responses on random trials are slower and less accurate than those on pattern trials, and that this difference increases across epochs for both groups. Furthermore, accuracy is high and relatively constant on pattern trials, but declines across epochs on random trials. This pattern of increasing errors on the unpredictable, random trials with practice is typical when probabilistic regularities are used (Curran, 1997a; Howard, Howard, Japikse et al., 2004; Schvaneveldt & Gomez, 1998). Participants often report that their fingers seem to take over leading them to make more "oops" errors. Unbeknownst to them, these errors occur primarily on the unpredictable random trials, and hence reflect learning of the sequence structure. Thus, when probabilistic sequences are used, errors are as sensitive to learning as are response times.

Although both groups show sequence learning, the dyslexics show significantly less learning than controls on both measures. This is supported by significant Trial Type × Group interactions for accuracy, $F(1,21) = 25.64$, MSE = .001, and speed, $F(1,21) = 4.61$, MSE = 226.58.

Fig. 2 also suggests that learning occurs more slowly for dyslexics in that the difference between pattern and random trials appears to develop more gradually with practice for the dyslexic than control groups. Despite this, the three-way interactions did not reach significance for either measure. This may reflect the relatively low power from our small sample size as well as the directional insensitivity of this omnibus test.

Follow-up two-way (Trial Type × Epoch) ANOVAs were carried out separately on the two groups. Results indicated that both groups showed significant learning on both measures. For the dyslexic group, the main effect of Trial Type was significant for the accuracy measure, $F(1,10) = 17.57$, MSE = 2.6E−4, and marginally significant for the speed measure, $F(1,10) = 3.31$, MSE = 280.99, $p < .10$, but with a significant Trial Type × Epoch interaction, $F(7,70) = 6.33$, MSE = 46.15. For the controls, there were significant Trial Type, $F(1,11) = 57.41$, MSE = .001, and Trial Type × Epoch interactions, $F(7, 77) = 4.96$, MSE = 3.91E−4 for accuracy and a significant Trial Type effect, $F(1,11) = 34.90$, MSE = 177.10, for speed.

Thus, although both groups reveal higher-order sequence learning, dyslexics show less learning than controls. This is consistent with a number of previous studies that have demonstrated higher-order sequence learning in college students (Curran, 1997a; Howard & Howard, 1997; Remillard & Clark, 2001), and also provides clear support for our hypothesis of impaired higher-order sequence learning in dyslexics.

2.1.2. Triplet effects on speed and accuracy

In our previous studies with the ASRT task we have shown that people do not become aware of the alternating structure of the sequence even after practicing for more than 10,000 trials (Howard, Howard, Japikse et al., 2004). We have also shown in trial-by-trial analyses that performance becomes increasingly sensitive to the local sequence context—specifically to the frequency with which runs of length three, i.e., triplets, occur (Howard, Howard, Japikse et al., 2004). Triplets are relevant

because in the alternating sequences we use (e.g., ArBrCrDr, ...) the lowest level of predictive relationship occurs between events that are separated by a lag of two trials (i.e., trial $n - 2$ predicts trial n or B predicts C in the above example). In the following we compare the sensitivity of the dyslexic and control groups to the triplet structure of the sequence.

There are two reasons why this analysis is important. First, pre-existing response tendencies exist for some triplets. For example, because of perceptual and/or motor priming people tend to respond very quickly to repetitions (e.g., CCC) whereas they respond slowly to trills (e.g., CDC) (Howard, Howard, Japikse et al., 2004; Remillard & Clark, 2001). Since repetitions and trills can end only on random trials in the alternating sequences, these tendencies may contaminate learning measures based exclusively on the Trial Type effect (i.e., pattern versus random trials) reported above. Second, we have shown that people often acquire declarative knowledge or inaccurate hypotheses about the likelihood of these distinctive triplets. For example, many people report (incorrectly) that repetitions occur frequently in the ASRT task (Howard, Howard, Japikse et al., 2004). Hence, in the following analysis we compare responses to high- and low-frequency triplets after responses to repetitions and trills have been removed. High-frequency triplets occur on all pattern trials and on some random trials by chance (e.g., AxB, BxC, etc., for the above example, where x reflects any of the four events) whereas low-frequency triplets occur only on random trials (e.g., AxD, DxB, etc.).

Each person's event sequence was parsed into a series of overlapping triplets using a sliding three-trial window (see Howard, Howard, Japikse et al., 2004 for details). Each triplet was then sorted into one of four categories; repetitions, trills, high or low frequency. *Repetitions* contain three successive identical events and *trills* begin and end with the same element but with a different middle element. For the reasons outlined above, these two triplet types were not included in the following analyses. *High-frequency triplets* included those ending on a pattern trial as well as those ending on random trials that by chance form a structure-consistent triplet. *Low-frequency triplets* included all the remaining triplets, i.e., those ending on random trials that are neither structure consistent, repetitions, or trills. Overall, there are 16 possible high-frequency triplets that occur on 62.5% of the trials and 32 low-frequency triplets that occur on 25% of the trials. The remaining 25% of the trials are either repetitions (4 kinds) or trills (12 kinds).

Three-way mixed ANOVAs (Group × Triplet Type × Epoch) revealed an identical pattern of results to those seen in the trial type data reported above for accuracy. However, for reaction time the Triplet Type × Group interaction did not reach significance despite a trend toward less learning for the dyslexic group. Hence, this analysis supports the overall conclusion that while both groups show higher-order implicit sequence learning, dyslexics are impaired in doing so.

2.1.3. Recognition analysis

The recognition data were analyzed by determining the mean rating assigned to the foils and targets for each individual (1: certain it did not to 4: certain it did). A preliminary compari-

Table 2
Mean recognition ratings (standard deviations), ASRT task

	Foil	Target
Control	2.55 (.92)	2.71 (.81)
Dyslexic	2.71 (.84)	2.71 (.95)

Table 3
Mean proportion "most often" category (standard deviations), ASRT task

	High frequency	Low frequency	Repetitions	Trills
Control	.58 (.11)	.51 (.10)	.48 (.30)	.39 (.13)
Dyslexic	.57 (.11)	.56 (.10)	.61 (.43)	.50 (.16)

son of the random (10 people) and backward (12 people) foils revealed no differences in recognition performance so this distinction was not considered further. Recognition data from one dyslexic participant were lost due to a computer error. As may be seen in Table 2, the mean ratings were virtually identical across sequence type for the two groups indicating that neither group was able to distinguish between the target and foil sequences. This was confirmed by a two-way (Group × Sequence Type) ANOVA that yielded no significant effects. Thus, people were unable to express knowledge of the sequence structure in an explicit recognition task, despite revealing sensitivity to it in their responding. This is consistent with previous findings in revealing that learning in the ASRT task is implicit.

2.1.4. Sorting task analysis

To determine if people were able to judge explicitly the relative frequency with which various triplets occurred, we calculated the mean proportion of times high-frequency (structure consistent) and low-frequency triplets were sorted into the "most often" category. For the reasons argued above, we also distinguished repetitions and trills for this analysis. The sorting data are shown in Table 3.

A two-way (Group × Triplet Type) ANOVA carried out on these data revealed no significant effects, indicating that neither the dyslexic nor control groups were able to explicitly evaluate the frequency with which the different triplet types occurred. Despite this, both groups reveal a non-significant tendency to rate trills as occurring less often than the other triplet types. This could reflect either a pre-existing bias or learning, but could not, in either case, have influenced the results of the high frequency versus low frequency analysis of learning above, in which both trills and repetitions were eliminated. Hence, in keeping with our previous findings, subjects were not able to express their knowledge of the temporal structure in an explicit sorting task adding to the evidence that learning is implicit.

2.1.5. Interview

Responses on the post-experimental interview were examined for evidence of declarative knowledge. They revealed no apparent differences between the two groups. Most people reported that they felt that there was some regularity, but that it was too subtle for them to pick up. No one reported they had found a pattern and, specifically, no one identified the alternating structure of the sequence.

When specifically told to guess, the most frequent descriptions were either vague, "... the lights moved in an orderly way," or incorrect "... some positions occurred more often than others," and "... doubles or triples of the same items were common." Although people could not describe the regularity, some felt that they were learning something, perhaps unconsciously, "... there was a pattern, but I can't describe what it is."

Thus, consistent with our earlier work with this task, people were unable to describe the regularities to which they had been exposed for thousands of trials. Nonetheless, most believed that there was a regularity that influenced their performance in some way. This is consistent with the evidence from the recognition and card-sorting tasks that the learning revealed by both groups was implicit and uncontaminated by explicit learning.

2.1.6. Correlations between implicit learning and individual reading ability

In addition to the group analyses reported above, we performed a series of correlations to examine the relationship between implicit sequence learning and reading ability as measured on two standardized tests of single real and pseudoword reading (Woodcock & Johnson, 1990). This was motivated by previous studies that have examined the relationship between individual reading ability and implicit learning (e.g., Waber et al., 2003). Word identification measures single real word reading and word attack is a measure of phonological decoding (as context or memory cannot be applied to name these non-words). Unlike the group comparisons, these correlations permit us to investigate the relationship between individual reading ability and implicit learning independent of diagnostic category.

Two measures of terminal sequence learning were determined by calculating the difference in mean accuracy (pattern accuracy − random accuracy) and mean reaction time (random RT − pattern RT) on the final testing epoch (epoch 8) for each individual. These values were then correlated with the single real word (WI) and single pseudoword reading (WA) scores described above. This revealed significant positive correlations between both measures of reading ability and the accuracy-based implicit learning score ($r = .59$, $p < .01$ and $r = .52$, $p < .01$ for WI and WA, respectively). Positive correlations were also observed between reading ability and the speed-based learning score ($r = .24$ and $.13$, respectively), but neither was statistically significant. These findings suggest that individuals in our sample with higher reading scores show greater implicit sequence learning. Scatter plots for the accuracy scores are shown in Fig. 3 for WI (upper graph) and WA (lower graph). These findings are consistent with the group analyses reported above as well as with our previous studies in which we have found speed to be a less sensitive measure of implicit sequence learning than accuracy (e.g., Howard & Howard, 1997).

Although our focus here is on the relationship between individual reading skill and implicit sequence learning, we also examined the pattern of correlations between implicit learning and the other standardized measures on which the two
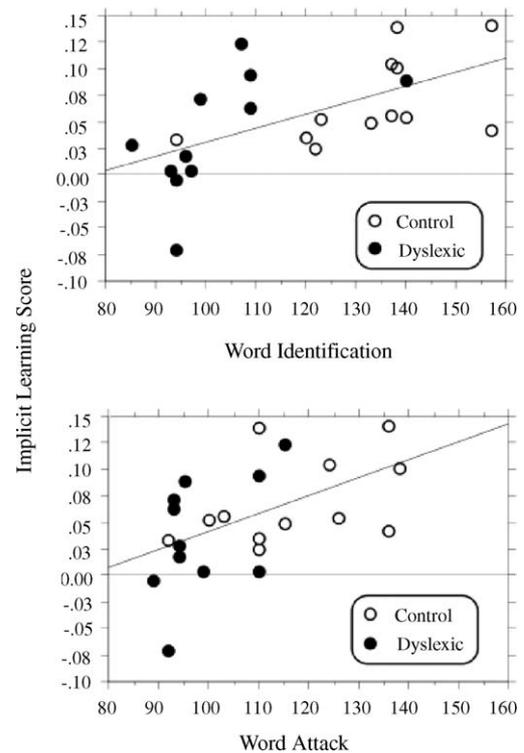

Fig. 3. Scatter plots showing the relation between implicit sequence learning score and individual-word reading score for word identification (upper graph) and word attack (lower graph) for both groups.

groups differed including spelling, phonological awareness, rapid automatized naming and WASI vocabulary (see Table 1). Of these, only individual spelling (TWS) revealed a significant correlation. As with the reading scores, spelling correlated positively with both dependent measures, but was only significant for accuracy ($r = .45$, $p < .03$ and $r = .24$ for accuracy and reaction time, respectively). However, the correlation between spelling and implicit learning was no longer significant when either word (WI) or pseudoword (WA) reading scores were partialed out.

Overall, these findings are consistent with the group analyses in supporting our hypothesis that higher-order sequence learning is impaired in dyslexia. Our results also underscore the importance of considering individual data since one individual in the control group had unusually poor reading scores characteristic of dyslexia (word identification = 94 and word attack = 92). This person's sequence learning scores were also among the lowest in the control group. Consistent with this, a precautionary re-analysis of the group data with this individual reclassified as dyslexic resulted in larger group differences in implicit learning than those reported above, but the overall statistical pattern of results remained unchanged. In addition, an individual in the dyslexic group had an unexpectedly high familiar word reading score (word identification = 140), but a non-word word reading score in the expected range for the group (word attack = 95). This very likely reflects memorization of word pronunciation, a pattern not unusual for academically successful dyslexics. Hence, the individual analyses not only supported the group findings, but also provided additional insights into individual differences within groups.

2.2. Spatial contextual cueing task

For this task, we tested the hypothesis that the same dyslexic college students who were impaired on implicit sequence learning will show normal implicit learning for spatial configurations. A mean RT was determined separately for correct responses to new and repeated configurations for each block and participant. Following the convention adopted in previous studies, these data were then averaged across successive blocks to obtain six five-block epochs for each individual and configuration type (new or repeated).

2.2.1. Response time analysis

The mean response times for each group are plotted in Fig. 4. These were subjected to a Group × Configuration × Epoch ANOVA with repeated measures on the latter two factors. Overall skill learning was reflected in a significant main effect of Epoch, $F(5,105) = 23.64$, MSE = .067, with both groups responding more quickly with practice. In addition, the dyslexic group was marginally slower overall than the control group, $F(1,21) = 3.41$, MSE = 1.849, $p = .08$. More importantly, a significant main effect of Configuration, $F(1,21) = 15.06$, MSE = .061 and a significant Configuration × Epoch interaction, $F(5,105) = 4.57$, MSE = .015, revealed spatial context learning. Furthermore, despite what appears to be substantially greater contextual cueing for the dyslexic than control group, the Group × Configuration interaction, $F(1,21) = 2.90$, MSE = .061, $p = .104$, only approached marginal significance. This occurred despite the fact that the terminal level (epoch 6) of spatial context learning was nearly three times greater for the dyslexic than the control group (.31 s versus .12 s difference between novel and repeated configurations for the dyslexic and control groups, respectively). The failure to find significance here may reflect low power from our relatively small sample size or the bi-directionality of the omnibus ANOVA test. In fact, a directional t-test of the epoch 6 learning scores revealed a significant difference between the two groups, $t(21) = 2.70$. Hence, the dyslexics reveal a trend toward stronger spatial context learning than controls. No other main effects or interactions were significant.

These findings are consistent with our hypothesis that dyslexics are as good as controls on implicit spatial context learning. However, it is possible that spatial context learning was inflated for the dyslexic group because of their marginally slower overall responding. To investigate this possibility, we calculated
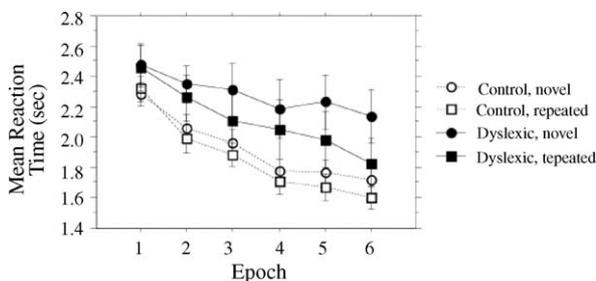

Fig. 4. Mean RT to novel and repeated configurations as a function of epoch for both groups on the spatial contextual cueing task.

learning scores for each individual normalized by the RT to new configurations ((new − repeated)/new), on each epoch. A Group × Epoch ANOVA carried out on these normalized learning scores revealed a significant main effect of Epoch, $F(5, 105) = 4.69$, MSE = .005, but neither the main effect of Group nor the Group × Epoch interaction were significant. Hence, the two groups do not differ significantly in context learning even when a proportional measure is used.

It is also possible that our control group showed particularly poor spatial context learning. To investigate this possibility we compared them to an age-matched group of 18 college students from an earlier study (Howard, Howard, Dennis, et al., 2004, Experiment 1). The present controls had very similar final contextual learning scores to the earlier group (epoch 6 differences of .116 and .127 s, respectively), and a three-way ANOVA carried out on the learning data produced no significant group differences. Hence, our controls do not appear to be atypical.

2.2.2. Error analysis

Although people in both groups made relatively few errors (4.5 and 4.0% for the dyslexic and control groups, overall), we carried out a similar analysis of the error data. This revealed only a significant main effect of Epoch, $F(5,150) = 7.20$, MSE = .001, reflecting an overall decrease in errors with practice (from 6.5 to 3.6%).

2.2.3. Recognition analysis

To investigate if learning was implicit, we calculated the rating accuracy for the repeated and novel configurations on the recognition block for each person. Accuracy was nearly identical across groups (52 and 55% for control and dyslexic, respectively) and configurations (53 and 55% for novel and repeated, respectively). A Group × Configuration ANOVA revealed no significant effects and accuracy was not significantly different from chance in any condition. Thus, spatial context learning occurs implicitly for both the dyslexic and control groups.

2.2.4. Interview

Comments from the post-experimental interview were examined for evidence of declarative knowledge. As with sequence learning, no systematic differences were evident between the two groups. On the open-ended questions people frequently indicated incorrectly that the target did not occur on some of the trials and very few said that they thought some displays repeated. Hence, the interview data are consistent with the recognition data reported above as well as with previous findings with this task in revealing no explicit knowledge of the repeated configurations.

2.2.5. Correlations between implicit spatial context learning and individual reading ability

The difference in mean response time between novel and repeated configurations on the final testing epoch (epoch 6) was determined for each individual. These learning scores were then correlated with the reading and spelling scores as in the sequence learning analysis described earlier. This revealed significant negative correlations between both measures of reading ability ($r = −.44$, $p < .05$ and $r = −.50$, $p < .05$ for WI and WA,
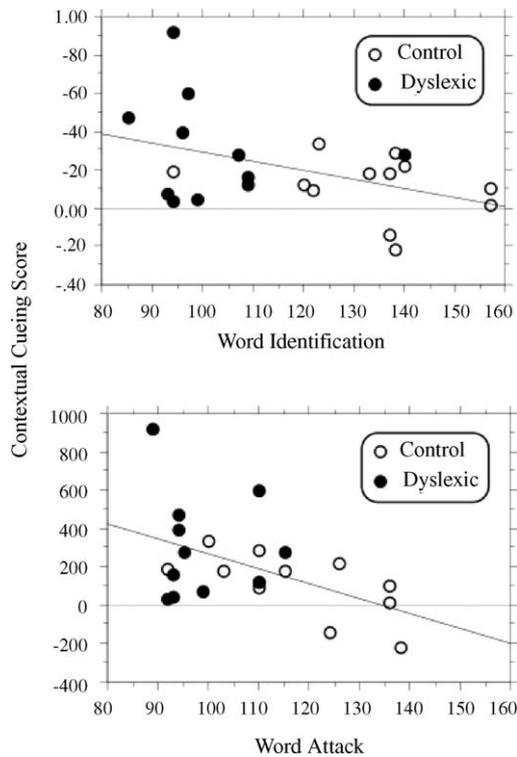
Fig. 5. Scatter plots showing the relation between implicit spatial contextual learning score and individual-word reading score for word identification (upper graph) and word attack (lower graph) for both groups.

respectively) as well as spelling ($r = -.44$, $p < .05$) and the spatial context learning score. As we found for sequence learning, the correlation with spelling was no longer significant with either reading measure was partialed out. These negative correlations are in contrast to the significant positive correlations found between implicit sequence learning and these measures and indicate that individuals in our sample with higher reading or spelling scores actually show less implicit spatial context learning. Scatter plots for the two reading scores are shown in Fig. 5 for WI (upper graph) and WA (lower graph). These results are also consistent with the group analyses reported above in which the dyslexic group revealed a trend toward greater spatial context learning than typical controls. Overall, these findings are consistent with the group analyses in supporting our hypothesis that spatial context learning is not impaired in dyslexia and they provide additional evidence that spatial context learning might actually be enhanced in college-student dyslexics.

3. General discussion

The present findings demonstrate that college students with a history of dyslexia are impaired in higher-order sequence learning, but unimpaired in spatial context learning. Furthermore, this group reveals a trend toward learning more than normal readers in the contextual cueing task. These conclusions were supported by both the group comparisons (based primarily on a childhood diagnosis of dyslexia) and the individual correlational analyses (based on single real and non-word reading scores). Thus these findings reveal a dissociation between two forms

of implicit learning in high-functioning dyslexic adults with a strong trend toward a double dissociation: college-age students with a history of dyslexia learn relationships among simultaneous spatial stimuli at least as well as controls, but they are poorer at learning relationships among non-adjacent events in temporal sequences. These results support and extend the existing literature on implicit learning in dyslexia in a number ways.

First, the present findings indicate that the impaired sequence learning observed in this and some previous research (Vicari et al., 2005) does not reflect a general cognitive or attentional deficit. If this were the case, dyslexic individuals should show impairment on both the sequence learning and contextual cueing tasks, rather than the selective impairment observed. Nor can poor learning on the serial reaction time task be attributed to the relative overall difficulty of the two tasks. There is no evidence that sequence learning was more difficult than contextual cuing for either group. On the contrary, most participants reported that contextual cueing was more difficult, an observation consistent with the substantially longer response times that occur in this task. Furthermore, the sample with a history of dyslexia showed the same pattern of overall performance compared to controls on both tasks; they were slower overall, but just as accurate.

Second, the results establish that deficits in implicit sequence learning occur even when explicit learning can be ruled out. We have demonstrated here and in earlier research (Howard, Howard, Japikse et al., 2004), that the present tasks tap relatively pure implicit learning, in the absence of explicit learning. In the present study, neither group showed evidence of declarative knowledge for either task in interviews or on other sensitive measures of explicit knowledge, including recognition and card sorting for sequence learning and forced-choice configuration recognition for contextual cueing. Furthermore, previous studies have reported impaired implicit but spared explicit learning in dyslexia (Sperling et al., 2004) suggesting that even if explicit learning had occurred during our task, which we believe to be unlikely, we would not expect it to affect the two groups differentially. As an added precaution we examined the possibility that some individuals gained awareness in a series of post hoc t-tests comparing individual recognition ratings for the foil and target sequences and "most often" card-sorting frequencies for the high- and low-frequency triplets. There were only two significant comparisons: a control subject had a significantly higher mean recognition rating for target than foil sequences and a dyslexic participant sorted the low-frequency triplets into the "occurred most often" category more often than the high-frequency triplets—the reverse of what actually occurred. Thus, only one person showed statistical evidence of awareness on the recognition task and no one showed such evidence on more than one of the explicit knowledge measures. Hence, the present findings cannot be explained by differences in explicit knowledge between the two groups.

While some earlier studies of dyslexic children had reported impaired non-linguistic sequential processing on the serial reaction time task (Vicari et al., 2003, 2005, however see Waber et al., 2003), the only previous study using the serial reaction time task in dyslexic adults (Kelly et al., 2002) did not leading to speculation that this discrepancy might be attributable to age

(Vicari et al., 2005). Our third conclusion is therefore, that our findings refute this supposition and suggest that sequence learning deficits are not limited to childhood, but do indeed occur in adults.

We need to consider why our findings differ from those reported by Kelly and coworkers, who found no sequence learning deficits. Since the two studies used comparable numbers of college students with a childhood history of dyslexia, it is unlikely that the different findings relate to sample selection. As is typical of dyslexic college students, their reading was in the normal range for the general population, but significantly worse than their non-dyslexic university peers. For both studies, the selection of university students means that there are limitations with regards to generalizing these results to the entire population. Future studies in adults that are more representative of the general population will need to be conducted.

Our dyslexic sample did include four subjects with ADHD, whereas Kelly and coworkers do not report if their sample was screened for ADHD. To rule out the possibility that participants with a comorbid diagnostic history (ADHD and dyslexia) were driving the effects, we re-analyzed the sequence learning data without these individuals and found an identical pattern of means and statistical significance. Thus, we can rule out any concern that the ADHD cases are responsible for the effects observed on the SRT task. Even if the presence of ADHD played a role in subject's performance on implicit learning, there is no reason to believe it would differentially affect the sequence learning and contextual cueing tasks.

The most likely explanation for the discrepancy between our findings and those of Kelly and coworkers is based on the serial reaction time task itself. For example, the fact that they used simple repeating sequences could account for the difference. Specifically, by demonstrating a deficit in higher-order implicit sequence learning, i.e., learning that requires integrating across at least three elements, the present study calls attention to the potential importance of sequence complexity in studies of implicit sequence learning in dyslexia. To date, sequence structure has not been varied systematically in studies of dyslexia, and previous studies have used relatively simple repeating patterns. There is evidence that different levels of structure call on different brain systems (Curran, 1997b; Fletcher et al., 2004; Howard, Howard, Dennis et al., 2004) raising the possibility that dyslexia may influence the learning of simple and complex sequences differently. Future studies need to examine this possibility systematically.

So what do our findings suggest about the role of poor implicit learning in individuals who are poor readers? First, it is important to underscore that our results demonstrate that dyslexics do not suffer from an overall deficit in implicit learning. Although both tasks investigated in the present study involve implicit learning, they were selected to complement each other: the alternating serial reaction time task has a strong sequencing component whereas the contextual cueing task does not. This distinction enables us to separate sequencing deficits from other forms of implicit learning deficits. The differences we report in implicit learning of sequential versus spatial information are consistent with results from a computer-based test in which children with

dyslexia showed impaired temporal processing with preserved spatial processing of visual stimuli (Eden, Stein, Wood, & Wood, 1995). Interestingly there is evidence of a higher prevalence of dyslexia among artists than non-artists at college (Wolff & Lundberg, 2002) suggesting that dyslexics may be relatively good at configural visual processing. It is possible that the discrepant findings from earlier studies are due in part to a failure to distinguish among these different kinds of implicit learning.

Our results suggest that the weakness in implicit learning can be narrowed down to paradigms that involve sequential processing. Furthermore, even within one form of implicit learning, such as implicit sequence learning, it is important to consider the level of structure that is present. A number of authors have argued for the importance of implicit learning in learning to read and in dyslexia (Gombert, 2003; Sperling et al., 2004). There are several plausible mechanisms by which a selective weakness in implicit learning of sequential information could account for the phonological processing and reading problems that are the cardinal feature of dyslexia. They are addressed below by considering the role of: (1) automaticity, (2) phonemic awareness and (3) orthographic awareness in attaining reading skills. Finally, the growing literature describing patient populations or employing functional brain imaging technology to study implicit learning will be considered to relate our findings to the functional anatomy of implicit learning.

Our results are consistent with earlier studies (Vicari et al., 2005) in indicating that the implicit sequence learning deficit is not limited to linguistic materials, but rather represents a more general sequencing problem. The concept of a deficit in non-linguistic processing in dyslexia has been described using different theoretical frameworks, such as impaired information processing attributed to low-level sensory perception (Stein & Walsh, 1997), a lack of automaticity in the context of dual task performance (Nicolson & Fawcett, 1999) or in the context of articulatory fluency (Wolf, Miller, & Donnelly, 2000). The current study was not designed to test any of these theories, but future studies could examine these aspects.

In the present study, we did measure rapid automatized naming skills (Wolf, 1986) and found these to be impaired in our sample with childhood reading deficits, consistent with the literature arguing that rapid naming problems in children with reading disabilities persists into adulthood (Korhonen, 1995). To explore ad hoc whether poor rapid automatized naming skills are related to "fluency" in performance of sequential learning, partial correlations were performed to explore the influence of RAN on the correlation between word reading (real and non-word) and the accuracy measure of implicit sequence learning described in the results section. The correlations remained the same with RAN partialed out, providing no evidence of a possible connection between SRTT performance and rapid automatized naming.

Our findings are more consistent with the explanation offered by Sperling et al. (2004) who have argued that poor implicit learning could hinder the establishment of good phonological processing as well as learning orthographic–phonological representations. Gombert (2003) proposed that children with dyslexia have a phonological deficit that prevents the implicit learning of linguistic regularities and, hence, interferes with

reading. However, the findings from Sperling et al. and the present study suggest that the causality may be somewhat more complex. For example, the combination of a phonological deficit with an impaired implicit sequence learning system could lead to the observed reading disabilities. This combination could manifest as a failure in applying implicit or probabilistic rules required for fluent application of grapheme–phoneme correspondences (Sperling et al., 2004). In our sample, skills that involve or require phonological processing (i.e., sound elision measured with the Test of Auditory Analysis Skills and non-word decoding measured via Word Attack), were impaired. Likewise, our dyslexic subjects had significant deficits in spelling. Residual deficits in encoding are often seen in adults with dyslexia even once they have overcome some of their reading problems (Flowers, 1995). Not surprisingly therefore, post hoc analysis of spelling ability (TWS) proved to correlate significantly with our most informative learning score (the accuracy measure of sequence learning). Spelling shares a great deal of variance with measures of reading due to their common reliance on phonological and orthographic processing. The former relationship was illustrated by the observation that the relationship between single real word reading (WI) and sequence learning remained significant when the spelling was partialed out (using TWS), but the relationship between sequence learning and non-word reading (WA) was no longer significant when spelling (TWS) was accounted for.

Surprisingly, adding other variables such as phonemic awareness (TAAS) and verbal working memory (digit span) had no effect and the correlations between implicit sequence learning and reading (WI and WA) remained largely the same under these conditions. Our data therefore do not provide a clear picture or allow for a straightforward interpretation of the relationship between implicit sequence learning and phonological processing.

However, it can be stated that not only is the relationship between sequence learning and real word reading the strongest, but it is also the most robust relationship, surviving the partial correlations with measures of spelling, phonemic awareness, rapid automatized naming and verbal working memory. It has been suggested that dyslexic, unlike typical readers who use a rule-based approach to sound out words, compensate by recollecting words by sight (Manis et al., 1987). We did not acquire a measure of predictable and unpredictable word reading, but noted in our sample of adults with a history of dyslexia that their performance was equal on the spelling of predictable and unpredictable words. The relationship between orthography, phonology and sequence learning therefore requires further study. A particularly interesting theoretical question would be the relationship between reading scores and the higher-order SRTT with differing word types, to test the prediction that the reading of words with more complex pronunciation rules would be more strongly predicted by measures of higher-order rather than simple sequence learning.

Turning to the anatomical correlates of learning, it is known that different forms of implicit learning make different cognitive demands and call on different neural substrates. The two tasks we investigated are thought to rely on different underlying brain systems (Howard, Howard, Dennis et al., 2004). This underscores the fact that implicit learning is not a unitary phenomenon dependent on a single brain system, but rather it represents a range of tasks that engage different neural systems.

Evidence from patient, functional neuroimaging, and transcranial magnetic stimulation studies indicates that sequence learning depends on fronto-striatal-cerebellar circuitry (Prull et al., 2000; Robertson, Tormos, Maeda, & Pascual-Leone, 2001). For example, patients with focal cerebellar or frontal lesions reveal impaired learning in an SRTT (Gomez-Beldarrain, Garcia-Monco, Rubio, & Pascual-Leone, 1998; Gomez Beldarrain, Grafman, Pascual-Leone, & Garcia-Monco, 1999; Gomez Beldarrain, Grafman, Ruiz De Velasco, Pascual-Leone, & Garcia-Monco, 2002) as do individuals with striatal disorders such as Huntington's (Willingham, Koroshetz, & Peterson, 1996) and Parkinson's disease (e.g., Dominey & Jeannerod, 1997; Helmuth, Mayr, & Daum, 2000; e.g., Jackson, Jackson, Harrison, Henderson, & Kennard, 1995). Functional neuroimaging (e.g., Grafton, Hazeltine, & Ivry, 1995; Rauch et al., 1997; Seidler et al., 2002) and transcranial magnetic stimulation (Robertson et al., 2001) studies have been generally consistent with the patient findings. Although there is some evidence that the medial temporal lobe may also be involved when higher-order sequences are used (Curran, 1997a; Fletcher et al., 2004; Schendan, Searl, Melrose, & Stern, 2003), the SRTT depends primarily on fronto-striatal-cerebellar circuits.

In contrast to sequence learning, the contextual cueing task seems to depend primarily on medial temporal lobe structures. For example, amnesic patients with lesions involving parahippocampal regions possibly involving the hippocampus are impaired in contextual cueing compared to healthy controls (Chun & Phelps, 1999; Manns & Squire, 2001). There is also preliminary evidence that contextual cueing is impaired in elderly mild cognitive impairment patients believed to have medial temporal lobe pathology (Negash et al., 2004). Consistent with this, functional neuroimaging studies have reported greater activation in medial temporal lobe structures, including hippocampus and parahippocampal areas, on contextual cueing trials with repeated compared to novel configurations (Greene & Gross, 2003; Preston, Saladis, & Gabrieli, 2001).

Thus, the present findings suggest that dyslexia is associated with selective deficits in the fronto-striatal-cerebellar circuits that underlie sequence learning. This is consistent with previous evidence that one or more of these regions are involved in the functional pathology of dyslexia (Eckert, 2004; Eden & Zeffiro, 1998; Nicolson, Fawcett, & Dean, 2001a).

It also could explain the results by Vicari et al. (2005) who showed that dyslexic children were impaired on two different implicit learning tasks, sequence learning and mirror drawing. There is evidence that these two tasks share a dependence on fronto-striatal brain circuits (see discussion below and Poldrack & Gabrieli, 2001). In contrast, our findings reveal that dyslexics are not universally impaired on implicit learning, showing selective deficits on some, but not other tasks depending on which brain systems are engaged.

The present data are also consistent with the argument that the medial temporal lobe system that underlies implicit learning in

the contextual cueing task is intact in dyslexia. In fact, the present data show a strong trend toward enhanced learning in dyslexic compared to typical college students on this task. Evidence for this occurred in both the group (significant post hoc comparison of learning on the final session) and individual analyses (significant negative correlations between individual learning and word reading scores). It is possible that this reflects compensation for impaired striatal, cerebellar or frontal function in the successful, dyslexic college students we tested. Many previous human and animal studies have suggested that compensation of this sort develops in the face of system-specific pathology (Eden et al., 2004; Poldrack & Packard, 2003; Ullman, 2004).

In summary, the present findings reveal that dyslexics are impaired in higher-order implicit sequence learning, but spared or even enhanced in the implicit learning of spatial context. This indicates that otherwise high-functioning college-student dyslexics have difficulty integrating information across temporally non-adjacent elements, but not in the spatial configural processing of information within a single display. This is consistent with previous behavioral and neurological evidence of fronto-striatal-cerebellar pathology in dyslexia and suggests that it is important to study the development of these different forms of implicit learning so as to determine if this pattern of spared and impaired ability reflects developmental compensation.

Acknowledgements

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