**Intact Forms of Procedural Memory in Adults with Dyslexia**

**Abstract**

Developmental dyslexia is characterized by reading difficulty and is known to be associated with atypical brain functions. One neuropsychological theory of dyslexia posits that dyslexia reflects a deficit in procedural memory (learning that is independent of the brain structures that support declarative or explicit memory). Here we examined multiple forms of procedural-learning related tasks in adults with developmental dyslexia and typically-reading adults. Adults with dyslexia exhibited typical learning on two perceptual-motor tasks -- mirror tracing and rotary pursuit -- that have been well-established as reflecting purely procedural memory and dependent on basal ganglia and cerebellar structures. They also exhibited typical statistical learning for visual material, but impaired statistical learning for auditory material. Auditory statistical learning proficiency correlated positively with single-word reading (decoding) performance across all participants and within the group with dyslexia, linking a major difficulty in dyslexia with impaired auditory statistical learning. These findings dissociate multiple forms of procedural memory that are intact in dyslexia from a specific impairment in auditory statistical learning that is associated with reading difficulty.

Keywords: dyslexia, procedural memory, statistical learning, mirror tracing, rotary pursuit

**Introduction**

Developmental dyslexia is characterized by inaccurate and dysfluent reading. Although individuals with dyslexia most consistently demonstrate difficulties with storing, retrieving, and/or manipulating phonological representations (Brady et al., 1983; Shankweiler et al., 1979; Snowling, 2000; Stanovich & Siegel, 1994; Vellutino et al., 1994), a range of non-linguistic deficits in the motor and perceptual domains have also been reported for this population (for reviews see Folia et al., 2008; Lum et al., 2013; Nicolson & Fawcett, 2019; West et al., 2021). Multiple theories have been developed to explain the neurocognitive underpinnings of dyslexia. One hypothesis proposes that dyslexia is caused by deficits in the implicit learning system, which is critically involved in extracting and learning the sequential or distributional regularities in language (e.g., Nicolson & Fawcett, 2007, 2011; Ullman, 2004; Ullman & Pierpont, 2005). Implicit learning refers to the acquisition of knowledge without conscious awareness or intention and is thought rely on the procedural memory system (Berry et al., 1993; Christiansen, 2019; Perruchet & Pacton, 2006; Shanks, 2005). In contrast to declarative memory, referring to conscious memory for facts and events (or “knowing that”), procedural memory refers to the unconscious learning of skills, rules, or patterned regularities in stimuli (Cohen & Squire, 1980).

*Skill learning* is a form of implicit learning that involves the acquisition of motor skills through practice and feedback. Tasks such as serial reaction time (SRT), mirror tracing, and rotary pursuit are often used to measure skill-based learning. These tasks involve explicit feedback to guide performance but do not rely on prior knowledge or conscious awareness of the skill being learned. Studies of amnesic patients with severe impairments in declarative memory have led to the procedural/declarative distinction in human learning, with patients showing intact skill learning but impaired declarative memory for the episodes during which they learned the skills. Tasks such as rotary pursuit and mirror tracing have been used to demonstrate the dissociation of the procedural memory system from the declarative system, with different forms of procedural memory having different neural substrates.

*Statistical learning* *(SL)* is a form of implicit learning that plays a fundamental role in the perception and categorization of environmental inputs. Learners are thought to automatically extract the co-occurring patterns of exemplars embedded in sensory input mostly through passive exposure. Modern theoretical frameworks often introduce SL as a broad construct that encompasses a range of incidental learning paradigms (Bogaerts et al., 2020; Conway, 2020; Frost et al., 2019; Thiessen, 2017), including category learning, SRT, artificial grammar learning, and embedded pattern learning. However, the relative contributions of declarative and procedural memory to most SL tasks are largely unknown (Conway, 2020; Frost et al., 2015). There are mixed findings with a few patients with memory disorders that may reflect either variation in SL paradigms, patient abilities, or both (Cerreta et al., 2018; Covington et al., 2018; Schapiro et al., 2014). Neuroimaging findings have revealed basal ganglia involvement across both SL and procedural learning tasks (Karuza et al., 2013; McNealy et al., 2006; Willingham et al., 2002; see Conway & Pisoni, 2008 for a review). while the hippocampus has also been shown sensitive to visual input structures (Schapiro et al., 2012; Tang et al., 2022; Wammes et al., 2022).

procedural memory system (or “knowing how”), which is critically involved in extracting and learning the sequential or distributional regularities in language (e.g., Nicolson & Fawcett, 2007, 2011; Ullman, 2004; Ullman & Pierpont, 2005). In contrast to declarative memory, referring to conscious memory for facts and events (or “knowing that”), procedural memory refers to the unconscious learning of skills, rules, or patterned regularities in stimuli (Cohen & Squire, 1980). *Procedural learning* is often used interchangeably with other terms such as *implicit learning* and *statistical learning* (Berry et al., 1993; Christiansen, 2019; Perruchet & Pacton, 2006; Shanks, 2005). The procedural deficit hypothesis is supported by the high rates of comorbidity of dyslexia with other disorders (Boada et al., 2012; Ramus, 2003; Wimmer et al., 1999), suggesting a broad deficit in learning that extends beyond the language system. In the current study, we tested for the presence of domain-general procedural deficits in developmental dyslexia in adults.

The procedural/declarative distinction in human learning arose from studies of intact skill learning in amnesic patients with severe impairments in declarative memory (Cohen & Squire, 1980). These patients had injuries to medial temporal-lobe or diencephalic brain regions. For example, the amnesic patient H.M. demonstrated intact learning skills for mirror tracing across days (Milner, 1962) and a year (Gabrieli et al., 1993) and for rotary pursuit (Corkin, 1968), but impaired declarative memory for the episodes during which he had learned the skills. Similar intact skill learning was shown by memory-impaired patients with Alzheimer’s disease on the same two tasks (Gabrieli et al., 1993a; Heindel et al., 1989), supporting the dissociation of the procedural memory system from the declarative system. Research with other neurological patient groups has suggested that rotary pursuit is dependent on the basal ganglia (Gabrieli et al., 1997; Heindel et al., 1989) and mirror tracing is dependent on the cerebellum (Laforce Jr & Doyon, 2001). Broadly, these studies also indicate that procedural memory is not a unitary neurobiological construct, but rather that different forms of procedural memory have different neural substrates.

Mirror tracing has been examined only once in children with dyslexia, who were slower in performance but demonstrated typical learning across trials (Vicari et al., 2005). Rotary pursuit has not been examined in dyslexia. Two other forms of learning, however, have been studied more extensively in dyslexia: serial reaction time (SRT) and statistical learning (SL). SRT is a spatio-motor skill learning task in which participants typically see four horizontal spatial locations on a monitor and are instructed to press the corresponding button (from among four horizontal buttons) as quickly as possible. In some blocks, the order of stimulus locations follows a sequential pattern; in others, stimulus locations are presented randomly. Amnesic patients show normal learning of the repeating stimulus sequence as evidenced by faster reaction times (Nissen & Bullemer, 1987) and typical participants can exhibit skill learning for the repeated sequence without declarative memory for the sequence, although those typical participants who do develop declarative memory for the sequence show greater learning (Willingham et al., 1989).

There are multiple reports of both intact and impaired SRT learning in dyslexia; a meta-analysis indicates that there appears to be a deficit in SRT learning in dyslexia (Lum et al., 2013; West et al., 2021). It is difficult to synthesize findings across studies, however, because sequences vary in their attentional demands and susceptibility to the development of declarative memory, both of which can influence learning (Cohen et al., 1990; Willingham et al., 1989) and may invoke cognitive processes beyond procedural memory. Further, there is some evidence that the SRT deficit is more pronounced in a task involving letters compared to a task involving nonlinguistic visual stimuli, suggesting that spatio-motor sequence learning in dyslexic individuals might be constrained by separate underlying learning systems (Gabay et al., 2012).

In the current study, we used a classic embedded-pattern learning paradigm (Saffran et al., 1996) to define and measure SL performance for the following reasons. First, we aimed to compare our findings with decades of empirical proof that typical adults are capable of robust SL across sensory modalities (e.g., visual shape and color sequences: Turk-Browne et al., 2008; auditory tones: Saffran et al., 1999; speech syllables: Saffran et al., 1996; see Frost et al., 2015 for a review on the domain-generality vs. modality-specificity debate). Second, successful embedded-pattern learning does not require explicit knowledge of the task goal or any motor engagement (Batterink et al., 2015; Song et al., 2007), which enabled us to test for a domain-general procedural deficit across SL and procedural learning tasks.

Because spoken and written language inputs are rich in regularities, SL has been proposed as an important mechanism underlying typical language and reading development (Arciuli, 2018; Aslin & Newport, 2008; Erickson & Thiessen, 2015; Romberg & Saffran, 2010; Sawi & Rueckl, 2019). Empirical evidence ties SL with reading skills in both first and second languages (Arciuli & Simpson, 2012; Frost et al., 2013; Qi et al., 2019; Spencer et al., 2015; Tong et al., 2019). In typically reading adults and children, reading skills were more strongly associated with auditory SL than with visual SL (Qi et al., 2019). In children, the relationship between auditory SL and reading skills was further mediated by an emergent literacy skill: phonological awareness. Implicit auditory sequence learning might therefore constitute an early step towards phonological awareness, a pivotal building block of literacy development.

There have been mixed findings of deficits in SL in individuals with dyslexia. In the visual modality, some studies reported similar learning patterns between dyslexic and typically reading individuals (Howard Jr et al., 2006; Nigro et al., 2016; Singh et al., 2018; van Witteloostuijn et al., 2021), while others have reported impaired SL learning in dyslexia (Sigurdardottir et al., 2017; Tong et al., 2019) In the auditory modality, however, findings are more consistent, especially in adult participants: Across both linguistic and nonlinguistic stimuli, dyslexic adults have less success in recognizing embedded auditory patterns (Dobó et al., 2021; Gabay et al., 2015; Singh & Conway, 2021, p. 202). The lack of consensus in the literature regarding the status of SL in dyslexia is consistent with the pluralist view of SL (Frost et al., 2019) positing that SL across modalities and domains operates through partially overlapping, but distinct mechanisms. Therefore, a direct comparison between auditory and visual SL tasks of similar design is necessary to reconcile whether certain types of SL are indeed more vulnerable than others in dyslexia.

The present study had two major aims. First, we asked whether adults with dyslexia would show intact or impaired procedural memory on two motor skill learning tasks that have been well established as reflecting purely procedural memory: mirror tracing and rotary pursuit. Intact learning in dyslexia would contradict the idea that there is a broad impairment of procedural memory in dyslexia. Second, given that reading development is built upon inputs from both the visual and auditory sensory modalities, we asked whether statistical learning in these domains is correlated with reading skill.

**Methods**

**Participants**

Twenty-six adults with dyslexia (16 female) and 27 typical readers (14 female) matched on age, sex ratio, and IQ (age 18-41 years, *M* = 26.6, *SD* = 6.3) participated in this study. All participants met eligibility criteria: being a native speaker of American English; born after at least 36 weeks’ gestation; no sensory or perceptual difficulties other than corrected vision; no history of head or brain injury or trauma; no neurological, neuropsychological, or developmental disorder diagnoses; no medications affecting the nervous system; nonverbal IQ standard score > 85 (Matrices subtest of the Kaufman Brief Intelligence Test/KBIT-2; Kaufman, 2004). Pure-tone audiometry was performed for all participants and those with atypical hearing thresholds were excluded. The study was approved by the Committee on the Use of Humans as Experimental Subjects (COUHES) at the Massachusetts Institute of Technology.

**Neuropsychological characterization**

All participants completed a comprehensive battery of standardized reading, language, and cognitive assessments, as well as a background questionnaire (**Table 1**). Measures included: the Sight Word Efficiency (SWE) and Phonemic Decoding Efficiency (PDE) subtests of the Test of Word Reading Efficiency (Torgesen et al., 2012); the Word ID (WID) and Word Attack (WA) subtests of the Woodcock Reading Mastery Tests-Revised/Normative Update (Woodcock, 2011); the Peabody Picture Vocabulary Test (Vocabulary; Dunn & Dunn, 2007); the Wechsler Adult Intelligence Scale (Adult-IQ; Wechsler, 2008); the Elision and Blending Words subtests of the Comprehensive Test of Phonological Processing (Wagner et al., 1999); ​​and the Digit Span subtest of the Wechsler Adult Intelligence Scale (WAIS-IV, Wechsler, 2008). Participants were included in the developmental dyslexia group (DD) based on performance below the 25th percentile on at least two out of four standardized subtests of timed or untimed word or nonword reading (SWE, PDE, WID, and WA). Participants were included in the typical readergroup (TYP) based on performance at or above the 25th percentile on all four of the above subtests. The sample’s demographic information is available in **Supplemental Table 2**. A majority of participants in the DD group also reported an external diagnosis of dyslexia (*N* = 20) and a history of reading delay (*N* = 19). One participant in each group had a diagnosis of ADHD.

**Table 1**. Behavioral Characterization of Participants.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Dyslexia (N=26) | Typical (N=27) | *p* value | *Cohen’s d* |
| Age | 26.35 (6.59) | 26.68 (6.58) | 0.848 | 0.18 |
| IQ | 107.30 (14.84) | 113.68 (13.97) | 0.106 | 0.28 |
| WID | 89.44 (9.54) | 110.75 (7.40) | < 0.001 | 2.54 |
| WA | 77.59 (9.71) | 102.46 (7.97) | < 0.001 | 2.81 |
| SWE | 89.19 (9.19) | 110.25 (12.50) | < 0.001 | 1.89 |
| PDE | 83.52 (8.19) | 106.54 (7.78) | < 0.001 | 2.87 |
| Vocabulary | 106.15 (10.02) | 113.93 (8.51) | 0.004 | 0.85 |
| Elision | 8.22 (2.31) | 9.89 (1.91) | 0.005 | 0.8 |
| Blending Words | 10.33 (3.16) | 12.50 (2.69) | 0.008 | 0.75 |
| Digit Span | 8.63 (2.37) | 11.04 (2.38) | < 0.001 | 1.01 |

**Tasks**

***Mirror Tracing***

Participants *(N:* DD = 26, TYP = 27) watched their hands in a mirror while tracing the outline of a six-sided star (Gabrieli et al., 1993; Milner, 1962). A Lafayette Instruments Auto-Scoring Mirror Tracer, a device that includes a metal stylus and a metal test plate (except for the star pattern), was used for this task (Model 58024A⁄C). When the stylus goes off the star and touches the metal plate, it completes an electrical circuit and an error is recorded. Participants were instructed to trace as quickly and accurately as possible while staying within the outline of the star. Participants first completed a practice trial and then traced four times. After 30 minutes of performing other tasks, participants traced five more times. Completion time and number of errors per trial were the dependent variables.

***Rotary Pursuit***

Participants *(N:* DD = 26, TYP = 27) used a stylus to maintain contact with a photoelectric target driven by a Lafayette photoelectric pursuit rotor (Lafayette Instruments, Model 30014). The target rotated around a rectangle with truncated corners. Participants first completed a 20-s practice trial to establish baseline speed (15, 30, 45, or 60 rotations per minute). The speed at which a participant’s time-on-target was closest to 5 s was selected as the baseline and used for all subsequent trials. Participants then completed four 20-s trials, took a break for 1 minute, and then completed four more 20-s trials. After 30 minutes of performing other tasks, participants completed eight more 20-s trials, taking a 1-minute break after the first four trials as before. The dependent measure was *proportion on*, computed as time on target/(time on target + time off target).

***Statistical Learning (SL)***

Participants (*N*: DD = 17, TYP = 24) were invited to complete one visual SL (VSL) task and one auditory SL (ASL) task by themselves, hosted on a secure website (<https://www.cogscigame.co>). Age and sex ratio are matched between DD and TYP. But DD group has a relatively lower nonverbal IQ, compared to TYP (DD: 105.5, TYP: 115.8, *p* = 0.02). The two tasks were arranged in a random order for each participant, and a sound volume check was included at the beginning to ensure that participants were able to hear the auditory stimuli and were sitting at a quiet environment. Materials for reproducing the tasks are available at <https://zenodo.org/record/3820620#.Y3eE--zMLvV>. The design and procedure of the SL tasks have been previously described in detail in Qi et al. (2019). For each SL task, a familiarization phase, in which participants performed a target detection task for approximately 5 min, was immediately followed by a test phase, in which a two-alternative forced-choice (2AFC) test was given.

In the familiarization phase, stimuli were presented in a continuous stream according to an embedded pattern of four unique triplets. In the VSL task, 12 unique cartoon alien images formed four target triplets. Each of the target triplets was repeated 24 times for a total of 96 triplets. Each image was presented one at a time at the center of the screen for 800 ms with a 200-ms inter-stimulus interval (stimulus onset asynchrony (SOA) = 1000 ms), lasting a total of 4 min 48 sec. Participants were instructed to press the spacebar as quickly as possible whenever the target alien appeared on the screen. The target alien image was always the third alien of one of the four base triplets so that online learning could be measured via response time acceleration over 24 target trials during exposure. In the ASL task, 12 unique monotones of the same duration (328 ms) formed four target triplets. Each triplet was repeated 48 times for a total of 192 triplets. The SOA was 480 ms, with the familiarization phase lasting 4 min and 36 sec. Presentation speed was faster in the auditory than visual tasks due to differences in perceptual preference (Conway & Christiansen, 2009; Emberson et al., 2011). The procedure was identical to that of VSL except that the target tones used in the target-detection task during familiarization were constrained to only the lowest and highest notes of the final tones of the four triplets to facilitate identification. Two practice trials before the continuous stream of tones ensured that participants could distinguish the target tone. Response time was measured over 48 target trials. This approach of measuring online learning has been validated in our previous work in adult learners: their responses to target stimuli accelerated more quickly in structured sequences, similar to the ones used here, than in random sequences where no triplets were formed and the same stimuli were displayed in a random order (Schneider et al., 2020; Tang et al., 2022). Significant RT acceleration was also observed in children using a tablet to respond to targets in the third position, but not the first position, of a triplet, indicating that they had learned the triplet structure and could anticipate the target (Zinszer et al., 2020).

In the 2AFC test phase, participants were asked to identify which of two triplets seemed more like what they saw during the familiarization phase. One option was a target triplet from the familiarization phase and the other was a foil triplet that was novel to the participant. Foil triplets were constructed so that the relative position of each image was the same as in the target triplet. The test phase consisted of 32 trials (4 target triplets x 4 foil triplets x 2 repetitions) presented in random order. The images and sounds within each triplet were presented one at a time at the same presentation rate as in the familiarization phase with a 1000-ms pause between the target and the foil triplets. There were no time constraints for responses and no feedback was given. The dependent measure was accuracy.

One participant in the DDgroup was removed from the ASL analyses and one participant in the TYP group was removed from the VSL analyses because their data were not recorded due to technical issues. Task order (VSL or ASL first) was counterbalanced across participants.

**Statistical Analysis**

For all four experiments, outcome variables were analyzed in R v3.5.0 (Team, 2013), using identical statistical thresholds (*p* < 0.05*)*, and maximal random effect structures (Barr, 2013), using the package *lme4* (Bates et al., 2007). The significance of fixed effects in the linear mixed-level models was tested in an ANOVA (using Satterthwaite approximations) and fit with restricted maximum likelihood (REML) using the package *lmerTest* (Kuznetsova et al., 2016). The significance of fixed effects in the generalized linear mixed-level models was estimated using personalized quasi-likelihood using the *glmmPQL* function of the package *MASS* to improve model convergence. The effect sizes for the fixed effects in these linear mixed models were computed via the coefficient of determination (R squared) using *r2beta* function of the package *r2glmm* (Jaeger, 2017; Nakagawa & Schielzeth, 2013). In all models, age, sex, and nonverbal IQ were included as nuisance covariates.

***​​Pairwise Correlation Analysis***

To test whether individuals’ performance across these different tasks is partially constrained by an underlying unified capacity, Pearson pairwise correlations were computed to test for cross-task associations using the Hmisc package in R (Harrell Jr & Harrell Jr, 2019). Completion time per trial was extracted for the MT and RP tasks, and the mean number of errors per trial was extracted for the MT task. Each participant’s SL performance was measured by 1) the linear slope of response-time acceleration over normalized response time, so that we are able to compare SL performance across individuals with different baseline speed, and 2) the proportion of correct responses during the 2AFC task. To avoid skewing our correlational analyses, we removed one TYP participant who showed an unusual deceleration over the course of ASL exposure (RT slope was more than 3 SD above the sample mean) from the correlations that involve ASL RT slopes. Bayesian correlations were computed using the BayesFactor package (Morey et al., 2015) with default priors comparing a null model of no correlation with the alternative model of correlation. Bayesian models provide good precision even in smaller data sets (Lee & Song, 2004). Importantly, Bayes factors provide a measure of how likely the data are under the null versus alternative hypothesis, allowing us to quantify and compare relative support for the existence of a relationship between each pair of variables. Based on previous work, Bayes factors larger than 1 were considered to provide positive evidence (albeit weak if under 3) in favor of the alternative hypothesis that two variables are correlated (Jeffreys, 1998; Wetzels et al., 2011).

**Results**

There were no significant group differences in age or IQ, but participants with dyslexia performed significantly worse than typical readers on the two measures of phonological awareness, short-term verbal memory, and vocabulary (Table 1).

**Rotary Pursuit**

The group performance by trial is shown in **Figure 1A**. There were no significant group differences in the baseline speed (*t*(45.39) = 0.06, *p* = 0.95, d = 0.02). Both groups showed substantial improvement across trials. To test for group differences in time on target, a linear mixed-effects model was conducted with *proportion on* as the dependent variable. Fixed factors in the model included *trial number* and *group* (DD vs. TYP); the model’s random effects structure included random intercepts by participants and by-participant random slopes for *trial number* (Jaeger, 2008). The main effect of *trial number* was significant (*b* = 0.01, SE = 0.002, *t* = 7.13, *p* < 0.001, 𝑅2𝑚 = 0.072), with an increase in the proportion of time on target across trials for both groups. The main effect of *group* was not significant (*b* = 0.01, SE = 0.04, *t* = 0.30, *p* = 0.77, 𝑅2𝑚 = 0). The interaction between *trial number* and *group* was marginal (*b* = -0.005, SE = 0.002, *t* = -1.86, *p* = 0.069, 𝑅2𝑚 = 0.005), suggesting a marginally steeper slope in the DD group (*b* = 0.01, SE = 0.001, *t* = 8.37, *p* < 0.001) than in the TYP group (*b* = 0.008, SE = 0.002, *t* = 4.15, *p* < 0.001).

**Mirror Tracing**

The completion time by trial and the number of errors by trial are shown in **Figure 1B** and **Figure 1C**,respectively. There were no significant group differences in the baseline time (*t*(24.60) = 0.46, *p* = 0.65, d = 0.14) or error (*t*(38.23) = 0.05, *p* = 0.96, d = 0.01) during the first practice trial. Both groups showed substantial reduction in completion time and number of errors across trials. To test for group differences, two linear mixed-effects models were conducted with completion *time* and total number of *errors* as the dependent variables. Fixed effects in the models included *trial number* (Trials 2–10 because the first trial was practice) and *group* (DD vs. TYP); the model’s random effects structure included random intercepts by participants and by-participant random slopes for *trial number*. Age, sex, and nonverbal IQ were included as nuisance covariates.

For the *time* model, the main effect of *trial number* was significant (*b* = -2.43, SE = 0.68, *t* = 3.59, *p* = 0.001, 𝑅2𝑚 = 0.043), with a reduced time on task across trials. Neither the main effect of *group* (*b* = 3.21, SE = 10.20, *t* = 0.32, *p* = 0.75, 𝑅2𝑚 = 0.001) nor the interaction between *trial number* and *group* (*b* = 0.14, SE = 0.94, *t* = 0.15, *p* = 0.88, 𝑅2𝑚 = 0) weresignificant. Similar results were revealed for the *error* model. The main effect of *trial* was significant (*b* = 1.88, SE = 0.43, *t* = 4.32, *p* < 0.001, 𝑅2𝑚 = 0.058), with a reduced number of errors across trials. Neither the main effect of *group* (*b* = 6.98, SE = 5.84, *t* = 1.20, *p* = 0.24, 𝑅2𝑚 = 0.01) nor the interaction between *trial number* and *group* (*b* = 0.71, SE = 0.61, *t* = 1.17, *p* = 0.25, 𝑅2𝑚 = 0.004) weresignificant.

**Auditory Statistical Learning**

Familiarization Phase: The time window for valid button presses for the target tones was defined from the onset of the previous stimulus to the onset of the next two stimuli (from -480 ms to 960 ms) to allow for anticipatory as well as delayed button presses for the target tones. The two groups were not significantly different in their baseline response time (*t*(27.2) = 0.84, *p* = 0.41, *d* = 0.29) or hit rate (*t*(37.8) = -0.31, *p* = 0.76, *d* = 0.1; **Supplementary Table 1**).

Graphical user interface, histogram

Description automatically generated

**Figure 1**. The time courses of procedural learning and implicit statistical learning. Performance for adults with dyslexia (DD, solid lines) and typical readers (TYP, dashed lines) is plotted across trials for rotary pursuit (A), mirror tracing (B, C), the familiarization phase of auditory statistical learning (D), and the familiarization phase of visual statistical learning €. The vertical dash-dotted lines in 1A-1C indicate task breaks.

The group performance by trial is shown in **Figure 1D**. Neither group showed a trend of acceleration over the course of familiarization. To test for group differences, a linear mixed-effect model was conducted with response *time* as the dependent variables. Fixed effects in the models included *trial number* (Trials 1–48), *group* (DD vs. TYP), and their interaction. Age, sex, and non-verbal IQ were included as covariates. The model’s random effects structure included random intercepts by participants and by-participant random slopes for *trial number*. There was no significant effect of *trial number* (*b* = -0.390, SE = 1.41, *t* = -0.28, *p* = 0.78, 𝑅2𝑚 = 0), *group* (*b* = -51.94, SE = 55.20, *t* = -0.94, *p* = 0.35, 𝑅2𝑚 = 0.002), or their interaction (*b* = 0.48, SE = 1.82, *t* = 0.26, *p* = 0.80, 𝑅2𝑚 = 0) on response time.

Test Phase: Participants’ overall accuracy in the 32-trial 2AFC test is depicted in **Figure 2**. Both groups performed significantly above the 50% chance level (DD: Mean = 0.55, SD = 0.09, *t*(15) = 2.19, *p* = 0.02; TYP: Mean = 0.66, SD = 0.13, *t*(23) = 6.22, *p* < 0.001). We compared the two groups using a generalized linear mixed model fit by maximum likelihood (Laplace Approximation). The dependent variable was each participant’s trial-by-trial binomial accuracy. The fixed effect was *group* (DD vs. TYP). Age, sex, and nonverbal IQ were included as covariates. The model’s random effects structure included random intercepts by participants and by trial. There was a significant main effect of *group*. The DD group had significantly lower accuracy in identifying the target tone triplets as compared to the TYP group (*b* = 2.43, SE = 0.65, *z* = 3.71, *p* < 0.001, 𝑅2𝑚 = 0.02).

**Visual Statistical Learning**

Familiarization Phase: The time window for valid button presses for the target tones was defined from the onset of the previous stimulus to the onset of the next two stimuli (from -1000 ms to 2000 ms) in order to allow for anticipatory as well as delayed button presses for the target tones. Participants performed the target detection task with high hit rates. As a result, all participants were kept in this analysis. The two groups were not significantly different in their baseline response time (*t*(34.5) = 0.70, *p* = 0.49, *d* = 0.23) or hit rate (*t*(21.7) = -0.70, *p* = 0.13, *d* = 0.57; **Supplementary Table 1**).

The group performance by trial is shown in **Figure 1E**. To test for group differences in response time changes over the course of familiarization, a linear mixed-effect model was conducted with response *time* as the dependent variable. Fixed effects in the models included *trial number* (Trials 1–24), *group* (DD vs. TYP), and their interaction. The model’s random effects structure included random intercepts by participants and by-participant random slopes on *trial number*. There was a significant effect of *trial number* (*b* = 2.56, SE = 0.91, *t* = 2.81, *p* = 0.008, 𝑅2𝑚 = 0.01) and a marginal interaction between *group* and *trial number* (*b* = 2.10, SE = 1.19, *t* = 1.76, *p* = 0.087, 𝑅2𝑚 = 0.004) on reaction time. The *group* difference in response time was not significant(*b* = -8.14, SE = 24.39, *t* = -0.33, *p* = 0.74, 𝑅2𝑚 = 0).

Test Phase: Participants’ overall accuracy in the 2AFC test following familiarization is depicted in **Figure 2**. Both groups performed significantly above the 50% chance level (DD: Mean = 0.72, SD= 0.21, *t*(16) = 4.39, *p* < 0.001; TYP: Mean = 0.67, SD = 0.23, *t*(22) = 3.55, *p* < 0.001). We compared the two groups using a generalized linear mixed model. The dependent variable was each participant’s trial-by-trial binomial accuracy. The fixed effect was *group* (DD vs. TYP). Age*,* sex*,* and nonverbal IQ were included as covariates. The model’s random effects structure included random intercepts by participants and by trial. The two groups did not significantly differ in accuracy (*b* = 0.75, SE = 1.67, *t* = 0.45, *p* = 0.65, 𝑅2𝑚 = 0.001).

**Comparison of Auditory Statistical Learning and Visual Statistical Learning**

Familiarization Phase: To compare the task demands during familiarization phase across the two SL tasks, we tested the interaction between *task* and *trial number* within the TYP group. The RT changes during the familiarization phase were similar between ASL and VSL tasks (*b* = 0.0006, SE = 0.004, *t* = 0.164, *p* = 0.87, 𝑅2𝑚 = 0). To compare the degree of group differences in response-time changes across the two SL tasks, we tested the interaction between *trial number, task,* and *group* in a linear mixed model. Our analysis revealed a marginal three-way interaction (*b* = 0.005, SE = 0.002, *t* = 1.84, *p* = 0.066, 𝑅2𝑚 = 0.002), that is, the group difference (DD quicker than TYP) in real-time VSL is marginally larger than the group difference in real-time ASL.

Test Phase: To compare the task demands during the test phase across the two SL tasks, we tested the main effect of taskswithin the TYP group. The TYP group performed similarly across ASL and VSL tasks (*b* = -0.18, SE = 0.26, *t* = -0.69, *p* = 0.49, 𝑅2𝑚 = 0). To compare the degree of group differences in test accuracy across the two SL tasks, we tested the interaction between *task* and *group* in a generalized linear mixed model. We found a significant difference in learning between the groups on the two SL tasks: the group difference (DD < TYP) was significantly greater in the ASL task than the VSL task (*b* = -0.77, SE = 0.21, *t* = -3.59, *p* < 0.001, 𝑅2𝑚 = 0.005). This suggests a dissociation in DD between ASL (reduced) and VSL (preserved).

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**Figure 2**. Implicit statistical learning performance during the test phase. Mean proportion of correct trials in adults with dyslexia (DD, darker grey) and typical readers (TYP, lighter grey) for auditory statistical learning and visual statistical learning. \*\*\*, *p* < 0.001.

**Pairwise Task Correlation Analysis**

all seven learning measuresAll seven task performance measures presented moderate-to-good internal consistency as measured by Cronbach’s alpha (**Supplementary Table 3**). There were no significant associations among the different learning tasks. This was confirmed using Bayes factors with no evidence against the hypothesis of cross-task associations. The only significant associations were between MT accuracy and response time and between VSL accuracy and response time. The former correlation represents a tradeoff between accuracy and response time. The latter relationship is consistent with previous research (Qi et al., 2019), suggesting that quicker response-time acceleration during exposure was associated with greater success in recognizing the learned triplets.

**Table 2.** Pairwise learning task correlations.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **1** | **2** | **3** | **4** | **5** | **6** |
| **1. Rotary Pursuit Mean Proportion On** | 1 |  |  |  |  |  |
| **2. Mirror Tracing Time** | 0.186  BF = 0.39 | 1 |  |  |  |  |
| **3. Mirror Tracing Error** | 0.104  BF = 0.37 | 0.368\*  BF= 5.407 | 1 |  |  |  |
| **4.Auditory SL Accuracy** | -0.014  BF = 0.37 | -0.052  BF = 0.399 | 0.132  BF = 0.274 | 1 |  |  |
| **5. Visual SL Accuracy** | -0.01  BF = 0.37 | -0.028  BF = 0.207 | 0.0431  BF= 0.211 | -0.116  BF= 0.253 | 1 |  |
| **6. Auditory SL RT Slope** | 0.221  BF = 0.56 | -0.028  BF = 0.229 | -0.223  BF= 0.443 | -0.034  BF= 0.223 | -0.230  BF= 0.469 | 1 |
| **7. Visual SL RT Slope** | -0.265  BF = 0.59 | -0.104  BF = 0.245 | -0.165  BF = 0.253 | 0.081  BF = 0.224 | -0.586\*\*  BF = 400.962 | -0.100  BF = 0.256 |

SL = statistical learning. RT = response time. \*p < 0.05, \*\* p < 0.001

**Relationship between learning and standardized tests of reading and phonological skills.**

To examine the relationships between learning performance and individuals’ reading abilities, we assessed the Pearson correlations between all seven learning measures and the average of Word ID and Word Attack from the WRMT-R/NU across the whole sample and within each group (**Table 3**). We hypothesized that greater learning performance (more negative slope and higher SL test accuracy) would be associated with better reading and phonological skills. We chose the untimed decoding skills because three out of seven learning measures involve response time and may inflate the correlations. Better decoding skills were significantly associated with greater ASL accuracy (**Figure 3A**; R = 0.49, one-tailed *p* = 0.001, Bonferroni-corrected *p* < 0.05, BF = 24.71), but not with VSL accuracy (R = -0.12, one-tailed *p* = 0.27, BF = 0.45). The two correlation strengths are significantly different (Hittner et al., 2003; *z* = 2.69, *p* = 0.007). Importantly, the ASL-decoding relationship was similarly strong within the DD group alone (R = 0.50, one-tailed *p* = 0.03, BF = 2.04), suggesting that the significant association in the whole sample was not simply due to the co-existing group differences on both ASL and decoding skills. We previously reported a strong relationship between ASL RT slope and nonword decoding, as opposed to real-word reading, in school-aged children, whose decoding skills were still developing (Qi et al., 2019). A similar trend was also found within the DD group in the current study: quicker ASL RT acceleration was marginally associated with better nonword decoding measured by Word Attack (R = -0.40, *p* = 0.07, BF = 1.21), but not related to real word decoding measured by Word Identification (R = -0.08, *p* = 0.78).

We also examined the correlations between learning performance and individuals’ phonological awareness skills, measured by the average of Elision and Blending Words from the CTOPP-2 (**Table 3**). A greater VSL response-time slope in the DD group correlated significantly with higher phonological awareness scores (**Figure 3B**; R= -0.85, one-tailed *p* < 0.001, Bonferroni-corrected *p* < 0.05, BF = 244.08). There was also a significant correlation between greater VSL accuracy and higher phonological awareness scores in the DD group (*R* = 0.54, one-tailed *p* = 0.02, BF = 2.853). No correlations survived corrections for multiple comparisons within the typical group, perhaps due to smaller variance in their reading and phonological awareness scores.

**Table 3.** Correlation coefficients between procedural/statistical learning and standardized reading and phonological test scores.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Learning | Decoding | | | Phonological Awareness | | | |
| All | DD | TYP | | All | DD | TYP |
| RP Mean Prop On | -0.11  BF = 0.41 | 0  BF = 0.42 | -0.07  BF = 0.44 | | 0.15  BF = 0.52 | 0.10  BF = 0.47 | 0.33\*  BF = 1.39 |
| MT Time | -0.02  BF = 0.32 | 0.16  BF = 0.55 | 0.26  BF = 0.88 | | 0.03  BF = 0.32 | 0.10  BF = 0.47 | 0.16  BF = 0.54 |
| MT Error | 0.02  BF = 0.31 | 0.14  BF = 0.51 | 0.31  BF =0.88 | | 0.02  BF = 0.31 | 0.01  BF = 0.43 | 0.23  BF = 0.74 |
| ASL Accuracy | 0.49\*\*  BF = 24.71 | 0.50\*  BF = 2.04 | 0.20  BF = 0.63 | | 0.26  BF = 1.07 | 0.21  BF = 0.65 | 0.01  BF = 0.45 |
| VSL Accuracy | -0.12  BF = 0.45 | -0.31  BF = 0.86 | 0.08  BF = 0.48 | | 0.23  BF = 0.83 | 0.54\*  BF = 2.85 | 0.19  BF = 0.62 |
| ASL RT Slope | 0.08  BF = 0.40 | -0.26  BF = 0.73 | 0.05  BF = 0.47 | | -0.06  BF = 0.39 | -0.32  BF = 0.87 | -0.02  BF = 0.46 |
| VSL RT Slope | 0.17  BF = 0.58 | 0.04  BF = 0.86 | -0.07  BF = 0.47 | | -0.11  BF = 0.43 | -0.85\*\*\*  BF= 244.08 | 0.14  BF = 0.53 |

Note: \* uncorrected p < 0.05; \*\* uncorrected p < 0.01; \*\*\* uncorrected p < 0.001. Underlined values represent significant correlations after Bonferroni corrections for 14 correlations within each group. RP = rotary pursuit. MT = mirror tracing. ASL = auditory statistical learning. VSL = visual statistical learning. RT = response time.



**Figure 3.** Relationships between statistical learning and reading-related skills. **A.** Auditory statistical learning accuracy and untimed word and nonword decoding skills. **B.** The response-time slope of visual statistical learning and phonological awareness.

**Discussion**

According to one influential theoretical framework, reading deficits in developmental dyslexia result from atypical domain-general procedural learning (Nicolson & Fawcett, 2011; Ullman et al., 2020; Ullman & Pullman, 2015). Here we tested this theory using four non-linguistic tasks that measure implicit learning in adults with and without dyslexia. We found no evidence for impaired learning in adults with dyslexia on rotary pursuit and mirror tracing, two classic and well-validated paradigms designed to measure procedural learning independent of declarative memory. In the auditory statistical learning task, individuals with dyslexia showed reduced learning as measured by test accuracy in post-learning triplet recognition. In contrast, individuals with dyslexia showed typical learning on the visual statistical learning task. Thus, these findings suggest that instead of a pervasive deficit in procedural learning, learning deficits in dyslexic adults are specific to the domain that shows the most consistent impairment in dyslexia: auditory processing.

The findings that adults with dyslexia show learning equivalent to that of typical readers on the two motor learning tasks challenge previous reports of broad procedural deficits in dyslexia (e.g., Lum et al., 2013; Nicolson & Fawcett, 2007, 2011; Ullman, 2004; Ullman & Pierpont, 2005). There is ample evidence that skill learning on both mirror tracing and rotary pursuit tasks is strongly dissociable from declarative or explicit memory (e.g., Corkin, 1968; Gabrieli et al., 1993b; Heindel et al., 1989; Milner, 1962). The absence of differences in learning between the typical and dyslexia group in the current study, combined with lack of convincing evidence for procedural deficits in dyslexia reported in two recent meta-analyses (Oliveira et al., 2022; West et al., 2021), point convincingly against broad deficits in procedural learning as the core deficit in dyslexia.

The statistical learning results further rule out a domain-general procedural learning deficit. We found that dyslexic adults showed an impairment in ASL, but intact ability in VSL. Moreover, reading skills, measured by word decoding, were strongly associated with ASL but not with VSL, across the entire sample. A similar relationship, albeit less robust, was found within the dyslexic group. These findings are consistent with the specific link between ASL and reading skills reported before in neurotypical adults and children (Qi et al., 2019). Our study extends the relationship between ASL and reading in adults from sentence level to word-level decoding. The complementary findings across the online and offline learning measures of ASL in the dyslexic group suggested that the relationship between ASL and word-level decoding might be particularly evident for cases when decoding is effortful and might overly rely on phonological processes (e.g., children, dyslexic individuals, and nonword reading).

The specificity of reduced ASL in the dyslexia group implies underlying low-level learning deficits that impair performance on both ASL and reading. Atypical auditory learning might be one of the underlying causes of challenges faced by dyslexic individuals in establishing grapheme-to-phoneme mapping. Decades of dyslexia research have documented the widespread and persistent deficits in auditory processing in individuals with dyslexia (Ahissar et al., 2000; Amitay et al., 2002; Goswami, 2002; Lorusso et al., 2014; Tallal & Piercy, 1973; Ziegler et al., 2009). Specifically, individuals with dyslexia consistently show elevated discrimination thresholds on tone-frequency discrimination tasks (reviewed in Witton et al., 2020). Processing of tone frequencies relies on sound representations in the earliest stages of the auditory system. Brainstem recordings in individuals with dyslexia revealed noisier and less congruent sound representations (Banai et al., 2009; Basu et al., 2010; Hornickel et al., 2011; Hornickel & Kraus, 2013) which may result in less efficient adaptation to sound statistics (Chandrasekaran et al., 2009). ). Therefore, poor auditory processing may attenuate learning on auditory tasks. Indeed, adults with dyslexia demonstrated reduced capacity for tone-frequency discrimination but benefitted to the same extent as typical readers when one comparison tone was held constant across trials (Ozernov-Palchik et al., 2022) Even when baseline auditory discrimination skills were equated across the groups in a word recognition experiment with acoustic distortion, dyslexic adults demonstrated attenuated gain in auditory perception from the feedback about the word identity in speech (Gabay et al., 2022; Gabay & Holt, 2015).

The current study is in part consistent with prior SL findings in the literature on dyslexia. To date, the majority of SL studies in dyslexic adults and adolescents have only investigated a single sensory modality, yet less efficient learning in ASL (Dobó et al., 2021; Gabay et al., 2015; Kahta & Schiff, 2019), as well as in VSL (Kahta & Schiff, 2016; Sigurdardottir et al., 2017) have been documented. Notably, the impairment in SL seems to hinge on the implicit nature of the task, because no behavioral difference was found when dyslexic adults were either informed of the embedded statistical patterns prior to learning or became vaguely aware of the embedded patterns after learning (Kahta & Schiff, 2016; Sigurdardottir et al., 2017). The visual saliency of our cartoon alien stimuli, together with our target-detection cover task, may have boosted attention to the stimuli and therefore facilitated learning (Schneider et al., 2020; Toro et al., 2005; Turk-Browne et al., 2005).

The positive relationship between visual statistical learning and phonological awareness in dyslexic adults was interesting and somewhat unexpected. This relationship was not found in a typically reading population (Qi et al., 2019). However, a reversed causal relationship between phonological skills and reading has been proposed in typical reading development as well: that is, school-aged children’s phonological abilities improve with reading experience (e.g., Castles & Coltheart, 2004). Similarly, dyslexic adults might also hone their phonological skills through reading and decoding practices and superior visual statistical learning might boost the benefits. This compensatory route might be especially valuable for learners whose spoken language and written language skills develop in tandem. This possibility has been recently supported by a study in a group of beginning readers of a second language. Children’s visual statistical learning was found to predict their phonological awareness in the second language (Zinszer et al., 2020). In another study with adults who were learning Hebrew as a second language, VSL was also related to their Hebrew reading skills, measured by a morphological priming effect in a lexical decision task (Frost et al., 2013).

Our study has a few methodological limitations. First, the modest number of participants could have obscured small learning deficits. There is evidence that group differences in SRT learning have small effect sizes, but such differences are more robust for SL (West et al., 2021). Further, the group with dyslexia had slightly stronger learning effects than the typically learning group on both VSL and mirror tracing. Thus, the overall findings of intact learning in the present study appear robust. Second, as indicated by a lower hit rate, the target detection cover task in ASL was a more difficult task than the one in VSL. As a result, ASL could have been more influenced by perceptual or attentional differences during learning. During ASL, neither group showed any evidence of response-time acceleration. Previous studies observed similar null results at the group level in ASL (e.g., Qi et al., 2019; Schneider et al., 2020), but individual differences in ASL response-time acceleration can still serve as a valuable predictor for reading-related skills. For example, neurotypical children’s ASL response-time slope was significantly related to decoding skills, which was mediated by phonological awareness (Qi et al., 2019). Third, our SL measures, despite capturing both online and offline learning, are not sufficient to tease apart learning and retrieval mechanisms. The above-chance 2AFC accuracy does not depend on RT acceleration, nor is RT acceleration solely driven by pattern learning. Future research, potentially with neuroimaging, is necessary to pinpoint which learning subprocesses are more vulnerable to disruption in dyslexia.

In conclusion, our study combining four classic procedural learning and statistical learning tasks provides converging evidence against a domain-general procedural learning deficit in dyslexic adults. Even though a shared subcortical contribution to procedural learning across all four tasks is well-documented (Janacsek et al., 2022), dyslexic adults show reduced performance only in auditory statistical learning, but typical performance in motor skill learning and visual statistical learning. Difficulties in learning phoneme-to-grapheme mapping in dyslexia, therefore, cannot be directly attributed to the procedural dysfunctions governed by the core subcortical circuitry involving basal ganglia (Krishnan et al., 2016; c.f. Ullman et al., 2020). Instead, our findings suggest reading acquisition in dyslexic individuals might be constrained specifically by neural substrates of auditory processing and learning, providing support for a multi-component and pluralist view of learning (Bogaerts et al., 2022; Frost et al., 2019).

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**Supplementary Table 1**. Performance during the familiarization phase of statistical learning.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Auditory SL | | Visual SL | |
| Mean (SD) | Mean RT (ms) | Hit rate | Mean RT (ms) | Hit rate |
| DD | 400.3 (102.6) | 0.51 (0.20) | 475.4 (70.8) | 0.96 (0.06) |
| TYP | 372.8 (88.76) | 0.53 (0.25) | 491.2 (70.1) | 0.99 (0.03) |

**Supplementary Table 2**. Demographic information.

|  |  |  |
| --- | --- | --- |
|  | DD (N=26) | TYP (N=27) |
| History of Reading Delay | 19 (73.1%) | 1 (3.7%) |
| History of Language Delay | 2 (7.7%) | 0 (0.0%) |
| Diagnosis of Dyslexia | 20 (76.9%) | 0 (0.0%) |
| Diagnosis of ADHD | 1 (3.8%) | 1 (3.7%) |
| Race |  |  |
| White | 22 (84.6%) | 24 (88.9%) |
| Black/African American | 4 (15.4%) | 3 (11.1%) |
| Hispanic | 0 (0.0%) | 1 (3.7%) |
| Income |  |  |
| <30k | 6 (24.0%) | 3 (11.5%) |
| 30-60k | 11 (44.0%) | 9 (34.6%) |
| 60-100k | 4 (16.0%) | 3 (11.5%) |
| >100k | 4 (16.0%) | 11 (42.3%) |
| Education |  |  |
| Less than 7th Grade | 0 (0.0%) | 0 (0.0%) |
| Junior High | 0 (0.0%) | 0 (0.0%) |
| High School | 1 (3.8%) | 0 (0.0%) |
| Partial College | 2 (7.7%) | 0 (0.0%) |
| College | 7 (26.9%) | 12 (44.4%) |
| Masters | 14 (53.8%) | 10 (37.0%) |
| Doctorate | 2 (7.7%) | 5 (18.5%) |

**Supplementary Table 3**. Cronbach’s alpha for all tasks.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Procedural Learning** | | | **Statistical Learning** | | | |
|  | Rotary Pursuit | Mirror Tracing - Error | Mirror Tracing - Time | Visual - RT | Visual - Accuracy | Auditory - RT | Auditory - Accuracy |
| Cronbach’s alpha | 0.98 | 0.68 | 0.56 | 0.94 | 0.89 | 0.89 | 0.65 |