

Delaying feedback compensates for impaired reinforcement learning in developmental dyslexia[☆]

Yafit Gabay^{*}

Department of Special Education, University of Haifa, Haifa, Israel

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

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ABSTRACT

A theoretical framework suggests that developmental dyslexia is characterized by abnormalities in brain structures underlying the procedural learning and memory systems while the declarative learning and memory systems are presumed to remain intact or even enhanced (Procedural Deficit Hypothesis). This notion has been supported by a substantial body of research, which focused on each system independently. However, less attention has been paid to interactions between these memory systems which may provide insights as to learning situations and conditions in which learning in dyslexia can be improved. The current study was undertaken to examine these important but unresolved issues. To this end, probabilistic reinforcement learning and episodic memory tasks were examined in participants with dyslexia and neurotypicals simultaneously within a single task. Feedback timing presentation was manipulated, building on prior research indicating that delaying feedback timing shifts striatal-based probabilistic learning, to become more hippocampal-dependent. It was hypothesized that if the procedural learning and memory systems are impaired in dyslexia, performance will be impaired under conditions that encourage procedural memory engagement (immediate feedback trials) but not under conditions that promote declarative memory processing (long delayed feedback trials). It was also predicted that the ability to incidentally acquire episodic information would be preserved in dyslexia. The results supported these predictions. Participants with dyslexia were impaired in probabilistic learning of cue-outcome associations compared to neurotypicals in an immediate feedback condition, but not when feedback on choices was presented after a long delay. Furthermore, participants with dyslexia demonstrated similar performance to neurotypicals in a task requiring incidental episodic memory formation. These findings attest to a dissociation between procedural-based and declarative-based learning in developmental dyslexia within a single task, a finding that adds discriminative validity to the Procedural Deficit Hypothesis. Just as important, the present findings suggest that training conditions designed to shift the load from midbrain/striatal systems to declarative memory mechanisms have the potential to compensate for impaired learning in developmental dyslexia.

1. Introduction

Developmental dyslexia is a neurobiological disorder characterized by selective impairment in reading skill acquisition despite conventional instruction, adequate intelligence, and sociocultural opportunity. It is one of the most prevalent neurodevelopmental disorders and has been identified as affecting roughly 7% of the population (Peterson & Pennington, 2015). Dyslexia has several negative emotional and social consequences, including reduced participation in the labor force,

increased dependence on government assistance, and diminished civic involvement (Livingston, Siegel, & Ribary, 2018).

The underlying psychological bases of dyslexia remain unclear despite extensive research (Démonet, Taylor, & Chaix, 2004). The central hypothesis regarding the etiology of dyslexia posits poor processing of or access to phonological information as the underlying cause of the disorder (Ramus & Szenkovits, 2008; Snowling, 2001). Although the exact nature of the phonological deficit is unclear (Ramus & Szenkovits, 2008), there is an agreement across researchers that phonological

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^{*} At: Department of Special Education, University of Haifa, Mount Carmel, Haifa 31905, Israel.

E-mail address: ygabay@edu.haifa.ac.il.

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deficits are one of the most prevalent symptoms associated with dyslexia. This is manifested in impaired phonological awareness, poor verbal short-term memory, and slow lexical retrieval (Vellutino, Fletcher, Snowling, & Scanlon, 2004), and is consistent with the phonological deficit account of dyslexia. Yet, phonological deficits may arise from a range of causes, and phonological impairments may be the result, rather than the cause of dyslexia (Gabay & Holt, 2015). Evidence has accumulated that individuals with dyslexia struggle with a range of nonlinguistic difficulties that are difficult to reconcile with a phonological account. These include problems with sensitivity to statistical structure (Gabay, Thiessen, & Holt, 2015; Sigurdardottir et al., 2017; Singh, Walk, & Conway, 2018), motor functioning (Fawcett & Nicolson, 1995; Hedenius, Lum, & Bölte, 2020; Orban, Lungu, & Doyon, 2008; Stoodley, Harrison, & Stein, 2006) and visual and auditory processing impairments (Farmer & Klein, 1995; Gabay, Najjar, & Reinisch, 2019; Goswami et al., 2002; Vandermosten et al., 2010). In light of the multifaceted nature of dyslexia, researchers have searched for a more broad explanatory framework to explain the diversity of deficits (Goswami, 2011; Jaffe-Dax, Daikhin, & Ahissar, 2018; Nicolson & Fawcett, 2019; Stein, 2019; Ullman, Earle, Walenski, & Janacek, 2020; Vidyasagar & Pammer, 2010), although there is no clear consensus on this issue.

1.1. Procedural learning dysfunction in dyslexia

One such broad conceptual framework suggests that domain-general procedural learning deficits play a role in its causation (Nicolson & Fawcett, 2007, 2011, 2019; Ullman, 2004; Ullman & Pierpont, 2005). This framework is based on a distinction between the declarative (“knowing that”) and procedural (“knowing how”) memory systems (Cohen, Poldrack, & Eichenbaum, 1997; Squire, 2004, 2009). The declarative memory system pertains to the acquisition of semantic and episodic memory, and is dependent on the integrity of medial temporal lobe structures, including the hippocampus (Squire, Stark, & Clark, 2004). The procedural memory system serves the acquisition of skills (the process of improving behaviors through repeated practice), habits (incremental learning of stimulus–response associations) and rules (Knowlton, Siegel, & Moody, 2017), mainly through structures in the cerebellum, basal ganglia, and neocortex (Gabrieli, 1998). It is assumed that in dyslexia, the procedural memory system malfunctions, causing problems with the acquisition and automaticity of reading, writing, and other language-related skills (the Procedural Deficit Hypothesis; PDH; Fawcett & Nicolson, 2019; Nicolson & Fawcett, 2011; Ullman et al., 2020).

The notion that procedural learning and memory systems may lie at the core of dyslexia is strengthened by the observations that children and adults with dyslexia tend to be impaired in a variety of motor, linguistic, and cognitive procedural learning tasks, such as motor adaptation tasks (Brookes, Nicolson, & Fawcett, 2007), serial reaction time tasks (Howard Jr, Howard, Japikse, & Eden, 2006; Lum, Ullman, & Conti-Ramsden, 2013; Stoodley et al., 2006), artificial grammar learning tasks (Pavlidou, Louise Kelly, & Williams, 2010; Pavlidou, Williams, & Kelly, 2009), weather prediction task (Gabay, Vakil, Schiff, & Holt, 2015), and multidimensional category learning tasks (Gabay, Dick, Zevin, & Holt, 2015; Sperling, Lu, & Manis, 2004). Problems are apparent not only in skill acquisition but also in reinforcement learning (Massarwe, Nissan, & Gabay, 2021). On the brain level, studies have revealed structural and functional abnormalities in core structures of the procedural memory systems, such as the cerebellum (Alvarez & Fiez, 2018; Finch, Nicolson, & Fawcett, 2002; Rae et al., 1998) and the basal ganglia (Brunswick, McCrory, Price, Frith, & Frith, 1999; Kita et al.,

2013; Richlan, Kronbichler, & Wimmer, 2011; Wang et al., 2019), in children and adults with dyslexia.

1.2. Declarative-based learning and memory in dyslexia

An extension of the procedural framework suggests that procedural memory impairment leads to greater dependence on the declarative memory system (the compensation hypothesis), enhanced functioning of that system (termed the “seesaw effect”) (Nicolson & Fawcett, 1990; Ullman & Pullman, 2015), or both. According to this assumption, people with dyslexia are more likely to use conscious strategies to compensate for their procedural learning impairments, which can lead to greater reliance on declarative memory processes or to enhanced functioning of this system. Consistent with this hypothesis, there is evidence that non-verbal declarative learning abilities of children with dyslexia are preserved (Li, Shu, McBride-Chang, Liu, & Xue, 2009; Messbauer & de Jong, 2003) or even enhanced (Hedenius, Ullman, Alm, Jennische, & Persson, 2013). Although evidence points to impaired episodic memory in children with dyslexia (Menghini, Carlesimo, Marotta, Finzi, & Vicari, 2010), this impairment is not observed in non-verbal episodic memory tasks (Hedenius et al., 2013). Likewise, implicit learning involving the striatum is impaired in adults with dyslexia but not to the extent that it relies on hippocampal functioning (Howard et al., 2006). Research has also revealed that better reading abilities are associated with better declarative memory (Hedenius et al., 2013) and larger hippocampal/medial temporal lobe (MTL) structures in children with dyslexia (Krafnick, Flowers, Napoliello, & Eden, 2011), as well as increased hippocampal activation and volumes in children and adults with dyslexia following reading intervention (Eden et al., 2004; Gebauer et al., 2012; Temple et al., 2003), suggesting increased reliance on these structures.

Although these findings are consistent with the PDH of dyslexia, learning tasks are likely to involve a mixture of declarative and procedural processes that interact in complex ways (Ashby & Crossley, 2010; Packard & Goodman, 2013; Sun, Slusarz, & Terry, 2005). Even quintessential procedural learning tasks are likely to involve both processes (Packard & Goodman, 2013; Sun et al., 2005). To date, the typical approach to studying the PDH in dyslexia has been to examine either declarative or procedural learning in isolation. In real-life learning situations, however, memory systems are likely to interact in complex ways, either cooperatively or competitively (Hartley & Burgess, 2005; McDonald, Devan, & Hong, 2004; Packard & Goodman, 2013). Yet few studies have examined these interactions in dyslexia in a given learning situation. In addition, because a learning impairment is unlikely to be an all-or-nothing phenomenon (Gabay, Shahbani-Khateb, & Mendelsohn, 2018), a critical goal is to delineate the learning environments and conditions in which learning behaviors in individuals with dyslexia can be improved. In particular, there are grounds to believe that relatively intact functions and circuits can play important compensatory roles in neurodevelopmental disorders (Ullman & Pullman, 2015), but few studies have examined whether the advantages of people with dyslexia can be exploited to mitigate their learning impairments (Vicari, Marotta, Menghini, Molinari, & Petrosini, 2003).

1.3. Feedback timing modulates the engagement of multiple memory systems

As noted above, although most studies make a distinction between declarative-based and procedural-based memory and learning systems, both systems are likely engaged in real-world learning environments (Crossley & Ashby, 2015; Packard & Goodman, 2013; Squire & Dede,

2015). The relative contribution of each system may be modulated based on task instructions (explicit vs. implicit) (Destrebecqz et al., 2005; Schendan, Searl, Melrose, & Stern, 2003), the presence of a secondary task (Foerde, Knowlton, & Poldrack, 2006; Waldron & Ashby, 2001), inclusion of feedback (Shohamy et al., 2004), or manipulation of the statistical structure to be learned (Nomura et al., 2007). Another important factor that contributes to the relative involvement of memory systems is the timing of feedback. Consider the probabilistic category learning task, which is one of the most common paradigms used to study habit learning in humans (Foerde, 2018; Knowlton, Mangels, & Squire, 1996; Poldrack et al., 2001; Shohamy et al., 2004). In this type of tasks, participants learn to associate cues with outcomes through trial and error. As there is no one-to-one mapping between cues and outcomes, optimal learning involves the use of response-contingent feedback across multiple trials to incrementally learn the most probable outcome. This type of reinforcement learning, which has been shown to engage the striatal-based memory system in neurotypicals (Knowlton et al., 1996; Poldrack et al., 2001; Shohamy et al., 2004), is impaired in populations with altered striatal function (Gabay & Goldfarb, 2017; Holl, Wilkinson, Tabrizi, Painold, & Jahanshahi, 2012; Shohamy et al., 2004). Although this type of learning is usually sensitive to striatal function, delaying feedback between stimulus and responses alters the learning process, making it more hippocampal-dependent (Foerde & Shohamy, 2011). Phasic dopamine responses to feedback, observed approximately 100 ms after a reward (Redgrave & Gurney, 2007), are thought to promote learning by facilitating cortico-striatal plasticity, presumably by reinforcing reward-related associations with relevant responses or stimuli (Reynolds & Wickens, 2002). The presence of a temporal gap between response and feedback, however, can fundamentally alter striatal neural responses and strengthen inappropriate synapses, suggesting that this mechanism is perhaps unsuitable for learning under delayed feedback conditions. Modeling-based functional imaging (fMRI) research provided direct evidence of the role of the declarative memory system in delayed feedback conditions. Foerde and Shohamy (2011) found that immediate feedback trials in a probabilistic learning task led to striatal activation in healthy individuals, as opposed to hippocampal activation under long delayed feedback trials. Learning in this task was observed to be impaired in disorders characterized by altered dopaminergic function in the striatum, but was intact when feedback was delayed for a few seconds (Foerde, Braun, & Shohamy, 2013; Gabay et al., 2018). The opposite pattern was observed in people who suffer from hippocampal damage, for whom learning was reduced in long delayed feedback condition but was preserved when feedback to choices was immediate (Foerde, Race, Verfaellie, & Shohamy, 2013). Consistent with this evidence, electrophysiological studies point to MTL involvement in long delayed feedback conditions (Arbel, Hong, Baker, & Holroyd, 2017; Hölting & Mecklinger, 2020). At the behavioral level, procedural learning tasks using delayed feedback seem to hamper visual categorization learning, but not when visual categorization is afforded based on declarative learning alone (Chandrasekaran, Yi, & Maddox, 2014; Maddox, Ashby, & Bohil, 2003; Maddox & David, 2005). These findings indicate that the nature of the training experience plays an important role in determining the neural processes and the underlying computational demands for successful learning. The different learning systems and neural processes engaged based on task features raise important issues in the study of neurodevelopmental disorders, and may be particularly relevant to the understanding and remediation of dyslexia, in which certain forms of learning are compromised.

1.4. The present study

The typical approach to studying the PDH in dyslexia was to investigate either declarative or procedural memory in isolation. Less attention has been paid to the interaction between multiple memory systems in dyslexia in a given learning situation. Most tasks harness a combination of learning and memory systems, therefore it is important to determine whether people with dyslexia are impaired in conditions that encourage mostly procedural-based memory involvement rather than in training conditions that favor declarative processing (Bogaerts, Siegelman, & Frost, 2021). It is also critical to determine whether dissociations between procedural and declarative functions can be observed in dyslexia. Investigating this question within a single task can add discriminant validity to the literature on the procedural learning deficit in developmental dyslexia. In addition, since learning impairment is unlikely to be an all-or-nothing condition, a critical goal is to delineate the boundaries and constraints of procedural learning in dyslexia and devise effective evidence-based remedies. Whether learning can be ameliorated in dyslexia remains largely uncharted territory. In particular, it is not clear whether learning in dyslexia can be amended by shifting the load from procedural memory systems to declarative memory mechanisms within a given learning situation. Although evidence suggests better learning of children with dyslexia in explicit than in implicit tasks (Vicari et al., 2003), it is not clear whether this is the result of differences in how a stimulus is processed or of a procedural learning dysfunction in dyslexia. Therefore, examining whether learning in dyslexia can be ameliorated within a single task under the same instructions can help clarify the role that multiple memory systems play in the etiology of dyslexia.

The present study explored these questions by assessing probabilistic learning and episodic memory formation simultaneously, within a single task, in young adults with developmental dyslexia. Feedback timing presentation was manipulated to assess how learning in dyslexia is affected by feedback timing presentation. To enable comparison between Foerde and Shohamy's (2011) study and the present study, and to adapt task difficulty to a population of young adults, an intermediate feedback delay was used in addition to a long delayed and immediate feedback conditions.

Imaging studies have shown that long delayed feedback can shift probabilistic learning to depend less on the striatum and rely more on the hippocampus (Foerde & Shohamy, 2011), and that this manipulation can be harnessed to resolve learning impairments in patient populations (Foerde, Braun, & Shohamy, 2012). Given that procedural, but not necessarily other learning systems, are disrupted in dyslexia (Nicolson & Fawcett, 2011; Ullman et al., 2020), it was predicted that probabilistic learning in participants with dyslexia will be impaired on immediate feedback trials but not on long delayed feedback trials, compared to neurotypicals. Furthermore, event-related potential (ERP) studies reported processing differences between immediate/intermediate vs. long delayed feedback conditions during probabilistic learning (Peterburs, Kobza, & Bellebaum, 2016; Weismüller & Bellebaum, 2016), therefore it was predicted that the performance of participants with dyslexia in the intermediate feedback trials would be similar to their performance in the immediate feedback trials, or in any case different from their performance in the long delayed feedback trials. Finally, based on the PDH, it was hypothesized that incidental episodic memory formation is preserved in individuals with dyslexia.

2. Methods

2.1. Participants

The sample included 50 university students: 25 with developmental dyslexia and 25 typical readers. All were native speakers of Hebrew, with no history of neurological disorders, psychiatric disorders. All the participants had normal or corrected-to-normal vision and normal hearing. The dyslexia group was recruited primarily through the Yael Learning Disabilities Center at the University of Haifa, Israel. The typical readers group was recruited by advertisements in universities and colleges and through social media. To be included in the dyslexia group, participants needed to have been diagnosed with developmental dyslexia by an authorized clinician. All candidates provided their psycho-educational or MATAL assessments to the experimenter before participating in the experiment. MATAL is a standardized, computer-based battery of tests for the diagnosis of learning disabilities in adults. The test was developed by the Israeli National Institute for Testing and the Israeli Council for Higher Education (Ben-Simon & Inbar-Weiss, 2012). To assess dyslexia, MATAL calculates performance on several tests, including vocal text reading, nonword reading, phonemic deletion, phoneme counting, rapid automatic naming, verbal fluency, and reading comprehension. For a full description of the MATAL test designed to assess dyslexia, including its psychometric properties, see Ben-Simon and Inbar-Weiss (2012). Participants who also had a formal diagnosis of attention deficit hyperactivity disorder (ADHD), assessed by a neurologist, or a specific language impairment, as evident from their clinical assessments, were excluded from the study. The absence of ADHD was also verified by a self-report questionnaire that participants completed based on DSM-5 criteria (American Psychiatric Association, 2013). A second inclusion criterion was a score of at least one standard deviation below the average of the local norm in tests of phonological decoding (non-word reading). Because there are no published standardized reading tests for adults in Hebrew, selection was

based on local norms collected from an independent sample of 191 readers (Weiss, Katzir, & Bitan, 2015), using similar criteria to those of other studies conducted on Hebrew readers with dyslexia (Gabay et al., 2019; Weiss et al., 2015; Weiss, Katzir, & Bitan, 2016). Scores of one standard deviation below the mean of the local norms were chosen, following the standard practice in the literature published in Hebrew (Brenzitz & Misra, 2003; Shany & Brenzitz, 2011). Based on this criterion, one participant with dyslexia was excluded from the sample. The control group included individuals who exhibited no difficulties in reading (e.g., were above the inclusion criteria of the dyslexia group on the nonword-reading test), and were at the same level of cognitive skills (assessed by the Similarities and Block Design subtests of the Wechsler intelligence test; Wechsler, 1997) as the dyslexia group. The Institutional Review Board of the University of Haifa approved the study, which was conducted in accordance with the Declaration of Helsinki, with written informed consent provided by all participants. Participants received a compensation of 120 NIS (approximately \$37) for participating in the study.

Participants underwent a series of cognitive tests to evaluate basic cognitive ability (assessed by the Similarities and Block Design subtests of the Wechsler intelligence test; Wechsler, 1997), verbal working memory, rapid automatized reading skills, and phonological processing. Details of these tasks are presented in Table 1. The results, shown in Table 2, indicate that the groups did not differ in age or cognitive abilities, but compared to the control group, the dyslexia group displayed a profile of reading disability compatible with the symptomatology of developmental dyslexia. This group differed significantly from the control group on both rate and accuracy measures of word reading and decoding skills. The dyslexia group demonstrated deficits also in the three key phonological domains: phonological processing (Spoonerism, phoneme segmentation, phoneme deletion), verbal working memory (digit span), and rapid naming (rapid automatized naming).

Table 1

Psychometric Tests.

The following tests were administered according to the test manual instructions:

1. *Block Design and Similarities Subtests.* Intelligence was assessed by means of two subtests of the Wechsler Intelligence test for adults (Wechsler, 1997). One was the non-verbal block design task, in which participants were required to rearrange blocks with different color patterns according to a stimulus presented to them on a card. The other was the verbal similarities subtest, in which participants were required to indicate what characteristic two words in a pair have in common (i.e., what do dog and cat have in common = both are animals).
2. *Digit Span Subtest.* verbal working memory was assessed with the Digit Span subtest from the Wechsler Intelligence test for adults (Wechsler, 1997). In this task, participants were required to recall the names of the digits presented auditorily in the order they appeared, with a maximum total raw score of 28. Task administration was discontinued after a failure to recall two trials with a similar length of digits. Test reliability coefficient was 0.9.
3. *Rapid Automatized Naming.* Naming skills were assessed with the Rapid Automatized Naming task (RAN) (Wolf & Denckla, 2005). The tasks require oral naming of rows of visually-presented exemplars drawn from a constant category (RAN colors, RAN categories, RAN numerals, and RAN letters). They require not only the retrieval of a familiar phonological code for each stimulus, but also coordination of phonological and visual (color) or orthographic (alphanumeric) information quickly.
4. The *One Minute Test of Words* (Shatil, 1995b) and the *One Minute Test of Non-words* (Shatil, 1995a) was used to assess the number of words and non-words accurately read aloud in one minute. The One Minute Test of Words contains 168 non-vowelized words of an equivalent level of difficulty, listed in columns. The One Minute Test of Non-words contains 86 increasingly difficult vowelized non-words, listed in seven columns. Both accuracy (number of correct words read per minute) and speed (number of items read per minute) were measured.
5. The *Phoneme Deletion Test* (Brenzitz & Misra, 2003), *Phoneme Segmentation Test* (Brenzitz & Misra, 2003), and *Spoonerism Test* (developed by Peleg & Ben-Dror) were used to assess phonological processing. The Phoneme Deletion Test contains 25 non-words. In this test, the experimenter read a word and a specific phoneme, and the participant was required to repeat the word without that phoneme. In the segmentation task, the experimenter read 16 non-words, and the participant was asked to segment the word into its basic phonological sounds as quickly as possible. In the Spoonerism Test, the participant was required to switch the first syllables of a word pair, then synthesize the segments to provide new words (for example, the word pair *brown sugar* becomes *srown bugar*). For all tests, both accuracy and the time participants needed to complete the task were measured.

Table 2

Psychometric results of the dyslexia and control groups.

Measurement	Dyslexia	Std. Deviation	Control	Std. Deviation	t value	p
Age (in years)	25.37	3.63	25.33	3.65	0.04	0.96
Decoding						
Oral words recognition accuracy	73.21	20.55	118.25	12.69	9.08	0.001
Oral words recognition speed	79.83	18.76	114.41	27.34	5.10	0.001
Oral non-words recognition accuracy	25.83	10.52	64.16	9.61	13.17	0.001
Oral non-words recognition speed	42.29	11.08	68.16	10.25	8.39	0.001
Naming skills						
Naming letters	25.95	4.21	21.87	2.81	-3.94	0.001
Naming objects	39.66	6.99	32.62	5.18	-3.96	0.001
Naming numbers	21.66	2.86	17.04	2.56	-5.89	0.001
Naming colors	31.51	6.72	28.25	6.07	-1.76	0.08
Phonological processing						
Phoneme segmentation (time)	137.29	50.49	70.62	16.54	-6.14	0.001
Phoneme segmentation (accuracy)	10.54	3.99	15.04	1.16	5.29	0.001
Phoneme deletion (time)	184.83	61.68	93.58	21.28	-6.85	0.001
Phoneme deletion (accuracy)	18.95	4.63	23.66	1.55	4.71	0.001
Spoonerism (time)	297.54	159.62	109.25	24.72	-5.71	0.001
Spoonerism (accuracy)	14.33	5.23	18.54	1.47	3.78	0.001
Verbal working memory						
Digit span ^a	9.91	2.20	12.25	2.80	-3.20	0.001
Intellectual ability						
Block design ^a	11.20	1.76	10.83	2.01	-0.68	0.49
Similarities ^a	13.08	3.29	12.95	3.04	-0.13	0.89

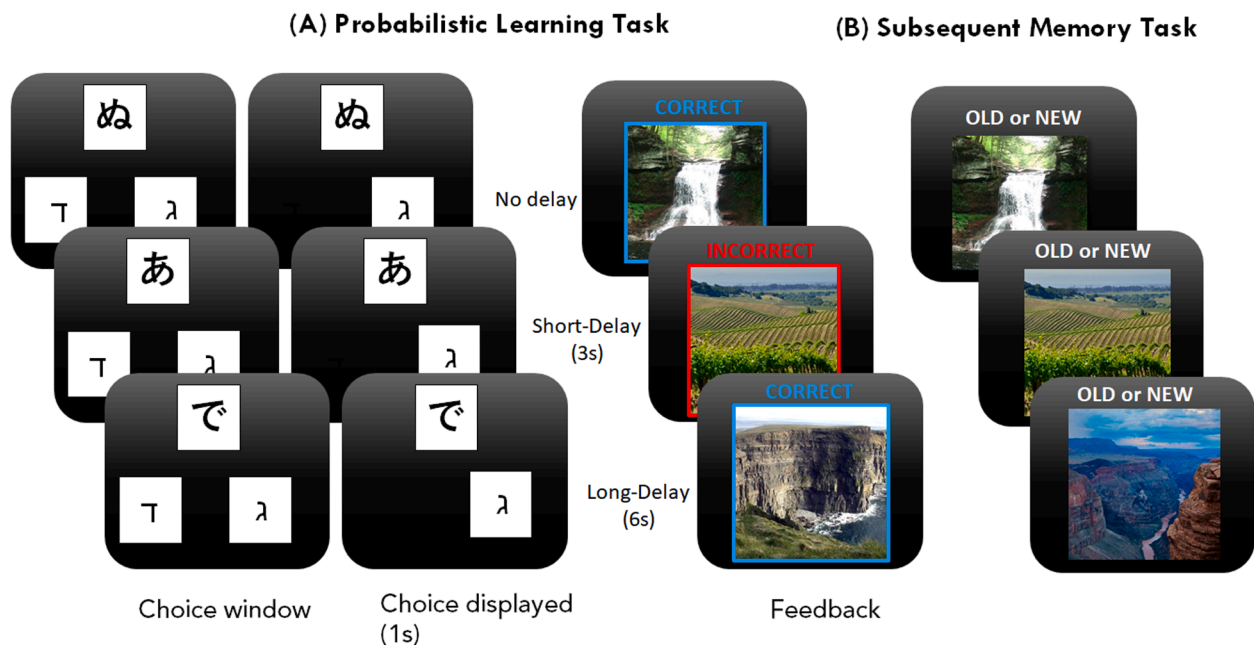
^a Standard scores; other scores are raw scores.

Fig. 1. Participants used trial-by-trial feedback to learn with which Hebrew letters (ט, λ) six different Hiragana characters were associated (learning phase, **A**). For one set of Hiragana characters feedback was presented immediately (0 s) after choice display. For another set of Hiragana characters, feedback was presented with an intermediate (3 s), or long (6 s) delay after choice display. After the learning phase ended, participants completed a probe task in which they continued to make predictions about associations between letters and characters, but they no longer received feedback, and the timing of all trial events was equal across trial types. Each Hiragana character was associated with one Hebrew letter in 80% of trials and with the other Hebrew letter in 20% of trials. Participant's episodic memory for feedback events was tested in a surprise subsequent memory phase (**B**).

2.2. Experimental design

The experiment consisted of two sessions. All sessions were conducted in a sound-attenuated booth in front of a 14-inch laptop monitor. Stimulus presentation and the recording of response time and accuracy were controlled by E-prime (Schneider, Eschman, & Zuccolotto, 2002). Participants filled out a background questionnaire at home and were invited to complete the linguistic and cognitive battery of tests in the first session. In the second session they completed probabilistic learning and episodic memory tasks.

2.2.1. Probabilistic learning task

Participants carried out a probabilistic learning task (see Fig. 1) similar to that used in previous studies (Ballan & Gabay, 2020; Foerde, Braun, et al., 2013; Foerde, Race, et al., 2013; Foerde & Shohamy, 2011; Gabay et al., 2018) and none of them had training with hiragana characters prior to task completion. The task included a training phase consisting of 120 trials (Fig. 1A), during which participants were presented with one of six different cues (Hiragana characters) and asked to predict with which of two outcomes (different Hebrew letters) the Hiragana character would be associated (Fig. 1A). None of the participants

was familiar with Japanese, therefore the cue stimuli had no associated meaning at the beginning of the task. The probabilities used were such that each Hiragana character predicted one of the two Hebrew letters yielded a rewarding outcome in 80% of trials and with the other in 20% of trials.

Following each response, feedback was provided after a fixed delay of 0 s (immediate feedback), 3 s (short delayed feedback; intermediate), or 6 s (long delayed feedback). The task was designed in such a way that each Hiragana character was associated with one of the delay durations, with two Hiragana characters assigned randomly to each delay. The assignment of cues (Hiragana characters) to outcomes (Hebrew letters) and conditions was counterbalanced across participants. Trial types for each feedback delay condition were interleaved throughout the training. Participants were given a maximum of three seconds to complete their response. After participants made their choice, a performance feedback display appeared in the form of the words “correct” or “incorrect,” along with an image of an outdoor scene in a colored frame (blue for correct and red for incorrect choices) presented on the screen for 1.5 s. The outdoor scenes were trial-unique to allow testing of later episodic memory for these feedback events. Outdoor images were taken from a public fMRI dataset (Chang et al., 2019).

After responding, participants were immediately shown their choice for 1 s, followed by the delay period (0, 3, or 6 s). The selected outcome and character were displayed throughout the delay to reduce the demand on working memory. Thus, the crucial manipulation was the interval between response and feedback. Because response times could vary across trials and participants, the overall trial length (character onset to feedback end) could also vary, but the time between response and feedback remained constant for each trial type. The behavioral measurement of performance in the task was based on the percentage of successful choices for each feedback delay condition (i.e., selecting letters that led to correct feedback for each cue) or on averaging the

response times of accurate trials. Participants completed 120 learning trials (four training blocks with 30 trials each) followed by a test phase (30 trials), where they were shown again the previously presented Hiragana characters and asked to repeat the task based on what they had learned. The testing phase was similar to the learning phase, but no feedback was provided.

2.3. Episodic memory task

Immediately after completing the probabilistic learning task, participants performed a surprise episodic memory task for the feedback images (outdoor scene) seen during the learning phase (Fig. 1B). All images shown during learning (targets) and an equal number of new images (foils) were tested. In each trial, a single image was presented and participants were instructed to determine whether the image was seen during learning (old) or not seen (new).

3. Results

3.1. Statistical analysis

Following previous research (Foerde & Shohamy, 2011), participants who did not reach accuracy above chance level in any of the feedback conditions during the test phase were excluded from the analysis. Based on this criterion, one control participant was excluded from the analyses. For the probabilistic category learning task, both accuracy (as determined by optimal choice - the degree to which participants selected the most likely outcome for each cue (Foerde & Shohamy, 2011) and response time measures were examined, because both have been shown to be influenced by feedback timing modulation (Gabay et al., 2018). Mixed ANOVA tests were used to examine the performance of the two groups in the learning phase and in the test

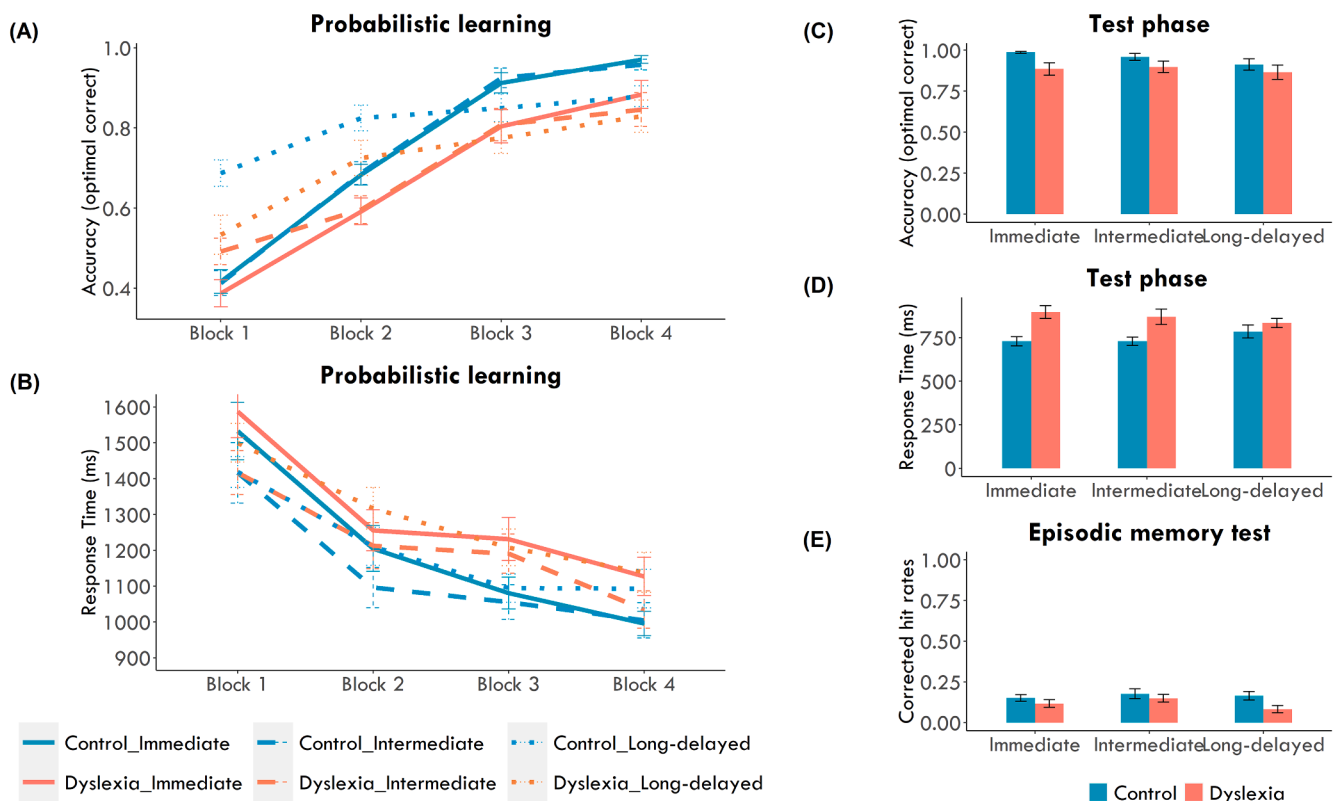


Fig. 2. Accuracy performance of the two groups during the learning phase (A) and test phase (C) across all feedback conditions. RT performance of the two groups during the learning phase (B) and test phase (D) across all feedback conditions. Memory for stimuli (scenes) at outcome phase by feedback condition and group (E). Means represent the proportion of high confidence hit responses (by condition) versus false alarms. Error bars represent standard error.

phase as a function of feedback timing. *A priori* planned comparisons were conducted with Bonferroni-corrected one-tailed *t*-tests. In the episodic memory task, the proportion of hits (recognizing previously seen images of outdoor scenes) associated with each feedback timing condition during learning and the proportion of false alarms (incorrectly identifying a new image as previously seen) were calculated, following the approach of Foerde and Shohamy (2011). The corrected hit rates were calculated by subtracting the proportion of false alarms from the proportion of hits and used them as the dependent measure. An ANOVA test was used to compare the performance of the two groups as a function of feedback timing condition, with Bonferroni correction for multiple comparisons. The Kolmogorov-Smirnov and the Levine tests were used to determine whether the distributions obeyed the assumptions of normality and homogeneity, respectively. Some of the variables had distributions that departed from normality and homogeneity assumptions. Therefore, theoretically important comparisons were also analyzed with non-parametric tests (one-tailed Mann-Whitney U-tests), with *p*-values Bonferroni-corrected for the number of multiple comparisons.

3.2. Probabilistic learning

3.2.1. Feedback-based learning across training-trial blocks

Accuracy analysis. A repeated measure ANOVA was conducted using group (dyslexia vs. control) as a between-subjects factor, feedback timing (immediate, intermediate, long delayed) and block (B1-B4) as a within-subject factor, and mean accuracy (optimal choices) as the dependent variable. Results are presented in Fig. 2A. The main effect of the group was significant, with the dyslexia group in general being less accurate than the control group, $F(1, 46) = 7.64, p = .008; \eta_p^2 = 0.14$. There was a main effect of block, indicating that participants improved at predicting the associated letters leading to correct outcomes across blocks, $F(3, 138) = 220.30, p = .001; \eta_p^2 = 0.82$. Further analysis using a linear contrast test revealed a significant linear trend, $F(1, 46) = 388.54, p = 0.001; \eta_p^2 = 0.89$, (with accuracy improving parametrically with training). The main effect of feedback was also significant, $F(2, 92) = 7.81, p = .001; \eta_p^2 = 0.14$, arising from the observation that participants were more accurate in the long delayed feedback condition than in the average of the immediate and intermediate feedback conditions, $F(1, 46) = 10.96, p = .001; \eta_p^2 = 0.18$. No performance difference was observed between the immediate and intermediate feedback conditions, $F < 1$ (with a *p* value less than the Bonferroni-corrected significant value of .025 (0.05/2) considered to be significant). The interaction of block by feedback was also significant, $F(6, 276) = 15.87, p = .001; \eta_p^2 = 0.25$. Further analysis demonstrated that the linear trend was stronger for the average accuracy of the immediate and intermediate feedback conditions than for the average accuracy of the long delayed feedback condition, $F(1, 46) = 58.54, p = .001; \eta_p^2 = 0.55$, but did not differ significantly across the immediate and intermediate feedback conditions, $F(1, 46) = 3.17, p = .08; \eta_p^2 = 0.05$ (with a *p* value less than the Bonferroni-corrected significant value of 0.025 (0.05/2) considered to be significant). Importantly, the triple interaction of group, block, and feedback was significant, $F(6, 276) = 3.361, p = .003; \eta_p^2 = 0.06$. *A priori* planned comparisons with Bonferroni-corrected one-tailed *t*-tests were conducted, to examine the differences between the two groups during early (first block) and later phases of learning (average of last three blocks of training) (with a *p* value less than the Bonferroni-corrected significant value of .008 (0.05/6) considered to be significant). The analyses revealed that in the first block of training there was no performance difference in the immediate feedback condition between the dyslexia and the control groups, $t(1, 46) = 0.65, p = .51$, Cohen's *d* = 0.19, whereas in the average of the last three blocks of training, group differences were apparent, with the dyslexia group performing significantly less accurately than the control group, $t(1, 46) = 2.97, p = .002$; Cohen's *d* = 0.92 (one-tailed). For the intermediate feedback condition, although no significant group differences were

observed in the first training block, $t(1, 46) = -1.75, p = .08$; Cohen's *d* = 0.51, the dyslexia group performed less accurately than the control group late in learning, $t(1, 46) = 2.90, p = 0.0025$; Cohen's *d* = 0.79 (one-tailed). In the delayed feedback condition, the performance difference between the two groups in the first training block did not survive Bonferroni correction, $t(1, 46) = 2.60, p = .012$, Cohen's *d* = 0.73 and no significant group differences were observed late in learning, $t(1, 46) = 1.69, p = .09$; Cohen's *d* = 0.54.

In addition to the ANOVA analyses, non-parametric Mann-Whitney U-tests were conducted to examine the differences between the two groups during early (first block) and later phases of learning (average of last three blocks of training) to address the possibility that variables departed from the assumptions of normality and homogeneity (with a *p* value less than the Bonferroni-corrected significant value of .008 (0.05/6) considered to be significant). This analysis revealed similar results to those of the ANOVA with regard to the immediate and long delayed feedback conditions. In particular, for the immediate feedback condition, no significant differences were observed during the first block of training (Mann-Whitney U test, $Z = 0.46, p = .64$), whereas the performance of the dyslexia group late in learning was significantly inferior to that of the control group (Mann-Whitney U test, one-tailed, $Z = 2.41, p = .007$). For the intermediate feedback condition, there were no group differences in the first block of training (Mann-Whitney U test, $Z = -1.80, p = .07$), and group differences late in learning did not survive Bonferroni correction for multiple comparisons (Mann-Whitney U-tests, one-tailed, $Z = 2.27, p = .011$). For the delayed feedback condition, the performance difference between the two groups during the first block of training did not survive Bonferroni correction for multiple comparisons (Mann-Whitney U-tests, $Z = 2.24, p = .02$) and there were no significant group differences late in learning (Mann-Whitney U test, $Z = 1.47, p = .14$).

Response time (RT) analysis. A repeated measure ANOVA was conducted using group (dyslexia vs. control) as a between-subjects factor, feedback timing (immediate, intermediate, long delayed) and block (B1-B4) as within-subject factors, and mean response times of accurate trials¹ as the dependent variable. Results are presented in Fig. 2B. The main effect of block was significant, $F(3, 132) = 65.57, p = .001, \eta_p^2 = 0.59$, indicating that participants from both groups improved their response times in predicting the associated letters leading to correct outcomes across trials. Further linear contrast tests revealed a significant linear trend, where as training progressed, RTs diminished, $F(1, 46) = 105.07, p = .001; \eta_p^2 = 0.70$. The main effect of feedback was also significant, $F(2, 92) = 3.58, p = .03; \eta_p^2 = 0.07$, with participants' response times being faster in the intermediate feedback condition than in the average response times of the delayed long and immediate feedback conditions, $F(1, 46) = 5.54, p = .02; \eta_p^2 = 0.11$, and there were no differences in RT between the long delayed and immediate feedback conditions, $F < 1$ (with a *p* value less than the Bonferroni-corrected significant value of .025 (0.05/2) considered to be significant). No other main effects or interactions with group were significant.

3.2.2. Test phase

Accuracy analysis. A repeated measure ANOVA was conducted with group (dyslexia vs. control) as a between-subjects factor, feedback timing (immediate, intermediate, long delayed) as a within-subject factor, and test phase accuracy as the dependent variable. Results are presented in Fig. 2C. None of the effects were significant.

RT analysis. A repeated measure ANOVA was conducted using group (dyslexia vs. control) as a between-subjects factor, feedback

¹ Two participants with dyslexia had missing values in one of the conditions in the first block of the probabilistic learning task (because they did not have any correct trials for that condition), which were replaced by the average reaction times of the dyslexia group for that condition. Also, excluding these participants from the analysis did not influence the results.

timing (immediate, intermediate, long delayed) as a within-subject factor, and test phase mean response times of accurate trials as the dependent variable. Results are presented in Fig. 2D. The main effect of group was significant, with the dyslexia group being significantly slower than the control group, $F(1, 46) = 9.22, p = .01, \eta_p^2 = 0.16$. There was a significant group by feedback interaction, $F(2, 92) = 3.61, p = .03, \eta_p^2 = 0.07$. Planned comparisons revealed that the response times of the two groups did not differ significantly in the long delayed feedback condition, $t(1, 46) = -1.04, p = .30$; Cohen's $d = 0.30$, but the dyslexia group performed significantly slower than the control group in the immediate, $t(1, 46) = -3.67, p = .003$; Cohen's $d = 0.51$ (one-tailed), and intermediate feedback conditions, $t(1, 46) = -2.80, p = .0035$; Cohen's $d = 1.06$ (one-tailed) (with a p value less than the Bonferroni-corrected significant value of .016 (0.05/3) considered to be significant).

In addition to the ANOVA analyses, non-parametric Mann-Whitney U -tests were conducted to address the possibility that variables departed from the assumptions of normality and homogeneity (with a p value less than the Bonferroni-corrected significant value of 0.0166 (0.05/3) considered to be significant). The results corroborated those of the ANOVA. There were no significant group differences in response times in the delayed feedback condition, (Mann-Whitney U test, $Z = -1.63, p = .10$), but the dyslexia group performed significantly slower than the control group in the immediate (Mann-Whitney U test, one-tailed, $Z = -3.24, p = .0005$) and the intermediate feedback conditions (Mann-Whitney U test, one-tailed, $Z = -2.52, p = .005$).

3.3. Episodic memory for feedback events

A repeated measure ANOVA was conducted using group (dyslexia vs. control) as a between-subjects factor, feedback timing (immediate, intermediate, long delayed) as a within-subject factor, and mean corrected hit responses (hit rate minus false alarm) during the episodic test phase as the dependent variable. Results are presented in Fig. 2E. None of the main effects or interactions with group were significant.

4. Discussion

The present study explored declarative and procedural learning and memory in adults with developmental dyslexia in a single task. Incremental learning of cue-outcome associations was examined, with an additional embedded subsequent surprise recognition memory test of episodic information. Feedback timing presentation was manipulated, building on previous research indicating differential engagement of multiple memory systems following the manipulation of feedback timing (Foerde & Shohamy, 2011; Lighthall, Pearson, Huettel, & Cabeza, 2018). Results of the probabilistic learning task suggest that learning was disrupted in the dyslexia group relative to the control group in the immediate feedback conditions, but not when feedback on choices was provided after a long delay. In particular, evidence of accuracy measures during the learning phase indicated that the learning of both groups improved as training progressed, but members of the dyslexia group were significantly less capable of improving their performance in the immediate feedback than in the long delay feedback trials. Examination of the learning phase in the immediate feedback trials revealed that there was no difference between the two groups during the first block of training, but the dyslexia group was significantly less accurate than the control group late in learning, indicating diminished capacity to learn in the immediate feedback condition. This was in contrast to results in the long delayed feedback trials, in which no group differences were observed late in learning. Findings of the test phase, where feedback was removed, corroborate the performance during the learning phase. In the test phase, the dyslexia group responded significantly slower than the control group in the immediate feedback condition but not in trials in which feedback during the learning phase was presented after a long delay. In the test phase, a significant interaction of group by feedback type was observed for RT

but not for accuracy measures, possibly owing to a ceiling effect in response accuracy. During the test phase, both groups showed high accuracy rates. Accuracy measures in the current high-functioning sample of neurotypicals and individuals with dyslexia may not have been sensitive enough to detect group differences in the test phase, which are more easily observed using RT measures.

The dyslexia group also differed from the control group in the intermediate feedback condition, at least in response times during the test phase. Previous neuroimaging studies revealed modulation of multiple memory systems by feedback timing presentation when comparing immediate and long delayed feedback conditions (Foerde & Shohamy, 2011; Lighthall et al., 2018). In both studies, which used the same task employed here, striatal engagement was found when feedback on choices was delivered immediately (no delay), and hippocampal engagement after a long (6-s) feedback delay in healthy young adults. But the feedback-related negativity (FNR) sensitivity to the timing of feedback measured in electrophysiological studies points to processing differences between immediate or short delay vs. long delay feedback in probabilistic learning (Peterburs et al., 2016; Weismüller & Bellebaum, 2016). Therefore, the conjecture that the performance of the dyslexia group in the intermediate feedback condition was likely to be similar to its performance in the immediate feedback condition was confirmed. In an electrophysiological study, Peterburs et al. (2016) examined a probabilistic learning task with a three-level manipulation of feedback timing, similar to the present study. Difference wave-based analyses showed that amplitudes decreased linearly with increasing feedback delay. Peterburs et al. (2016) speculated that the gradually reduced difference wave signal may reflect a gradual shift away from processing in frontostriatal circuits toward medial temporal involvement. The present behavioral findings revealed a similar pattern of performance for the immediate and intermediate feedback trials in the dyslexia group (in response times during the test phase). Future electrophysiological studies, therefore, could shed light on the possible differences between deferred feedback timing manipulations on reinforcement learning in dyslexia.

Observation of the impaired learning of individuals with dyslexia in the immediate feedback condition reproduces earlier findings in which striatal-mediated implicit learning (Howard et al., 2006) and reinforcement learning abilities (Gabay, Vakil, et al., 2015; Massarwe et al., 2021) were reduced in people with dyslexia. It extends previous research by showing that learning in general is not impaired in dyslexia, and introducing a temporal gap between rewards and choices has the potential to compensate for impaired reinforcement learning in dyslexia. A similar dissociation between immediate vs. delayed reinforcement-based learning was observed in populations that suffer from basal ganglia alterations (Foerde, Braun, et al., 2013; Foerde & Shohamy, 2011; Gabay et al., 2018), but not in amnesic patients, who learned better under immediate feedback conditions but not in conditions in which feedback was delayed (Foerde, Race, et al., 2013).

Results from the episodic memory test revealed no group differences. These findings contradict earlier ones, which demonstrated that episodic knowledge is compromised in children with dyslexia (Menghini et al., 2010). At the same time, previous findings also pointed to the possibility that children with dyslexia were not impaired in episodic tasks that did not involve verbal materials (Hedenius et al., 2013). The episodic memory task used in the present study did not contain verbal components. Therefore, the finding that episodic memory abilities were preserved in dyslexia in the present study is consistent with the assumption that episodic knowledge that does not involve verbal knowledge is spared in people with dyslexia (Hedenius et al., 2013). Taken together with the intact learning of the dyslexia group in the delayed feedback condition, the observation of intact performance in the episodic memory task is consistent with previous findings showing that hippocampal mediated implicit learning is intact in adults with dyslexia (Howard et al., 2006).

The present study supports the hypothesis that procedural and

declarative memory processing can be dissociated in dyslexia. In the same task, it has been shown that incremental learning of cue-outcome associations is impaired in participants with dyslexia relative to neurotypicals in the immediate feedback conditions, but not when there is a long delay between choices and feedback. Neuroimaging studies suggest that immediate-feedback conditions recruit the striatum, whereas delayed-feedback conditions engage the hippocampus (Foerde & Shohamy, 2011), with patients with basal ganglia damage showing deterioration in learning in immediate feedback conditions but not in delayed feedback conditions (Foerde, Braun, et al., 2013). Therefore, the finding that the performance of the dyslexia group was impaired in the immediate but not in the long delayed feedback conditions is consistent with the PDH (Fawcett & Nicolson, 2019; Nicolson & Fawcett, 2011; Ullman et al., 2020). Furthermore, the observation that within the same task learning under delayed feedback conditions and episodic memory were preserved in those with dyslexia adds discriminative validity to the PDH. Rather than having general learning impairments, individuals with dyslexia are impaired in conditions that encourage mostly procedural memory processing but not in those that involve hippocampal memory-dependent capacities.

It is still unknown whether procedural learning dysfunction in dyslexia leads to greater dependence on the declarative system, or even to enhanced functioning of that system (Ullman & Pullman, 2015). Previous research presented mixed findings with regard to non-verbal declarative memory processing in children with dyslexia, with some studies reporting intact (Li et al., 2009; Messbauer & de Jong, 2003) or even enhanced performance of individuals with dyslexia (Hedenius et al., 2013). In the present study, the dyslexia group showed no performance advantage in the delayed feedback condition or in the episodic memory task over neurotypicals. Therefore, it appears that no declarative enhancement was observed. Neuroimaging investigation could shed light on the role that the declarative memory system plays in dyslexia. Special populations learn in different ways. Therefore, brain imaging studies of the learning process in dyslexia may produce insights that are not achievable from behavior alone. In neurotypical participants, neural engagement during probabilistic learning is modulated by feedback timing, with greater activity observed in the striatum for immediate feedback and superior hippocampal engagement in delayed feedback conditions (Foerde & Shohamy, 2011; Lighthall et al., 2018). Based on the present behavioral findings, one could expect reduced striatal activation during immediate feedback events in individuals with dyslexia relative to controls, and greater or similar activation in medial temporal lobe regions for delayed feedback in individuals with dyslexia relative to neurotypical participants. Such investigation could help determine whether there is greater declarative dependence or even declarative enhancement in individuals with dyslexia.

The present behavioral investigation does suggest that probabilistic learning could be restored in dyslexia by manipulations designed to shift the load from procedural to declarative memory processing. In particular, learning under the long delayed feedback condition was intact in the dyslexia group compared to the control group. Therefore, the declarative learning and memory systems seem to play a compensatory role in dyslexia even when the same information is being learned. Some training interventions are designed to help people with dyslexia benefit from explicit teaching of phonological rules (Alexander & Slinger-Constant, 2004; Ehri, Nunes, Stahl, & Willows, 2001), an approach that encourages reliance on the declarative rather than the procedural memory system. The current findings suggest that such approaches can benefit the learning abilities of people with dyslexia. Future research is required to examine whether such benefits can be extended to the learning of language-related skills as well. Many language structures can be described as probabilistic in nature, making them well suited for learning by the procedural memory system, which may lead to concerns regarding the ability to learn these structures under declarative memory deployment (Krishnan, Watkins, & Bishop, 2016; Kuppuraj, Rao, & Bishop, 2016). The current findings suggest that manipulations that

encourage declarative engagement can enable intact learning in individuals with dyslexia even when probabilistic information is being learned. Future studies are required in order to examine whether the current manipulation can benefit learning in dyslexia using tasks that are closely related to language acquisition, such as artificial grammar learning (Opitz, Ferdinand, & Mecklinger, 2011) or the acquisition of speech sound categories (Chandrasekaran et al., 2014), in which feedback timing seems to modulate learning performance as well. It is also important to consider whether compensation in adults with dyslexia observed in the present study extends also to children with dyslexia. In the current study, the participants with dyslexia were young adults who presumably had a longer time to practice compensatory declarative mechanisms, and their declarative memory system was likely to be more fully developed than that of younger individuals with dyslexia (Finn et al., 2016). Therefore, further studies are needed to determine whether training conditions designed to shift the load from midbrain/striatal systems to declarative memory mechanisms have the potential to compensate for impaired learning in children with dyslexia.

The procedural learning impairments of the dyslexia group observed in the present study are difficult to explain by a strictly phonologically-based account. The PDH, however, can provide a mechanistic understanding of both procedural learning impairments observed in the present and previous studies and phonological deficits that characterize those with dyslexia. In particular, the learning of speech categories represents the learning of procedural knowledge that cannot be explicitly verbalized, which requires integration across multiple acoustic dimensions (Gabay, Dick, et al., 2015; Holt & Lotto, 2010), and is believed to take place via striatal reinforcement learning mechanisms (Ashby & Ennis, 2006; Chandrasekaran et al., 2014; Gabay, Dick, et al., 2015; Lim, Fiez, & Holt, 2019; Yi, Maddox, Mumford, & Chandrasekaran, 2016). Gabay and Holt (2015) found that high-functioning young adult university students with a childhood diagnosis of dyslexia were impaired in incidental auditory category learning relative to age- and intelligence-matched neurotypicals, and that greater impairments were associated with slower phonological processing. These findings point to a possible link between a procedural learning deficits and phonological impairments. Future research needs to determine whether the procedural learning deficit is casually related to or independently co-occurs with the ubiquitous phonological deficits observed in individuals with dyslexia.

In the present study, a dissociation was observed between procedural and declarative learning in dyslexia in the same task. Young adults with dyslexia exhibited preserved nonverbal episodic memory abilities. They were impaired in probabilistic learning in immediate feedback trials, but exhibited intact learning in long-delayed feedback trials. The findings imply that shifting the load from procedural to declarative processing can enable intact learning in dyslexia, and therefore, that training interventions designed to help people with dyslexia should focus on encouraging declarative memory engagement. Recent intriguing findings suggest the possibility that even when the declarative learning system controls behavior, the procedural learning system still learns (Crossley & Ashby, 2015). This calls into question whether the intact declarative learning system can be used to bootstrap the malfunctioning procedural learning system in dyslexia. Further studies are needed to investigate this question, but the present findings highlight the importance of encouraging declarative training conditions in individuals with developmental dyslexia.

CRediT authorship contribution statement

Yafit Gabay: Conceptualization, Methodology, Software, Formal analysis, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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