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Dyslexia and the failure to form a perceptual anchor

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In a large subgroup of dyslexic individuals (D-LDs), reading difficulties are part of a broader learning and language disability. Recent studies indicate that D-LDs perform poorly in many psychoacoustic tasks compared with individuals with normal reading ability. We found that D-LDs perform as well as normal readers in speech perception in noise and in a difficult tone comparison task. However, their performance did not improve when these same tasks were performed with a smaller stimulus set. In contrast to normal readers, they did not benefit from stimulus-specific repetitions, suggesting that they have difficulties forming perceptual anchors. These findings are inconsistent with previously suggested static models of dyslexia. Instead, we propose that D-LDs' core deficit is a general difficulty in dynamically constructing stimulus-specific predictions, deriving from deficient stimulus-specific adaptation mechanisms. This hypothesis provides a direct link between D-LDs' high-level difficulties and mechanisms at the level of specific neuronal circuits.

Developmental dyslexia was first documented more than 100 years ago. Yet the essence of the difficulties that impede reading acquisition in 5%–10% of the population is still heatedly debated[1]. It is now largely agreed that the majority of individuals for whom reading remains a struggle have phonological impairments rather than difficulties in visual identification of letter sequences[2]. Thus, most dyslexics have difficulties in manipulating and accurately repeating sequences of speech sounds. Still, it is not clear whether these phonological deficits are the core difficulties or are manifestations of a broader fundamental impairment[3,4].

It has been suggested that dyslexics' phonological deficits stem from a broader perceptual deficit[5]. Indeed, many, albeit not all, dyslexics show poor psychoacoustic performance[5–12], particularly in frequency discrimination[8,12–14]. Dyslexic individuals with poor psychoacoustic abilities typically show a broad pattern of learning deficits that span mathematics and language skills[7,8,12,15]; we use the acronym 'D-LD' to denote these dyslexic individuals with additional learning difficulties. Nevertheless, their general reasoning abilities are well within the normal range, as evidenced by their adequate nonverbal reasoning scores (block design test)[16].

D-LDs' poor psychoacoustic ability has been amply replicated[6–15], but this finding has not resolved the debate on the nature of their core deficit. Many researchers argue that because D-LDs have a broad pattern of cognitive difficulties and because the ability to perform perceptual discriminations is correlated with general cognitive ability[17,18], D-LDs' psychoacoustic impairments may be related to their cognitive, rather than to their reading, difficulties[19,20]. Indeed, the tasks that pose the greatest difficulties to D-LDs are those that are demanding in terms of working memory load[21].

We now sought to determine whether the core deficit underlying D-LDs' poor psychoacoustic performance with simple tones (Study I) and with speech sounds (Study II) reflects a perceptual (low-level) or a cognitive (high-level) difficulty. To our surprise, D-LDs performed as well as controls in a difficult comparison task requiring both perceptual and cognitive skills. However, they were unable to benefit from the use of a small, consistent stimulus set, suggesting that they may have difficulties in forming perceptual anchors. This finding suggests that their major deficit may be in the dynamics of switching from computation-based perception (stimulus comparison) to memory retrieval. We propose that D-LDs are at both a perceptual and a cognitive disadvantage in conditions that allow the general population to replace online operations with retrieval of stored representations but do not allow D-LDs to do so. Such conditions are abundant in academic environments.

RESULTS

Frequency discrimination and speech perception (Study I)

We designed two seemingly similar frequency discrimination tasks. In both tasks, participants were asked which of two sequentially presented tones had the higher pitch. However, in one condition ('standard'), a standard tone (1,000 Hz) was present in each trial (in either the first or second interval), and the other tone was always higher. In the other condition ('no-standard'), there was no standard tone. The two conditions were thus indistinguishable at the single-trial level, but in the standard condition, listeners could gradually form a perceptual anchor based on the repeated standard, which was always the lower tone. Therefore, after several trials with the standard condition, inter-stimulus comparison was no longer strictly required; subjects could associate stimuli with 'high' if they did not match the anchor. In the no-standard condition, however, successful performance required listeners to actively compare the two tones presented in each trial; that is, to manipulate the representations of the two tones using high-level

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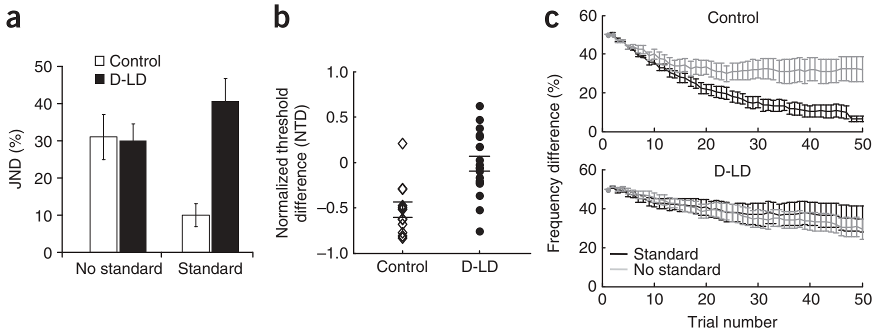

Figure 1 Study I: frequency discrimination JNDs with and without stimulus repetition across trials among D-LDs and control individuals. The effects of discrimination condition (standard versus no standard) differed significantly between the groups. (**a**) Average thresholds show that D-LDs had significantly higher JNDs in the standard condition. (**b**) Single-subject data of the normalized difference in threshold (NTD) between the standard and the no-standard conditions. NTD = (standard – no standard)/(standard + no standard). Filled circles: D-LDs; open diamonds: control individuals. (**c**) Assessment protocol for control individuals (top) and D-LDs (bottom) in the two procedures shows a gradual effect of using a consistent reference for control individuals but not for D-LDs. Error bars denote 1 s.e.m.

'executive' operations of working memory (the differences between these tasks has been studied in the tactile domain[22]). Such comparisons are more difficult and do not yield optimal perceptual resolution, yet they allow us to handle *ad hoc* conditions when there is no effective reference on which to anchor our decisions.

We expected that D-LDs' performance would be impaired in both conditions and that if they were indeed impaired in stimulus manipulation (an executive function, commonly thought to be problematic for D-LDs[23,24]), the no-standard condition would be particularly challenging. As expected, D-LDs' performance on the standard task was very poor (**Fig. 1a**). However, their performance on the difficult manipulation task, no-standard, did not differ from that of their class peers with normal reading abilities (**Fig. 1a**). In fact, D-LDs' performance did not differ between the standard and no-standard conditions (**Fig. 1a**). The group results are a good reflection of individual performance as measured by the normalized threshold difference between performance on the standard and no-standard (**Fig. 1b**). All but one control subject had lower thresholds when there was no standard tone, with a group average of –0.52 ± 0.29, whereas D-LDs' differences are scattered around 0, with an average of –0.02 ± 0.35 ($t = 4.2$; $P < 0.001$). A significant group × condition interaction term (repeated measures analysis of variance (ANOVA): $F_{1,29(\text{condition})} = 6.15$, $P = 0.019$; $F_{1,29(\text{group})} = 4.47$, $P = 0.043$; $F_{1,29(\text{group} \times \text{condition})} = 14.28$, $P = 0.001$) confirmed that use of the standard tone had a different impact on the performance of the two groups, inducing an advantage only for control individuals. Further distinction between the two groups was apparent when examining the trial-by-trial dynamics of the assessment protocols by group for the two conditions (**Fig. 1c**). In control individuals, a clear dissociation in perception was evident by the 20th trial. In D-LDs, the graphs were nearly overlapping throughout the assessments, and both were similar to that of control individuals' no-standard condition. These results suggest that D-LDs' tone perception and comparison abilities, as measured by the no-standard condition, are adequate. However, they seem unable to use across-trial repetitions to bypass the need for actual comparisons and do not sharpen their discrimination when a potential anchor is provided.

Performance of D-LDs in the standard condition, but not in the no-standard condition, correlated with their verbal working memory scores (digit span task, **Table 1**; digit-backward subtest, **Fig. 2**), suggesting that their well-documented memory impairments are related to difficulties that the standard condition poses to them. Control individuals' pattern of correlations showed the reverse trend. Their verbal working memory scores correlated with their performance on the no-standard condition (**Table 1**), which was the more difficult, performance-limiting condition for them. Phonological skills were also significantly correlated with the standard condition, though only when calculated for the whole group ($r = –0.53$, $P = 0.001$). None of the auditory scores were correlated with spatial reasoning abilities in either population (block design, **Table 1**), indicating that performance on these tasks was not limited by general reasoning abilities. We should note that the frequency thresholds that

Table 1 Correlations (*r* values) between measures of frequency discrimination and measures of verbal memory (digit span) and spatial reasoning (block-design) among D-LDs, control individuals and the entire group

	D-LD (n = 19)	Control (n = 12)	All (n = 31)
Standard			
Digit span	–0.65**	–0.34	–0.71***
Block design	–0.16	–0.03	–0.26
No-standard			
Digit span	–0.16	–0.61*	–0.30
Block design	–0.32	0.01	–0.21
NTD			
Digit span	–0.69***	0.06	–0.63***
Block design	0.11	0.20	–0.07

Frequency discrimination tests include the standard and no-standard conditions and NTD, their normalized threshold difference. Standard scores of digit span and block design were used.
$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P \leq 0.001$.

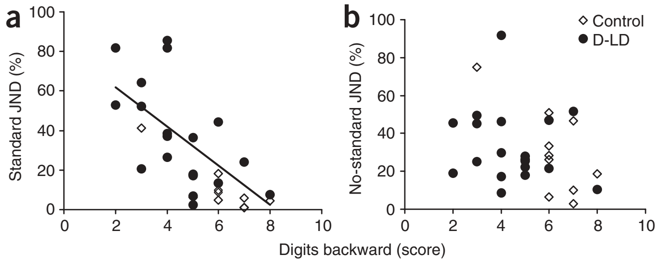

Figure 2 Correlation between frequency discrimination thresholds and working memory scores (digits backward test). (**a**) With a standard reference (standard), we found a significant correlation within each of the groups and for the entire group ($r = 0.73$, $P < 0.0001$). Note that although the regression line was drawn for D-LDs, control individuals' data points reside along this line. (**b**) Without a reference (no standard), we did not find any significant correlation among D-LDs or within the group as a whole. This correlation was significant among control individuals ($r = 0.65$, $P = 0.02$). Filled circles: D-LDs; open diamonds, control individuals.

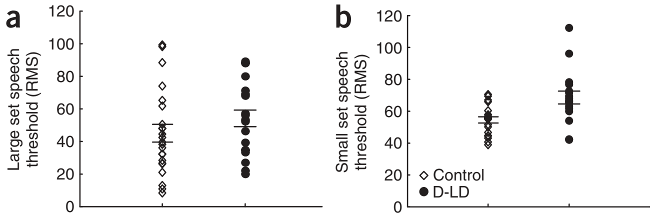

Figure 3 Speech perception thresholds of D-LDs and control individuals for large and small stimulus sets. (**a**) Individual thresholds for the large set in noise (Study I, D-LDs and Control-2 individuals). Thresholds of controls and D-LDs do not significantly differ. (**b**) Individual thresholds for the small set (Study II, D-LDs and Control-2 individuals) in noise. Most D-LDs perform worse than most control individuals.

we measured, even those of the control participants, are high compared with thresholds (~1%) typically reported for at least moderately trained adults. This higher range of thresholds is common for naive teenagers tested with brief stimuli with only several dozen trials. The specific choice of test paradigm also affects the measured thresholds.

In addition to frequency thresholds, Study I included measurements of thresholds for speech perception in noise. We were surprised to find no significant difference between threshold levels of D-LDs and control individuals ($t = 1.7$, $P = 0.1$). We also administered the same test of speech perception to an additional control group (Control-2) from a regular school, as part of a broader evaluation battery. Again, we did not find any significant intergroup difference. When we compared the distribution of performance of D-LD participants with that of their regular-school counterparts, it was apparent that the control individuals' scores were scattered and did not significantly differ from those of the D-LDs (**Fig. 3a**). Overall, there was no difference between the average thresholds measured for the three groups ($F_{2,49} = 1.44$, $P = 0.25$).

Having found no D-LD deficit in the speech perception in noise task compared with either control group, we reasoned that the lack of intergroup difference might be consistent with the lack of intergroup difference in the no-standard frequency discrimination condition and might stem from the large set of stimuli (40 pseudowords) used in this evaluation. Under these conditions, which contained almost no repetitions, anchoring was not a possibility for any group.

Speech perception in quiet and in noise (Study II)

We asked D-LDs and Control-2 participants of Study I to return for another assessment, with two speech perception experiments. In the first experiment, we repeated the adaptive assessment of speech perception applied in Study I but now used a small stimulus set (a subset of ten pseudo-words chosen from the larger set). Subjects were asked to repeat the pseudoword that they vaguely heard, and the experimenter pressed the 'right' or 'wrong' key so that the intensity of the next pseudoword would adequately adapt to the subject's performance. We measured thresholds (minimal intensity levels needed to attain 80% correct single-word repetitions) first in quiet and then shortly thereafter using the same limited vocabulary superimposed on speech noise. In contrast to the results with the previously administered large-set study (Study I, **Fig. 3a**), D-LDs' thresholds under small-set conditions (**Fig. 3b**) were significantly higher than those of control individuals, in both quiet and noise (repeated measures ANOVA: $F_{1,37(\text{group})} = 12.38$, $P = 0.001$; $F_{1,37(\text{condition})} = 808.40$, $P < 0.0001$; $F_{1,37(\text{interaction})} = 7.70$, $P = 0.01$; a *post hoc* intergroup Tukey test was significant ($P < 0.05$) for both the quiet and noise conditions).

At the end of the adaptive assessment of speech perception, we asked participants whether they could recall the vocabulary used (five pairs of pseudowords, with only one phoneme difference between pseudowords in each pair; for example, /barul/ and /parul/). Typically, neither D-LDs nor control individuals could reconstruct the whole set, despite its small size. In order to assess participants' implicit ability to use repetitions, we analyzed their pattern of errors. Control individuals erred on 18% ± 3% (mean ± s.d.) of the 200 pseudowords (20 repetitions of each of the ten words) and D-LDs on 20% ± 4% (note that error rates were kept constant by adapting stimulus intensity). We classified errors as 'no-response' (1.8% ± 1.4% for control individuals; 2.4% ± 1.5% for D-LDs), 'within-set' (that is, a wrong word that belonged to the small vocabulary used in the assessment; 11.2 ± 3.0% for control individuals and 7.5 ± 2.3% for D-LDs) or 'non-set' (that is, a wrong word that was not part of the vocabulary; 4.6% ± 4.3% for control individuals and 9.8% ± 4.6% for D-LDs). We reasoned that if control individuals, but not D-LDs, implicitly retain traces of the repeated words, then control individuals will have a lower fraction of errors with non-set guesses, whereas D-LDs' choice of words may be more random. Indeed, the overall proportion of incorrect responses that were taken from outside the stimulus set was significantly smaller in control individuals ($t = 4.1$, $P = 0.0002$, two-tailed t-test, for combined quiet and noise).

Analysis of the dynamics of the error pattern showed that control individuals had a significantly larger proportion of 'within-set' errors compared with D-LDs, starting from the third block of 20 trials (at which time each pseudoword had been presented approximately four times) measured in quiet (**Fig. 4**; repeated measures ANOVA: $F_{1,35(\text{group})} = 7.41$, $P = 0.01$; $F_{2,70(\text{block})} = 3.46$, $P = 0.04$; $F_{2,70(\text{interaction})} = 1.05$ (not significant (n.s.))). In noise, measured immediately afterwards, the group difference was apparent from the first block and was constant throughout the assessment (repeated measures ANOVA: $F_{1,32(\text{group})} = 13.76$, $P = 0.001$; $F_{4,128(\text{block})} = 0.17$, n.s.; $F_{4,128(\text{interaction})} = 0.07$, n.s.). Thus, whereas control individuals implicitly learned the stimulus set, no such learning was evident among D-LDs.

In addition to the small-set adaptive study, we administered a nonadaptive, large-set evaluation, using the same vocabulary as in the adaptive large-set study (Study I). Participants were asked to repeat the pseudowords presented in a pseudorandom sequence of quiet and noisy backgrounds and with various list lengths (one to six pseudowords). Both groups were nearly perfect in repeating single

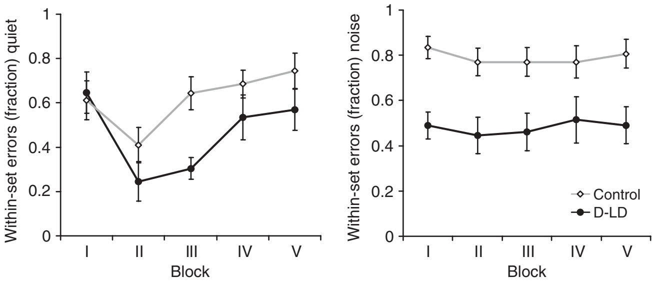

Figure 4 Fraction of 'within-set' speech perception errors as a function of block number. Group averages of the proportion of incorrect responses that were words from the small experimental vocabulary, in quiet (left), administered first, and in noise (right). Whereas in the first block there was no intergroup difference, toward the end of the assessment, the majority of errors made by control individuals were words from the stimulus set, whereas D-LDs were equally likely to use a within-set or a non-set word. Error bars denote 1 s.e.m.

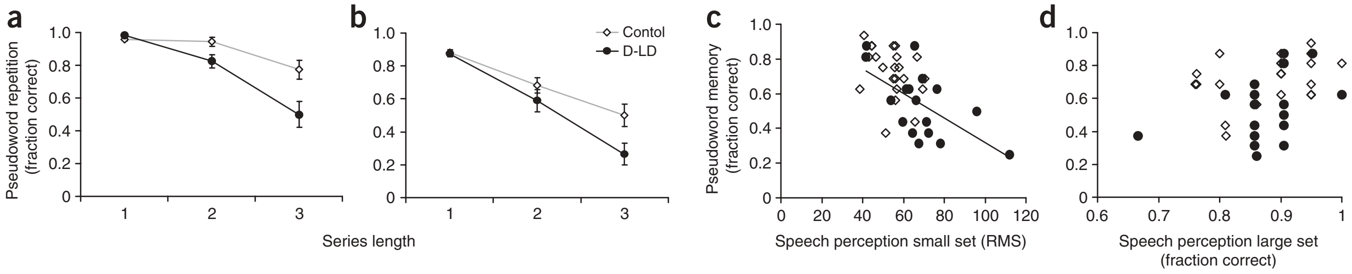

Figure 5 Perception and memory measured by pseudoword list repetition. (**a**,**b**) Fraction of correct repetition of pseudoword lists for list lengths of one, two and three words using a large stimulus set, in quiet, suprathreshold conditions (**a**) and in noise (**b**). All conditions (quiet, noise, list lengths of 1–6) were administered in a mixed order. Performance for single words does not significantly differ between groups, whereas performance for longer sequences is significantly poorer in the D-LD group. (**c**,**d**) Correlation between pseudoword memory scores (averaged over list lengths of two and three and over the quiet and noise conditions) and speech perception in noise as measured with a small stimulus set using the adaptive protocol (**c**) and with the large stimulus set using the nonadaptive protocol as part of the same assessment (**d**). The regression line in **c** shows the significant correlation for D-LDs in the small set. Control individuals' data points reside along an almost identical regression line. Filled circles: D-LDs; open diamonds: control individuals. Error bars denote 1 s.e.m.

pseudowords presented in quiet, at a comfortable intensity level (**Fig. 5a**). Both groups had errors in single-word repetitions in the noise condition (**Fig. 5b**; an average of ~87% correct for each group). However, in line with the previous results of speech perception with a large set, there was no intergroup difference for single-word repetitions (**Fig. 5a**,**b**), with even a mild, marginally significant, advantage for D-LDs in the quiet condition. With lists of two and three words, D-LDs showed the expected, well-known characteristic of impaired pseudoword repetition, demonstrating their impaired phonological memory (longer lists were not analyzed, because both groups scored very poorly). There was a clear advantage for control individuals in both the quiet and noise conditions (repeated measures ANOVA: quiet condition: $F_{1,37(\text{group})} = 7.99$, $P = 0.008$; $F_{2,74(\text{list length})} = 39.75$, $P < 0.0001$; $F_{2,74(\text{interaction})} = 7.37$, $P = 0.004$; noise condition: $F_{1,37(\text{group})} = 4.96$, $P = 0.03$; $F_{2,74(\text{list length})} = 59.58$, $P < 0.0001$; $F_{2,74(\text{interaction})} = 3.18$, $P = 0.05$).

In order to assess whether D-LDs' difficulties in phonological memory were related to their speech perception, we plotted an average memory score for each individual (fraction of correct list repetition averaged across lists of two and three pseudowords in quiet and in noise, combined) versus her single-word perception in noise with small and large stimulus sets (**Fig. 5c** and **d**, respectively). Among D-LDs, memory scores were not correlated with single-word perception in the large set ($r = 0.38$, $P = 0.13$; **Fig. 5d**) even though single words and word sequences were measured as part of the same evaluation. However, memory scores were significantly correlated with single-word perception as measured in the adaptive procedure with the small set ($r = -0.62$ and $P = 0.008$, Pearson correlation; $r = -0.56$ and $P = 0.02$, Spearman correlation, insensitive to outliers; **Fig. 5c**). These findings suggest that a common deficit underlies D-LDs' poorer speech perception (with a small vocabulary) and their difficulties with phonological memory.

DISCUSSION

We have found that D-LDs' difficulties both in tone and in speech perception are demonstrated only when a limited set of stimuli is used repetitively. Under these conditions, perception of normal readers sharpens compared with their perception with large stimulus sets, whereas the perception of D-LDs does not. The degree of this failure to form perceptual anchors is correlated with the degree of their difficulties in phonological and working memory tasks, suggesting that D-LDs' attentional[11] and working memory[25] impairments may result from the same core deficit. We suggest that this behavioral difficulty stems from impaired stimulus-specific adaptation processes. Taken together with other studies (for example, ref, 21), our data suggest that it is the resilience of these adaptation processes in the presence of intervening stimuli that is impaired among D-LDs, rather than the initiation of fast adaptation between consecutive stimuli. We note that despite the fact that all our participants were female, we do not believe that this deficit is gender specific because, to the best of our knowledge, there have been no reports of gender-specific perceptual deficits in dyslexia. However, further study is needed to confirm this generalization.

We selected D-LDs for the current study, rather than recruiting dyslexics in general, because previous findings had indicated that D-LDs have greater psychoacoustic difficulties (for example, see refs. 8,13). Determining whether dyslexics with only mild difficulties in auditory tasks also have a similar anchor-memory impairment requires further study. In the following discussion of the literature, we focus on studies of dyslexic groups with cognitive characteristics that are similar to those of our D-LD participants.

The 'stimulus-specific adaptation hypothesis' suggested by the combination of our results and previous studies accounts not only for our own findings but also for a range of other puzzling and seemingly inconsistent results and hypotheses regarding the underlying perceptual deficits. Prominent recent suggestions for the identity of these deficits include a deficit in perceiving briefly presented stimuli[5], a deficit in detecting the temporal structure of stimulus amplitude modulation[9], a lower resilience to external noise[26] or a generally noisier auditory system[27]. We now propose that these various manifestations are all the outcome of deficient stimulus-specific adaptation and the concomitant difficulty in acquiring a perceptual anchor. In each case, the assessment method used relied on such an anchor, either by using a small set of stimuli[5], by relying on the formation of a reference for comparison with subsequent stimuli[9] or on tuning to a specific repeated stimulus to improve its extraction from noise[26]. The difficulty in forming an anchor results in a less efficient perceptual system[7,27], which requires a comparatively larger signal-to-noise ratio when limited stimulus sets are used. This hypothesis further explains the results of another study, which systematically measured auditory performance among D-LDs and found deficits in several tasks, and yet could not isolate a specific, confined auditory mechanism that is selectively impaired[7].

The most commonly reported psychoacoustic deficit in dyslexics is poor frequency discrimination[6,10,12,14,28]. This finding, though consistent, is hard to reconcile with any of the previously suggested hypotheses. The adaptation hypothesis suggests that in this case, too, impairments are related to the assessment procedure. The most prevalent method for assessing frequency discrimination is based on comparisons with a standard tone that is repeated in every trial[8,12,29] and is typically used as an anchor providing improved thresholds (similar to the standard condition we used here). Thus, listeners improve their performance by forming a stimulus trace of the repeated reference and replacing actual comparisons with stimulus-response mapping. This method has dominated the field for technical reasons, as early studies found that when a standard is present, listeners attain lower thresholds[30,31]. Under these conditions (that is, in the presence of a repeated standard), our hypothesis is that D-LDs' perception will be impaired.

Furthermore, we would not expect impaired performance by D-LDs, compared with normal readers, when the formation of a reference is not feasible for any participant (for example, in roving conditions such as our no-standard test) or when its formation is particularly easy, as with consecutive presentations of the reference stimulus. Indeed, a previous study has reported that dyslexics' difficulties with frequency discrimination depend on the number of consecutive repetitions of the standard[14]. Their frequency discrimination was adequate when several consecutive repetitions of the standard were presented before the target, but it was deficient when only a single exemplar of the standard was given on every trial. In previous studies in our laboratory[21], we have found that D-LDs' two-tone same or different frequency discrimination was adequate, but when they needed to compare the tone with a nonconsecutive reference (three-tone same or different), their performance was significantly impaired (see also ref. 12).

Notably, D-LDs' intensity discrimination has been consistently reported to be adequate[6,12]. The discrepancy between adequate intensity discrimination and poor frequency discrimination may stem from the difference in the mechanisms underlying adaptation to these two sound features. Unlike frequency discrimination, intensity discrimination is largely disrupted by intervening masking stimuli[32] and is abruptly degraded with interstimulus intervals larger than 500 ms[33]. Thus, adaptation processes for intensity do not seem to normally produce robust references that are resilient to intervening stimuli. Hence, intervening stimuli may disturb intensity comparisons to the same degree in both controls and D-LDs.

Stimulus-specific adaptation processes can be further assessed by mismatch negativity responses (MMN). The MMN is an automatic response produced by the auditory cortex, with a frontal contribution, when an oddball (rare) stimulus is presented within a sequence of identical stimuli[34]. Detecting the oddball requires formation of a stimulus-specific memory trace for the repeated standard. Several studies have assessed MMN responses to both frequency and phonetic deviants in dyslexic individuals[35,36,37] and among children with a familial risk of dyslexia[38]. Typically, they report a diminished discriminative response to the oddball tone in dyslexics, supporting the stimulus-specific adaptation[39] hypothesis. However, abnormal MMN does not dissociate between impaired long-term representations and impaired dynamics of adaptation, as both must be intact to allow the formation of a normal MMN response. A recent study compared dyslexics' deficits using a standard MMN protocol and a protocol with an irrelevant variability in the properties of the standard[40]. Dyslexics' deficits were significantly greater with the increased variability, in line with the hypothesis that their formation of an internal reference (anchor) is more sensitive to stimulus interference.

Stimulus-specific adaptation processes characterize not only the auditory[41] but also the visual[42] modality. Recent findings suggest that dyslexics' adaptation processes in the visual domain may also be impaired. Dyslexics were found to have deficits in implicit learning, but not in explicit learning, of visual categorization[43], as well as difficulties in identifying simple stimuli when these were masked by external visual noise[26]. Both sets of findings were interpreted as indicating that dyslexics have difficulties in implicit formation of stimulus-specific templates. Other studies showing that dyslexics' visual difficulties are not specific to stimulus characteristics but rather to task conditions that require retain-and-compare operations[44,45] are also in line with the stimulus-specific adaptation hypothesis. A genetic deficit affecting these adaptation processes could be the cause of the pan-sensory impairment.

D-LDs suffer not only from a multisensory impairment but also from broader cognitive difficulties, apparent particularly in tasks requiring adequate working memory abilities[8]. As a deficit in mechanisms underlying stimulus-specific adaptation probably limits retention of recently presented information across intervening stimuli, it may also underlie these deficits and impede D-LD's achievements despite their adequate reasoning abilities. Given that adaptation mechanisms can also be studied at the level of single neurons in sensory cortices[46,47], the adaptation hypothesis links high-level skill effects with the dynamics of networks of single-neuron responses.

METHODS

Participants, Study I. Thirty-one seventh-grade female students (ages 13.1 ± 0.4) participated in the study. They were all selected from a private school for students with learning disabilities. None of the students had a history of hearing problems, and all had I.Q. scores in the normal range (>80; a requirement for admission to the school). The parents of all participating students in Study I and Study II gave their consent after receiving letters with information regarding the study. The study was approved by the ethics committee of the Department of Psychology at the Hebrew University of Jerusalem.

Classification of D-LDs and education-matched controls. The students were classified into two groups: those with reading disabilities (the dyslexic group) and those without reading disability (Control-1). Classification was based on two measures: accuracy of reading pseudowords and phonological awareness (see task descriptions below), based on current definitions stressing the significance of phonological deficits to the diagnosis of dyslexia (for example, see refs. 1,48). Based on these measures, we calculated a combined phonological

Table 2 Reading-related, language and cognitive scores (mean ± s.d.)

	D-LD ($n = 19$)	Control 1 ($n = 12$)	Control 2 ($n = 22$)
Non-word reading			
Accuracy (% correct)	56 ± 14	91 ± 7***	87 ± 10***
Rate (words/min)	34 ± 11	48 ± 11*	53 ± 15***
Phonological awareness			
Spoonerism (% correct)	52 ± 22	83 ± 16***	86 ± 15***
Word segmentation[a]	4.7 ± 3	7.9 ± 2*	7.5 ± 2.5***
Spoken language			
Analyze inflected forms	54 ± 7	59 ± 4*	60 ± 3***
Production (machine test)	37 ± 13	45 ± 6	54 ± 6***
Cognitive ability			
Digit span[b]	7.9 ± 1.9	10.2 ± 1.6*	10.5 ± 2.9**
Block design[b]	9.6 ± 2.8	11.1 ± 2	13 ± 1.7***
Vocabulary[b]	7.3 ± 1.9	7.6 ± 1.8	11 ± 2.2***

Control groups 1 and 2 did not significantly differ from each other on any of the measures except for block design ($P = 0.048$), vocabulary ($P < 0.001$) and the machine test ($P = 0.029$).

[a] Scores. [b] Standard scores. $^{*}P < 0.05$; $^{**}P < 0.01$ and $^{***}P \leq 0.001$ in a Bonferroni-corrected *t*-test between D-LDs and each of the control groups.

score with respect to students of the same age with normal learning ability. Students whose phonological score was lower than the average previously measured in the general population[21] by 1.5 s.d. or more were classified as dyslexic (D-LD, $n = 19$, age: 13.3 ± 0.4). The others, whose phonological abilities were normal (that is, within 1.5 s.d. of the above measure), were classified as controls (group Control-1; $n = 12$, age: 12.9 ± 0.5). In Study I, we measured standard reading, phonological, language and cognitive scores of all participants (D-LDs and groups Control-1 and Control-2, described below) (**Table 2**). For a full description of the cognitive and reading tests, see ref. 21; for a description of the language tests, see ref. 49. These characteristics show that although group Control-1 was composed of students in the same school (that is, a school for individuals with learning difficulties), their general performance did not differ from that of the general population, except that they had a poorer vocabulary, a measure known to be related to education level. In line with the formal assessments, the informal evaluation by their teachers did not distinguish them from their peers in regular schools. We thus concluded that their mild academic difficulties were related to some educational disadvantage rather than to an inherent learning disability. As some educational disadvantage is probably shared by both groups, these individuals form an education-matched control group for D-LDs. Furthermore, in previous studies, we established that their performance on standard psychoacoustic procedures, including protocols with standard tones used in this study (see below), is also adequate[21].

Study II. Participants of Study I were asked to participate in another 2-h testing session conducted in the lab a year later, and 17 of the 19 D-LD individuals agreed. As only a few of the education-matched peers (Control-1) agreed to make the trip to the laboratory, a group of 22 female students from a regular school was recruited to serve as controls (Control-2). This school has a similar student population (including many of the siblings of the D-LD study). This group had already participated in a study we conducted several months earlier, during which (among other evaluations) their cognitive profile was assessed (**Table 2**) and a speech perception protocol was administered (**Fig. 3a**). When Study II was conducted, D-LDs were 14.3 ± 0.5 and individuals in group Control-2 were 13.8 ± 0.3 years old.

Auditory frequency discrimination (Study I). All stimuli were presented binaurally through Sennheiser HD-265 linear headphones using a TDT System III signal generator (Tucker Davis Technologies) controlled by in-house software in a quiet room in the school. Tone intensity was 65 dB.

Two conditions of frequency discrimination, using a two-interval, two-alternative forced choice (2AFC) procedure were used. The frequency of the test (higher) tone was changed in a two-down/one-up staircase procedure converging on 71% correct (with step size decreasing every four reversals from 40 to 25 to 5 Hz). In one condition ('standard'), the frequency of the fixed reference (non-test) tone was constant in all trials (1,000 Hz). In the other condition ('no-standard'), there was no fixed reference. Instead, the lower tone was randomly selected every trial from the interval of 1,000–1,400 Hz. The higher tone was then determined based on the appropriate frequency difference for the current trial based on the subject's performance. The two conditions were identical in all other aspects: participants were asked to indicate which of the two tones in a trial was higher, and a pleasant visual feedback was provided for correct responses. Testing continued for 70 trials or 16 reversals (changes in the direction of the frequency difference between successive trials). Discrimination thresholds were determined as the mean of the frequency differences in the last seven reversals. One assessment was carried out in each condition. Tone duration was 50 ms, initial frequency difference was 500 Hz and interstimulus interval (ISI) was 950 ms.

Before actual testing on any of the conditions, participants were given a practice block of 15 trials with a 1,000-Hz difference between the two tones to familiarize them with the task. They had to score at least 80% correct on the practice block for testing to begin and were given two opportunities to reach this criterion. All participants in the current study reached this criterion.

Speech perception with a large stimulus set, adaptive protocol (Study I). Stimuli were disyllabic pseudowords (for example, /di-len/) designed to resemble Hebrew sound structure and word morphology. Two instances of each pseudoword were recorded in a sound-attenuated room by a female native Hebrew speaker. Root mean square amplitudes of these stimuli were then equated, and the length of each stimulus was set to 0.8 s using the Praat stretching algorithm (P. Boersma and D. Weenik; see http://www.praat.org).

Forty different disyllabic pseudowords were used in this assessment. In each trial, a single word was presented on a background of an 83 dB sound pressure level (SPL) masking noise[49], and subjects were asked to repeat it. Subjects named the word, and the experimenter wrote down the word and pressed the 'right' or 'wrong' response key to allow administration of the staircase procedure. Feedback was given in the form of a happy or sad cartoon face, respectively. The intensity of the pseudowords was adapted in a three-down/one-up staircase procedure (converging on ∼80% correct), and the noise level remained fixed. Each assessment terminated after 85 trials or 15 reversals. Identification threshold (JND) was taken as the mean of the intensities in the last ten reversals. Data from this phase are described in ref. 49 and were used here both as a pilot study and as a comparison for the small-set condition.

Measurements of frequency discrimination and speech perception in Study I were conducted in a quiet room at school in two separate sessions, respectively. Cognitive and reading abilities (detailed in **Table 2**; test details and norms are described in http://micro5.mscc.huji.ac.il/~ahissar/db.html under 'Hebrew Reading Norms') were also measured in these sessions.

Speech perception with a small stimulus set, adaptive protocol (Study II). Based on the large-set data and further pilot studies, we chose a set of ten pseudowords (composed of five minimal contrast pairs, such as /barul/ and /parul/) from the larger 40-word vocabulary. Subjects were familiarized with the stimuli by hearing all the words in the set twice at 45 dB-SPL, a level at which subjects were able to correctly repeat 100% of the stimuli. Thereafter, we determined the thresholds for perception of the pseudowords in quiet and in noise. In an assessment, subjects heard 100 trials of the pseudoword stimuli (stimuli were randomly selected on each trial from the set of ten pseudowords). Task administration proceeded as in Study I. The noise level remained fixed. Feedback was given as a sad or happy cartoon face, and after every trial, the word was presented again, at 45 dB-SPL, in quiet.

This assessment procedure was applied twice: first in a quiet background (with initial level of the speech stimulus at 45 dB-SPL) and then, after a short break, in the presence of a 60 dB SPL masking noise (initial stimulus level 56 dB SPL). The noise was a standard noise designed for use in audiological examinations of speech perception (ICRA speech noise[50]). Identification thresholds (JND) for speech perception in quiet and in noise were calculated as the average level in the last five reversals in the staircase procedure.

Speech perception with a large-set, nonadaptive protocol (Study II). Speech stimuli were played using the same system described above. Stimuli (pseudowords and noise) were the same as in the large stimulus set of Study I (except for two pseudowords that differed). Assessments were composed of 82 trials: 21 single words in quiet, 21 single words in noise and four repetitions of lists with each length from two to six words in quiet and in noise. These stimuli were presented in a pseudorandom order (speech token level was constant in quiet and noise).

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AUTHOR CONTRIBUTIONS

M.A. supervised the project and wrote the manuscript; Y.L. conducted Study II, statistical analyses and proofreading; H.P.-K. co-administered Study I and designed the nonadaptive speech perception test and K.B. designed, administered and analyzed the frequency discrimination tests.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

1. Demonet, J.F., Taylor, M.J. & Chaix, Y. Developmental dyslexia. *Lancet* **363**, 1451–1460 (2004).
2. Shovmann, M.M. & Ahissar, M. Isolating the impact of visual perception on dyslexics' reading ability. *Vision Res.* **46**, 3514–3525 (2006).
3. Ramus, F. Neurobiology of dyslexia: a reinterpretation of the data. *Trends Neurosci.* **27**, 720–726 (2004).
4. Wright, B.A. & Zecker, S.G. Learning problems, delayed development, and puberty. *Proc. Natl. Acad. Sci. USA* **101**, 9942–9946 (2004).
5. Tallal, P. Auditory temporal perception, phonics, and reading disabilities in children. *Brain Lang.* **9**, 182–198 (1980).
6. Ahissar, M., Protopapas, A., Reid, M. & Merzenich, M.M. Auditory processing parallels reading abilities in adults. *Proc. Natl. Acad. Sci. USA* **97**, 6832–6837 (2000).
7. Amitay, S., Ahissar, M. & Nelken, I. Auditory processing deficits in reading disabled adults. *J. Assoc. Res. Otolaryngol.* **3**, 302–320 (2002).
8. Banai, K. & Ahissar, M. Poor frequency discrimination probes dyslexics with particularly impaired working memory. *Audiol. Neurootol.* **9**, 328–340 (2004).
9. Goswami, U. *et al.* Amplitude envelope onsets and developmental dyslexia: a new hypothesis. *Proc. Natl. Acad. Sci. USA* **99**, 10911–10916 (2002).
10. McAnally, K.I. & Stein, J.F. Auditory temporal coding in dyslexia. *Proc. Biol. Sci.* **263**, 961–965 (1996).
11. Hari, R. & Renvall, H. Impaired processing of rapid stimulus sequences in dyslexia. *Trends Cogn. Sci.* **5**, 525–532 (2001).
12. Mengler, E.D., Hogben, J.H., Michie, P. & Bishop, D.V. Poor frequency discrimination is related to oral language disorder in children: a psychoacoustic study. *Dyslexia* **11**, 155–173 (2005).
13. Ben-Yehudah, G., Banai, K. & Ahissar, M. Patterns of deficit in auditory temporal processing among dyslexic adults. *Neuroreport* **15**, 627–631 (2004).
14. France, S.J. *et al.* Auditory frequency discrimination in adult developmental dyslexics. *Percept. Psychophys.* **64**, 169–179 (2002).
15. Heath, S.M., Hogben, J.H. & Clark, C.D. Auditory temporal processing in disabled readers with and without oral language delay. *J. Child Psychol. Psychiatry* **40**, 637–647 (1999).
16. Wechsler, D. *Wechsler Adult Intelligence Scale (WAIS-III) Administration and Scoring Manual* (The Psychological Corporation, San Antonio, Texas, 1997).
17. Raz, N., Willerman, L. & Yama, M. On sense and senses: intelligence and auditory information processing. *Pers. Individ. Dif.* **8**, 201–210 (1987).
18. Deary, I.J., Bell, P.J., Bell, A.J., Campbell, M.L. & Fazal, N.D. Sensory discrimination and intelligence: testing Spearman's other hypothesis. *Am. J. Psychol.* **117**, 1–18 (2004).
19. Goswami, U. Why theories about developmental dyslexia require developmental designs. *Trends Cogn. Sci.* **7**, 534–540 (2003).
20. Hulslander, J. *et al.* Sensory processing, reading, IQ, and attention. *J. Exp. Child Psychol.* **88**, 274–295 (2004).
21. Banai, K. & Ahissar, M. Auditory processing deficits in dyslexia: task or stimulus related? *Cereb. Cortex.* **16**, 1718–1728 (2006).
22. Romo, R. & Salinas, E. Flutter discrimination: neural codes, perception, memory and decision making. *Nat. Rev. Neurosci.* **4**, 203–218 (2003).
23. Brosnan, M. *et al.* Executive functioning in adults and children with developmental dyslexia. *Neuropsychologia* **40**, 2144–2155 (2002).
24. Helland, T. & Asbjornsen, A. Executive functions in dyslexia. *Child Neuropsychol* **6**, 37–48 (2000).
25. Swanson, H.L. Working memory in learning disability subgroups. *J. Exp. Child Psychol.* **56**, 87–114 (1993).
26. Sperling, A.J., Lu, Z.L., Manis, F.R. & Seidenberg, M.S. Deficits in perceptual noise exclusion in developmental dyslexia. *Nat. Neurosci.* **8**, 862–863 (2005).
27. Hartley, D.E. & Moore, D.R. Auditory processing efficiency deficits in children with developmental language impairments. *J. Acoust. Soc. Am.* **112**, 2962–2966 (2002).
28. McArthur, G.M. & Bishop, D.V.M. Frequency discrimination deficits in people with specific language impairment: reliability, validity, and linguistic correlates. *J. Speech Lang. Hear. Res.* **47**, 527–541 (2004).
29. Halliday, L.F. & Bishop, D.V. Frequency discrimination and literacy skills in children with mild to moderate sensorineural hearing loss. *J. Speech Lang. Hear. Res.* **48**, 1187–1203 (2005).
30. Harris, J. Discrimination of pitch: suggestions toward method and procedure. *Am. J. Psychol.* **61**, 309–322 (1948).
31. König, E. Effect of time on pitch discrimination thresholds under several psychophysical procedures; Comparison with intensity discrimination thresholds. *J. Acoust. Soc. Am.* **29**, 606 (1957).
32. Mori, S. & Ward, L.M. Intensity and frequency resolution: masking of absolute identification and fixed and roving discrimination. *J. Acoust. Soc. Am.* **91**, 246–255 (1992).
33. Clement, S., Demany, L. & Semal, C. Memory for pitch versus memory for loudness. *J. Acoust. Soc. Am.* **106**, 2805–2811 (1999).
34. Näätänen, R. *Attention and Brain Function* (L. Erlbaum, Hillsdale, New Jersey, 1992).
35. Baldeweg, T., Richardson, A., Watkins, S., Foale, C. & Gruzelier, J. Impaired auditory frequency discrimination in dyslexia detected with mismatch evoked potentials. *Ann. Neurol.* **45**, 495–503 (1999).
36. Renvall, H. & Hari, R. Diminished auditory mismatch fields in dyslexic adults. *Ann. Neurol.* **53**, 551–557 (2003).
37. Banai, K., Nicol, T., Zecker, S.G. & Kraus, N. Brainstem timing: implications for cortical processing and literacy. *J. Neurosci.* **25**, 9850–9857 (2005).
38. Maurer, U., Bucker, K., Brem, S. & Brandeis, D. Altered responses to tone and phoneme mismatch in kindergarteners at familial dyslexia risk. *Neuroreport,* **14**, 2245–2250 (2003).
39. Haenschel, C., Vernon, D.J., Dwivedi, P., Gruzelier, J.H. & Baldeweg, T. Event-related brain potential correlates of human auditory sensory memory-trace formation. *J. Neurosci.* **25**, 10494–10501 (2005).
40. Kujala, T., Lovio, R., Lepistö, T., Laasonen, M. & Näätänen, R. Evaluation of multi-attribute auditory discrimination in dyslexia with the mismatch negativity. *Clin. Neurophysiol.* **117**, 885–893 (2006).
41. Baldeweg, T. Repetition effects to sounds: evidence for predictive coding in the auditory system. *Trends Cogn. Sci.* **10**, 93–94 (2006).
42. Grill-Spector, K., Henson, R. & Martin, A. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* **10**, 14–23 (2006).
43. Sperling, A.J., Lu, Z.L. & Manis, F.R. Slower implicit categorical learning in adult poor readers. *Ann. Dyslexia* **54**, 281–303 (2004).
44. Ben-Yehudah, G., Sackett, E., Malchi-Ginzberg, L. & Ahissar, M. Impaired temporal contrast sensitivity in dyslexics is specific to retain-and-compare paradigms. *Brain,* **124**, 1381–1395 (2001).
45. Ben-Yehudah, G. & Ahissar, M. Sequential spatial frequency discrimination is consistently impaired among adult dyslexics. *Vision Res.* **44**, 1047–1063 (2004).
46. Ulanovsky, N., Las, L. & Nelken, I. Processing of low-probability sounds by cortical neurons. *Nat. Neurosci.* **6**, 391–398 (2003).
47. Ulanovsky, N., Las, L., Farkas, D. & Nelken, I. Multiple time scales of adaptation in auditory cortex neurons. *J. Neurosci.* **24**, 10440–10453 (2004).
48. Lyon, G.R. Toward a definition of dyslexia. *Ann. Dyslexia* **45**, 3–27 (1995).
49. Putter-Katz, H., Banai, K. & Ahissar, M. Speech perception in noise among learning disabled teenagers. in *Symposium on Plasticity of the Central Auditory System and Processing of Complex Acoustic Signals* (eds. Syka, J. & Merzenich, M.M.) 251–257 (Springer, New York, 2005).
50. Dreschler, W.A., Verschuure, H., Ludvigsen, C. & Westermann, S. ICRA noises: artificial noise signals with speech-like spectral and temporal properties for hearing instrument assessment. International Collegium for Rehabilitative Audiology. *Audiology* **40**, 148–157 (2001).