

## Title: **Shorter neural adaptation to sounds accounts for dyslexics' abnormal perceptual and reading dynamics**

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### 1 **Abstract**

2 Dyslexia is a prevalent reading disability whose underlying mechanisms are still disputed. We  
3 studied the neural mechanisms underlying dyslexia using a simple frequency-discrimination  
4 task. Though participants were asked to compare the 2-tones in each trial, implicit memory of  
5 previous trials affected their responses. We hypothesized that implicit memory decays faster  
6 among dyslexics. We tested this by increasing the temporal intervals between consecutive  
7 trials, and measuring the behavioral impact and ERP responses from the auditory cortex.  
8 Dyslexics showed a faster decay of implicit memory effects on both measures, with similar  
9 time constants. Finally, faster decay also characterized dyslexics' benefits in oral reading rate.  
10 It decreased faster as a function of the time interval from the previous reading of the same non-  
11 word. We propose that dyslexics' shorter neural adaptation paradoxically accounts for their  
12 longer reading times, since it induces noisier and less reliable predictions for both simple and  
13 complex stimuli.

14

15

## 16 **Introduction**

17 Dyslexics are diagnosed on the basis of their persistent difficulties in acquiring peer-level  
18 reading skills despite adequate education. Their general reasoning skills are within the normal  
19 range (or above), but they consistently show difficulties in some language related skills such as  
20 verbal working memory (e.g. Torgeson and Goldman, 1977), and phonological manipulations  
21 (which typically also load on short term memory; e.g. Landerl et al., 1997). Dyslexics also often  
22 have higher thresholds in simple perceptual discrimination tasks (McAnally and Stein, 1996;  
23 Witton et al., 1998; Hämäläinen et al., 2013), particularly when administered with serial  
24 presentations (Ben-Yehudah and Ahissar, 2004; discussed in Ramus and Ahissar, 2012). In most  
25 of these protocols participants can be more successful by taking into account the statistics of  
26 previous stimuli (Ahissar et al., 2006; Oganian and Ahissar, 2012).

27 The putative causes of dyslexics' difficulties on simple serial tasks have been studied in a series  
28 of works using 2-tone frequency discrimination. Ahissar et al. (2006) measured the impact of  
29 sound regularities on dyslexics' performance. They assessed a well-documented observation  
30 (Harris, 1948), that listeners use a repeated reference tone as an "anchor" and improve their  
31 performance compared with a no-reference protocol. Dyslexics' benefit from this repetition was  
32 smaller than good readers'. A similar deficit was found in dyslexics benefit from repetition of  
33 speech sounds. This led to the hypothesis that dyslexics have a deficit in using sound stimuli as  
34 perceptual anchors for the formation of sound predictions (Ahissar et al., 2006; Ahissar, 2007;  
35 Oganian and Ahissar, 2012).

36 Raviv et al. (2012) extended the protocol-specific account of benefits from stimulus repetition  
37 to a computational model which takes the experiment's statistics into account. This model  
38 assumes that listeners implicitly infer the mean (frequency) even when it is not presented

39 explicitly. The inferred mean of previous stimuli (prior) is combined with the representation of  
40 the current stimulus, and forms an integrated percept (posterior). The resulting percept is  
41 contracted (biased) towards that mean (the “contraction bias”; Woodrow, 1933; Preuschhof et  
42 al., 2010). This bias is advantageous when the observation of the current stimulus is noisy, and  
43 hence integration with prior knowledge is likely to improve its accuracy. Indeed, in the general  
44 population, “noisier” listeners weigh the prior more than “less noisy” listeners when they  
45 integrate it with current representation, resulting in their larger contraction bias. Jaffe-Dax et al.  
46 (2015) found that dyslexics’ bias is smaller than controls’ even though they tend to be “noisier”  
47 listeners.

48 The representation of the first tone is contracted towards the prior more than the second tone,  
49 due to the noise added to its representation during the inter-stimulus time interval. The  
50 contraction of the first tone towards the prior can increase the perceived difference between the  
51 two tones in the trial, and hence improve discrimination (*Bias+* trials; e.g., trial  $t$  in Fig. 1A); or,  
52 decrease the perceived difference between the two tones and disrupt performance (*Bias-*; e.g.,  
53 trial  $t - 1$  in Fig. 1A). The difference in performance between *Bias+* and *Bias-* trials reflects the  
54 magnitude of the contraction bias (i.e. context effect). Dyslexics’ underweighting of the prior  
55 yields a smaller contraction bias, namely a smaller performance difference between these two  
56 types of trials (Jaffe-Dax et al., 2015).

57 Using this measure of contraction bias, we studied the dynamics of controls’ and dyslexics’  
58 benefits from the statistics of recent sound stimuli in both simple discriminations and in oral  
59 reading. We found that dyslexics are similarly affected (biased) by recent stimuli, but less  
60 affected by earlier stimuli, as expressed both behaviorally and in the dynamics of the compulsory  
61 ERP components (N1 and P2) produced by the auditory cortex. These observations suggest that  
62 dyslexics’ automatic integration of previous sounds spans shorter time intervals, and is therefore

63 noisier and produces less reliable priors. We propose that noisier predictions impede dyslexics'  
64 acquisition of expert-level performance in a range of tasks, including reading. These  
65 observations also pave the way to pursuing the deficits underlying dyslexia in non-human  
66 animals.

67

## 68 **Results**

69 *Dissociating the contraction to the most recent trial from the contraction to all*  
70 *previous trials*

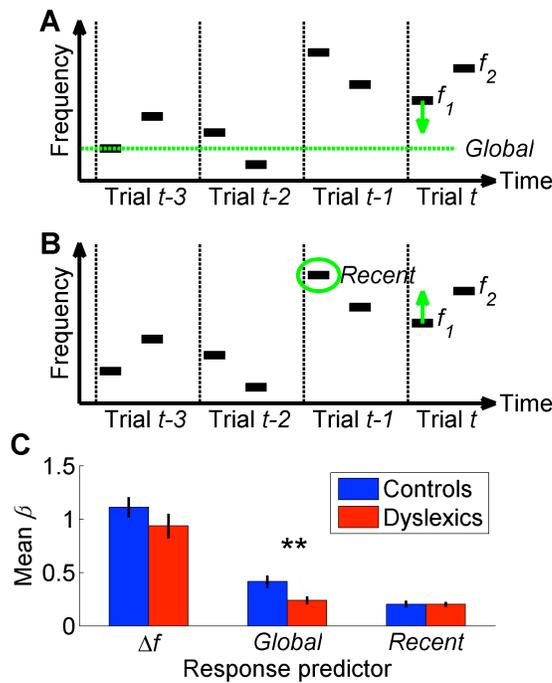
71 Performance in the 2-tone frequency discrimination task is affected by two basic components  
72 (Raviv et al., 2012, 2014). First, the frequency difference between the two tones composing each  
73 trial - participants are more accurate when this difference is larger. Second, the context effects;  
74 namely, the perceptual bias induced by contracting the first tone towards the estimated mean-  
75 frequency in previous trials (Woodrow, 1933; Preuschhof et al., 2010; see Introduction and Fig.  
76 1A-B). This estimated prior can be viewed as a combination of a recent component and a global  
77 component. The most recent one is the frequency of the previous trial (Fig. 1B ), whose impact  
78 on the estimated prior is substantially larger than that of any other previous trial (“recency  
79 effect”; Schab and Crowder, 1988; Stewart and Brown, 2004; Fischer and Whitney, 2014). The  
80 global prior (illustrated in Fig. 1A) is the mean frequency of all previous trials.

81 As described above, dyslexics' discrimination behavior is less affected by the statistics of  
82 previous trials (Jaffe-Dax et al., 2015). We now aimed to decipher whether dyslexics' deficit  
83 encompasses both the recent and the global context effects. To test this, we designed a novel  
84 protocol for the 2-tone frequency discrimination task, which allowed us to assess the contribution  
85 of recent and earlier trials' on performance separately. Unlike in most sequences where the

86 recent and more global contexts tend to have the same direction, and are therefore very difficult  
87 to dissociate, in the new sequence the recent and the global contexts were not correlated (the  
88 constraints that this sequence satisfies are described in the Methods).

89 The overall accuracy of the two groups in this task did not differ (controls' mean % correct  $\pm$   
90 SEM:  $75.3 \pm 1.6$ , dyslexics':  $73 \pm 1.9$ ;  $z = 1.3$ , *n.s.* Mann-Whitney U test), as predicted given that  
91 the use of experiment's statistics was not expected to be significantly beneficial in this stimulus  
92 series (replicating Ahissar et al., 2006). We calculated a GLM model with 3 predictors ( $\beta$ s) for  
93 each participant ( $n = 60$ ; 30 control and 30 dyslexic participants) by estimating the magnitude of  
94 the contribution of each of the following components to participants' responses: 1. Frequency  
95 difference in the current trial; 2. Contraction bias of the first tone toward the global mean of  
96 previous trials; 3. Contraction bias of the first tone towards the most recent trial. Dyslexics'  
97 frequency difference predictor did not differ from controls' (Fig 1C;  $z = 1.6$ , *n.s.*). Namely, the  
98 frequency difference within the trial had a similar impact on the response in the two groups  
99 (similar levels of sensitivity). The impact of the context effect of the most recent trial (ITI  $\approx 1.5$   
100 sec) was also similar in the two groups ( $z = 0.05$ , *n.s.*). However, dyslexics' bias towards the  
101 global mean was significantly smaller than controls' ( $z = 2.7$ ,  $p < 0.01$ ). Indeed, the difference in  
102 controls between the contributions of the *Global* (all previous trials except the most recent one)  
103 and *Recent* contexts was larger than that found in dyslexics ( $z = 2.4$ ,  $p < 0.05$ . Mann-Whitney U  
104 tests). Importantly, among both groups, the contribution on *Recent* context was significantly  
105 above zero (controls:  $z = 4.4$ ,  $p < 0.0001$ ; dyslexics:  $z = 4.7$ ,  $p < 0.00001$ ). Thus floor effect  
106 cannot account for this interaction.

107



108

109 **Figure 1.** The three parameters that additively determine performance in frequency  
110 discrimination: *frequency difference within a trial* ( $\Delta f$ ), *Global context* (the difference between  
111 the current  $f_1$  and the global mean) and *Recent context* (the difference between the current  $f_1$   
112 and the previous  $f_1$ ). **A.** A schematic illustration of the *Global bias* - four trials and the direction  
113 of the contraction, which contracts the representation of the first tone in the trial towards the  
114 global mean. **B.** A schematic illustration of the same four trials and the direction of the *Recent*  
115 *bias*, which pulls the representation of this tone towards the recent frequency. **C.** The estimated  
116 contribution ( $\beta$ ) of each the three parameters to the overall performance of each group.  
117 Dyslexics differed from controls only in the smaller magnitude of the contribution of their  
118 *Global* predictor ( $p < 0.01$ ). Filled bars denote the mean  $\beta$  values; controls in blue and dyslexics  
119 in red. Error bars denote SEM.

120

121 *Comparing the behavioral and neural dynamics of context effects*

122 The observation that dyslexics assign less weight to earlier trial statistics than controls can  
123 result from either of following two mechanisms. The first is that dyslexics experience larger  
124 interference effects, and intervening trials mask each other. The second is that dyslexics'  
125 memory trace decays faster in time, even without intervening sounds. To dissociate between  
126 these alternatives, we manipulated the time interval between consecutive trials. We reasoned that  
127 if dyslexics' memory trace decays faster we might be able to track the neural correlate of this  
128 behavioral dynamics.

129 We administered the 2-tone frequency discrimination task with four different Inter-Trial  
130 Intervals (ITIs; i.e. interval between the 2<sup>nd</sup> tone of the previous trial and the 1<sup>st</sup> tone of the  
131 current trial), in four separate blocks. We chose ITIs of 1.5, 3, 6 and 9 sec (roughly; see  
132 Methods), based on previous reports of cortical adaptation duration (N1 and P2 components;  
133 Hari et al., 1982; Lu et al., 1992; Sams et al., 1993).

134 **Assessing the time constant of the behavioral context effect**

135 We quantified behavioral performance in terms of sensitivity to the difference between the two  
136 tones. As a measure of sensitivity we used  $d'$ , which was calculated as the difference between the  
137 correct rate (HR) and the incorrect rate (FA), transformed by inverse cumulative standard  
138 distribution function (Macmillan and Creelman, 2004):  $d' = \Phi^{-1}(HR) - \Phi^{-1}(FA)$ . For both  
139 groups, performance was better at longer ITIs (mean  $d' \pm$  SEM for the four ITIs was  $0.48 \pm 0.05$ ,  
140  $0.57 \pm 0.05$ ,  $0.71 \pm 0.06$  and  $0.78 \pm 0.06$ , respectively;  $\chi^2 = 54.2$ ,  $p < 10^{-10}$ . Friedman test). The  
141 slight improvement in  $d'$  with longer ITIs is probably related to having “time outs” for  
142 responding. These “time-outs” were enforced due to the co-registration of ERP with behavioral  
143 performance, and probably introduced a slightly larger stress with short ITIs.

144 Across all ITIs, controls' ( $n = 23$ ) performance was slightly more accurate than dyslexics'  
145 performance ( $n = 25$ ; mean  $d' \pm$  SEM of controls:  $0.71 \pm 0.07$ , dyslexics:  $0.56 \pm 0.07$ ;  $z = 2.0$ ,  $p$   
146  $< 0.05$ . Mann-Whitney U test). There was no significant interaction between group and ITI  
147 (group X ITI;  $F_{3,46} = 1.4$ , *n.s.* Repeated Measures ANOVA test). Controls' slightly better  
148 performance is interesting, particularly since no group difference was found for the same  
149 participants in Experiment 1. The group difference was small, and was within the range of the  
150 estimated group variability. It may, however, reflect slightly better learning of the task's  
151 characteristics by the control participants.

152 We calculated the behavioral context effect as the difference (in  $d'$ ) between performance on  
153 trials for which contraction to the prior was beneficial (*Bias+*) and performance on trials for  
154 which this contraction was disruptive (*Bias-*). Previous studies have found that the impact of  
155 earlier stimuli decayed exponentially as a function of number of trials which had passed (Raviv  
156 et al., 2012) or the time interval (Lu et al., 1992) or both (Fischer and Whitney, 2014). Thus, to  
157 quantify the dynamics of this effect, i.e. its magnitude as a function of the time interval from  
158 previous trials, we fitted the calculated bias ( $\Delta d'$ ; difference between individual  $d'$  in *Bias+*  
159 trials and in *Bias-* trials) as a function of the ITI to an exponential decay model:  
160  $\Delta d'(t) = \alpha + \beta \exp(-t/\tau)$ , where  $\alpha$  denotes the estimated  $\Delta d'$  at  $t \rightarrow \infty$  (asymptotic level);  $\beta$   
161 denotes the difference between the  $\Delta d'$  at  $t = 0$  and at  $t \rightarrow \infty$  (decay magnitude); and  $\tau$   
162 denotes the time it takes for  $\Delta d'$  (at  $t = 0$ ) to decay to  $1/e$  (~37%) of its initial value (temporal  
163 slope parameter). A small  $\tau$  indicates fast decay;  $t$  is the ITI.

164 Evaluating the dynamics of the contraction bias as a function of ITI showed that its decay was  
165 significantly faster among dyslexics, as illustrated in Fig. 2B *bottom* (controls'  $\tau = 6 \pm 0.9$  sec,  
166 dyslexics'  $\tau = 2.9 \pm 0.8$  sec; mean  $\pm$  SEM;  $z = 2.2$ ,  $p < 0.05$ ). The two other parameters did not

167 differ between the two groups ( $\alpha$ : controls =  $0.7 \pm 0.1 d'$ , dyslexics:  $\alpha = 0.5 \pm 0.1 d'$ ;  $z=1$ , *n.s.*;  
168  $\beta$ : controls =  $2.3 \pm 0.8 d'$ , dyslexics =  $4 \pm 0.9 d'$ ;  $z = 1.9$ , *n.s.* Mann-Whitney U tests), in line  
169 with our hypothesis.

## 170 **Assessing the dynamics of the neural trace**

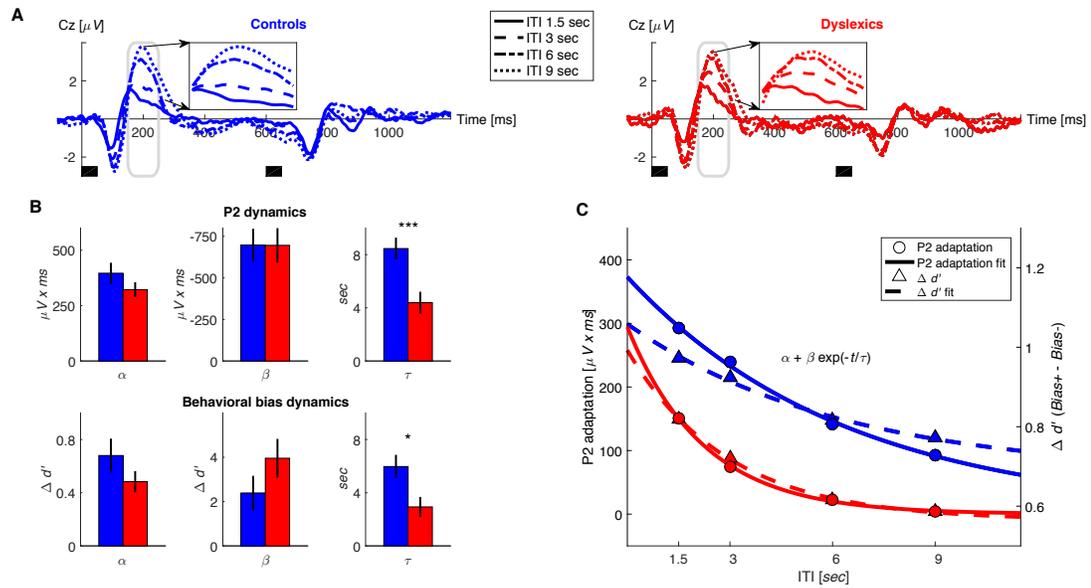
171 We hypothesized that the neural mechanism that mediates the inference of the prior frequency  
172 is neural adaptation, which is an automatic, stimulus-specific form of memory (Ulanovsky et al.,  
173 2003). Importantly, it was found that the time constant of context effects in sound discrimination  
174 is the same as that of cortical adaptation to sounds (Lu et al., 1992). The two prominent ERP  
175 components that are automatically produced by the auditory cortex are N1 and P2 (Sheehan et  
176 al., 2005; Mayhew et al., 2010), which peak at 100 and 200ms from stimulus onset, respectively.  
177 Whether they are produced by a single cortical generator (evolving in time) or by two is still  
178 debated (Lanting et al., 2013). Both were found to have some sensitivities to stimuli statistics  
179 (Tremblay et al., 2010; Herrmann et al., 2015). However, in our previous study where we  
180 assessed sensitivity to frequency prior, only the magnitude of P2 showed such sensitivity. We  
181 therefore hypothesized that P2 would be directly associated with the contraction bias. Still, given  
182 the mixed results regarding the distinction between N1 and P2 sensitivities, we analyzed the  
183 dynamics of both components. We hypothesized that for each group, behavioral context effects  
184 and cortical adaptation (N1 and/or P2) would have the same time constants and that these time  
185 constants would be shorter among dyslexics.

186 In both groups, the magnitude of the P2 responses was the smallest in the block with the  
187 shortest ITI (1.5 sec), when P2 adaptation was substantial, and increased (recovered) with longer  
188 ITIs, as adaptation gradually decayed ( $\chi^2 = 65.7$ ,  $p < 10^{-13}$ . Friedman test). Among dyslexics, P2  
189 reached its peak magnitude by 6 sec ITI (Fig. 2A, red dot-dashed line), whereas controls' P2 was

190 larger at 9 than at 6 sec ITIs (Fig. 2A, blue dotted line). To quantify the dynamics of P2  
191 adaptation under active discrimination, we fitted each individual's areas of P2 elicited by the first  
192 tone, in each of the 4 ITIs to the same equation of exponential decay. Figure 2B top shows the  
193 cumulative distribution of the 3 fitted parameters for each of the two groups. It shows that the  
194 groups did not differ in the estimated amplitudes of P2 at either maximal or minimal adaptation  
195 ( $\alpha$  : controls =  $396 \pm 47 \mu V \times ms$ , dyslexics =  $322 \pm 33 \mu V \times ms$ ;  $z = 1.1$ , *n.s.*;  $\beta$  : controls =  $-696$   
196  $\pm 99 \mu V \times ms$ , dyslexics =  $-696 \pm 103 \mu V \times ms$ ;  $z = -0.1$ , *n.s.* Mann-Whitney U tests). However, as  
197 with behavior, the rate at which adaptation decayed was significantly faster among dyslexics ( $\tau$  :  
198 controls =  $6.3 \pm 0.8$  sec, dyslexics =  $2.2 \pm 0.8$  sec; mean  $\pm$  SEM;  $z = 3.5$ ,  $p < 0.0005$ . Mann-  
199 Whitney U test).

200 As was evident when comparing the time constant of the recovery of P2 (time constant of its  
201 adaptation) and the time constant of the behavioral context effect, the two were very similar.  
202 This similarity was also found in the dyslexic group. Figure 2C plots the estimated dynamics (the  
203 fitted  $\alpha + \beta \exp(-t/\tau)$  curves) of P2 adaptation and the behavioral contraction bias in the same  
204 graph. For clarity, the dynamics of the ERP component is plotted as decaying to zero, i.e. the  
205 fitted curve was subtracted from  $\alpha$  (the asymptotic level of maximal P2 magnitude) to depict the  
206 decay of adaptation. Dyslexics' behavioral and P2 adaptation curves were very similar. Controls'  
207 behavioral and P2 adaptation were also similar and both were significantly slower than  
208 dyslexics' (Fig. 2B).

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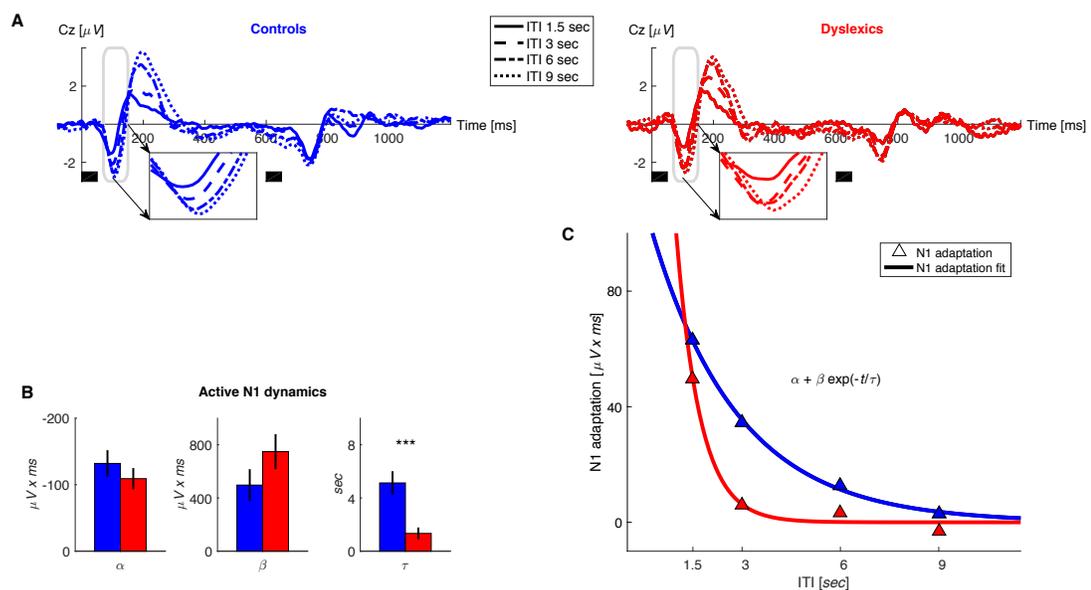
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211 **Figure 2.** Dyslexics' decay of both neural adaptation and behavioral contraction bias was faster  
 212 than controls'. **A.** Grand average ERPs, plotted separately for blocks with different ITIs, for  
 213 controls ( $n = 23$ ; blue, left) and dyslexics ( $n = 25$ ; red, right). Timing of the 2 tones in each trial  
 214 is denoted by the short black bars under the plots. **Middle insets:** P2 range (denoted in gray)  
 215 enlarged. Dyslexics' P2 area was similar for 6 and 9 second ITIs, whereas controls' P2 was  
 216 larger for the 9 second interval. **B.** Groups' mean and SEM of individually fitted estimated  
 217 parameters of the exponential decay model of P2 recovery from adaptation (**top**) and contraction  
 218 bias decay (**bottom**). In both, dyslexics differed from controls solely on the estimated rate of  
 219 decay (P2:  $p < 0.0005$ ;  $\Delta d'$ :  $p < 0.05$ ). **C.** The decrease in P2 adaptation (solid lines, circles, left  
 220 scale; estimated magnitude at asymptote minus fitted curve) and the decrease in contraction bias  
 221 (dashed lines, triangles, right scale; reflecting implicit sec memory decay) as a function of ITI. Data  
 222 in markers, fitted exponential decay model in lines. Controls in blue, dyslexics in red.

223

224 We further analyzed the dynamics of N1. In this component as well, dyslexics showed a faster  
225 recovery from adaptation than controls. As illustrated in Figure 3 A and C, dyslexics' N1 almost  
226 fully recovered (regained full magnitude) at an ITI of 3 seconds, whereas controls' N1 at this ITI  
227 was still substantially "adapted". Applying the same model, again we found that only the rate of  
228 decay differed between the two groups (Fig. 3B;  $\tau$ : controls =  $4.5 \pm 0.8$  sec, dyslexics =  $0.7 \pm$   
229  $0.4$  sec; mean  $\pm$  SEM;  $z = 4.2$ ,  $p < 0.0001$ . Mann-Whitney U test), whereas the two other  
230 estimated parameters were similar ( $\alpha$ : controls =  $-131 \pm 20 \mu V \times ms$ , dyslexics =  $-109 \pm 16 \mu V \times$   
231  $ms$ ;  $z = 0.7$ , *n.s.*;  $\beta$ : controls =  $497 \pm 120 \mu V \times ms$ , dyslexics =  $750 \pm 132 \mu V \times ms$ ;  $z = 1.1$ , *n.s.*  
232 Mann-Whitney U tests). Across groups, N1 adaptation was significantly shorter than that of P2 ( $z$   
233 =  $3.7$ ,  $p < 0.0005$ . Wilcoxon test). There was no group X ERP component interaction effect for  
234 the rate of decay of adaptation ( $z = 0.7$ , *n.s.* Mann-Whitney U test).

235



236

237 **Figure 3.** Dyslexics' decay of N1 adaptation was faster than controls'. **A.** Grand average ERPs,  
238 plotted separately for blocks with different ITIs, for controls ( $n = 23$ ; blue, left) and dyslexics ( $n$

239 = 25; red, right). Timing of the 2 tones in each trial is denoted by the short black bars under the  
240 plots. **Middle insets:** N1 range (denoted in gray) enlarged. Dyslexics' N1 almost reached its full  
241 magnitude at an ITI of 3 sec, whereas controls' N1 reached its near-full magnitude only at an ITI  
242 of 6 sec. **B.** Groups' mean and SEM of individually fitted estimated parameters of the  
243 exponential decay model of N1 recovery from adaptation. Only  $\tau$  differed between the two  
244 groups ( $p < 0.0001$ ). **C.** The decrease in N1 adaptation (circles) and the fitted exponential decay  
245 model (lines) as a function of ITI. Controls in blue, dyslexics in red.

246

### 247 *Comparing the dynamics of passive adaptation between controls and dyslexics*

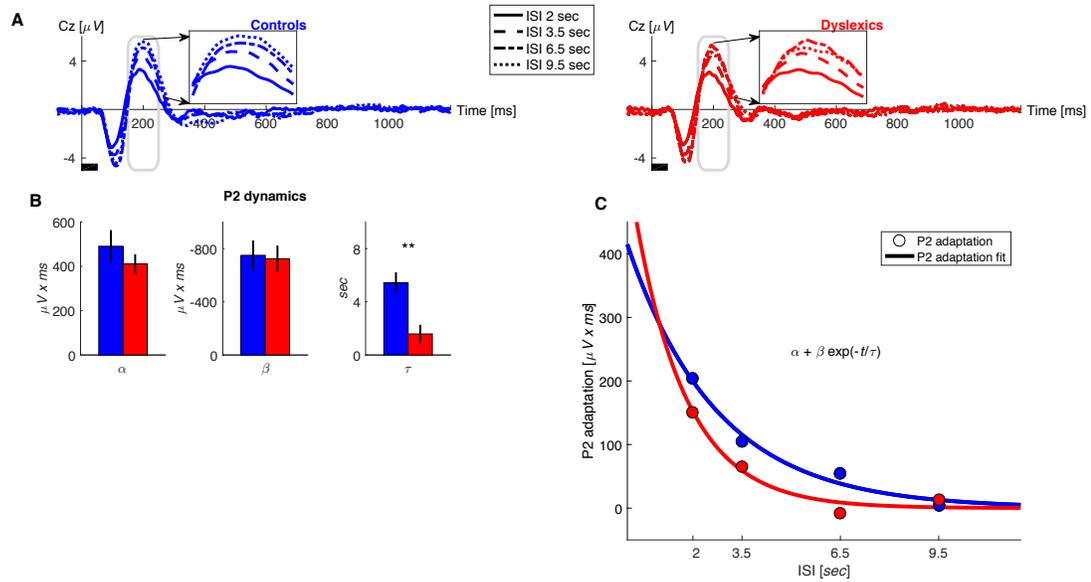
248 After showing that adaptation under active performance decays faster among dyslexics, we  
249 further asked whether this group-difference was an automatic characteristic that could also be  
250 detected in the absence of a behavioral task. To evaluate the dynamics of dyslexics' passive  
251 adaptation, we administered a sequence of pure tones in four blocks, each with a different ISI,  
252 while participants watched a silent movie (ISIs: 2, 3.5, 6.5 and 9.5; same TOAs as those used for  
253 the active condition, but without the second tone).

254 To quantify the dynamics of adaptation of P2 and N1, we fitted the P2 and N1 areas, to the  
255 exponential decay model described above. We found that controls' P2 recovery was significantly  
256 slower than dyslexics'. Importantly, the only significant difference between the two groups was  
257 in  $\tau$  ( $\tau$ : controls =  $4.2 \pm 0.8$  sec, dyslexics =  $2.1 \pm 0.7$  sec; mean  $\pm$  SEM;  $z = 3.3$ ,  $p < 0.005$ .  
258 Mann-Whitney U test; Fig. 4B). The other two parameters did not differ between the two groups  
259 ( $\alpha$ : controls =  $490 \pm 73 \mu V \times ms$ , dyslexics =  $410 \pm 44 \mu V \times ms$ ;  $z = -0.04$ , *n.s.*  $\beta$ : controls =  $-750$   
260  $\pm 112 \mu V \times ms$ , dyslexics =  $-724 \pm 100 \mu V \times ms$ ;  $z = -0.1$ , *n.s.* Mann-Whitney U tests).

261 N1 adaptation was not significantly shorter among dyslexics ( $\tau$ : controls =  $5 \pm 0.9$  sec,  
262 dyslexics =  $2.6 \pm 0.9$  sec;  $z = 1.7$ ,  $p = 0.05$ .  $\alpha$ : controls =  $-132 \pm 20 \mu V \times ms$ , dyslexics =  $-114 \pm$   
263  $16 \mu V \times ms$ ;  $z = 0.37$ , *n.s.*  $\beta$ : controls =  $497 \pm 120 \mu V \times ms$ , dyslexics =  $615 \pm 132 \mu V \times ms$ ;  $z =$   
264  $0.02$ , *n.s.* mean  $\pm$  SEM; Mann-Whitney U tests). In line with previous studies of passive  
265 presentation (Hari et al., 1982), we did not find a difference between the time scales of  
266 adaptation of P2 and N1 ( $z = 1.6$ , *n.s.* Wilcoxon test) nor was there a group X ERP component  
267 interaction ( $z = 1.4$ , *n.s.* Mann-Whitney U test).

268 Figure 4A shows the average ERP responses in the different blocks, for controls ( $n = 23$ ; blue,  
269 left) and dyslexics ( $n = 25$ ; red, right), respectively. It focuses on P2, since only P2 showed a  
270 significant group difference (insets in Figure 4A). In both groups, P2 responses were the smallest  
271 in the block with the shortest ISI (2 sec), when P2 adaptation was still substantial, and increased  
272 (recovered) with longer ISIs, as adaptation gradually decayed ( $\chi^2 = 60.3$ ,  $p < 10^{-12}$ . Friedman  
273 test). Among dyslexics, P2 reached its peak magnitude by 6.5 sec ISI (Fig. 4A, red dot-dashed  
274 line), whereas controls' P2 was larger at 9.5 than at 6.5 sec ISIs (Fig. 4A, blue dotted line).

275



276

277 **Figure 4.** Under passive conditions, dyslexics' P2 adaptation is shorter than controls'. **A.** Grand  
278 average ERPs, plotted separately for blocks with different ISIs, for controls (blue, left) and  
279 dyslexics (red, right). **Middle insets:** P2 range (denoted in gray) enlarged. Dyslexics' P2 area was  
280 largest for the 6.5 second ISI, whereas controls' P2 was largest for the 9.5 second ISI. **B.** Groups'  
281 mean and SEM of individually fitted estimated parameters of the exponential decay model of P2  
282 recovery from adaptation. Controls in blue; dyslexics in red. Dyslexics differed from controls  
283 only in the estimated rate of decay ( $p < 0.005$ ). **C.** The magnitude of P2 adaptation as a function  
284 of time from the previous stimulus (ISI) under passive condition (triangles) and fitted  
285 exponential decay model (solid line). Controls in blue; dyslexics in red.

286

287 Interestingly, among controls, the estimated duration of adaptation was longer in the active than  
288 in the passive condition (P2:  $z = 3$ ,  $p < 0.005$ . N1:  $z = 4.2$ ,  $p < 0.00005$ ). This was not observed  
289 in the dyslexic group (P2:  $z = 0.5$ , *n.s.* N1:  $z = 0.1$ , *n.s.* Wilcoxon tests). The interaction (in the  
290 estimated time constant of adaptation) between group and condition (passive/active) was

291 significant for N1 ( $z = 2.7, p < 0.01$ ), but not for P2 adaptation ( $z = 1.8, n.s.$  Mann-Whitney U  
292 tests). Thus, controls' but not dyslexics' N1 adaptation was prolonged by introducing a  
293 behavioral context.

294

### 295 *Comparing the dynamics of context effects in reading rate*

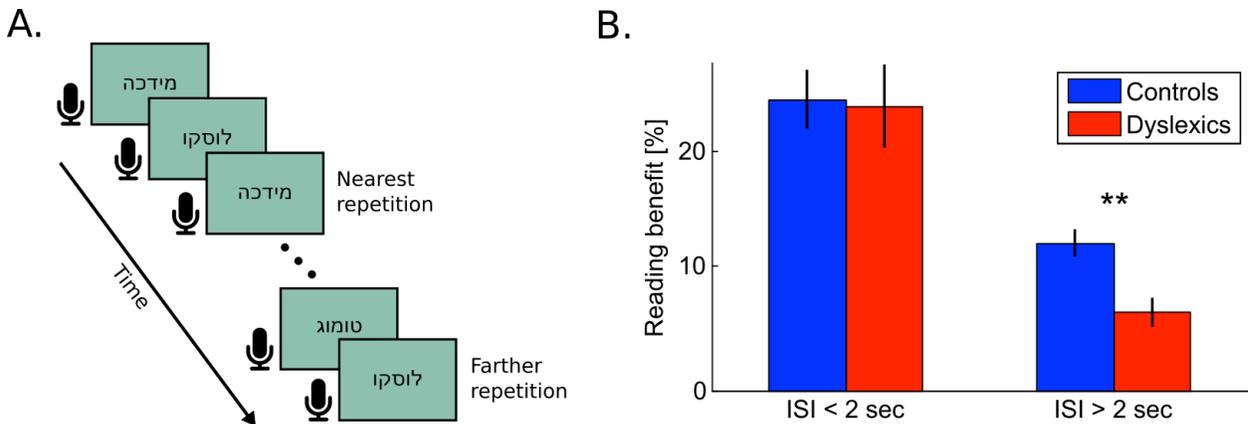
296 As shown above, dyslexics benefit less from recent sound statistics. We hypothesized that a  
297 similar observation would be found for recent encounters with complex sound stimuli and  
298 particularly with novel syllabic combinations. If demonstrated, this correlate would provide  
299 support for the relevance of the observations of Experiments 1-2 to the context of reading. To  
300 assess the dynamics of the simplest context effect in reading, we administered an oral reading  
301 task in which participants were asked to read single simple disyllabic non-words aloud, and  
302 measured repetition effects. The non-words were presented on a screen, one at a time, and  
303 participants were asked to read them as quickly (and accurately) as they could. Consecutive non-  
304 words were presented at an individually paced rate. Non-words were repeated throughout the  
305 block with various intervals (i.e. with a different number of other intervening non-words), as  
306 schematically illustrated in Figure 5A.

307 Participants' response times (RTs, measured as vocal response onset) were shorter in the  
308 second presentation of the same non-word. However, the magnitude of this improvement  
309 declined as the time interval from the previous presentation of the same non-word increased (i.e.  
310 there were more intervening words). Overall, dyslexics' RTs were longer than controls'  
311 (controls:  $n = 29$ ; mean RT per word  $\pm$  SEM =  $725 \pm 28$  ms; dyslexics:  $n = 23$ ; mean RT  $\pm$  SEM  
312 =  $929 \pm 47$  ms;  $z = 3.3, p < 0.001$ . Mann-Whitney U test) and they were less accurate (controls:

313 mean % correct  $\pm$  SEM =  $98.6 \pm 0.3$ ; dyslexics:  $96.0 \pm 1.4$ ;  $z = 3.2$ ,  $p < 0.005$ . Mann-Whitney U  
314 test), as expected.

315 Both groups showed large recent context (repetition) effects. Specifically, both groups showed  
316 substantially faster reading RTs in the second than in the first encounter with the same non-word,  
317 when the words were proximal in time ( $< 2$  sec interval), even though they were never  
318 consecutive. The smallest interval between two presentations of the same non-word was with one  
319 intervening word. Since word presentation rate was based on reading rate, and dyslexics are  
320 slower readers, we equated the inter-word time interval in the two groups by considering only  
321 trials in which the second presentation occurred within  $< 2$  sec ITI (offset of the first presentation  
322 to the onset of the second presentation of the same non-word). In these trials dyslexics' benefit  
323 from repetition was similar to controls' (Fig. 5B; controls:  $25 \pm 2$  % or  $170 \pm 19$  ms, dyslexics:  
324  $23 \pm 3$  % or  $177 \pm 20$  ms; mean benefit  $\pm$  SEM;  $z = 0.1$ , *n.s.* Mann-Whitney U test). However, in  
325 trials with larger inter-word intervals, dyslexics' benefits were overall smaller. Importantly,  
326 dyslexics' benefits were smaller than controls', even though their starting point had longer RTs,  
327 as explained above (mean ITI of 42 sec, max ITI of 163 sec. controls:  $12 \pm 1$  % or  $90 \pm 10$  ms,  
328 dyslexics:  $6 \pm 1$  % or  $52 \pm 8$  ms; mean benefit  $\pm$  SEM;  $z = 3$ ,  $p < 0.005$ . Mann-Whitney U test).  
329 Indeed, among dyslexics the difference in benefit from repetitions with small ( $< 2$  sec) compared  
330 to larger ( $> 2$  sec) intervals was greater than this difference among controls ( $z = 2.2$ ,  $p < 0.05$ .  
331 Mann-Whitney U test).

332



333

334 **Figure 5.** Dyslexics' benefit from a previous exposure to the same non-word decayed faster  
335 than controls'. **A.** Schematic illustration of the reading task. Subjects were asked to read the non-  
336 words aloud as quickly as possible. Presentation switched to the next word with the subject's  
337 voice offset. The closest repetition of the same non-word was with one intervening non-word  
338 (i.e. an ITI of < 2 sec). **B.** Benefit in RTs (response times from visual word presentation to vocal  
339 onset) as a function of the time interval between the first and second presentation of the same  
340 non-word. Improvement was calculated as the difference in RT between the first and second  
341 presentation of the same non-word in the block. At very short intervals (< 2 sec) the benefit was  
342 similar for both groups. However, this benefit decayed faster (at interval > 2 sec) among  
343 dyslexics (red) than among controls (blue;  $p < 0.005$ ). Error bars denote standard error (SEM).

344

345 Note that for short inter-word intervals, dyslexics' RT benefits do not differ from controls' in  
346 spite of an intervening word. Thus, here too, dyslexics' faster decay is consistent with a time  
347 based effect rather than with an enhanced interference effect.

348

349

## 350 **Discussion**

351 We characterized the dynamics of context effects, and found that they differ consistently  
352 between dyslexics and good readers. Dyslexics' behavioral benefits declined faster, both in the  
353 context of reading and in sound discrimination. In both groups, the behavioral dynamics  
354 reflected the dynamics of cortical adaptation, which decayed faster in dyslexics, both when  
355 actively performing a task and in passive listening.

356

### 357 *Accounting for Dyslexics' "slower processing speed"*

358 We propose that dyslexics' shorter time constant of adaptation reflects a shorter time constant  
359 of implicit sound integration. Dyslexics' faster decay decreases the time constant of their  
360 integration of sound statistics, and consequently reduces the reliability of their implicitly  
361 calculated priors. Due to their noisier priors, attaining the same level of processing reliability  
362 requires extraction of more on-line information, which requires more processing time, leading to  
363 the stereotypic "slower processing time" in dyslexia.

364 This account explains dyslexics' often poorer performance on rapidly presented brief auditory  
365 stimuli for both simple tones (Tallal, 1980; Temple et al., 2000) and speech (McArthur and  
366 Bishop, 2005; Boets et al., 2007). Moreover, it resolves seemingly inconsistent observations in  
367 dyslexics' pattern of perceptual difficulties. On the one hand, dyslexics' poor short term memory  
368 impairment is amply documented (Beneventi et al., 2010; Banai and Yifat, 2012) and suggests  
369 that their performance should improve when memory load is reduced by decreasing task's  
370 retention intervals. On the other hand, dyslexics are known to perform poorly with short stimuli  
371 presented at brief intervals (Tallal, 1980), suggesting that they should gain from longer inter-  
372 stimulus intervals.

373 We claim that these seemingly contradictory observations result from the same basic  
374 impairment. The key feature is the proportion of on-line computations that need be allocated to  
375 solve the task. The more predictable the stimuli are for controls, both locally within session and  
376 globally in terms of long-term regularities (such as in language) the greater relative slowness  
377 (“slow processing speed”) dyslexics are expected to show (consistent with Ahissar et al., 2006).  
378 This slowness stems from their poor implicit memory mechanisms; namely, their faster decay of  
379 the neural trace that integrates the statistics of recent stimuli.

380

### 381 *Dyslexics’ deficit as a process rather than a representational impairment*

382 Dyslexics’ phonological and reading skills reflect the outcome of long-term learning processes  
383 which are difficult to track. The use of a simple task of discrimination of pure tones (which are  
384 physically simple but very infrequent environmentally) enabled us to observe the dynamics of  
385 context effects in a relatively novel situation. It served to dissociate the benefits of very short-  
386 term (< 2 sec; the scale attributed to working memory processes; Baddeley, 2010) implicit  
387 effects from somewhat longer term effects. Dyslexics’ only benefitted less from prior statistics in  
388 the latter case.

389 Dyslexics’ noisier priors (predictions based on past experiences) may lead to slower long-term  
390 learning of characteristic sound regularities, such as those in the native language (Nicolson et al.,  
391 2010). It follows that dyslexics should benefit less than controls from a given number of  
392 experiences, and that group differences should increase with additional specific experiences.  
393 Thus, though both good and poor readers are expected to improve with practice, dyslexics’  
394 benefits per exposure are expected to be smaller. Hence, counter intuitively, dyslexics’ relative  
395 difficulties are expected to be greater for highly trained stimuli.

396 Our observation of reduced repetition effects in dyslexics' reading rate is compatible with  
397 imaging observations by Pugh et al. (2008), who compared the impact of word repetition in  
398 reading on BOLD activation in posterior reading-related areas, in dyslexics versus controls. They  
399 found that although both populations gained from such repetitions, the impact differed between  
400 groups. Whereas controls' activation was monotonically reduced with repetitions, dyslexics'  
401 activation initially increased. They interpreted this pattern in a manner consistent with ours by  
402 suggesting that dyslexics' pattern seemed similar to that expected after a lesser amount of  
403 exposure to these words; i.e., slower long-term learning of these (sound) patterns. Interestingly,  
404 dyslexics' slower learning rate per event (or exposure) was also recently proposed by Nicolson et  
405 al., (2010), who based their argument on slower learning curves in a different context. They  
406 found that dyslexics exhibit slower learning of simple motor tasks, which perhaps tap  
407 mechanisms partially common to those used in serial comparison tasks.

408

#### 409 *The complex relationships between mechanisms and sites*

410 We found that dyslexics' P2 component had a shorter adaptation duration under both active and  
411 passive conditions. We also found that their N1 had a shorter adaptation duration under active  
412 condition when compared to controls. The P2 (which peaks 200ms after tone onset) component  
413 was shown to reflect the accumulation of sound statistics (Tremblay et al., 2010; Jaffe-Dax et al.,  
414 2015) automatically, without explicit attention (Sheehan et al., 2005). Moreover, it was shown to  
415 be abnormal among dyslexics (Bishop and McArthur, 2004; Jaffe-Dax et al., 2015). Indeed, its  
416 dynamics matched that of the behavioral context effects measured simultaneously. However,  
417 even the earlier N1 component (100ms) had a shorter time constant here among dyslexics under  
418 the active condition. Whether these two components originate from one or two cortical

419 generators is still unclear (e.g. Mayhew et al., 2010; Lanting et al., 2013). Nevertheless, recent  
420 studies have found that the magnitude of adaptation of both is sensitive to the statistics that  
421 characterize the experiment (e.g. Herrmann et al., 2015). We found a shorter time constant of  
422 adaptation in N1 than in P2.

423 These observations suggest that the dynamics of adaptation in the auditory cortex of dyslexics  
424 differs from that of controls. But they do not directly point to the anatomical source of this  
425 abnormality, since by 100-200 ms ERP signals reflect the combined contribution of various brain  
426 sites. Thus, the abnormally fast decay of N1 and P2 adaptation may reflect a different anatomy of  
427 the auditory cortex, as suggested in a recent longitudinal study (Clark et al., 2014), or impaired  
428 long-range connectivity between posterior and frontal areas (Boets et al., 2013; Ramus, 2014).  
429 Alternatively, it may correspond to impaired top-down control (Díaz et al., 2012) or unreliable  
430 bottom-up processing (Hornickel and Kraus, 2013).

431 Importantly, the involvement of the auditory cortex does not exclude the contribution of sub-  
432 cortical regions. Both the cerebellum and the basal ganglia are involved in the process of  
433 integrating sound regularities into improved perceptual performance with reduced reliance on  
434 on-line working memory processes and increased reliance on specific sound predictions (Daikhin  
435 and Ahissar, 2015). Thus, the hypothesis linking dyslexics' reduced rate of automatization (in  
436 reading and in other tasks) with impaired usage of cerebellar processes (Nicolson et al., 2010) is  
437 also in line with our findings and interpretation.

438 The attempts to map dyslexics' processing difficulties to several potentially relevant anatomical  
439 abnormalities suggest that there may not be a single anatomical source of difficulty, and that the  
440 issue of the core deficit underlying dyslexia, should be seen as a process- rather than structure-  
441 related. Our observation that the process of dyslexics' neural adaptation is abnormally short

442 paves the way to studies of reading difficulties in non-humans, which are essential for  
443 understanding the complex relationships between the dynamics of cognitive processes and their  
444 underlying neural mechanisms.

445

#### 446 *The prevalence of shorter adaptation in dyslexia*

447 About half of our dyslexic participants showed adaptation time scales that were within the  
448 range of controls (Figs. 2-4). This partial overlap between the two groups could have stemmed  
449 from the low reliability of our measurements. Another potential source for this variability might  
450 be different types of dyslexia among our dyslexic participants, which may relate to different  
451 underlying neural mechanisms. Our standard reading tests that were used for inclusion or  
452 exclusion of participants might not have been fine-grained enough to define participants along  
453 the dimensions that map to different sources of underlying difficulties (Zoccolotti and  
454 Friedmann, 2010).

455

#### 456 *The putative functional relationship between shorter adaptation and long-term effects*

457 We only tracked the short-term effects of dyslexics' faster decay of memory trace. Therefore,  
458 we can only speculate about the relationship between these observations and dyslexics'  
459 difficulties in acquiring expert-level proficiency in reading. One putative conceptual link may be  
460 provided by the Bayesian framework, when the principle of efficient coding is introduced (Wei  
461 and Stocker, 2015). This principle predicts that more likely stimuli gradually acquire denser,  
462 more reliable representations. The gradual enhancement of the representation of more likely  
463 stimuli may be reduced in dyslexia, leading to reduced sensitivity to the specific phonological

464 and morphological forms that characterize their native language. Assessing this hypothesis  
465 experimentally requires long-term tracking of the learning of novel sound statistics.

466

## 467 **Materials and Methods**

### 468 *Participants*

469 Sixty native Hebrew speakers (30 dyslexics and 30 good readers), all of whom were students at  
470 the Hebrew University [mean age (STD) = 24.2 (5.4) years; 36 females] were recruited for this  
471 study. Recruitment was based on ads at the Hebrew University. Monetary compensation for  
472 participation was according to standard student rates. The study was approved by the Hebrew  
473 University Committee for the Use of Human Subjects in Research. All dyslexic participants had  
474 been diagnosed as having a specific reading disability by authorized clinicians. Reading related  
475 measures were also assessed in our lab (detailed in Table 1). Participants with more than 2 years  
476 of formal musical education were excluded, so that musical training would not be a major  
477 contributor to their pitch sensitivity (Micheyl et al., 2006; Parbery-Clark et al., 2011).  
478 Participants with poor Block Design scores (lower than a normalized score of 7) were also  
479 excluded from the study. All participants filled in a questionnaire regarding any neurological or  
480 psychiatric disorders. None of the participants reported any such disorders. None of them had  
481 ever participated in a similar auditory experiment in our lab.

482

483

484 *Experimental Procedure*

485 Participants were administered 4 sessions on 4 different days:

486 In session 1 participants were administered a series of cognitive assessments. 30 dyslexics and  
487 30 controls were admitted to this session.

488 In session 2 participants performed a 2-tone frequency discrimination task with a specially  
489 designed sequence of trials (Experiment 1; Fig. 1A-B). The same 30 dyslexics and 30 controls  
490 participated in this session.

491 In session 3, ERPs were recorded both passively and while performing the discrimination task.  
492 First, participants watched a silent movie while a series of single tones was presented to them in  
493 four blocks of four different Inter Stimulus Intervals (ISI) of 2, 3.5, 6.5 or 9.5 seconds  
494 (Experiment 2b), in a random order. Second, participants actively engaged in the 2-tone  
495 frequency discrimination task in four blocks with different Inter-Trial-Intervals (ITI – time  
496 interval between the second tone in the trial and first tone in the following trial) of 1.4, 2.9, 5.9  
497 and 8.9 seconds (Experiment 2a). The ISI between the two tones in the trial was 600 ms. Thus, in  
498 both passive and active conditions, the Stimulus Onset Asynchronies (SOA), i.e. the time  
499 intervals between the onset of the first tones in adjacent trials were 2, 3.5, 6.5 and 9.5 seconds. A  
500 subgroup of 25 dyslexics and 23 controls participated in this session.

501 In session 4 participants performed a fast reading task of visually presented single non-words.  
502 Voice response was recorded (Experiment 3; Fig 4A). Both rate and accuracy were obtained. 29  
503 dyslexics and 23 controls participated in this session.

504 All sessions were administered in a sound-attenuated room. Sounds and visual presentations  
505 were produced using Matlab (The Mathworks, Inc., Natick, MA). Tones were presented and

506 voice response was recorded by Psychtoolbox and Psychportaudio (Kleiner et al., 2007) through  
507 a Saffire 6 USB audio interface (Focusrite Audio Engineering Ltd., High Wycombe, UK).

508

509 *Cognitive assessments*

510 General cognitive abilities and phonological skills were assessed using standard tasks:

511 A. Non-verbal reasoning ability. This was measured with the Block Design, a standard test for  
512 assessing visuo-spatial reasoning (WAIS-III; Wechsler, 1997).

513 B. Short-term verbal memory. This was evaluated with the standard Digit Span task (forward  
514 and backward; Hebrew version of WAIS-III; Wechsler, 1997).

515 C. Phonological decoding and single word reading. Pseudo-word and single word reading were  
516 assessed using standard Hebrew lists designed by Deutsch and Bentin (1996).

517 D. Word pattern recognition. Subjects were presented with 24 pairs, each composed of a word  
518 and a pseudo-homophone, and were asked to point to the word in each pair.

519 E. Fluent reading. Subjects read an academic level passage of 150 words followed by a  
520 comprehension question.

521 F. Phonological awareness was assessed using the Spoonerism task (MacKay, 1970; Möller et  
522 al., 2007). Participants heard (Hebrew) word pairs and were asked to switch the first phonemes  
523 of the two words and respond vocally (e.g.: /laila tov/, “good night” in Hebrew, should be  
524 switched to /taila lov/).

525 In all phonological and reading tasks both accuracy and rate were scored.

526

Test	Control (STD) N=30	Dyslexic (STD) N=30	Mann- Whitney  z value
Age (years)	25.8 (3.0)	24.3 (3.1)	1.6
<b>General cognitive (scaled)</b>			
Block Design	12.4 (2.9)	12.1 (3.5)	0.3
Digit Span	11.1 (2.8)	7.8 (1.7)	4.7***
<b>Phonological Speed [items/minute]</b>			
Pseudo-word Reading Rate	58.4 (24.4)	32.2 (10.5)	4.4***
Single-word Reading Rate	96.8 (32.5)	68.3 (25.8)	3.3**
Word Pattern Recognition Rate	68.1 (15.2)	39.9 (13.5)	5.6***
Passage Reading Rate	140.4 (23.8)	97.8 (22.3)	5.7***
Spoonerism Rate	10.0 (3.0)	5.8 (3.2)	4.6***
<b>Phonological Accuracy [% correct]</b>			
Pseudo-word Reading Accuracy	89.7 (11.2)	62.4 (18.3)	5.1***
Single-word Reading Accuracy	97.1 (4.3)	87.6 (8.3)	4.8***
Word Pattern Recognition Accuracy	100 (0)	96.2 (6.4)	4.3***
Passage Reading Accuracy	98.6 (1.4)	94.8 (4.5)	4.9***
Spoonerism Accuracy	92.2 (6.8)	77.9 (18)	3.2**

527 \* $p < 0.05$ ; \*\* $p < 0.005$ ; \*\*\* $p < 0.0005$ .

528 **Table 1.** Cognitive scores for the dyslexic and control groups (mean and standard deviation).  
 529 Dyslexics differed from their good-reader peers in all phonological tasks and verbal working  
 530 memory, but not in their general reasoning skills (Mann-Whitney U tests).

531

532

533 *Stimuli for dissociating between context effects of recent versus earlier trials -*

534 *Experiment 1*

535 Participants performed 4 blocks of 150 trials of the 2-Tone Frequency Discrimination task.  
536 Each trial contained a tone pair (50 ms, 70 dB each tone; 600 ms inter-tone intervals). They were  
537 asked to indicate which of the 2 tones had a higher pitch. A short demo of 10 trials preceded the  
538 actual experiment. Feedback was provided only in the demo trials. 80% success on the 10 demo  
539 (easy) trials was a prerequisite for continuing the task. We did not administer feedback during  
540 the assessment because we did not want to affect the magnitude of the listeners' contraction bias.

541 The task was administered with a set of constant stimuli that we designed specifically for this  
542 experiment (available at: [elsc.huji.ac.il/sites/default/files/glocal\\_tones.xls](http://elsc.huji.ac.il/sites/default/files/glocal_tones.xls)). Its design allowed us  
543 to evaluate the contribution to the context effect of the most recent trial separately from that of  
544 all previous trials. Assessing these effects separately required a specifically designed sequence,  
545 since these effects are typically correlated. Specifically, the direction of the frequency distance  
546 between the first tone of the current trial and that of the most recent trial, and the direction of the  
547 distance from that tone to the average across trials, are typically correlated. In the design of this  
548 series we ensured that they were not correlated. In other words, the sign of the global context  
549 ( $G$ ):  $G(t) = \text{sign}(f_1(t) - \langle f_1 \rangle)$  and that of the recent context ( $R$ ):  
550  $R(t) = \text{sign}(f_1(t) - f_1(t-1))$ , in each trial were not correlated. In this sequence the overall  
551 contribution of both the local and global context was positive, yet small.

552

553

554 *Stimuli for assessing the impact of time intervals - Experiments 2a and 2b*

555 In the active condition (Experiment 2a) participants were administered 4 blocks of 100 trials  
556 each of the 2-tone frequency discrimination task. Each trial contained a tone pair (50 ms, 70 dB  
557 each tone; 600 ms inter-tone intervals), and listeners were asked to indicate which of the 2 tones  
558 had a higher pitch. The sequence of trials was randomly drawn for each participant. In each trial,  
559 a tone was chosen randomly from 800 Hz to 1,250 Hz. The other tone was chosen randomly-to  
560 have a frequency difference (plus or minus) between 1% and 30% from the previously chosen  
561 tone. The order of the tones was also randomly chosen. Trial onset asynchrony (TOA) was fixed  
562 for each block at 2, 3.5, 6.5 or 9.5 seconds. Block order was counterbalanced across subjects.

563 In the first, passive, part of the session (Experiment 2b), only the first tone in each pair was  
564 presented. We compensated for it by increasing the Inter-Stimulus Intervals (between the tone's  
565 offset on the previous trial and the onset of the current trial) in this condition by 0.6 sec.  
566 Consequently, the onset-to-onset intervals between first tones of adjacent events were the same  
567 in the two conditions. Subjects watched a silent movie and were asked to ignore the tones.

568

569 *Stimuli for assessing the dynamics of benefits in oral reading rate - Experiment 3*

570 Participants were presented with 6 blocks of 120 non-words and were asked to read them aloud  
571 as fast as they could. Voice onset and offset were acquired. Each non-word was presented 500  
572 ms after the voice offset of the preceding non-word. Presentation remained until the voice offset  
573 of the current non-word. Non-words were randomly generated by conjunction of two randomly  
574 chosen valid Hebrew syllables (consonant-vowel and consonant-vowel-consonant, or vice versa).

575

576 *ERP recordings and analyses*

577 Electrophysiological activity was recorded from 32 active Ag-AgCl electrodes mounted on an  
578 elastic cap using the BioSemi ActiveTwo tools and recording software (BioSemi B.V.,  
579 Amsterdam, Netherlands). Electrode sites were based on the 10-20 system (American  
580 Electroencephalographic Society, 1991). Two additional electrodes were placed over the left and  
581 right mastoids. Horizontal EOG was recorded from two electrodes placed at the outer canthi of  
582 both eyes. Vertical EOG was recorded from electrodes on the infraorbital and supraorbital  
583 regions of the right eye in line with the pupil.

584 EEG and EOG signals were sampled at 256 Hz, amplified and filtered with an analogue band-  
585 pass filter of 0.16 – 100 Hz. Offline analysis was performed using Brain Vision Analyzer 1.05  
586 software (Brain Products GmbH, Gilching, Germany) and EEGLAB toolbox for Matlab  
587 (Delorme and Makeig, 2004). The EEG signal was digitally band-pass filtered between 1 Hz and  
588 30 Hz to remove large drifts in signal and high frequency noise. ICA analysis was trained on the  
589 entire length of each block and on all scalp electrodes to identify components that reflect eye  
590 blink or eye movement evoked electrical activity. An eye related component was identified by its  
591 time-correlation with the occurrence of blinks or saccades. This relationship between the  
592 identified component and eye blink activity was verified by controlling that the component's  
593 scalp distribution was typical of eye-related electrical activity (Delorme et al., 2007). Data were  
594 referenced to the nose channel to remove external electrical influence. Artifact rejection was  
595 applied to the non-segmented data according to the following criteria: any data point with an  
596 EOG or EEG  $> \pm 100 \mu\text{V}$  was rejected along with the data  $\pm 300$  ms around it. In addition, if the  
597 difference between the maximum and the minimum amplitudes of two data points within an  
598 interval of 50 ms exceeded  $100 \mu\text{V}$ , data  $\pm 200$  ms around it were rejected. Finally, if the  
599 difference between two adjacent data points was more than  $50 \mu\text{V}$ , the data  $\pm 300$  ms around it

600 were rejected. Trials containing rejected data points were omitted from further analysis. Groups  
601 did not differ on the number of trials that were analyzed (active condition: controls:  $387 \pm 6$ ;  
602 dyslexics:  $382 \pm 5$ ;  $z = 1.6$ , *n.s.*; passive condition: controls:  $394 \pm 4$ ; dyslexics:  $394 \pm 4$ ;  $z = -0.2$ ,  
603 *n.s.*; mean number of trials  $\pm$  SEM, Mann-Whitney U tests)

604 For ERP averaging across trials, the EEG was parsed to 2,000 ms epochs starting 500 ms  
605 before the onset of the first stimulus in each pair, and averaged separately for each electrode. The  
606 baseline was adjusted by subtracting the mean amplitude of the pre-stimulus period (500-150 ms  
607 before the onset of the first stimulus in the trial) of each ERP from each data point in the epoch.  
608 The pre-stimulus baseline period was calculated from this time interval to exclude effects of  
609 anticipatory responses that preceded informative anticipated stimuli (CNV; Walter et al., 1964).

610 ERP analysis was based on the epochs that were recorded with electrode Cz (at the vertex of  
611 the scalp). This electrode measured the most prominent response to the auditory stimuli. Data  
612 from each acquisition session were analyzed separately. The magnitude of the ERP components  
613 was calculated as the area under the curve between 70 ms and 130 ms after first tone's onset for  
614 N1 and 150-250 ms time range for P2. We repeated the entire analysis for adjacent electrodes  
615 (Fz, FC1, FC2, C3, C4, CP1, CP2 and Pz) and found similar results.

616

### 617 *Estimation of the dynamics of recovery from adaptation*

618 Context effects and ERPs in each of the four different ITIs (experiment 2) were fitted with an  
619 exponential decay model for each participant separately. This model was previously used to  
620 characterize the decay of context effects both behaviorally and for MEG measurements (Lu et  
621 al., 1992; Sams et al., 1993). In a previous study, the effect of context as a function of number of  
622 trials back was quantitatively measured and indeed resembled an exponential decay (Raviv et al.,

623 2012). Following that quantitative description, we found that the exponential decay of previous  
624 trials captures context effects on this task (Jaffe-Dax et al., 2015). In the current study we  
625 modeled the impact of previous trials as a function of the temporal interval instead of number of  
626 trials. The model,  $\alpha + \beta \exp(-t/\tau)$ , had three parameters:  $\alpha$  – asymptote after recovery; i.e.,  
627 the value expected when  $t \rightarrow \infty$ ,  $\beta$  – the magnitude of adaptation; i.e., the value expected at  
628  $t = 0$  minus  $\alpha$ ,  $\tau$  – time constant of adaptation; i.e., the time it takes for the measure expected  
629 at  $t = 0$  to decay to  $1/e$  (~37%) of its initial value. A small  $\tau$  indicates fast decay and a large  $\tau$   
630 indicates a slow decay.

631 Formally, we searched for the triplet of parameters that minimizes the squared difference  
632 between the data and the model prediction: The units of  $\alpha$  and  $\beta$  are those of the fitted measure  
633 ( $d'$  for behavioral bias,  $\mu V X msec$  for ERP). In the passive condition,  $t$  is the Inter-Stimulus  
634 Interval (ISI) between the offset of a tone and the onset of the consecutive tone. In the active  
635 condition,  $t$  is the Inter-Trial Interval (ITI) between the offset of the second tone and the onset of  
636 the first tone in the consecutive trial. Fitted parameters were estimated by minimizing the  
637 squared error of the exponential decay model in a limited range. For the ERP adaptation, limits  
638 were from 0 to 15,000 for  $\alpha$  and from -15,000 to 0 for  $\beta$ . For the  $d'$  difference, the limits were  
639 from 0 to 100 for  $\alpha$  and  $\beta$ . For both measures,  $\tau$  was limited to be from 0 to 100 seconds. The  
640 groups did not differ on the exponential curve's Goodness-of-Fit for any of the analyzed  
641 measurements ( $z < 1.8$ , n.s. Mann-Whitney U tests). The exponential decay model captured the  
642 ERP adaptation decay well for both groups ( $R^2 > 0.4$ ). The model was less able to account for the  
643 behavioral bias decay, especially for controls ( $R^2 = 0.2$ ), suggesting a more complex mechanism  
644 than could be well described by a single exponential decay.

645 For purposes of compatibility with our previous studies (Raviv et al., 2012; Jaffe-Dax et al.,  
646 2015) and to avoid assumptions of normal distribution, we used conservative, non-parametric  
647 tests, throughout the study. Using standard parametric tests yielded similar statistical  
648 significance.

649

## 650 **Conflict of interests**

651 The authors declare no competing financial interests.

652

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