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In search for the relevant space of implicit memory deficit in dyslexia

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Abstract

Studies of dyslexics, whose implicit memory is impaired, suggest that their implicit inference of sound statistics and its integration into perception is inefficient. Specifically, dyslexics' implicit memory decays faster and consequently only accumulates information over shorter temporal windows. We now ask whether this abnormal dynamic is domain general by measuring its cortical distribution. We measure the dynamics of behavioral context effects and the concurrent neural adaptation during fast acquisition fMRI. We find a similar pattern of fast decay of adaptation across a broad range of cortical areas, though most significant effects are found in auditory cortex. This broad neural distribution suggests that the relevant aspect of implicit statistical inferences is not the nature of stimuli, but their temporal distribution.

Keywords: implicit memory; adaptation; fMRI; dyslexia, anchoring hypothesis of dyslexia; Bayesian inference; statistical learning.

Background

Implicit statistical learning has a profound measurable effect on performance in perceptual discrimination tasks. Seemingly simple and unbiased, serial discrimination places an asymmetric memory load on sequentially presented stimuli. The stimulus presented first has the highest memory load, since it needs to be retained until the subsequent stimulus is presented. Hence, relying on priors to compensate for noisy representations is crucial for accurately inferring the perceived stimulus. Priors can be utilized to modify noisy representations into a maximum likelihood estimate of stimuli, those based on previous exposures that led to the formation of priors. The integration of priors has been modeled computationally in the context of auditory perception for signal detection tasks (Treisman & Williams, 1984) and recently for 2-tone frequency discrimination (Raviv et al., 2012, 2014; reviewed in Bausenhardt, Bratzke, & Ulrich, 2016). Raviv et al. (2012) model asserts that participants do not compare the representations of the first and second tones, as requested to do and as they introspectively do. Rather, they compare the representation of the second tone to the integrated representation of the first tone with the estimated mean (prior) of previous stimuli. Thus, the representation of the first tone is contracted towards the mean of previous trials, and when this contraction is in

the direction of the correct response, the success rate will increase.

Accordingly, trials in this serial discrimination task can be divided into those in which contraction increases the perceived difference between the two stimuli, hence increasing success rate (*Bias+*), and trials in which contraction decreases the perceived difference, and decreases the success rate (*Bias-*). The magnitude of the contraction can be quantified as the difference in performance on these two types of trials.

Contraction bias in serial comparison tasks has been observed in the visual (Ashourian & Loewenstein, 2011; Fischer & Whitney, 2014; Lages & Treisman, 1998; Liberman, Fischer, & Whitney, 2014), auditory (Lu, Williamson, & Kaufman, 1992; Raviv et al., 2012; Treisman & Williams, 1984) and tactile (Hairston & Nagarajan, 2007) modalities, and was even observed in tactile velocity discrimination tasks in rats (Fassihi, Akrami, Esmaeili, & Diamond, 2014) and vibro-tactile discriminations in monkeys (Romo, Hernández, Zainos, Lemus, & Brody, 2002).

Dyslexia is a wide spread learning disability which poses an obstacle in acquiring academic education. It is probably the most prevalent learning disability. Defined as a “specific and significant impairment in the development of reading skills that is not accounted for by mental age, visual acuity problems, or inadequate schooling” (WHO, 2010), it affects 5% of the world’s population (Lindgren, De Renzi, & Richman, 1985).

Dyslexics are diagnosed by their reading difficulty but are also consistently found to have difficulties in non-linguistic perceptual tasks (McAnally & Stein, 1996; Sperling, Lu, Manis, & Seidenberg, 2005). Specifically, dyslexics exhibit poorer utilization of implicit memory to compensate for noisy observation (Ahissar, Lubin, Putter-Katz, & Banai, 2006; Jaffe-Dax, Raviv, Jacoby, Loewenstein, & Ahissar, 2015; Oganian & Ahissar, 2012). We recently accounted for this deficient memory usage by faster recovery from neural adaptation, as measure in Event Related Potential (ERP; Jaffe-Dax, Frenkel, & Ahissar, 2017). Importantly, dyslexics also exhibit poorer utilization of implicit memory in visual discrimination tasks (Jaffe-Dax, Lieder, Biron, & Ahissar, 2016). Namely, their implicit memory impairment is not modality-specific, but rather general multi-modal.

Importantly, even in linguistic tasks, compared to good readers, dyslexics perceptual performance is adequate when the stimuli are equally unfamiliar to both groups, and only differ from peers in familiar contexts (Perrachione, Del Tufo, & Gabrieli, 2011). This accumulative body of research stands in contrast to both the traditional phonological deficit theory of dyslexia (Snowling, 2000) and the claim for dyslexics' overall noisy neural representation (Hancock, Pugh, & Hoeft, 2017).

Implicit memory is an inaccessible cognitive module which has precise resolution, large capacity and long term retention (Schacter, 1987). Contemporary studies define implicit memory as a memory which does not depend on Medio-Temporal lobe activity, or inaccessible to subject's awareness. This negative definition has been recently challenged by a general theory of wide-spread cortical plasticity in response to perceived events (Reber, 2013). Implicit memory utilization has been recently quantified using a heuristic approximation of Bayesian inference in simple perceptual task (Raviv et al., 2012). This well-defined grounded model of high level cognitive aptitude paved a way for a search for well-defined neural mechanism which would give rise to implicit memory.

While neural adaptation has a long history of research and has been studied intensively in human and animals (Khoury & Nelken, 2015), its cognitive role and behavioral implication are yet poorly understood. The time scale of recovery from neural adaptation has been linked with the time scale of implicit memory trace (Lu et al., 1992). Our preliminary findings of fast decay suggest that this rate of decay of adaptation is a crucial machinery for statistical learning. Though traditionally adaptation was considered as reflecting fatigue, we gradually understand that it is used for statistical learning and updating of categories (Kleinschmidt & Jaeger, 2016).

In the current study, we used fMRI to localize dyslexics' cortical site of fast decay of adaptation. We expected that, if their deficit was specific to speech sounds, the difference in dynamics would affect only specific areas of the temporal lobe, and perhaps also some parietal areas. However, if their deficit was domain general, then all areas activated by these stimuli would show a similar pattern compared with controls.

Our results show, that all active regions exhibit faster recovery from adaptation among dyslexics. We also found additional support to the relation between implicit memory and the time-scale of recovery from adaptation by replicating the parallel finding of shorter adaptation and shorter implicit memory in a special population - dyslexics. Our findings suggest that neural adaptation in cortical areas that correspond to the specific perceptual event carries implicit memory.

This current study shows that dyslexics' implicit memory impairment is dictated by the dynamic decay of their representation throughout the cortex and not by a modality-specific difficulty.

Results

We administered two-tone frequency discrimination to 20 dyslexics and 19 good readers in four conditions of trial intervals: 3, 6, 9 and 15 seconds (trial onset to trial onset; TOA). Implicitly, the representation of the first tone is degraded and contracted towards the mean of previously experienced tones (contraction bias). In *Bias+* trials this bias extended the perceived difference between the current pair and improve their detectability; while in *Bias-* trials this bias decreased the perceived difference between the current two tones and hence hampered performance (Raviv et al., 2012). We previously found that this implicit memory impact decayed with the extension of inter-trial intervals – it was weaker in conditions of longer inter-trials intervals than in conditions with short inter-trial intervals (Jaffe-Dax et al., 2017). We measured implicit memory as the difference in sensitivity (d') between *Bias+* and *Bias-* trials and modelled its decay using an exponential decay: $\Delta d'(TOA) = a + b \exp(-TOA/\tau)$, where a denotes the estimated $\Delta d'$ at $t \rightarrow \infty$ (asymptotic level); b denotes the difference between the $\Delta d'$ at $t = 0$ and at $t \rightarrow \infty$ (decay magnitude); τ denotes the time it takes for $\Delta d'$ (at $t = 0$) to decay to $1/e$ (~37%) of its initial value (temporal slope parameter). A small τ indicates fast decay.

In this current study, we replicate faster implicit memory decay among dyslexics outside of the magnet (in a training session), but surprisingly not in-scan. In the training session dyslexics' implicit memory decay was faster than controls' (group $\tau \pm$ IQR: controls: 2.3 ± 3.4 ; dyslexics': 0.4 ± 0.4 ; $z = 2$, $p < 0.05$, Mann-Whitney U-test). Figure 1 shows the difference in d' between the trials that benefit from prior integration and trials that loose from it as a function of inter-trial interval. For both groups, we did not observe a significant decay of implicit memory in the scanner. Perhaps the scanner noise forced the subjects to compensate for their noisy perception in all TOA conditions.

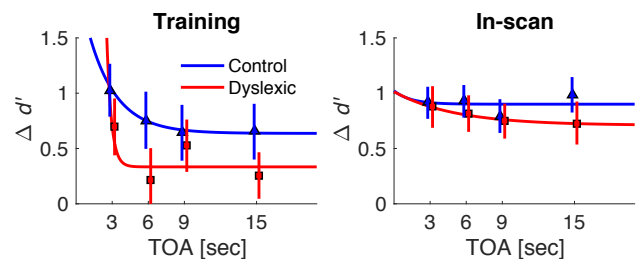


Figure 1. Implicit memory decay is faster among dyslexics in the training session, but not in-scan. Controls in blue; dyslexics in red.

We expected an attenuation of neural activity in the conditions with short inter-trial interval relative to the conditions with long inter-trial intervals, as neural adaptation decays. Specifically, we fitted their BOLD activity in the four ITI conditions to an exponential decay model ($\beta(TOA) = a + b \exp(-TOA/\tau)$) and searched for regions in which the

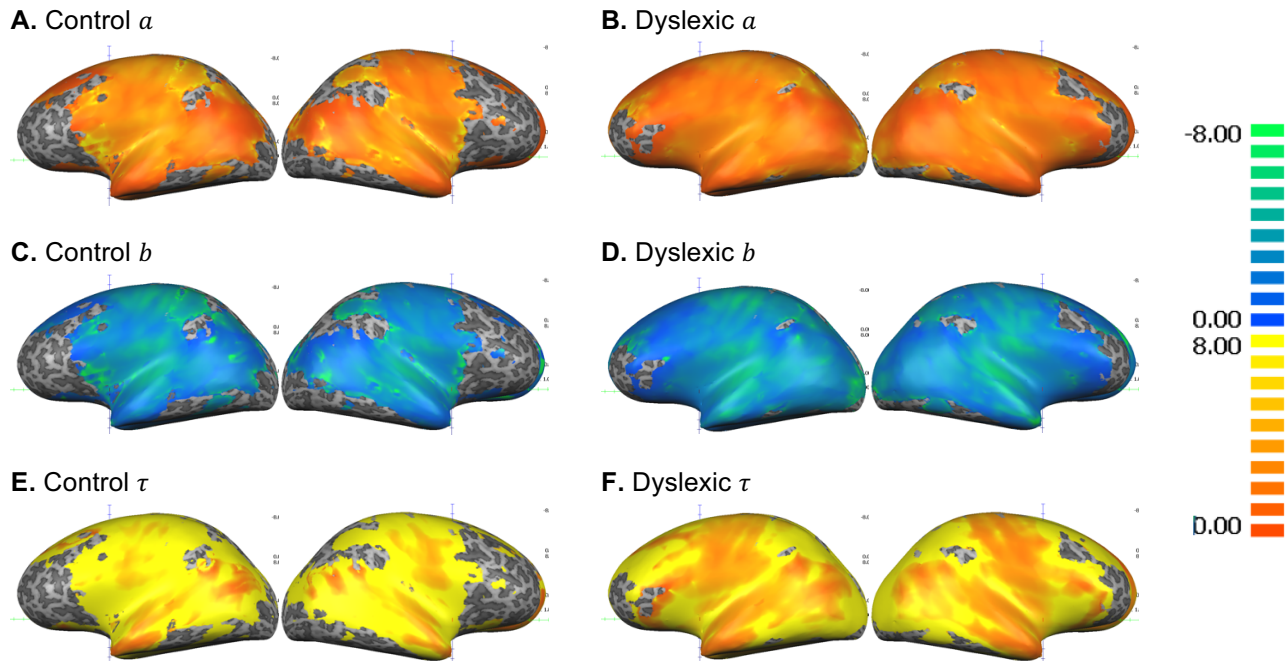


Figure 2. Estimated groups' model parameters for exponential BOLD decay across the cortex. **A.** Controls' asymptote level (*a*). **B.** Dyslexics' asymptote level (*a*). **C.** Controls' magnitude of decay (*b*). **D.** Dyslexics' magnitude of decay (*b*). **E.** Controls' decay time (τ). **F.** Dyslexics' decay time (τ).

model parameters (*a*, *b* or τ) differed significantly between the groups. Figure 2 shows the average groups' parameters of the exponential decay model. Throughout the cortex, dyslexics' estimated decay rate was faster than controls' (i.e. shorter τ). This confirms our prior hypothesis regarding their faster recovery from adaptation. Unexpectedly, the asymptote level (*a*) of the model also differed between the groups. Specifically, the overall BOLD level of controls was higher than dyslexics'. This could be attributed to overall lower signal-to-noise ratio in dyslexics' BOLD signal, but surely worth further investigation and verification.

We compared the individually estimated parameters of BOLD decay between the groups and found that the decay time differed significantly in the left primary auditory cortex (group $\tau \pm$ IQR: controls: 25.4 ± 990.9 ; dyslexics': 9.1 ± 113.2 ; $z = 2.2$, $p < 0.05$, Mann-Whitney U-test). Unexpectedly, the asymptotic level differed significantly in this region (group $a \pm$ IQR: controls: 10.4 ± 298 ; dyslexics': 9.1 ± 113.2 ; $z = 2.5$, $p < 0.05$), in the left central gyrus (controls: 7.7 ± 230.9 ; dyslexics': 3.9 ± 12.5 ; $z = 2$, $p < 0.05$) and in the right ventral frontal cortex (controls: 6.6 ± 180.1 ; dyslexics': 2.2 ± 55 ; $z = 2.1$, $p < 0.05$, Mann-Whitney U-tests). Figure 3 shows the clusters which revealed significant difference in estimated parameters between the groups.

These significant group differences were mostly apparent in the cortical regions that are known to be most active during this task (Daikhin & Ahissar, 2015). Recent study with multiple types of stimuli reported reduced stimulus specific adaptation in dyslexics across all related cortical regions (Perrachione et al., 2016). In line with these findings, we

argue that shorter time scale of recovery from adaptation is a general property of dyslexics' cortex, which accounts for their shorter retention of implicit memory.

Discussion

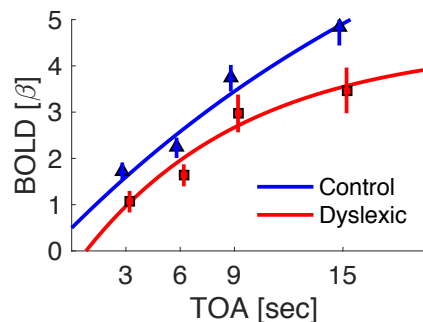
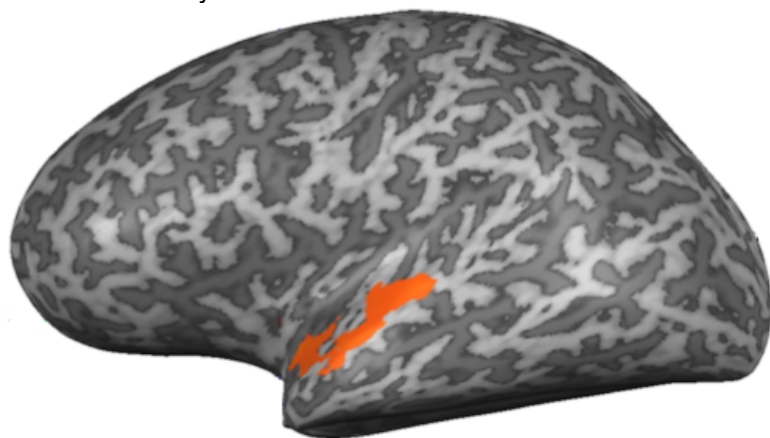
Adaptation is a simple, well defined candidate for the neural basis of implicit memory. Assuming a labelled line of input units, adaptation from previous stimuli should attenuate responses to upcoming stimulus as a function of its proximity to the previous stimuli. This proximity has both temporal and parametric dimensions, such that similar stimuli should yield a more attenuated response than dissimilar stimuli, and rapid repeating stimuli should yield a more attenuated response than slow repetitions.

In this work, we have presented evidence that neural adaptation in modality specific cortical region decayed faster in a special population of subjects, who also exhibited faster decay implicit memory to the same modality. Taken together, these parallel findings support the purposed model for implicit memory.

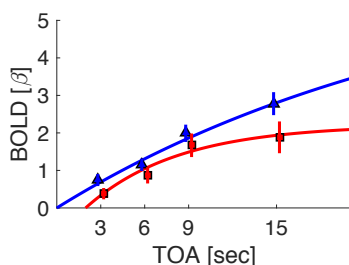
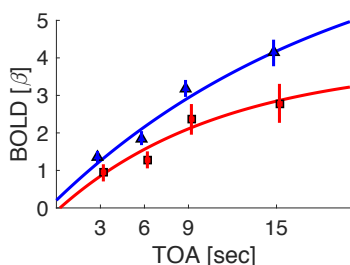
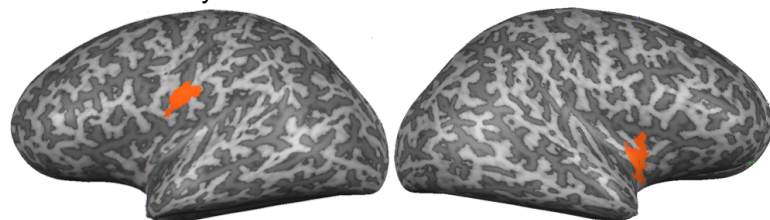
A recent imaging study compared adaptation to similar stimuli within a category among dyslexics and good readers. Our suggestion is in line with the researchers' findings of deficient adaptation in dyslexics in every category-specific cortical region that was measured (Perrachione et al., 2016).

Our findings suggest that the property of adaptation which is impaired in dyslexics is the temporal dimension rather than the similarity between stimuli. Namely, their adaptation decay as a function of time and not as a function of representational similarity (which was recently found intact

A. Control $\tau >$ Dyslexic τ



B. Control $a >$ Dyslexic a



z value

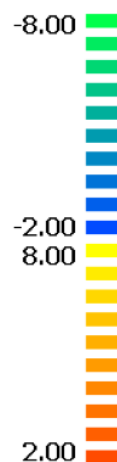


Figure 3. Group effect in estimated decay model parameters. **A.** Controls’ estimated decay time (τ) was longer than dyslexics’ in superior temporal gyrus. **B.** Controls’ estimated asymptote level (a) was higher than dyslexics’ in central sulcus and in ventral frontal cortex.

in dyslexics ;Boets et al., 2013). Thus, it is this dynamic feature that governs implicit memory skills and deficits.

Methods

The demographic, cognitive and reading assessments of this cohort is described in Jaffe-Dax et al., 2017.

In the two-tone frequency discrimination task, subjects were asked to indicate which of the two tones had a higher pitch. The tones were drawn from a uniform distribution between 800-1250 Hz and the frequency difference within each pair was randomly drawn between 1-20%. Each subject performed 12 blocks of 16 trials. Each block had a constant Trial Onset Asynchrony (TOA) of 3, 6, 9 or 15 seconds (in random order). Subjects performed the task outside of the scanner (training) and in-scan.

Stimuli were digitally constructed using Matlab 2015b (The Mathworks Inc., Natwick, MA) and administered

through inserted sound attenuating MR compatible S14 earphones (Sensimetrics Corporation, Malden, MA).

Prior to the functional scan, a high-resolution ($1 \times 1 \times 1$ mm resolution) T1-weighted magnetization-prepared rapid acquisition gradient-echo (MPRAGE) images were acquired using a 3-T Magnetom Skyra Siemens scanner and a 32-channel head coil, at the ELSC Neuroimaging Unit (ENU). The functional MRI protocols were based on a multislice gradient echo-planar imaging and obtained under the following parameters: TR = 1 s, TE = 30 ms, flip angle = 90° , imaging matrix = 64×64 , field-of-view = 192 mm; 42 slices with 3 mm slice thickness and no gap, were oriented in AC-PC plane, covering the whole brain, with functional voxels of $3 \times 3 \times 3$ mm and multiband parallel imaging with acceleration factor = 3 (Moeller et al., 2010).

Each condition was modelled separately to account for its contribution to the measured BOLD signal in each voxel, i.e., its β values for each TOA condition. A spherical searchlight with 4 voxels radius was performed centered at each voxel to

average β values for each condition. An exponential decay model (see Results) was fitted to the smoothed β values and its parameters were estimated for each center voxel.

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