Does neuronal recycling result in destructive competition?

The influence of learning to read on the recognition of faces

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Abstract

Written language, a human cultural invention, is far too recent for dedicated neural infrastructure to have evolved in its service. Culturally newly acquired skills (e.g. reading) thus ‘recycle’ evolutionarily older circuits that originally evolved for different, but similar functions (e.g. visual object recognition). The destructive competition hypothesis predicts that this neuronal recycling has detrimental behavioral effects on the cognitive functions a cortical network originally evolved for. In a study with 97 literate, low-literate, and illiterate participants from the same socioeconomic background we find that even after adjusting for cognitive ability and test-taking familiarity, learning to read is associated with an increase, rather than a decrease, in object recognition abilities. These results are incompatible with the claim that neuronal recycling results in destructive competition and consistent with the possibility that learning to read instead fine-tunes general object recognition mechanisms, a hypothesis that needs further neuroscientific investigation.

Learning to read has a profound impact on people's lives, changing not just their socioeconomic perspectives, but how they relate to the world. The broad significance of literacy has led researchers to investigate the cognitive (e.g., Dehaene et al., 2015; Huettig et al., 2018) and neural (e.g. Carreiras et al., 2009; Dehaene et al., 2010; Hervais-Adelman et al., 2019; Skeide et al., 2017) processes that underlie the acquisition of this culturally transmitted, evolutionarily very recent skill. A hallmark finding is that in literates a region in the left occipito-temporal lobe becomes specialized for the processing of the visual word forms (hence labeled visual word form area, VWFA, Cohen et al., 2002; cf. Price & Devlin, 2003). This 'specialization' is not unusual; the region is located near other high-level visual cortical areas that respond selectively to specific visual categories (e.g., faces, tools; Dehaene et al., 2010). Given that categories such as faces have had considerable evolutionary relevance for our species for a long time, it is not surprising that the brain has evolved dedicated cortical networks to process them effectively. Written language, however, poses an interesting puzzle as human writing systems have only been invented over the last 6000 years, which is too recent for a dedicated cortical system to have evolved in its service.

To account for this phenomenon, researchers have invoked the notion of neuronal recycling, according to which acquiring cultural skills involves the re-purposing of circuits related to evolutionarily older but similar functions (Dehaene & Cohen, 2007). There is strong experimental support for this general notion, the exact mechanisms of this repurposing of preexisting cortical mechanisms however are hotly debated (e.g., Carreiras et al., 2009; Dehaene-Lambertz et al., 2018; Hervais-Adelman et al., 2019).

According to the initial formulation of the neuronal recycling hypothesis, reading acquisition involves destructive competition in the form of an 'invasion' into neuronal space that was formerly specialized for the processing other visual categories, such as faces or tools (Dehaene & Cohen, 2007). Different visual categories are assumed to compete for limited neuronal resources and the acquisition of a new category encroaches upon populations of neurons that previously performed similar computations. The converse possibility is that neuronal recycling results in a general fine-tuning of object recognition mechanisms and enhanced responses to other visual categories in the ventral visual system surrounding the VWFA (Hervais-Adelman et al., 2019).

Previous fMRI studies with participants with varying literacy level, using very similar visual stimuli, have reported contradictory findings (some evidence in line with destructive competition, Dehaene et al., 2010, but also for general fine-tuning of object recognition, Hervais-Adelman et al., 2019). Here we conducted behavioral tests to distinguish the two accounts. Behavioral testing is crucial because a main prediction of destructive competition is that it entails "small losses in perceptual and cognitive abilities due to competition of the new cultural ability with the evolutionarily older function in relevant cortical regions" (Dehaene & Cohen, 2007). By contrast, the visual fine-tuning view predicts that additional training of low-level visual circuits on complex visual stimuli during reading also benefits recognition in other visual categories. It thus predicts that reading acquisition is associated with similar or better performance in tasks that involve other visual categories. We tested object recognition memory of different categories (faces, cars, and bicycles) in a large-scale study with illiterates, low-literates, and literates of Tamil script in Chennai, India.

Discussion

Our findings are incompatible with destructive competition and consistent with neuroimaging evidence (Hervais-Adelman et al., 2019) that learning to read may fine-tune object recognition mechanisms, namely, that reading acquisition results in increased sensitivity to visual stimuli in addition to reading-related enhanced attentional and oculomotor capacities (Kastner et al., 2004; Skeide et al., 2017).

Importantly, the comparatively better object recognition abilities of literates than illiterates appear to be directly related to reading acquisition and are very unlikely to be a secondary effect of literacy such as increased verbal working memory (Demoulin & Kolinsky, 2016; Smalle et al., 2019) or general cognitive ability or familiarity with test taking, since in the present study we regress out common variance associated with these traits. To more directly assess causality, further investigation of the results from the present large-scale cross-sectional study with a longitudinal design would be beneficial (cf. Goswami, 2015; Huettig et al., 2018). The positive relationship between reading ability and object recognition memory in the present study casts serious doubts on the viability of the destructive competition hypothesis. Whereas the competition hypothesis views the brain as a system with finite processing resources that different functions are competing for, the present findings raise the intriguing possibility that a remarkable capacity of the brain is to support new abilities in such a way that related older abilities can be enhanced rather than impaired. Further behavioral and neuroscientific research could explore this possibility in more detail, for instance whether literates' better object recognition abilities are related to shared (neural) processing between face and word reading as both skills require sophisticated foveal processing.

Methods

Participants

97 participants were recruited through a nongovernmental organization (NGO) working to improve living conditions for people of lower socioeconomic status in Chennai, capital city of Tamil Nadu state, India. 35 participants were registered with the NGO as illiterate, 30 were registered as low-literate, and 32 were registered as literate. We originally set a target of 30 participants per group as the maximum feasible sample size in the time available on site; that slightly more illiterate and literate participants took part is due to varying numbers of illiterate, low-literate, and literate participants being available on any given day. The groups were matched for age and socioeconomic status, but there was a marked difference in the average number of completed years of education between the three groups (see Table 1 in supplementary online materials). Participants were allowed to wear glasses or contact lenses. The tests reported below were conducted as part of a larger battery of tests that took each participant approximately three hours to complete. Participants received 2400 INR (roughly equivalent to 30 Euro) as compensation for their participation, equivalent to about two months' pay at the mean salary in our sample.

Design and procedure

In order to apply a conservative test of the behavioral consequences of literacy on object recognition we selected participants with differing literacy from the same communities and socio-economic backgrounds and statistically corrected reading proficiency for cognitive ability and familiarity with formal test-taking settings. For this purpose, we collected word and pseudoword reading scores to assess the reliability of participants' self-reported literacy status, as well as measures of non-verbal intelligence (Raven's Progressive Matrices, Bilker et al., 2012; Raven, 1938) and working memory (digit span) to enable us to statistically control for participants' secondary effects of literacy such as working memory and general cognitive ability.

All tasks were administered using a laptop computer to record participant responses, with spoken instructions prerecorded in Tamil and played automatically for each participant to ensure that literate and illiterate participants received identical instructions in a format that they could understand. Items in the visual tasks were displayed on the laptop screen in a size corresponding with roughly 5 degrees of visual angle.

Word reading. The word reading section of the test battery consisted of word and pseudoword reading. For both words and pseudowords, participants were given 60 seconds to read up to 100 items from a list presented on paper. Responses were recorded and scored for number of words read correctly. A native speaker of Tamil designed the Tamil pseudowords used in this task to ensure all pseudowords were phonotactically legal. Response scoring was also performed by a native speaker.

Digit span. Forward and backward digit span tasks were conducted to assess the working memory capacity of the participants. For both forward and backward digit span, the participant heard a series of numbers sequences. The sequences increased in length from 2 numbers to 10 numbers for forward digit span and from 2 numbers to 8 numbers for backward digit span. Number sequences were pre-recorded in Tamil by a native Tamil speaker. After each number sequence was presented, participants repeated back the sequence in the original order (for forward digit span) or in reverse order (for backward digit span). Each task was stopped when participants made two mistakes consecutively. Responses for both forward and backward digit span were recorded and scored based on the longest sequence repeated correctly before the task was stopped.

Raven's Progressive Matrices. General cognitive ability was measured using the Raven's Standard Progressive Matrices task (Raven, 1938). Because of time constraints we used a shortened version constructed by Bilker and colleagues (2012) by selecting two lists of nine items from the original, redundant list of 60 items using item-response theory to ensure that sensitivity is preserved. Our task consisted of both nine-item lists; each list was presented as a block of items in order of increasing difficulty. Raven's SPM items consist of a display of a visuospatial pattern from which a section is missing. Participants must select the section that best fits in the empty spot from a multiple choice (6 or 8 options) display of possible replacement sections. Answer options are traditionally numbered, with responses delivered using a keyboard or in writing. To adapt this paradigm for illiterate participants, we presented the answer options with colored labels that corresponded with colored keys on a keyboard.

Cambridge Recognition Memory Tasks. The Cambridge Face Memory Task (Duchaine & Nakayama, 2006), Cambridge Car Memory Task (Dennett et al., 2012), and Cambridge Bicycle Memory Task (Dalrymple et al., 2014), which we collectively refer to as the Cambridge Recognition Memory Tasks (CRMT), are a set of tasks meant to test object recognition memory. Participants are first familiarized with six different items (either faces, cars, or bicycles) through a series of practice questions in the following format:

1. A single target item is presented three times: Once rotated 30 degrees to the left, once head on, once rotated 30 degrees to the right. Each of these presentations lasts three seconds.

2. A display of three items is presented, one of which is the previously presented item. Participants are instructed to select the previously presented item with a keypress.

Step 2 is repeated three times per target item. The sequence is repeated six times with different items, so the participant is familiarized with six target items. Object recognition for these six target items is then tested using the following format:

1. A display of all six target items is presented for 20 seconds, with the instruction to memorize these items.

2. A display of three items is presented, one of which is an item presented in the memorization display. Participants are instructed to select the memorized item with a keypress.

Step 2 is repeated 30 times.

The test phase consists of two parts. In the first half the memorization display and test display images are drawn from the same set. In the second half, the procedure is repeated as described above, but Gaussian visual noise is added to the answer slide images to increase the recognition difficulty.

The usual format for the CRMT is to have written instructions presented on-screen and response options labeled with numbers that participants then press on a keyboard. Presenting written instructions and numerals to illiterate participants is not possible, so we adapted the task to illiterates by replacing the written instructions with prerecorded instructions in Tamil, replacing the on-screen response labels with (primary) color swatches, and putting corresponding color patches on the physical response keys.

Statistical modeling. Statistical analyses were performed using Bayesian linear and logistic (where appropriate) mixed-effects regression implemented with the BAMBI package for Python, using the PyMC3 backend. We placed moderately regularizing priors on both fixed and random effects, in the form of narrow ($\sigma = .2$ on a partial correlation scale) zero-centered normal distributions. Models were estimated by Markov Chain Monte Carlo sampling, using the No-U-Turn Sampler (NUTS). The starting point for the Markov Chains was obtained through Automatic Differentiation Variational Inference (ADVI). Four chains were run for 2500 tuning samples, after which 5000 posterior samples were obtained per chain, for 20000 posterior samples in total per model. For each experiment, we fitted models with various permutations of effects and performed model selection based on model fit. The nature of the predictor matrix for the models predicting CRMT scores (no items repeated across categories; adjusted reading score as a between-participants predictor) meant that the data did not support even a minimal random effects structure. For the CRMT scores we therefore fitted only various permutations of fixed effects and their interactions. In the interest of parsimony, model fits were compared using Leave-One-Out Information Criterion with Pareto-Smoothed Importance Sampling (PSIS-LOOIC), a Bayesian index of model fit that penalizes model complexity. Sampling diagnostics indicate no sampling problems for the selected model (*minimum* $n_{effective} > 8000$, $r_{hat} < 1.001$). Full details on model comparison and the full range of models considered can be found in the Supplementary Materials.

Data and code availability

Data and code for fully reproducing all analyses in this manuscript are available online at https://doi.org/10.5281/zenodo.3543572. Additionally, the behavioral test suite administered to participants in this study is also available online at https://doi.org/10.5281/zenodo.3543296.

Results

Object recognition memory was assessed in Tamil illiterates, low-literates and literates (see supplementary materials for the relationship between self-reported literacy and reading scores) to test whether literacy acquisition comes with a cost for other visual categories, such as faces. Participants performed the Cambridge Face Memory Task (Duchaine & Nakayama, 2006), Cambridge Car Memory Task (Dennett et al., 2012), and Cambridge Bicycle Memory Task (Dalrymple et al., 2014), collectively referred to as the Cambridge Recognition Memory Tasks (CRMT). In these tasks, participants see arrays of six target items (faces, bicycles, cars, in separate blocks) and are then presented with three items one of which appeared in the six-item arrays. Their task is to select that item. In the second half of the task, Gaussian noise is added to increase difficulty.

Adjusting reading scores

As expected for different, but related measures of cognitive ability, participants' Raven's Progressive Matrices scores and digit span are moderately correlated (ρ = .48, see Figure 1). Both Raven's Progressive Matrices scores and digit span are also moderately correlated with Tamil word reading score (ρ = .51 for both measures, see Figure 1). These correlations indicate common variance between the three tasks. Previous research suggests that literacy is associated with increased verbal working memory (Demoulin & Kolinsky, 2016; Smalle et al., 2019) and Raven's scores (Hervais-Adelman et al., 2019; Skeide et al., 2017). However, despite poverty and other socioeconomic factors being the main reasons for illiteracy in India, it cannot be conclusively ruled out that 'literacy-unrelated' general cognitive ability and familiarity with formal test-taking settings underlie some of the common variance between Raven's, digit span, and reading scores. To solve this issue, and to achieve a strong test of our experimental hypothesis, we regress out common variance attributable to general cognitive ability and familiarity with test-taking, whilst preserving the variance that is uniquely associated with literacy. To adjust the raw (contaminated) reading scores, we construct a Bayesian binomial (generalized linear) mixed-effects model to predict the proportion of correctly read words and pseudowords in the reading task from the proportion of correct responses in the Raven's Progressive Matrices task and the mean of forward and backward digit span. After fitting the model, we extract the means of the posterior samples for the by-participant intercepts from this model for use as predictors in the statistical model for the Cambridge Recognition Memory Tasks. In line with our expectations, the new, adjusted reading score is no longer correlated with the cognitive ability measures (ρ = .03 for Raven's, ρ = .02 for digit span, see Figure 1) but still strongly correlated with the original, unadjusted reading score (ρ = .71).

Full details on the model fitting procedure and the construction of the Raven's and digit span predictors can be found in the Supplementary Materials.

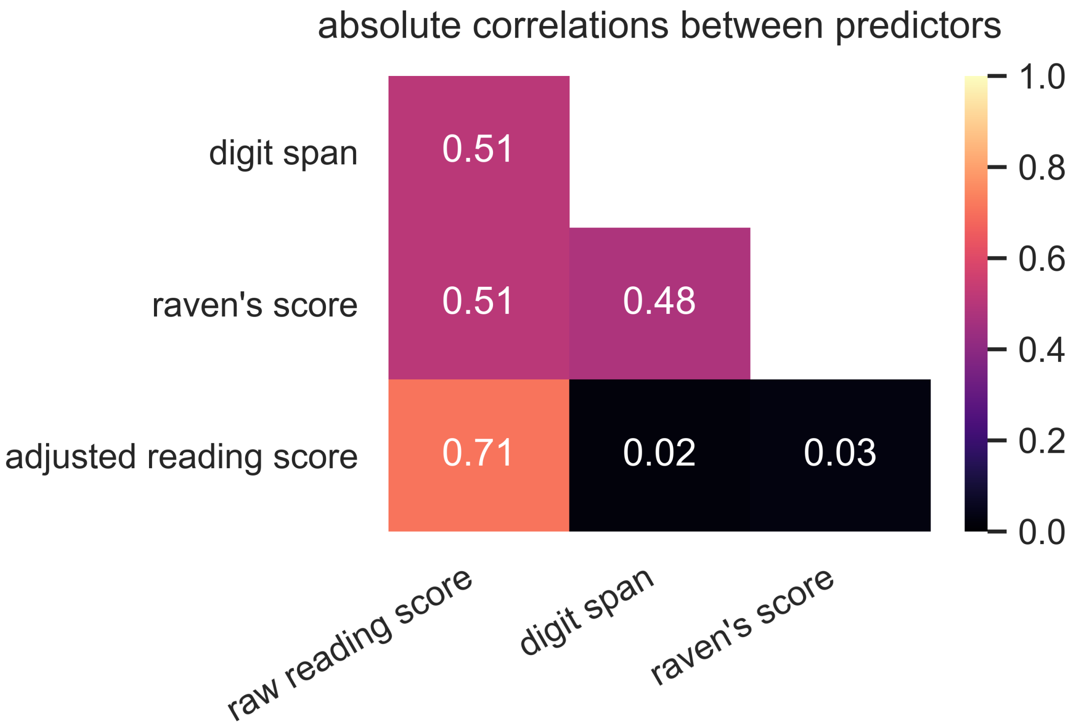

Figure 1. *Heatmap of absolute correlations between uncorrected and literacy-corrected predictors.*

Relationship between literacy and object recognition memory

For modeling the association between literacy and performance on the Cambridge Recognition Memory Tasks, we take each trial as a Bernoulli trial, using a Bayesian generalized linear model to predict the odds of successfully answering a given trial. We pool the data from all three tasks (bicycles, faces, and cars), creating a dummy coded predictor for each task. Similarly, we create dummy coded predictors for the visual noise and no visual noise conditions. Which conditions are used as reference levels in our analysis is arbitrary and does not affect our results, since we compute conditional effects post-hoc for each condition from posterior samples.

Based on model comparisons using Pareto-Smoothed Importance Sampling Leave-One-Out Information Criteria (PSIS-LOOIC), we select a model with the predictors *visual noise, object category,* and *adjusted reading score* and the interactions between *visual noise* and *object category.*

The main result is that higher reading scores are associated with higher recognition memory scores (see Fig. 2). Crucially, this is the case both for the raw and the adjusted reading scores; even when regressing out variance that can be attributed to general cognitive capacity and test-taking familiarity, there is no evidence for decreased object recognition abilities in literates. Rather, literacy is associated with slightly better object recognition; a result that contrasts with the central tenet of the destructive competition hypothesis that literacy acquisition has detrimental effects on other visual abilities such as face recognition (Dehaene & Cohen, 2007). This result is consistent with the visual fine-tuning account of neuronal recycling and with recent evidence for enhanced responses to visual stimuli around the VWFA and in early visual cortex (Hervais-Adelman et al., 2019). Because the model selection prefers a model with a single slope for literacy across all visual categories, we observe a positive relationship between literacy and object recognition memory for all visual categories (faces, bicycles, and cars; see supplementary materials).

An additional, possibly cultural effect on object recognition memory manifested itself in the relatively large difference in performance between the cars and bicycles categories. Improved recognition memory for bicycles compared to cars is likely largely due to the better familiarity of our low SES participants with bicycles than with cars. Participants largely used bicycles and motorcycles for transportation in daily life, and even when they encountered cars, those cars were unlikely to be the early 90s models of cars sold in Western Europe that were used in the Cambridge Car Memory Test.

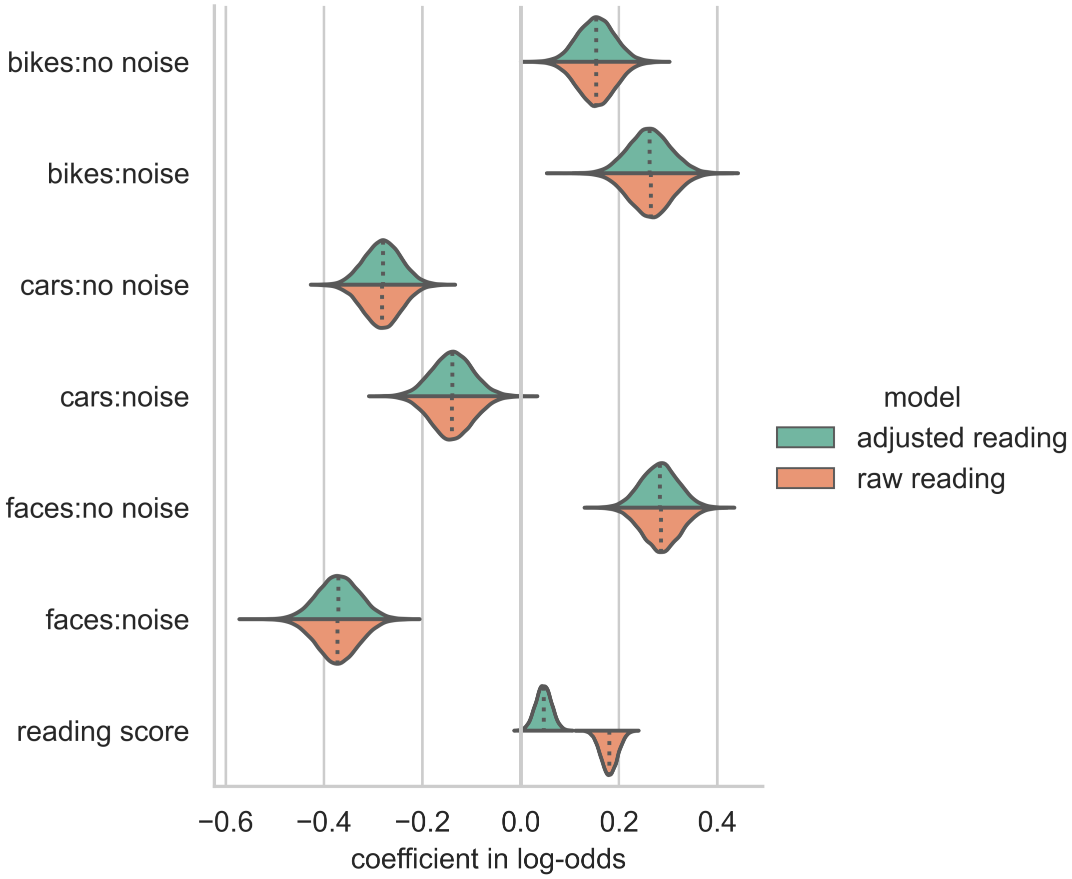

Figure 2. Densities of posterior estimates *in each object category and noise condition, and the overall effect of reading score for the model with raw reading score as a predictor (in orange) and the model with adjusted reading score as a predictor (in green). Coefficients are presented as log-odds, on a linear scale, for ease of visual comparison. Object category and visual noise coefficients are highly similar in both models, whereas the adjusted reading score coefficient is markedly lower than the coefficient for the raw reading score. Crucially, both are positive; log-odds ratio for adjusted reading score is .05 (95% credible interval [.02, .08]). Conditional effects were re-referenced post-hoc for ease of visual comparison.*

Besides these main results, there is strong evidence for a varying interaction between *object category* and *visual noise*, with bicycles and cars appearing slightly easier to recognize in the noise condition than in the no-noise condition (difference in log-odds ratio is .11 for bicycles, 95% CI [.00, .22]; .14 for cars, 95% CI [.03, .25]), whilst for faces, the noise condition appeared much *more* difficult than the no-noise condition (difference in log-odds ratio is -.65, 95% CI [-.76, -.54]).

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