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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 a development for dedicated neural infrastructure to have evolved in its service. Newly acquired cultural skills, such as 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 for which a cortical network originally evolved. In a study with 97 literate, low-literate, and illiterate participants from the same socioeconomic background, we found that even after adjusting for cognitive ability and test-taking familiarity, learning to read was 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 are consistent with the possibility that learning to read instead fine-tunes general object-recognition mechanisms, a hypothesis that needs further neuroscientific investigation.

Keywords

reading, face perception, literacy, neuroimaging, open data, open materials

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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, Kolinsky, & Lachmann, 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 recent skill. A hallmark finding is that in literate people, a region in the left occipitotemporal lobe becomes specialized for the processing of the visual word forms (hence *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 been invented only over the last 6,000 years, which is too recent for a dedicated cortical system to have evolved in their service.

To account for this phenomenon, researchers have invoked the notion of *neuronal recycling*, according to

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which acquiring cultural skills involves the repurposing of circuits related to evolutionarily older but similar functions (Dehaene & Cohen, 2007). There is strong experimental support for this general notion, although the exact mechanisms of this repurposing 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 of 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 on 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 functional MRI studies with participants of varying literacy levels, using very similar visual stimuli, have reported contradictory findings—some evidence in line with destructive competition (Dehaene et al., 2010), but also with 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, p. 385). 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.

Statement of Relevance

A main characteristic of our species is its ability to invent technologies that have transformed life on Earth. During reading acquisition, a cultural skill has to be accommodated in a cognitive and neural system that does not provide a dedicated processing pathway because writing systems have been used only for the last 6,000 years, which is too short a time for neural networks to have evolved in their service. Reading has to create its own niche by modifying preexisting brain networks that evolved for different but related abilities (e.g., face recognition). In a large-scale study with literate, low-literate, and illiterate participants in India, we observed that such neuronal recycling improves face-recognition abilities rather than weakening them (as had previously been suggested). Reading thus makes use of the remarkable capacity of the brain to support new abilities in such a way that related older abilities can be enhanced rather than impaired.

Method

Participants

Ninety-seven participants were recruited through a nongovernmental organization (NGO) working to improve living conditions for people of lower socioeconomic status (SES) in Chennai, the capital city of Tamil Nadu, India. Thirty-five 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 SES, but there was a marked difference in the average number of completed years of education among the three groups (see Table 1 in the Supplemental Material available online). 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 3 hr to complete. Participants received 2,400 Indian rupees (roughly equivalent to €30) as compensation, equivalent to about 2 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 socioeconomic backgrounds and statistically corrected reading proficiency for cognitive ability and familiarity with formal test-taking settings. We collected word-reading scores and pseudoword-reading scores to assess the reliability of participants' self-reported literacy status, as well as measures of nonverbal 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. Spoken instructions were 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 to roughly 5° 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 s 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 that 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 number sequences. The sequences increased in length from two numbers to 10 numbers for forward digit span and from two numbers to eight numbers for backward digit span. Number sequences were prerecorded in Tamil by a native Tamil speaker. After each number sequence was presented, participants repeated 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 on the basis of the longest sequence repeated correctly before the task was stopped.

Raven's Standard 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; we used item-response theory to ensure that sensitivity was 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 Standard Progressive Matrices 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 display of six or eight possible replacement sections. Answer options are traditionally numbered, and responses are delivered using a keyboard or in writing. To adapt this paradigm for illiterate participants, we presented the answer options with colored labels that corresponded to colored keys on a keyboard.

Cambridge Recognition Memory Tests. The Cambridge Face Memory Test (Duchaine & Nakayama, 2006), Cambridge Car Memory Test (Dennett et al., 2012), and Cambridge Bicycle Memory Test (Dalrymple et al., 2014), which we refer to collectively as the Cambridge tests, are a set of tasks meant to test object-recognition memory. Participants are first familiarized with six different items (faces, cars, or bicycles) through a series of practice questions. In Step 1, a single target item is presented three times: once rotated 30° to the left, once head on, and once rotated 30° to the right. Each of these presentations lasts 3 s. Then in Step 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 by pressing a key. 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. In Step 1, a display of all six target items is presented for 20 s, and participants are instructed to memorize these items. This is followed by Step 2, in which a display of three items is presented, one of which was presented in the memorization display. Participants are instructed to select the memorized item by pressing a key. Step 2 is repeated 30 times.

The test phase consists of two parts. In the first half, the images in the memorization display and test display 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 recognition difficulty.

The usual format for the Cambridge tests 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 (Yarkoni & Westfall, 2018), using the PyMC3 back end (Salvatier et al., 2016). We placed moderately regularizing priors on both fixed and random effects, in the form of narrow (σ = .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; Hoffman, & Gelman, 2014). The starting point for the Markov chains was obtained through automatic differentiation variational inference (ADVI). Four chains were run for 2,500 tuning samples, after which 5,000 posterior samples were obtained per chain, for 20,000 posterior samples in total per model. For each test, we fitted models with various permutations of effects and selected models on the basis of fit. The nature of the predictor matrix for the models predicting Cambridge-test 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 Cambridge-test scores, we therefore fitted only various permutations of fixed effects and their interactions. In the interest of parsimony, model fits were compared using pareto-smoothed importance sampling with a leave-one-out information criterion (PSIS-LOOIC), a Bayesian index of model fit that penalizes model complexity. Diagnostics indicated no sampling problems for the selected model (minimum $n_{\text{effective}} > 8{,}000$, $\hat{r} < 1.001$). Full details on model comparison and the full range of models considered can be found in the Supplemental Material.

Results

Object-recognition memory was assessed in Tamil illiterates, low literates, and literates (see the Supplemental Material 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 Test, Cambridge Car Memory Test, and Cambridge Bicycle Memory Test. In these tests, participants see arrays of six target items (faces, bicycles, and cars, in separate blocks) and are then shown 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 scores were moderately correlated (ρ = .48; see Fig. 1). Both Raven's Progressive Matrices scores and digit-span scores were also moderately

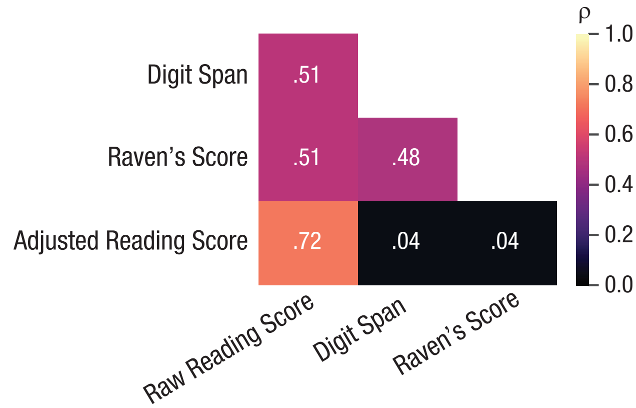

Fig. 1. Heat map showing absolute correlations between digit span, Raven's Standard Progressive Matrices score, and both raw and adjusted reading score.

correlated with Tamil word-reading scores (ρ = .51 for both measures; see Fig. 1). These correlations indicate common variance among 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, although poverty and other socioeconomic factors are 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 among Raven's, digit-span, and reading scores.

To solve this issue, and to achieve a strong test of our experimental hypothesis, we regressed out common variance attributable to general cognitive ability and familiarity with test taking while preserving the variance uniquely associated with literacy. To adjust the raw (contaminated) reading scores, we constructed 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 extracted 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 tests. In line with our expectations, the new, adjusted reading score was no longer correlated with the cognitive-ability measures (ρ = .03 for Raven's Progressive Matrices, ρ = .02 for digit span; see Fig. 1) but was 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 Supplemental Material.

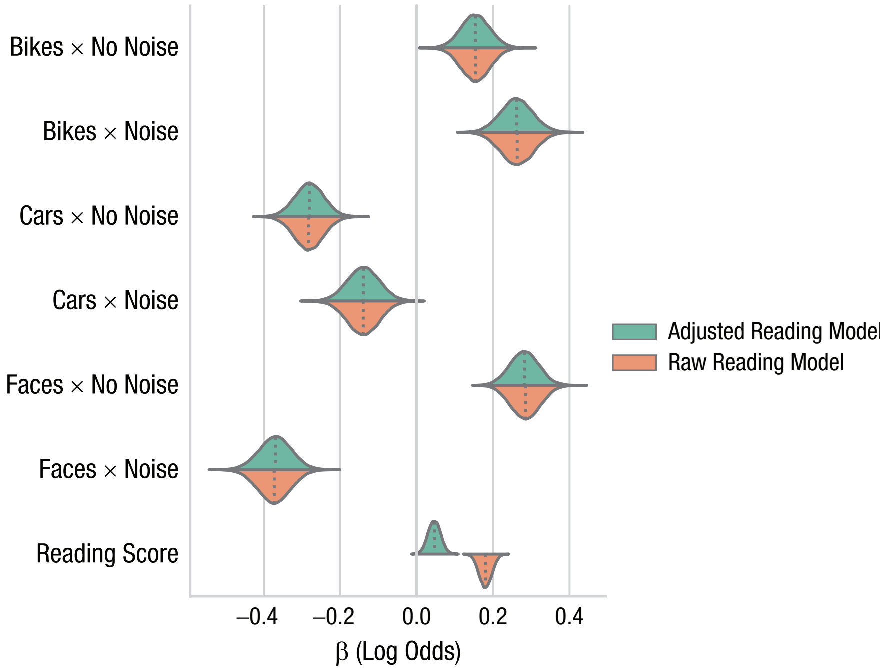

Fig. 2. Densities of posterior estimates in each object category and noise condition and the overall effect of reading score for the model with raw reading score as a predictor and the model with adjusted reading score as a predictor. Coefficients are presented as log odds, on a linear scale, for ease of visual comparison. Conditional effects were rereferenced for ease of visual comparison.

Relationship between literacy and object-recognition memory

For modeling the association between literacy and performance on the Cambridge tests, we took each trial as a Bernoulli trial, using a Bayesian generalized linear model to predict the odds of successfully answering a given trial. We pooled the data from all three tasks (bicycles, faces, and cars), creating a dummy-coded predictor for each task. Similarly, we created dummy-coded predictors for the *visual noise* and *no-visual-noise* conditions. Which conditions were used as reference levels in our analysis was arbitrary and did not affect our results, because we computed conditional effects for each condition from posterior samples.

On the basis of model comparisons using PSIS-LOOIC, we selected 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 was that higher reading scores were associated with higher recognition-memory scores (see Fig. 2). Crucially, this was the case both for the raw and the adjusted reading scores; even when we regressed out variance that could be attributed to general cognitive capacity and test-taking familiarity, there was no evidence for decreased object-recognition abilities in literates. Rather, literacy was 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 preferred a model with a single slope for literacy across all visual categories, we observed a positive relationship between literacy and object-recognition memory for all visual categories (faces, bicycles, and cars; see the Supplemental Material).

An additional, possibly cultural effect on object-recognition memory manifested itself in the relatively large difference in performance between the car and bicycle categories. Improved recognition memory for bicycles compared with 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 1990s models sold in Western Europe that were used in the Cambridge Car Memory Test.

Besides these main results, there was strong evidence for a varying interaction between object category and visual noise: It appears that bicycles and cars were slightly easier to recognize in the noise condition than in the no-visual-noise condition. The difference in log-odds ratio was 0.11 for bicycles (95% credible interval [CI] = [0.00, 0.22]) and 0.14 for cars (95% CI = [0.03, 0.25]). By contrast, for faces, the noise condition appeared to be much more difficult than the no-visual-noise condition (difference in log-odds ratio = −0.65, 95% CI = [−0.76, −0.54]).

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. Such abilities are very unlikely to be a secondary effect of literacy, such as increased verbal working memory (Demoulin & Kolinsky, 2016; Smalle et al., 2019), general cognitive ability, or familiarity with test taking, because in the present study we regressed out common variance associated with these traits. To more directly assess causality, we recommend further investigation of the results from the present large-scale cross-sectional study with a longitudinal design (cf. Goswami, 2015; Huettig, Lachmann, 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 this hypothesis views the brain as a system with finite processing resources for which different functions are competing, the present findings raise the intriguing possibility that the brain, remarkably, is able 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, examining whether literates' better object-recognition abilities are related to shared (neural) processing between face and word reading, as both skills require sophisticated foveal processing.

Transparency

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Author Contributions

J. van Paridon, M. Ostarek, M. Arunkumar, and F. Huettig designed the study. M. Arunkumar collected the data, and J. van Paridon and M. Ostarek analyzed the results. All of the authors wrote the manuscript and approved the final version for publication.

Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

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Open Practices

All data and analysis code have been made publicly available via Zenodo and can be accessed at https://doi.org/10.5281/zenodo.3543572. The behavioral test suite administered to participants in this study is available at https://doi.org/10.5281/zenodo.3543296. The design and analysis plans for this study were not preregistered. This article has received the badges for Open Data and Open Materials. More information about the Open Practices badges can be found at http://www.psychologicalscience.org/publications/badges.

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Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/0956797620971652

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