Developmental Science (2011), pp 1–11 DOI: 10.1111/j.1467-7687.2011.01102.x

PAPER

Reading acquisition enhances an early visual process of contour integration

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Abstract

The acquisition of reading has an extensive impact on the developing brain and leads to enhanced abilities in phonological processing and visual letter perception. Could this expertise also extend to early visual abilities outside the reading domain? Here we studied the performance of illiterate, ex-illiterate and literate adults closely matched in age, socioeconomic and cultural characteristics, on a contour integration task known to depend on early visual processing. Stimuli consisted of a closed egg-shaped contour made of disconnected Gabor patches, within a background of randomly oriented Gabor stimuli. Subjects had to decide whether the egg was pointing left or right. Difficulty was varied by jittering the orientation of the Gabor patches forming the contour. Contour integration performance was lower in illiterates than in both ex-illiterate and literate controls. We argue that this difference in contour perception must reflect a genuine difference in visual function. According to this view, the intensive perceptual training that accompanies reading acquisition also improves early visual abilities, suggesting that the impact of literacy on the visual system is more widespread than originally proposed.

Introduction

Integration of contours across the visual field is an essential step in vision, which has been related to the basic architecture of horizontal connections in early visual cortices (Gilbert & Wiesel, 1979, 1989). Here we examine whether even such a basic visual process can be influenced by the acquisition of reading, a major culture-dependent event with an extensive impact on cerebral organization (Dehaene, 2009). Functional neuroimaging studies have shown that learning to read leads to the development of a strong response to letter strings in the fusiform cortex in the left hemisphere, a region known as the visual word form area (Cohen, Lehericy, Chochon, Lemer, Rivaud & Dehaene, 2002; Dehaene, Pegado, Braga, Ventura, Filho, Jobert, Dehaene-Lambertz, Kolinsky, Morais & Cohen, 2010b; Fiez, Balota, Raichle & Petersen, 1999; Price, Wise & Frackowiak, 1996; Puce, Allison, Asgari, Gore & McCarthy, 1996). Anatomically, literate subjects show an increase of grey matter volume in several areas involved in language processing (Carreiras, Seghier, Baqueiro, Estévez, Lozano, Devlin & Price, 2009), and of white matter in the splenium of the corpus callosum (Carreiras *et al*., 2009; Castro-Caldas, Petersson, Reis, Stone-Elander & Ingvar, 1998) whose tracts may link the occipital, temporal and inferior parietal regions of both hemispheres. Learning to read also enhances phonemic awareness, the ability to explicitly manipulate the smallest units of spoken language (Morais, Bertelson, Cary & Alegria, 1986). Finally, recently, literacy has been shown to induce a broad enhancement of visual responses to non-letter stimuli such as simple checkerboards in lateral and mesial occipital cortices, including the primary visual area (Dehaene *et al*., 2010b; see also Szwed, Dehaene, Kleinschmidt, Eger, Valabregue, Amadon & Cohen, 2011). The latter findings led us to ask whether learning to read could also have a behaviorally detectable effect on one of the basic features of the visual system, namely contour integration.

Recognition of everyday objects relies crucially on our ability to detect and integrate contours into coherent

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D E S C 1 1 0 2 B Journal Name Manuscript No. Dispatch: 27.9.11 Journal: DESC CE: Blackwell Author Received: No. of pages: PE: Priya

percepts. A long line of research starting with Gestalt psychology (Köhler, 1947) has been devoted to this subject. In particular, it is known that the capacity to integrate contours matures late. Five-year-old children are much worse at integrating contours than 8-year-old children, and adult-level performance is reached only around the age of 13 (Kovacs, Kozma, Feher & Benedek, 1999). This improvement in contour integration roughly coincides in time with the acquisition of literacy. This coincidence might be accidental. However, some have argued that learning to read involves visual perceptual learning, a form of implicit learning that involves improvement in visual discrimination by repeated exposure to sensory stimuli (Fahle & Poggio, 2004). A key consequence of such perceptual learning would be to achieve fast reading by integrating the features of several letters in parallel (Nazir, 2000; Nazir, Ben-Boutayab, Decoppet, Deutsch & Frost, 2004; Nazir & Huckauf, 2008; Szwed *et al.*, 2011). This raises the possibility that such perceptual learning, while initially associated to reading, could eventually enhance general contour detection ability.

Integration of information across the visual field has been extensively studied using the contour integration paradigm (reviewed in Hess, Hayes & Field, 2003; Kovacs, 2000). In this paradigm, observers are presented with a contour made out of local elements (Gabor patches) embedded in an array of distractors (Figure 1). To detect the contour, the observer has first to perceive the local orientation of the individual elements and then to connect them into a coherent contour by relying solely on collinearity cues. By manipulating only the orientation of elements, it is possible to make contours more or less salient. In this way, long-range cortical interactions underlying contour integration can be studied selectively.

Here we propose that the several thousands of hours spent on learning to read would not only make one an expert reader, but also lead to improvements in fine-grained visual integration in general. This hypothesis predicts that in a contour integration task, illiterate subjects should have a lower performance than ex-illiterate and literate controls closely matched in age, socioeconomic and cultural characteristics (Table 1).

Methods

Contour detection task – stimuli

We used a variant of the contour integration task developed by Kovacs and colleagues (Gervan & Kovacs, 2010; Kovacs & Julesz, 1993; Kozma-Wiebe, Silverstein, Feher, Kovacs, Ulhaas & Wilkniss, 2006). The stimuli consisted of a closed chain of Gabor patches forming an egg shape within a background of randomly oriented Gabor stimuli. The egg was pointing either left or right (Figure 1A, B).

Stimuli were generated using a Monte Carlo technique, where the contour and the background were controlled

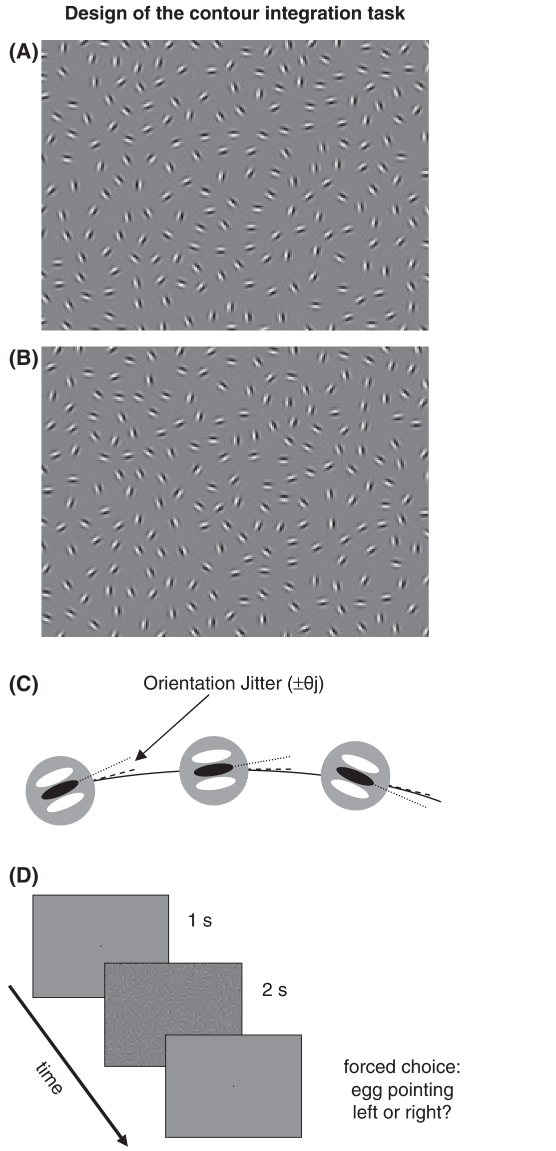

Figure 1 *Stimuli and experimental design. (A, B) Samples of stimuli used. The images consisted of a closed chain of Gabor patches forming an egg-like shape within a background of randomly oriented Gabor stimuli. The egg was pointing either left or right. (A) Egg with 0° jitter pointing left. (B) Egg with 11–12° jitter pointing right. (C) The orientation jitter (θ_j) controlled the orientation of the element with respect to the contour, and thus, the stimulus difficulty (θ_j = 0° – perfect alignment). (D) Experimental design. The subjects performed a two-choice forced orientation judgment task. These images in (A, B) are published with the kind permission of I. Kovács, and are equivalent to those employed in Kozma-Wiebe et al (2006) and in Gerván and Kovács (2010).*

independently (Kozma-Wiebe *et al.*, 2006). The carrier spatial frequency of the Gabor patches was 5 c/deg and their contrast was 95%. The spacing between the contour elements was kept constant (8λ, where λ is the wavelength of the Gabor stimulus), as was the average spacing between the background elements. The D value (average background spacing/contour spacing) of each image was 0.9. This means that the distance between distractor

Table 1 *Subject populations. Ex-illiterates and illiterates were defined as adults who had received no early schooling during childhood. Among this population, ex-illiterates had fulfilled adult literacy courses, while illiterates were still unable to read even simple words (but could identify some letters). Literate subjects had received a normal education in literacy at an early age and were all normal readers. All subjects were of gipsy ethnicity, lived in a small town in the outskirts of Lisbon, were fully functional in their daily lives and socially integrated. They were thus matched as closely as possible on socioeconomic and cultural characteristics. The values given are mean ± SD and SEM*

Gabor patches was on average equal to 0.9 of the distance between Gabor patches forming the egg contour. It is known from previous results that with such stimuli (D < 1), the contour can only be detected on the basis of long-range horizontal interactions between the adjacent elements and not on the basis of first-order density cues. This is because the distance between target elements is larger than the distance between targets and distractors.

The difficulty of the task was varied by jittering the orientation of the Gabor patches forming the contour. The orientation jitter (θj) controlled the orientation of the element with respect to the contour (Figure 1C). The orientation jitter of the contour elements was varied between 0 and 24 degrees across six difficulty levels (0 deg, 7–8 deg, 11–12 deg, 15–16 deg, 19–20 deg, 23–24 deg). Figure 1 A, B shows two contours, one (A) with 0 deg jitter pointing left, another with 11–12 deg jitter pointing right.

Testing was performed in a dimly lit room. Day-to-day consistency of illumination was verified with a luminance meter (Sekonic). The images subtended an area of 12.8 × 9.6 degrees of visual field. The mean luminance of the monitor was 16.5 cd/m^2.

Contour detection task – experimental procedure

The experimental procedure is depicted in Figure 1D. Each trial began by 1 s fixation. The stimulus was then shown for 2 s. It was followed by a fixation cross that remained on the screen until the subjects gave an answer. Subjects performed a two-choice forced orientation judgment task in which they had to decide whether the contour was pointing left or right. Since subjects were not familiar with computers, the answer was given vocally. The experimenter then recorded the response with the keyboard. Before the experiment, the subjects were familiarized with the task, first using a PowerPoint presentation followed by a short trial session in which feedback was provided (10 stimuli at each of the 0, 11–12 and 19–20 deg difficulty (jitter) levels). In the main experiment subjects saw 60 stimuli at each of the six difficulty (jitter) levels. The stimuli were presented starting with the easiest (0 level) and ending with the most difficult (23–24 level). No feedback was provided.

In our experiment, we used a two-choice forced discrimination task. Contour integration can be studied both with discrimination tasks and simple detection tasks (e.g. Field, Hayes & Hess, 1993; Kovacs *et al*., 1999) and the results obtained with the two types of task are generally consistent (e.g. Kuai & Yu, 2006). Here we chose to use a discrimination task rather than a detection task because we were concerned that illiterate subjects might have less self-confidence than ex-illiterates and literates. In a detection paradigm, this could lead them to give up more easily on more difficult stimuli and to report 'not detected'. To avoid such a situation of 'stereotype threat' (Smith, 2004), where illiterates think of themselves as less able and less skilled and act according to this self-image, we used a forced-choice procedure that required subjects to respond on every trial and minimized this potential confound.

Subjects

Three groups of subjects were tested in Portugal: literates (n = 17), ex-illiterates (n = 17), and illiterates (n = 14). Ex-illiterates and illiterates were defined as adults who had received no early schooling during childhood. Among this population, ex-illiterates had fulfilled adult literacy courses (and typically went on to use reading on a daily basis at home and at work), while illiterates were still unable to read even simple words (but could identify some letters). Finally, literate subjects, who had received 4 years of normal education at an early age and were all normally proficient readers, were matched to these groups in age ($F(2, 47) < 1$, p = .86). This design allowed us to separate between the effects of literacy *per se* and the broader effects of schooling, which include literacy but also a variety of other learned abilities (e.g. numeracy, mathematics, social skills, executive control, etc.).

Details of the three groups are summarized in Table 1. All subjects were of gipsy ethnicity and all lived in social projects in a small town in the outskirts of Lisbon. They were thus matched as closely as possible on socioeconomic and cultural characteristics, and all came from very similar households. All subjects had normal or corrected-to-normal visual acuity (Snellen chart for illiterate subjects). The average acuities for the three groups were 18.6/20, 19.8/20 and 18.6/20 for illiterate, ex-illiterate and literate groups, respectively (difference not significant, ANOVA, $F(2, 95) = 1.78$; p = .19), and all subjects' acuities were equal or superior to 15/20. All the subjects were fully functional in their daily lives and socially integrated. The subjects were recruited through a Portuguese non-governmental agency (AMUCIP; Association of the Gipsy Women of Portugal). Subjects received 40 Euros for their participation. All subjects underwent a battery of simple tests in order to verify their reading skills. In the letter identification task, the subjects were asked to name the 23 printed letters of the

Latin alphabet commonly used in the Portuguese language. The word reading task comprised six simple words to be read aloud. For pseudoword reading, eight simple pseudowords were created by changing the first phoneme of real words (e.g. 'tavalo' instead of 'cavalo', which means 'horse' in Portuguese). The sentence reading task was a validated Portuguese version of the 'Lobrot' test (Sucena & Castro, 2009), which comprises 36 sentences that must be completed with one word, chosen among five options, in 5 minutes or less. A 100% correct performance in the Lobrot test is reached by the majority of children in the 4th grade.

Further details of the three groups are summarized below and in Table 1.

Illiterates

The illiterate subjects did not attend school at all as children. They were able to identify five letters, on average, but they were unable to read words or pseudowords.

Ex-illiterates

Like the illiterates, ex-illiterates had not attended school during childhood. All had attended and fulfilled adult literacy courses (one subject for 3 years; all the others for 4 years). Two subjects had attended a professional training program (aimed at learning a job; Portuguese government New Opportunity Program), one for 3 months and another for 9 months. Ex-illiterates identified all single letters, and were very good at reading simple words and pseudowords. In the sentence-level reading test (Lobrot), this group was only slightly worse than the literates ($t(32) = 2.65$, $p < .01$).

Literates

The literates comprised subjects from the same community as the illiterate and ex-illiterate groups, but with 4 years of early education. As expected, reading performance was very good in all literate subjects.

Data analysis

We fitted individual psychometric curves with a logistic function using a Maximum Likelihood (ML) criterion. The fitting was done in Matlab using the Palamedes toolbox (Prins & Kingdom, 2009). The detection threshold was defined as 75% correct performance. The results were analyzed in Minitab (Minitab, Inc) and R (http://www.r-project.org/).

Results

Figure 2 shows the percentages of correct responses for contours of increasing difficulty plotted for each group of subjects. All subjects were very accurate for contours

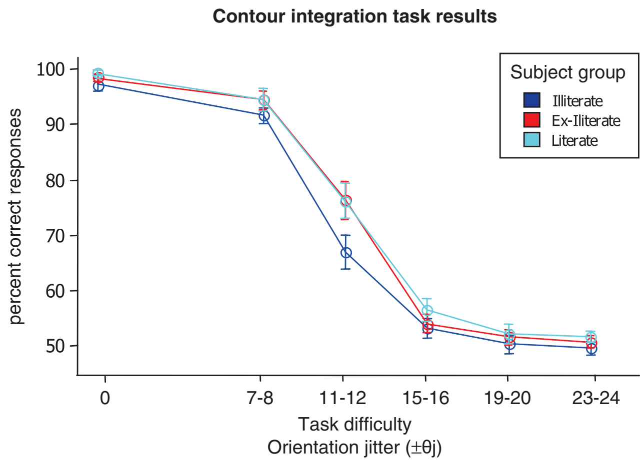

Figure 2 *Contour integration task results. The percentages of correct responses for contours of increasing difficulty are plotted for each subject group (group sizes: n = 14 for illiterates, and n = 17 for ex-illiterates and literates). There was a significant effect of literacy on the subjects' capacity to correctly detect contours (p = .029). Pairwise comparisons revealed significant differences between the illiterates and literates (p = .043) and the illiterate and ex-illiterates (p = .013). Chance level is 50%. Error bars denote SEM.*

with no jitter (0 deg difficulty; all scores > 88%), indicating excellent task comprehension and compliance in all three groups. Median performances at this easiest level of difficulty were 98.33% for the illiterate and ex-illiterate groups and 100% for the literate group (difference non-significant, $p = .25$, Kruskal-Wallis test for non-normally distributed data). All performed at chance level (50%) for the two most difficult conditions: 19–20 deg and 23–24 deg.

We analyzed the data in an ANOVA with group and difficulty level as factors. Group was treated as a between-subjects factor and task difficulty as a within-subject factor. There was a significant effect of literacy on the subjects' capacity to correctly detect contours (ANOVA: $F(2, 45) = 3.83$; $p = .029$, no significant interaction with difficulty level, $F(10, 225) = 0.94$; $p = .49$). Pairwise comparisons revealed significant differences between the illiterates and literates ($F(1, 29) = 4.48$; $p = .042$) and the illiterate and ex-illiterates ($F(1, 29) = 7.03$; $p = .012$). The difference between the ex-illiterates and literates was non-significant ($F(1, 32) = 0.37$; $p = .54$). We conclude that illiterates have lower performance in the contour integration task.

The responses of a subject to a physical parameter – in our case the visibility of a contour – can be modeled by a psychometric function. This approach allows one to compute a single parameter, the detection threshold, which summarizes the subjects' responses across several difficulty levels. We estimated the individual subjects' detection thresholds by fitting a logistic function to their responses, with the slope and lapse rates as free parameters (the lapse rate is the percentage of errors made under optimal viewing conditions that is not attributed to the failure of the detection process itself but rather to sub-optimal efficiency of higher cognitive processes such as attention or concentration; Kingdom & Prins, 2010; Wydell, Vuorinen, Helenius & Salmelin, 2003). Figure 3A depicts an example of curve fitting for one subject (DA).

Figure 3B shows the individual subjects' psychometric curves for the illiterate, ex-illiterate and literate groups. Figure 3C shows the estimated detection thresholds for the illiterate, ex-illiterate and literate groups. Detection thresholds were lower for the illiterate group (9.7 ± 0.5 deg, mean ± SEM), than for the ex-illiterate group (11.5 ± 0.4 deg, mean ± SEM) and the literate group (11.8 ± 0.4 deg, mean ± SEM). There was a significant effect of group on the subjects' capacity to correctly detect contours (ANOVA, $F(2, 47) = 6.65$, $p = .003$). Pairwise comparisons revealed significant differences between the illiterate and literate groups ($F(1, 30) = 12.65$, $p = .001$) and the illiterate and ex-illiterate groups ($F(1,30) = 8.14$, $p = 0.008$). The difference between the ex-illiterate and literate groups was non-significant ($F(1, 32) = 0.55$, $p = .35$). We conclude again that illiterates have lower performance in the contour integration task.

To make sure that our result does not rely on a few subjects who failed to properly understand instructions, we repeated our analysis this time removing three illiterate subjects who scored below 92% in the easiest condition. The main effect remained significant, with an overall effect of literacy ($F(2, 44) = 3.70$; $p = .033$) and a significant difference between the illiterate and ex-illiterate populations ($F(1, 27) = 4.33$; $p = .047$). This leads us to the conclusion that that the effect of literacy on contour detection is robust, and does not rely unduly on a few illiterate subjects with the lowest scores.

Discussion

Our results indicate that illiterate subjects are less efficient at integrating visual contours than matched ex-illiterate and literate subjects. To our knowledge, this is the first demonstration of an impact of literacy on early visual processes. Indeed, as reviewed below, previous demonstrations of the impact of literacy on visual cognition were restricted to late and possibly strategic aspects of visual analysis.

Previous studies on the impact of literacy on visual cognition

Aspects of visual cognition which have been studied in illiterates included both early perceptual processes and post-perceptual processes involved in the conscious, intentional analysis of the visual world.

Early perceptual processes in illiterate and literate adults were studied by Kolinsky, Morais and Verhaege

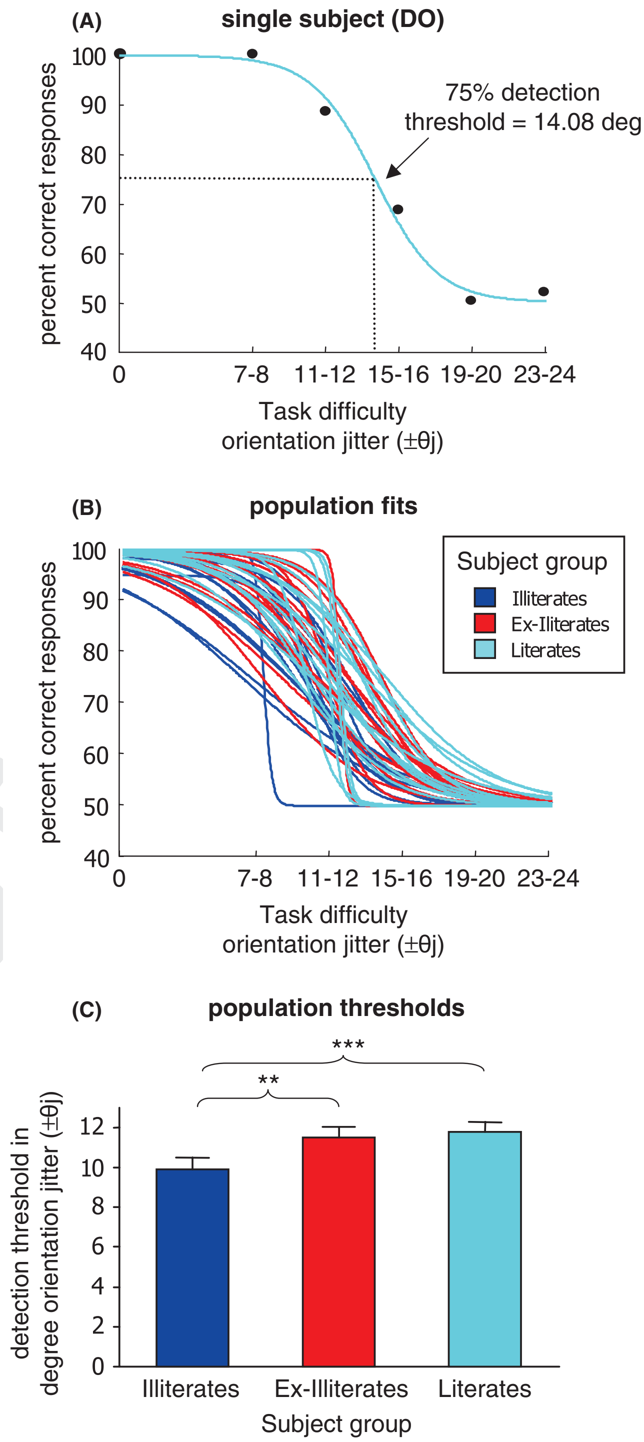

Figure 3 *Psychometric curves and contour detection thresholds. We estimated the individual subjects' psychometric curves using a logistic function. (A) Example fitting for subject DA, a literate. A logistic function is fitted to the results (dots), and threshold is determined at 75% correct performance. (B) Individual subjects' psychometric curves for the illiterate, ex-illiterate and literate groups. The resulting 75% detection thresholds are depicted in (C). Significance levels: ** p = .008; *** p = .001; Error bars in (C) denote SEM.*

(1994) using illusory contour stimuli. The authors found no differences in the rate of observed illusory contours between these subject groups.

In contrast, several differences between illiterate and literate subjects have been reported for conscious, post-perceptual analytic processes. A first set of reports focused on the processing of whole–part relationships. In a task in which subjects had to detect a part made of three segments within a figure made of six segments, Kolinsky, Morais, Content and Cary (1987) found that illiterates and ex-illiterates performed at the same level, and that both those groups did less well than literate children attending the second grade. In another study, Ventura, Pattamadilok, Fernandes, Klein, Morais and Kolinsky (2008) used the Framed-Line-Test, in which subjects have to draw a line that is identical to a reference line embedded in a square frame. Depending on the task, what should be matched is either the absolute length of the model line (absolute task) or its ratio to the surrounding frame (relative task). They found that schooled literates performed better on the absolute than on the relative task. However, both illiterate and ex-illiterate subjects showed the reverse pattern. Thus, both studies were taken as an indication that performance depends not on literacy *per se* but on schooling, since differences were found between, on the one hand, schooled literate adults, and on the other hand unschooled subjects irrespective of their reading ability.

However, literacy, rather than schooling, was shown to be critical in the Cooper visual task (Brito-Mendes, Morais & Kolinsky, 2005). Cooper and Podgorny (1976) attempted to distinguish between holistic and analytic processing using a same–different decision task on visual patterns. Asking subjects to classify pairs of closed and irregular black-colored shapes as same or different, she found that some subjects used a holistic strategy ('same' responses were faster than 'different' responses, and the degree of dissimilarity did not affect 'different' responses), whereas others used an analytic strategy ('same' responses were not faster than 'different responses', and latency to 'different' responses increased as similarity increased). Examining illiterate, ex-illiterate, and literate people in this task, Brito-Mendes *et al.* (2005) found that illiterates displayed clear signs of holistic processing, whereas both ex-illiterates and literates showed a more analytic processing.

A second set of studies on high-level visual tasks in illiterate subjects focused on the ability to discriminate mirror images (enantiomorphy). Most natural categories are invariant for left–right inversion. Accordingly, our visual system readily performs mirror-image generalization, a process that has been explored at the level of single inferotemporal neurons (Logothetis & Pauls, 1995; Rollenhagen & Olson, 2000), and using fMRI in healthy humans (Dehaene, Nakamura, Jobert, Kuroki, Ogawa & Cohen, 2010a). However, mastering the Latin alphabet requires taking mirror-image contrasts into account, in order to distinguish e.g. p from q and b from d. Hence, learning to read may push the beginning reader to 'unlearn' invariance for mirror symmetry even for non-linguistic stimuli (e.g. Dehaene *et al.*, 2010a). Under such a view, a perceptual sensitivity to enantiomorphy would develop under the pressure of literacy acquisition. In a recent study (Kolinsky, Verhaege, Fernandes, Mengarda, Grimm-Cabral & Morais, submitted) this hypothesis was evaluated by comparing the performance of unschooled illiterate adults, schooled literates and unschooled adults alphabetized at adult age (i.e. ex-illiterates) in various sorting and same–different comparison tasks. Illiterates performed far worse than all other subjects when the task required paying attention to enantiomorphic differences. Learning a writing system that incorporates enantiomorphic letters thus reduces the default invariance for mirror symmetry, a process which seems to generalize to non-linguistic stimuli.

In summary, literacy has been shown to improve performance in high-level visual tasks such as the Cooper task (Brito-Mendes *et al.*, 2005). The present study shows that such improvement extends to an early visual contour detection task. We believe that similar results should be obtained with all contour stimuli that form a good continuity such as circles (e.g. Kuai & Yu, 2006), as previous work shows that contour detection is particularly enhanced whenever the contour is a closed shape with good Gestalt continuity (Kovacs & Julesz, 1993). On the other hand, it is less certain whether the improvements due to literacy would extend to contour stimuli that do not form good Gestalt continua like the lines used by Field and colleagues (1993). As will be discussed now, our findings suggest that low-level peceptual mechanisms involved in contour detection may be modified by the acquisition of reading.

Reading, contour integration and low-level visual processing

Reading has been traditionally viewed as a high-level process, yet fast reading of small letter size text puts heavy demands on early visual processing. Indeed, it has also been suggested that early visual cortex may develop preferential tuning for letters (Nazir, 2000; Nazir *et al.*, 2004; Nazir & Huckauf, 2008). Nazir and colleagues have argued that the capacity to detect several letters in parallel, which is the hallmark of skilled reading, relies on perceptual learning in early visual areas.

Perceptual learning is a form of implicit learning that leads to performance improvement through repeated exposure to stimuli (reviewed in Fahle & Poggio, 2004). It is known that perceptual learning can lead to functional changes in early sensory cortices (e.g. Karni & Sagi, 1991; Sasaki, Nanez & Watanabe, 2010; Schoups, Vogels, Qian & Orban, 2001; Sigman, Pan, Yang, Stern, Silbersweig & Gilbert, 2005) and that these modifications sometimes occur in parallel with the modifications of connections between the visual and 'decision-making' areas of the brain (Chowdhury, DeAngelis & Fine, 2008; Law & Gold, 2008).

It is well established that contour integration is associated with the same neural structures, i.e. the early visual cortex (area V1) in conjunction with higher-level areas that provide top-down contextual control. These neural correlates of contour processing have been firmly established by psychophysical methods (Fahle & Poggio, 2004), fMRI (Kourtzi, Tolias, Altmann, Augath & Logothetis, 2003; Schwartz, Maquet & Frith, 2002) and primate electrophysiology (Kourtzi *et al*., 2003; Li, Piech & Gilbert, 2008). In particular, it is known that contour integration relies on horizontal connections in the primary visual cortex which connect distant orientation columns sharing the same line orientation preference (Gilbert & Wiesel, 1979, 1989).

The idea that reading acquisition might also partially rely on changes in early visual cortex has received relatively less attention (see however Nazir, 2000; Nazir *et al*., 2004; Nazir & Huckauf, 2008). Nevertheless, that idea has been recently substantiated by two fMRI experiments. Szwed and colleagues (2011) studied activations to words and objects in early and intermediate visual areas (V1, V2, V3v, V4) in adult readers. Consistent with previous reports (see for example Grill-Spector & Malach, 2004), these areas were either equally or more activated by scrambled objects than by intact objects. However, for words the pattern was reversed, as words caused more activation than scrambled words. Thus early visual cortices exhibited a preference for written materials. This effect could reflect early visual perceptual learning under the pressure for fast, parallel processing that is more prominent in reading than other visual cognitive processes.

In a second study, Dehaene and colleagues (2010b) measured brain activation to various stimulus classes including faces, objects, words and horizontal and vertical checkerboards in literate and illiterate adults. Among other findings, Dehaene and colleagues found that literacy increases occipital responsivity to essentially all the contrasted black-and-white visual stimuli used in their study. Furthermore, literacy enhanced responses in the primary visual cortex not only to written words, but also to horizontal checkerboards presented at the foveal and horizontal location in which words are commonly perceived (Rayner, 1998). Thus, the perceptual learning associated with the acquisition of literacy seems to generalize to checkerboard stimuli presented at the trained location.

Along the same lines, we suggest that some visual expertise associated with literacy is generic enough to facilitate contour integration beyond alphabetic stimuli. Letters are made of small high-contrast contours. We speculate that detecting letters in a rapid and effortless manner – a key ability in skilled reading – relies on contour detection more than other forms of visual cognition such as object recognition, which is less parallel and also relies on cues such as texture or movement. Under such a view, learning to read would involve extensive training in contour detection leading to changes in early visual cortex (area V1) and higher-level visual areas that are commonly associated with visual perceptual learning (Chowdhury *et al*., 2008; Karni & Sagi, 1991; Law & Gold, 2008; Sasaki *et al*., 2010; Schoups *et al*., 2001; Sigman *et al*., 2005).

Underlying neural mechanisms

What exactly are the neuronal integration mechanisms that are left underdeveloped in illiterates, and what are the changes in learning? The detection of contours relies on perceptual binding of individual elements into a coherent shape. On a neuronal level, the individual elements – line fragments of a given orientation – are detected by cells in primary visual area V1 which are sensitive to line orientation (Hubel & Wiesel, 1968). V1 cells respond to lines of a preferred orientation (e.g. vertical) falling into their receptive field, which is a quite small fragment of the visual field (0.2–1 deg). Importantly, their responses are also influenced by the presence of other line fragments beyond the classical receptive field. On a behavioral level, these influences have been extensively explored in the collinear facilitation (or lateral facilitation) paradigm, which studies contrast detection of elements within a contour (e.g. Polat & Sagi, 1993; Solomon & Morgan, 2000; Wehrhahn & Dresp, 1998; Yu & Levi, 2000), (for a recent review, see Loffler, 2008). In this paradigm, observers are required to detect the presence of a near-threshold Gabor patch flanked by other, clearly visible Gabor patches ('flankers'). The detection of the target is usually facilitated when the flankers are collinear.

It has been established that on a neuronal level these influences arise predominantly from horizontal interactions between neighboring V1 cells (e.g. Kapadia, Ito, Gilbert & Westheimer, 1995) which are carried out by the plexus of connections in superficial layers of the cortex (e.g. Gilbert & Wiesel, 1989). These connections provide the substrate for complex computations engaged in binding distinct elements into one contour. Critically, it has been shown that the functioning of these connections can be modified by training. Thus, extensive training can alter response properties of V1 cells, and induce in them strong responses to contours that lie beyond their classical receptive field (Li *et al*., 2008). V1 cells can be therefore made to 'pay attention' to more complex features.

A person learning to read has to learn quick and parallel detection of complex visual targets – letters. We argue that this learning process involves plastic changes in early visual cortex parallel to those described in primates by Li *et al*. (2008). Such changes would lead to remodeling of the plexus of connections in superficial layers of the early visual cortex (e.g. Gilbert & Wiesel, 1989) accompanied by changes in the way that these connections can be modulated by higher order areas (McManus, Li & Gilbert, 2011).

While the few anatomical studies comparing illiterate subjects to literate controls did not find evidence of grey matter changes in early visual areas (Carreiras *et al*., 2009), several experiments have nevertheless shown that the adult human brain can undergo structural plasticity (indexed by grey matter changes) in response to the acquisition of a new skill (e.g. Maguire, Gadian, Johnsrude, Good, Ashburner, Frackowiak & Frith, 2000). Notably, Kwok, Niu, Kay, Zhou, Mo, Jin, So and Tan (2011) have recently demonstrated that such changes can occur in the visual system: learning new color categories can produce rapid increase in grey matter in areas V2/V3 of adult human subjects after as little as 2 hours of training. We believe that similar changes in early visual areas driven by the acquisition of literacy could underlie the improvement in contour detection capacity reported here.

The role of attention and development and implications for dyslexia

Several factors, such as attention, executive control, psychiatric or neurological disorders, can impact performance on the task we used. It has been reported, for example, that schizophrenic patients show decreased performance on the same contour integration task as used here (Silverstein, Hatashita-Wong, Schenkel, Wilkniss, Kovacs, Feher, Smith, Giocochea, Uhlhaas, Carpiniello & Savitz, 2006; Silverstein, Kovacs, Corry & Valone, 2000; Uhlhaas, Phillips, Mitchell & Silverstein, 2006). Studies using another visual grouping task also reported impairments of visual organization in schizophrenic patients (van Assche & Giersch, 2009). Both types of study have linked the deficit in schizophrenic patients to volitional deficits that lead to reduced top-down feedback from attention regions (Silverstein, Berten, Essex, Kovacs, Susmaras & Little, 2009; van Assche & Giersch, 2009). In the case of our study, however, it was unlikely that the differences found could be due to attention deficits or education since we tested groups of ex-illiterate control subjects closely matched in age, socioeconomic and cultural characteristics (Table 1, Methods).[1] Therefore, we believe that the differences in contour integration reported in this paper reflect genuine differences in low-level visual function.

The late development of contour integration in children has been linked (Kovacs, 2000) to the time course of the maturation of the visual system (Burkhalter, 1993; Burkhalter, Bernardo & Charles, 1993). This maturation results from the interplay of innate properties and of environmental stimulations and interactions. In cases where the visual input is abnormal, for example in amblyopic subjects, contour integration is impeded (e.g. Hess, McIlhagga & Field, 1997). Our paper demonstrates that in an opposite manner, intensive perceptual training such as that involved in the acquisition of reading may improve contour integration abilities above the level reached by subjects matched in all respects except literacy.

[1] Moreover, we have recently tested the very same subjects in a different visual cognition task that does not put a heavy weight on early visual processing: the part-probe verification task adapted from Palmer (Kolinsky, Morais & Brito-Mendes, 1990; Kolinsky *et al*., 1987; Palmer, 1977). We did not find any differences in performance between illiterates and ex-illiterates. Thus, the illiterates and ex-illiterates tested in this experiment have different performance in the contour integration task but similar performance in a different visual cognition task. In our opinion, it is therefore very unlikely that our results could be driven by an attentional deficit.

Our results might also bring a new argument into the ongoing debate on dyslexia and whether its causes are visuospatial or phonological (Ahissar, Lubin, Putter-Katz & Banai, 2006; Di Filippo, Zoccolotti & Ziegler, 2008; Valdois, Bosse & Tainturier, 2004; Vidyasagar & Pammer, 2010; Ziegler & Goswami, 2005; Ziegler, Pech-Georgel, Dufau & Grainger, 2010; Bosse, Tainturier & Valdois 2007; Lallier, Donnadieu, Berger & Valdois, 2010; Peyrin, Demonet, N'Guyen-Morel, Le Bas & Valdois, 2011). Previous research has found that among several visuospatial deficits, dyslexic subjects have inferior contour integration abilities (Simmers & Bex, 2001). Our results raise the possibility that this deficit, rather than being a cause of dyslexia, could be in fact its consequence. According to this explanation, the putative phonological deficit at the source of the dyslexia would disrupt reading acquisition and therefore, as an indirect consequence, the contour integration abilities of dyslexic subjects would fail to improve as they do in normal readers. This hypothesis might also explain the reduced ability to recognize line drawings of objects observed in dyslexic subjects, which also show reduced PET activations in high-order visual system to both words and drawings (McCrory, Mechelli, Frith & Price, 2005). If more evidence confirms this possibility, and if other visuospatial deficits observed in dyslexia (e.g. Ziegler *et al*., 2010) could be explained in a similar manner, it might become possible to reconcile the two apparently contradictory visuospatial and phonological theories of dyslexia.

Acknowledgements

This work was supported by a grant from the Fundação para a Ciência e a Tecnologia – Ministério da Ciência, Tecnologia e Ensino Superior – (Project PTDC/PSI-PCO/099526/2008 'Analytic vs. holistic thinking') to PV, by the Centro de Psicologia Clínica e Experimental – Desenvolvimento, Cognição e Personalidade of the Universidade de Lisboa, by INSERM and by a grant from the Agence Nationale de Recherche to LC and SD (CORELEX). MS was supported by a Human Frontier Science Program Organization Long-Term Fellowship. We thank the subjects for their participation, the Association of Gipsy Women of Portugal for help in recruiting subjects, Moti Salti and Regine Kolinsky for helpful comments on the previous versions of this manuscript, Laurence Labruna for administrative support, and Ilona Kovacs and Patricia Gervan for their generous advice and for sharing their experimental stimulation protocol.

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Received: 7 October 2010
Accepted: 24 July 2011

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