**Evolution of reading and face circuits
during the first three years of reading acquisition**

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20 **Highlights**

21 • While written words and faces activate neighboring areas of the fusiform gyri, their
22 developmental trajectory is different.

23

24 • The growth of word-induced activation at the classical coordinates of the VWFA is
25 primarily due to schooling.

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27 • The growth of face responses, particularly in the right hemisphere, is primarily
28 affected by age rather than by schooling.

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30 • Word and face-related areas exhibit distinct functional connectivity even prior to
31 reading acquisition: VWFA with left-hemisphere spoken language areas, FFA with
32 contralateral FFA and amygdala.

33

Abstract

Although words and faces activate neighboring regions in the fusiform gyrus, we lack an understanding of how this category selectivity emerges during development. To investigate the organization of reading and face circuits at the earliest stage of reading acquisition, we measured the fMRI responses to words, faces, houses, and checkerboards in three groups of 60 children: 6-year-old pre-readers, 6-year-old beginning readers and 9-year-old advanced readers. The results showed that specific responses to written words were absent prior to reading, but emerged in beginning readers, irrespective of age. Likewise, specific responses to faces were weak or absent in pre-readers, but they emerged more slowly and continued to evolve in the 9-year-olds, primarily driven by age rather than by schooling. Crucially, the sectors of ventral visual cortex that become specialized words and faces harbored their own functional connectivity prior to reading acquisition: the VWFA with left-hemispheric spoken language areas, and the FFA with the contralateral region and the amygdalae. The results support the view that reading acquisition occurs through the recycling of a pre-existing but plastic circuit which, in pre-readers, already connects the VWFA site to other distant language areas. Furthermore, reading acquisition does not compete with the face system directly, through a pruning of preexisting face responses, but indirectly, by partially reorienting the slow growth of face responses to the right hemisphere.

Keywords: Neuroimaging, Reading development, Visual word form area, Fusiform face area, Functional connectivity

1. Introduction

Learning to read is a cultural invention that deeply modifies the brain (Dehaene et al., 2015; Dehaene et al., 2010). The development of specific responses to the learned script in a left fusiform area, called the visual word form area (VWFA), is the major signature of a literate brain, and numerous studies have reported robust correlations between the level of literacy and activations in this region independently of age, scripts, in normal readers as well as dyslexics (Brem et al., 2020; Cohen et al., 2004; Dehaene et al., 2015; Feng et al., 2020; Martin et al., 2015; McCandliss et al., 2003; Richlan et al., 2011; Shaywitz et al., 2002). The VWFA develops rapidly in children, such that an initial activation to the learned script can already be detected after a few weeks of reading instructions (Brem et al., 2010; Dehaene-Lambertz et al., 2018). In all readers, this activation is systematically located within the occipito-temporal sulcus, just lateral to the fusiform gyrus, surrounded by face- and object-responsive regions (Puce et al., 1996; Weiner et al., 2016). This entire region shows late developmental plasticity and develops at a slower pace than the neighboring collateral sulcus (Gomez et al., 2017). The precise location of the VWFA in each individual is thought to be determined, at least in part, by its pre-existing connectivity, particularly to left-hemispheric temporal language areas (Bouhali et al., 2014; Li et al., 2020; Saygin et al., 2016) and parietal areas (Moulton et al., 2019; Yu et al., 2018).

In adults, ventral responses to visual categories are spatially organized in a robustly reproducible way, even in illiterate people (Dehaene et al., 2010): buildings and landscapes elicit preferential responses medially in the parahippocampal gyrus (PPA), bordered externally by a fusiform region responding to faces (FFA), then by an area in the lateral occipital cortex (LOC) responding more to objects than to scrambled images (Downing et al., 2006; Grill-Spector and Weiner, 2014; Hasson et al., 2003; Haxby et al., 2001; Weiner et al., 2016). In the context of such a reproducible organization, the culture-dependent emergence of the VWFA offers a unique opportunity to explore how new cultural representations exploit the margin of available plasticity and encroach within a mosaic of pre-existing robust specificities (Dehaene and Cohen, 2007).

The spatial organization of category-specific responses is known to develop slowly during childhood and even adolescence (Golarai et al., 2007; Grill-Spector et al., 2008). In infants, a rough medial-to-lateral gradient is already observed during the first year of life, with medial responses to places and lateral responses to faces and tools, yet the activations to faces have been reported to be initially indistinguishable from those to tools (Deen et al., 2017). It was rather unexpected that faces, which are both an important ecological stimulus and the visual category most frequently encountered by infants and children, do not elicit large visual MRI activations unique to this category in early childhood. On the contrary, face responses, while clearly present in pre-readers (Dehaene-Lambertz et al., 2018), continue to slowly grow and change during childhood and adolescence (Cantlon et al., 2011; Golarai et al., 2007).

These results contrast with behavioral and event-related potential (ERP) results in infants, showing (1) a strong attraction towards faces in infants (Johnson et al., 1991), perhaps even in utero (Reid et al., 2017); and (2) the recording, in the first year of life, of face-specific ERP components, such as N290 and P400 (de Haan et al., 2003; Farroni et al., 2002; Gliga and Dehaene-Lambertz, 2005, 2007) and right-lateralized responses compatible with the right hemispheric bias described in adults (Adibpour et al., 2017; de Heering and Rossion, 2015; see also Otsuka et al., 2007 using NIRS). These differences between methods, while confusing, might suggest that dedicated face-responsive neurons are present early on, yet with a spatial dispersion and intermingling with other neurons, such that face responsivity only gets slowly and progressively focused onto dedicated cortical patches with very high specificity for faces (Hesse and Tsao, 2020; Tsao and Livingstone, 2008; Tsao et al., 2008).

The protracted maturation of ventral visual areas opens opportunities for any stimulus, close enough to fit within the same biological constraints, to encroach on these areas. For instance, playing a video game for hours in childhood, or learning to read music, both lead to an increase in ventral visual responses to those stimuli in adulthood (Gomez et al., 2019a; Mongelli et al., 2017). More crucially, in all literate brains, the “neuronal recycling hypothesis” (Dehaene and Cohen, 2007) proposes that reading is one of the main beneficiaries of this phenomenon. Indeed, several studies have observed an impact of reading acquisition on the

113 activations to faces and objects (Centanni et al., 2018; Dehaene-Lambertz et al., 2018;
114 Dehaene et al., 2010; Li et al., 2013; Monzalvo et al., 2012). In illiterate and literate adults,
115 higher reading ability is associated with reduced responsivity to faces in the left fusiform and
116 increasing the right-hemispheric advantage for faces (Dehaene et al., 2010). An increased
117 rightward bias for faces was also found in typical 9-year-old readers relative to less efficient
118 dyslexic children (Monzalvo et al., 2012), and also in 7-year-olds readers compared to the
119 same children a few month earlier, prior to reading acquisition (Dehaene-Lambertz et al.,
120 2018). In those cases, however, the right-hemisphere increase, while positively correlated
121 with reading scores, was not associated with a diminution of face responses in the left-
122 hemisphere. In 6-year-old children with different reading performances (i.e. able to read from
123 0 to 80 words), Centanni et al (2018) found that the extent of the VWFA was negatively
124 correlated with the extend of the left face fusiform area (FFA). Finally, young struggling
125 readers had lower word selectivity in the VWFA, not because of a lack of response to words
126 but because of larger responses to objects (Kubota et al., 2019). It is important to stress that
127 those cortical changes can occur without necessarily having any measurable behavioral
128 impact – in fact, recent behavioral studies suggest that both word and face processing improve
129 steadily during this period, without interfering with each other (Kühn et al., 2021; Van Paridon
130 et al., 2020; Ventura et al., 2013). Furthermore, two different views on cortical competition
131 can in fact explain these brain-imaging findings. One possibility is that neurons are initially
132 committed, for instance to faces, and must change their preferred stimuli during reading
133 acquisition, such that any increase in reading-related responses implies a decrease in face
134 responses (pruning model) (Cantlon et al., 2011; Kubota et al., 2018). Alternatively, however,
135 both faces and words may compete for a pool of initially uncommitted neurons; in this case,
136 the growth of reading-related responses in the left hemisphere would block that of face-
137 related responses and force them to occur in the right hemisphere (blocking model); again,
138 this changing lateralization would not necessarily impact on behavior, but would be solely
139 seen through brain imaging.

140 To investigate those possibilities, we recently performed a longitudinal fMRI study in
141 which we were able to repeatedly scan 10 children during their first year of school, thus

allowing us to probe the responsivity of VWFA voxels prior to reading acquisition (Dehaene-Lambertz et al., 2018). We observed that words invaded a left-hemispheric site that was initially largely uncommitted, only slightly responsive to tools, and lateral to a region that was already face-selective. Neither face nor object responses in the vicinity decreased during reading acquisition. Thus, reading acquisition did not seem to prune away those initial responses, but blocked the further development of face-selective responses in the left hemisphere, and induced it to occur in the right hemisphere.

Here, our aim was to refine our understanding of the spatial organization of the ventral visual areas at the onset of reading acquisition. A major difficulty confronting prior studies is that age is often systematically confounded with reading acquisition, thus making it difficult to separate the cultural and maturational causes of brain development. To partially decorrelate age and reading acquisition, we recruited three groups of typical children who varied in age and reading expertise: 6-year-old pre-readers, 6-year-old beginning readers, and 9-year-old advanced readers. Pre-readers and beginning readers were approximately the same age (~ 6y) but exhibited very different expertise in reading due to the gap between the civil year beginning in January and the academic year beginning in September. Thus, pre-readers and beginners had roughly the same age, but a difference of one year in formal education. To further disentangle the variables, we also made a special effort to identify a few kindergartners who were already somewhat efficient in reading. As a contrasting point, the advanced readers were 9-year-old children with three years of reading experience.

Our first goal was to study how the development of a preferential response to words correlates with the development of preferential responses to other visual categories (e.g. faces). Second, we aimed to disentangle the effects of maturation (age) and reading acquisition on the spatial organization of ventral visual areas. Third, we were interested in investigating the biased connectivity hypothesis, according to which the preference for words and faces that occur at the specific location of the ventral occipital-temporal cortex are due to their privileged connections with cortical language and face network respectively (Hannagan et al., 2015; Li et al., 2020; Saygin et al., 2012; Saygin et al., 2016).

2. Material and methods

2.1 Subjects

A total of sixty typically developing children (31 boys and 29 girls) were included in the present study. These children could be divided into two groups according to their chronological age (6- and 9- year-olds children) or three groups according to their reading experience (pre-readers, beginning readers and advanced readers).

Children in the younger group (37 children, 59 to 87 months-old, 24 boys and 13 girls) were all following a normal curriculum. The difference in reading performance and age was related to the fact that, in France, all children who are born in a given calendar year (January to December) enter first grade. Thus, the oldest children in kindergarten and the youngest in first grade are separated by only a few months of age, but have different reading instruction. We assessed children's reading level with "Lecture en une minute" (LUM), a standardized list of words that children were asked to read as fast as possible in one minute. All children in 1st-grade (n=13) were considered beginning readers. Due to some variability in early exposure to print (both at school and in the family), we also included another six children who were in kindergarten but already able to read more than 15 words/mn. Thus, beginning readers comprised 19 children (10 boys and 9 girls) who were 80 ± 7 months-old and could read 19 to 72 words/mn (41 in average). The pre-readers (73 ± 5 months-old, 9 boys and 9 girls) were all kindergartners who did not receive formal reading instruction and could read less than 15 words/mn (6 in average). Although we greatly reduced the age difference between pre-readers and beginning readers while keeping an important difference in reading experience, the beginning readers were still 7 months older, on average, than the pre-readers (see Fig. 1 and Table 1). Below, we use a multiple regression approach to further disentangle the variables.

The oldest 9-year-old group (23 children, 115 ± 6 months-old, 12 boys and 11 girls) or the group of advanced reader had three complete years of reading experience (80 words/min in average. Their data were previously published in Monzalvo et al (2012).

Fig. 1. Age distribution (A) and reading performance distribution (B) in pre-readers, beginning readers and advanced readers.

Children were also tested on several cognitive skills that have been proven to be important for the acquisition of the reading abilities: Phonological awareness was tested with a French standardized test (EVALEC) consisting of the deletion of the first syllable in 10 trisyllabic words, then of the first phoneme in 12 CVC words, and finally in 12 CCV words (Sprenger-Charolles et al., 2005). Rapid automatic naming (RAN) of pictures was measured. Vocabulary level was determined with DEN48, consisting in the number (on 48) of pictures correctly named (Jambaqué and Dellatolas, 2000). Verbal short-term memory was assessed with forward and backward digit span and a sentence span (correct repetition of sentences of increasing length).

Pre-readers differed from beginning readers in phonological abilities, rapid automatic naming but not in vocabulary and verbal-short-term memory. Beginning readers differed from advanced readers in all the behavioral tests, including phonological abilities, rapid automatic naming, vocabulary and verbal short-term memory (**Table 1**).

Table 1
Characteristics of three groups (mean and standard deviation)

	6-Year-olds		9-Year-old advanced readers	F (2,59)	Pre-readers vs. beginners (p value)	Beginners vs. advanced readers (p value)
	Pre-readers	Beginning readers				
N	18	19	23			
Age/months	73 (5)	80 (7)	115 (6)	295.84* *	0.001***	<0.001***
Sex	9M 9F	10M 9F	12M 11F			
Handedness (Left/Right)	4/14	2/17	2/21			
Number of words read in 1 min	6 (5)	41 (15)	80 (13)	205.89* **	<0.001***	<0.001***
Phonological awareness	14.90 (9.07)	24.95 (7.89)	30.96 (3.95)	26.09** *	<0.001***	0.025*
Rapid automatic naming (time in sec)	25.97 (7.32)	20.93 (4.82)	16.22 (3.16)	17.73** *	0.014*	0.015*
Number of correctly named images	31.61 (4.33)	31.63 (8.09)	37.30 (5.23)	6.23***	n.s	0.011*
Verbal short-term memory	13.06 (3.31)	13.90 (3.86)	18.70 (4.74)	11.50** *	n.s	0.001***

218 Note: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$

219

220 None of the children had a history of neurological, psychiatric or hearing deficit. Their
221 vision was normal or corrected and their IQ estimated by two subtests of the verbal and
222 perceptual domains of the Wechsler's WISC 3 or 4 was in the normal range. All parents and
223 children gave their written informed consent. The study was approved by the local ethical
224 committee for biomedical research.

225

226 2.2 Stimuli and experimental task

227 The stimuli and experimental paradigm were the same as in Monzalvo et al (2012). Four
228 categories of visual stimuli (words, faces, houses, and an expanding checkerboard) were used
229 in a block paradigm. 30 four-letter regular French words and 30 different black and white
230 pictures of unknown people and of houses were used. The words were frequent words
231 encountered by young readers, as specified in Manulex, a lexicon basis comprising occurrence

frequency of words in 54 scholar French reading books (Lété et al., 2004).

In each block, 10 pairs of different images of the same category were presented (200 ms presentation for the first picture/word, 200 ms inter-stimulus, 500 ms presentation for the second picture/word) with an inter-pairs interval of 600 ms. The block was followed by a fixation cross during 10.5 s. For the entire block, images in a pair were either repeated or different, with in both cases, a size-factor difference for pictures, and an upper-lower case transformation for words. The initial goal was to study repetition suppression effects, but this variable had little or no effect and is not studied here. For the checkerboard category, a round black and white checkerboard picture was smoothly rotated during 15 s followed by a cross fixation image during 10.5 s. In each block, two stars were randomly inserted during the visual stimuli presentation, either on the right or the left side of the screen. The child was instructed to press the left button as soon as he/she saw a star. This incidental task was designed to keep the child's attention toward the visual stimuli. In each run, there were two blocks of each visual category and only one block of checkerboards. All blocks were presented in a random order. A run duration was 3 min 21s and all the children performed four runs.

Before MRI acquisition, each child was trained in a fake MRI, in which the real experiment was simulated using recorded MRI noises and a shortened version of the functional study. They also saw all the words used during the fMRI experiment, in randomly order and case, at their own pace. They were instructed to read what they could. The responses were either the correct word, letters from the word, or "I don't know". 500 ms after any child's response, the following word was presented with no feedback. The pre-readers had on average 33.8% correct (whole-word) responses vs 93% and 98.9% for the one-year- and three-year-readers.

2.3 fMRI Acquisition Parameters

Magnetic resonance was performed on a Siemens Tim Trio 3.0 Tesla scanner. Stimulus presentation and behavioral response collection were done with E-prime. Children were protected with noise-protection ear-phones and a mirror system above the child's head allowed them to see the visual stimuli presented on a screen at the end of the tunnel. T1

images were acquired for anatomical reference (TR = 2300 ms, TE = 4.18, voxel size = 1×1×1 mm, matrix 256×256×176). During the structural acquisition, children were looking at cartoons. For functional imaging, EPI volumes were acquired (TR = 2400 ms, TE = 30ms, matrix = 64×64× 40, voxel size =3×3×3mm). Each visual run comprised 84 volumes.

2.4 Data preprocessing

Preprocessing and analyses of the data were conducted using SPM12. The functional images were first corrected for differences in slice-acquisition time and realigned to the first volume in the scanning session. ArtRepair toolbox was used for detecting and repairing bad volumes (43). Two criteria were used to detect bad volumes: (1) 1.5 % variation in the global average BOLD signal from scan to scan, and (2) 0.5 frame-wise displacement, reflecting the sum of all head movements from scan to scan (calculated from realignment parameters). The damaged volumes that exceeded these criteria were replaced by linear interpolation of previous and subsequent images or by nearest-neighbor interpolation when several consecutive images were affected.

For the anatomical image, we first checked for scanner artefacts and gross anatomical abnormalities, then we manually set the origin of T1 image to the anterior commissure for each subject. We normalized each child anatomy to the Montreal Neurological Institute (MNI) template using the DARTEL approach to improve segmentation accuracy and local registration among participants. Functional images were co-registered to their corresponding anatomy. Then the parameters obtained during the DARTEL wrapping process were applied to the functional images which were finally smoothed using a 6 mm Gaussian kernel.

2.5 Statistical analyses

2.5.1 Category-specific activations:

In each subject, a general linear model was built in which a hemodynamic response function and its time derivative were convolved with block onsets for each category and the 6 motion parameters entered as regressors of non-interest. We implemented a mixed-model

analysis of variance (ANOVA) with Group (pre-readers vs. beginning readers vs. advanced readers) as a between-subject factor and Category (Words vs. Faces vs. Houses vs. Checkerboards) as a within-subject factor. We first examined the category-specific activation through the contrasts of one category versus the mean of the other three categories, across the entire set of participants ($N = 60$), then in each group, and finally compared the 9- and 6-year-olds activations.

2.5.2 Effect of age and reading expertise on brain activity:

In order to disentangle effects related to reading from those related to age on brain activity, we conducted two distinct whole-brain regression analyses. First, to investigate the effect of reading acquisition while controlling for age, we focused only on the two groups of 6-year-olds (total $n=37$) who had approximately the same age but different expertise in reading. We computed analyses with reading performance (number of words read in one minute) as a regressor and with age as a regressor of non-interest. Second, conversely, to examine the effect of age on brain activity, we analyzed the data from all 6- and 9-years-old (total $n=60$; age range 59-130 months) and entered age as a regressor of interest and reading performance as a regressor of non-interest.

For all analyses, we report effects at a threshold of $p < 0.001$ at the voxel level and $p < 0.05$ family wise error (FWE) corrected for multiple comparisons at the cluster level (the cluster-level corrected p value is denoted as $p_{\text{FWE_corr}}$).

2.5.3 Number of significant voxels in ventral visual areas

It might be possible that activation is present but more spatially variable or dispersed in younger and/or less expert children, something that would be missed in classical group analyses. To investigate this point, we considered all the voxels showing a preference for one category over the others in a ventral visual mask. The ventral visual mask comprised bilateral inferior temporal gyri and fusiform gyri as defined in the AAL template (Gao et al., 2017; Hervais-Adelman et al., 2019). Category-specific voxels were defined as any voxel in the mask having a z -value > 2.58 ($p < .005$) for the contrast of this category superior to the mean of the

three other visual categories. The number of specific voxels in each child was entered in an ANOVA with Group (pre-readers vs. beginning readers vs. advanced readers) as between-subjects factor, Category (Words vs. Faces) and Hemisphere (Left vs. Right) as within-subject factors. To investigate the effect of reading and age, we also conducted two regression analyses as above: 1) in an analysis restricted to 6-year-olds, the number of words read in one min (LUM) was entered as a continuous predictor variable, while age was the regressor of non-interest; and 2) conversely, in an analysis grouping all 60 children, age was entered as a predictor of interest while reading score (LUM) was a regressor of non-interest.

2.5.4 Medial-lateral and anterior-posterior selectivity

To better investigate the functional organization of the visual cortex, we recovered the activations within 6-mm spheres regularly spaced out along the x axis ($x = \pm 57, \pm 52, \pm 47, \pm 42, \pm 37, \pm 32, \pm 27$) at constant y-coordinate (-57) and z-coordinate (-12) on each hemisphere and for each of the categories (words, faces, houses, checkerboard) minus fixation (Cantlon et al., 2011; Dehaene et al., 2010). The y- and z-coordinates were based on our previous work on illiterates (Dehaene et al., 2010), children (Feng et al., 2020) and the classic coordinates of the VWFA (Cohen et al., 2002).

The same ROIs approach was also performed along the anterior-posterior axis ($y = -80, -68, -54, -42, -30$) at the 'x' privileged position for words ($x = \pm 48$) and faces (± 39) at constant z coordinate ($z = -12$) in both hemispheres, since an increasing specificity has been described along this axis (Van der Mark et al., 2009; Vinckier et al., 2007). The x and z coordinates were based on the peak of the word- and face-specific activation across all participants.

We first confirmed that we obtained the classic mosaic of preferences for the different visual categories, then we studied the degree of selectivity (selectivity index SI) to words and faces in each ROI and group. We used the simplest definition of SI, namely $SI_{\text{word}} = R_{\text{word}} - R_{\text{(average of others)}}$ where R_{word} is the BOLD response for words (as estimated by the beta coefficient for words vs. fixation) and $R_{\text{(average of others)}}$ is the averaged BOLD response for other categories (Faces vs. fixation, Houses vs. fixation, and Checkerboard vs. fixation). A positive SI denotes a preference for words relative to the other categories, whereas a negative SI denotes a greater

response to other categories compared to words.

We computed separate independent-samples t-test among the three groups at each ROI (FDR correction for repeated measures), then conducted our two regression analyses to separate age from reading score, as described above.

2.5.5 Functional connectivity analyses.

Since the biased connectivity hypothesis claims that the location of category-specific areas in the ventral visual cortex arises from their prior connectivity, we used the spheres defined above as seeds to analyze their “functional connectivity” pattern (i.e. correlation of fMRI signals to other brain sites). Van der Mark et al (2011) found that only the VWFA, but not the adjacent anterior-posterior areas exhibited functional connectivity with the spoken language network in the left hemisphere. To investigate how reading acquisition and age/maturation change these connectivity patterns, we focused on anterior-posterior regions near the VWFA and FFA within the occipitotemporal cortex. For the FFA, studies have revealed that in the adult brain, FFA exhibited functional connectivity with an extended face processing network, e.g. amygdala, inferior frontal gyrus, and occipital face area (Kleinhans et al., 2008).

Functional connectivity was computed using a seed-voxel correlation mapping analysis (Biswal et al., 1995). The ROIs defined above along the posterior-anterior axes and centered on one hand on the VWFA ($x = -48, z = -12, y = -80, -68, -54, -42, -30$) (**Fig. 6A**), and on the other hand on the bilateral FFA ($x = \pm 39, z = -12, y = -80, -68, -54, -42, -30$) (**Fig. 6D, 6F**) were used as seeds. In each child, we extracted the mean BOLD time series of the voxels comprised in each seed in each word (or face) block, z-scored the signal, and concatenated it across all word (or face) blocks and across the four runs. Three frames (7.2 s) after the end of each task block were included and three frames at the beginning of each task block were excluded in order to account for the hemodynamic delay (Fair et al., 2007). We then computed the temporal correlation between this signal and the similarly processed signal from all the other voxels in a mask defined by the contrast of [(words + faces) > fixation] across all participants. The correlation coefficients were further transformed to Fisher's Z scores for statistical analyses. Subject-specific contrast images reflecting standardized correlation coefficients

were used for the second-level analysis in SPM (Schurz et al., 2015). For each of the five seeds, one-sample t-tests were computed on correlation coefficients to yield functional connectivity maps for each group separately which allowed us to examine seed-specific connectivity (van der Mark et al., 2011).

To further examine the group differences, two-sample t-tests were first computed to determine whether there were reliable group differences in functional connectivity. We then implemented regression analyses with reading performance and age as described above, in order to find regions whose functional connectivity with seeds varied with reading experience independently of age, and vice-versa.

3. Results

3.1 Behavioral results

Due to unexpected technical problems, the inside-scanner behavioral data of 9 children (2 pre-readers and 7 beginning readers) were missing. The remaining data showed that pre-readers responded slower to the target star than beginning and advanced readers (main effect of Group: $F(2, 50) = 3.822$, $p = 0.029$, pre-readers: 782.72 ± 71.48 ; beginning readers: $669.85.39 \pm 86.42$; advanced readers: 696.04 ± 100.98). However, the induced activation in the right motor cortex (left hand response, $[39 -21 60]$) was similar in all groups, confirming that all the children were similarly engaged in the task.

3.2 fMRI results

3.2.1 Category-specific activations

To determine the local specificity of the activations to the different categories, each category was compared to all others. As shown in **Fig. 2A and 2E**, when all children were analyzed together, the different categories elicited localized activations along a medial-lateral axis in the ventral areas, from checkerboard in the primary visual and surrounding areas,

bordered externally by houses and then faces, and finally words only in the left hemisphere.

Beyond ventral activations, activations to faces were observed in both amygdala whereas words elicited activations in the posterior superior temporal region, prefrontal regions and angular gyrus in the left hemisphere, and the posterior superior temporal sulcus and angular gyrus in the right hemisphere (**Supplementary Table S1**).

We then examined the responses in each group (**Fig. 2B-D, 2F-H**). A preferential response to checkerboard and houses was seen in each group, and the response to words was present as expected, only in the two groups of readers. More surprisingly, the responses to faces also showed striking differences between groups. In the 9-years-old group, the preferential response to faces was firmly established in the occipital and fusiform regions associated with the bilateral amygdala (**Supplementary Table S2**). In the 6-years-old beginning readers, specific activation for faces was observed in the same locations. However, in the 6-years-old pre-readers, activation in the fusiform regions were not significant at the classical p_{FWE_corr} threshold. Only by lowering the threshold could we find activation at the classical site of bilateral face fusiform areas (left fusiform gyrus: $[-39, -51, -21]$, 5 voxels, $z = 3.37$, $p_{FWE_corr} = 0.965$; right fusiform gyrus: $[42, -48, -21]$, 5 voxels, $z = 3.61$, $p_{FWE_corr} = 0.965$).

Fig. 2. Category-specific circuits. Whole-brain views of words > [other visual categories] for all participants (A), 6-year-old pre-readers (B), 6-year-old beginning readers (C), and 9-year-old advanced readers (D). Horizontal and sagittal slides showing category-specific activations for all participants (E), 6-year-old pre-readers (F), 6-year-old beginning readers (G), and 9-year-old advanced readers (H). Green: regions selectively activated by words (Word > [Face, House, Checker]); Red: face-selective regions (Face > [Word, House, Checker]); Yellow: houses-selective regions (House > [Word, Face, Checker]); Cyan: checkers-selective regions (Checker > [Word, Face, House]). All the regions are reported at the threshold of voxel-level $p < 0.001$ with cluster-level FWE corrected $p < 0.05$.

When the 6- and 9-year-old children were compared, no difference of activation for the checkerboard condition was observed, but there was a general increase with age in activation in the right hemisphere for all the other stimuli vs. fixation (words: $[27 -75 -6]$ $z = 4.84$, 185 voxels, $p_{FWE_corr} < 0.001$; faces: $[27 -69 -5]$ $z = 5.49$, 741 voxels, $p_{FWE_corr} < 0.001$ and houses: $[27 -72 -6]$ $z = 5.31$, 512 voxels, $p_{FWE_corr} < 0.001$). There was no significant difference in specific contrasts (one category vs. the others) between the 6- and 9-year-olds.

We then examined the differences between the two 6-year-old groups who were at the same age but had very different reading experience. No significant differences were found in the whole-brain analysis. We then focused on the regions with significant activation to a given category in the 9-year-old advanced readers. These regions were used as masks, to which the comparison between the two 6-year-old groups was confined. The only difference was found for words minus others, near the classical VWFA site ($[-45 -60 -12]$ $z = 3.39$, 8 voxels, $p_{FWE_corr}=0.05$), i.e. the expected result of reading acquisition.

3.2.2 Regression analyses: Dissociation of the effects of reading expertise and of age/maturation on brain activations

To evaluate the respective effect of reading expertise and age on brain activity to each visual category, we performed two independent whole-brain regression analyses with reading (estimated by the number of words read in 1 min) and age as regressors with one or the other factor cancelled. The goal was to find out which brain regions had activity that varied more with age than with reading level and vice versa.

As expected, specific activations to words (Words > others) correlated with reading level, independently of age, in the left occipitotemporal cortex around the VWFA site when the 6 years-olds were considered (38 voxels, $p_{FWE_corr} = 0.03$, $z = 4.32$ at $[-45 -63 -9]$, **Fig. 3A**). This cluster was also significant when all children were considered (42 voxels, $p_{FWE_corr} = 0.02$, $z = 4.12$ at the peak). No other effect of reading level on brain activations to the other visual categories was observed, neither in contrasts such as [one category vs fixation] nor in contrasts [one category vs all others].

The converse analysis, examining the effect of age independently of reading expertise, revealed a significant cluster in response to faces vs fixation in the right medial fusiform ($[33 -66 -15]$ $z = 4.14$, 108 voxels, $p_{FWE_corr} = .002$, **Fig. 3B**) when all children were considered. Note that this cluster was only significant when the voxel-level threshold was lowered to $p=0.005$ but it survived cluster-level FWE corrected $p < 0.05$. The same analysis showed no significant cluster when only the 6-year-olds were considered. No significant effect of age on brain activity to other visual categories was observed, neither in the contrast of [one category vs

fixation] nor the contrast of [one category vs all others].

Fig. 3. Regression of brain activity with reading and age. (A) Effect of reading experience (number of words read in 1 min) on word-evoked activations relative to others in a model in which age was regressed out in 6-year-olds. (B) Age effect on the activation evoked by faces relative to fixation while reading experience was regressed out across all children. No significant effect was seen for the other categories.

To summarize our results, learning to read rapidly changes the brain, allowing the left-hemispheric spoken language network to be activated by written words (Fig. 2A- D) and reorganizing the visual cortices (Fig. 2E-H). While the ventral visual activation to written words was mainly driven by expertise in reading (Fig. 3A), the activation to faces was dependent on age (Fig. 3B) and was particularly weak in our youngest group.

3.2.3 Number of category-specific voxels in the visual areas

The above group analyses implicitly assume that there is a reproducible brain localization across children, whereas more variability might be present in younger and less expert children. To circumvent this difficulty, we also performed a localization-independent analysis on the number of voxels showing a preference for one category (words or faces) over

the others in a ventral visual mask. We observed a significant interaction of Group $\times$ Category $\times$ Hemisphere ($F(2, 57) = 4.992, p = 0.01$), thus confirming the existence of different selectivity patterns to words and faces in the left and right ventral visual cortex among the three groups (Fig. 4).

For words, post-hoc analyses revealed that readers (both beginning and advanced readers) had greater word-specific voxels than pre-readers in the left ventral visual cortex (beginning vs. pre-readers: $p_{\text{FDR_corr}} = 0.002$; advanced vs pre-readers: $p_{\text{FDR_corr}} = 0.003$) and also exhibited a left-lateralized pattern with a greater number of word-specific voxels in the left than in the right hemisphere in these two groups (beginning readers: $p_{\text{FDR_corr}} = 0.007$, advanced reader: $p_{\text{FDR_corr}} = 0.001$) with no difference in the number of word-specific voxels between the two groups of readers ($p_{\text{FDR_corr}} = 0.89$) and no difference between left and right hemispheres in pre-readers ($p_{\text{FDR_corr}} = 0.516$) (Fig. 4A). In the 6-year-old children, multiple regression revealed that the number of word-specific voxels in both hemispheres was significantly correlated with reading performance (left: $r = 0.522, p = 0.001$; right: $r = 0.374, p = 0.025$) when age was controlled for.

For faces, the number of face-specific voxels in the right hemisphere increased with age: 9-year-old advanced readers had greater face-specific voxels than the two 6-year-old groups (advanced vs. pre-readers: $p_{\text{FDR_corr}} = 0.003$; advanced vs. beginning readers: $p_{\text{FDR_corr}} = 0.045$), whereas there was no significant difference between the two 6-year-old groups in either hemisphere (left: $p_{\text{FDR_corr}} = 0.121$; right: $p_{\text{FDR_corr}} = 0.137$) (Fig. 4B). Besides, 9-year-olds had a right-lateralized pattern with a greater number of face-specific voxels in the right than in the left hemisphere (advanced readers: $p_{\text{FDR_corr}} = 0.004$), but this was not the case in the two groups of 6-year-olds (pre-readers and beginning readers, both $p_{\text{FDR}} > 0.1$). Interestingly, the number of face-specific voxels in the right hemisphere was also significantly correlated with age when reading performance was controlled for across all participants ($r = 0.286, p = 0.028$). Restricted to the 6-year-olds, neither an effect of reading (left: $p = 0.328$, right: $p = 0.518$), nor an effect of age (left: $p = 0.839$, right: $p = 0.449$) were found on face-specific voxels in either hemisphere.

No significant difference between groups (see Supplementary Fig. S1) was found for

the number of selective voxels for the house category.

Fig. 4. Number of voxels specifically responding to words and faces in the left and right ventral visual cortex in each group. (A) Number of word-specific voxels. The number of word-specific voxels in beginning and advanced readers were significantly larger than that in pre-readers and exhibited a significant left lateralization. **(B)** Number of face-specific voxels. The number of face-specific voxels increased with age and became larger in the right hemisphere than in the left hemisphere in advanced readers. *: $p < 0.05$; **: $p < 0.01$, ***: $p < 0.005$

3.2.4 ROI analyses of the medial-lateral and anterior-posterior functional organization

Our subsequent analyses were focused on the organization of the ventral visual cortex. Using regularly spaced 6-mm spheres along the x axis ($x = \pm 57$ to ± 27) at constant y-coordinate (-57) and z-coordinate (-12), we recovered the classic mosaic of preference for the different visual categories along this axis in each group except the pre-readers, who had no word-specific activation at the location of the VWFA (**Supplementary Fig. S2A**). We also performed the same ROIs approach along the anterior-posterior axis [$y = -80$ to -30] at the 'x' privileged position for words ($x = 48$) and faces ($x = 39$) in both hemispheres at constant z coordinate ($z = -12$) (**Supplementary Fig. S2B**). No region anterior or posterior to the classic location of VWFA showed word-specific activation in pre-readers.

In each of the above ROIs, we first compared the selectivity index across the 3 groups (independent-samples t-test), then conducted regression analyses controlling for age and

reading performance (Fig. 5). The word selectivity index was related to reading performance independently of age around the VWFA [$x = (-47)$, $y = -57$, $z = -12$;] (Fig. 5A) whereas the face selectivity index was related to age in both hemispheres around the FFA [left: $x = -39$, $y = (-68)$, $z = -12$; right: $x = 39$, $y = -54$, $z = -12$] (Fig. 5D).

Fig. 5. Word- and face-selectivity index in the three groups, along the x axis (A, B) and y axis (C, D). The pink rectangle in the left graphs indicates the locations (in A) [$x = (-52)$, $y = -57$; $z = -12$], and in (C) [$x = -48$; $y = (-68)$; $z = -12$] where significant differences were observed between pre-readers and each of the two other groups ($p_{FDR_cor} < 0.05$). The blue rectangle in the right graphs indicates the locations (in B) [$x = (-32)$, $y = -57$, $z = -12$], and in (D) [$x = -39$, $y = (-68)$, $z = -12$] in the left hemisphere; in (B) [$x = (32, 37, 42)$, $y = -57$, $z = -12$] and in (D) [$x = 39$, $y = (-54)$, $z = -12$] in the right hemisphere where significant differences were

observed between 9-year-olds and each of the 6-year-old groups ($p_{\text{FDR_corr}} < 0.05$). The red stars further indicate locations in which the word-selectivity index was significantly correlated with reading performance in 6-year-olds when age was controlled; and the blue stars indicate the locations in which the face-selectivity index was significantly correlated with age across all children when reading performance was controlled.

3.2.5 Functional connectivity along the anterior-posterior axis of the fusiform gyri

We examined the functional connectivity of the ROIs defined above with all the other voxels activated by words and faces (**Fig. 6**). Along the word axis, all seeds except seed 5 ($y = -80$) showed significant correlations with left posterior superior temporal gyrus and angular gyrus. Besides, seed 3, which fell closest to the classical coordinates of the VWFA, exhibited the strongest connections with traditional left-hemispheric language areas (left inferior frontal gyrus, inferior parietal lobule and superior temporal gyrus). Crucially, this pattern was significant in all 3 groups, including the pre-readers (see **Fig. 6B**), and we did not observe any significant group differences for any seed in this analysis. In the regression analyses, when we controlled age and examined the effect of reading performance in 6-year-olds, we found that the functional connectivity between seed 3 and left middle temporal gyrus increased with reading performance (3 voxels, $z = 3.23$ at $[-60, -36, 9]$; see **Fig. 6C**). However, this cluster did not survive correction for multiple comparisons.

The ROIs around the left and right FFAs showed functional connectivity with its contralateral region and bilateral amygdala (left FFA: **Fig. 6E**, right FFA: **Fig. 6G**). We didn't observe significant group difference in pair-wise group comparisons. Besides, neither an effect of age on functional connectivity across all children nor an effect of reading restricted to 6-year-olds were observed.

Fig. 6. Functional connectivity maps. Illustration of the 5 Seeds in the VWFA-System ($x = -48$) (A) and FFA-System ($x = \pm 39$) (D, F): Seed1 (red) was located most anterior, Seed5 (yellow) most posterior in the left occipitotemporal cortex. Seed3 (green) of the VWFA-System corresponds to the center of the VWFA described in previous studies. (B) Functional connectivity maps for pre-readers, beginning readers and advanced readers. (C) Reading effect on functional connectivity: regions whose functional connectivity with seed 3 positively correlated with reading performance (LUM) in 6-year-olds when age was controlled. (E, G) Functional connectivity maps with seeds in bilateral FFA-System for pre-readers, beginning readers and advanced readers.

4. Discussion

The ventral visual cortex displays a consistent and robust functional organization, fairly consistent in primates, for natural categories such as faces, bodies, objects and houses. Reading is a recent cultural invention based on arbitrary visual symbols that must intrude into this pre-existing organization. To examine the relative roles of age and reading experience in this transformation, we compared three groups of children of different ages and different reading experiences: 6-year-old pre-readers, 6-year-old beginning readers, and 9-year-old advanced readers. The two 6-year-olds groups had a minimal difference of age, contrasting with an entire school year of reading experience (1st grade, when the acquisition of reading is concentrated in the French education system). The few months of age-difference (~7 months) that remained between the two groups were further taken into account by including age as a regressor of non-interest in all our analyzes.

The fMRI results showed that, although written words and faces elicited specific activations in neighboring areas in the fusiform gyri, their developmental trajectory was different. On the one hand, a few months of school were sufficient to observe word-specific activation at the classical coordinates of the VWFA. This area was functionally correlated to the spoken language network in all three groups, even before reading acquisition, and with minimal differences in functional correlations between groups. On the other hand, face responses were affected by age, notably in the right hemisphere. Functional correlations were mainly found with the contra-lateral region and both amygdalae. Finally, the activation evoked by places was not affected either by age or by reading expertise.

4.1 Reading development

Learning to read comprises many stages over the course of several years, each of which could leave its own signature in the brain (Stuart and Coltheart, 1988). According to an accepted developmental hypothesis (Pugh et al., 2001), at the beginning of formal reading instruction, children primarily make use of the temporoparietal regions to decode written

words in a laborious letter-by-letter manner. Through continuous practice and in tight coupling with the temporoparietal regions, processing in the occipitotemporal VWFA becomes increasingly routinized and unconscious, ultimately resulting in automatic and fluent lexical access and reading performance.

Our findings on pre-readers, beginning reader and advanced readers support this developmental hypothesis. In pre-readers, we found that the contrast of words versus other visual categories only activated the left temporoparietal region. This activation, which lies outside of the ventral visual pathway, might indicate that children without formal reading instruction grope with letters and attempt to guess either their pronunciation (the supra-marginal region being involved in covert articulation; e.g. (Price, 2010) or to guess words they know by recovering semantic information (Binder et al., 2009).

In beginning readers, we found that the left temporal-occipital region (VWFA), inferior parietal lobule, left temporal middle gyrus and other regions showed a selective response to words (**Fig. 2**). Even after controlling the effect of age, the VWFA still showed significant group differences between the two groups of 6-year-olds, suggesting that the increased activation of this area was caused by children's reading experience rather than by mere brain maturation. The same conclusion is afforded by other studies which found differences in this reading circuit when comparing literate versus illiterates (Dehaene et al., 2010; Hervais-Adelman et al., 2019) or known versus unknown scripts (Agrawal et al., 2019; Baker et al., 2007; Szwed et al., 2014). The present research first shows that this transformation can start at a very young age, as it was found even six-year-olds with only a short period of reading experience. Again, this is convergent with previous longitudinal fMRI training studies (Brem et al., 2010; Dehaene-Lambertz et al., 2018).

Finally, advanced readers, who had 3-years of reading experience activated classical reading areas comprising a large activation in the posterior superior temporal sulcus and the left inferior frontal gyrus. These activations are similar to adults in a similar task (Dehaene et al., 2010). They indicate that by 3 years of reading experience, an automatic and efficient access to the language network from visual symbols may already be in place.

4.2 Reading experience rapidly shapes the word specification in VWFA

Previous studies have found that the emergence of VWFA is dependent on the reading experience but this relation was confounded with age. Here, we decorrelated the two effects by comparing two groups of typical children of approximately the same age but with different reading experience simply due to the gap between the academic and the civil year. Pre-readers were exposed to books and some reading/writing in kindergarten and were able to slowly decipher some of the presented words (~38%), but their familiarity with print was not sufficient to obtain significant word-specific activation in this region. By contrast, although their reading performance remained modest (41 words/min in average, half the performance of the advanced readers 80/min), the few months of intense instruction that beginners had received was sufficient to strongly modify this region. The VWFA is thus one of the most robust and macroscopic evidence of how learning transforms a brain. Brem et al (2010) also reported a fast training effect on brain visual activity in 6-year-old kindergarten children using the *graphogame*, a computer game to teach grapheme-phoneme correspondence. After 8 weeks (3.6 hours), children improved their knowledge but with only slight reading gain. Print-selectivity (Words > False font) increased but in more posterior ROIs than here (i.e. corresponding to our ROIs 4 and 5). Both results emphasize the plasticity of the anterior-posterior axis at the lateral level of the VWFA.

4.3 Word vs Face-specific activations

The rapid change in responsivity to written words stands in contrast with the slow development of the face-specific response, whose activation increased between 6 and 9 years (**Fig. 2-5**), notably in the right hemisphere. Since the first reports of a weak fusiform response to faces in young children (Golarai et al., 2007; Scherf et al., 2007), with a protracted development until adolescence, this observation has questioned models of neural development. Faces are the most frequent and important stimulus with which children are exposed from birth, and young children are already expert to discriminate and memorize faces

(De Heering et al., 2012). Even if performance continues to improve until adulthood (Kühn et al., 2021; Van Paridon et al., 2020; Ventura et al., 2013), peculiarities of face perception such as the face-inversion effect or the other-race effect already arise during infancy (Hayden et al., 2007; Sangrigoli and De Schonen, 2004). Faces are not only important social stimuli but are also crucial for speech perception. Since the first weeks, infants are able to link visual facial movements and the produced speech sound (Bristow et al., 2009; Kushnerenko et al., 2008; Weikum et al., 2007; Yeung and Werker, 2013). Furthermore, although lip-reading mainly involves the left posterior superior temporal sulcus, the size of the McGurk effect, indicating audio-visual integration of face and speech information, is also correlated with the activity in the fusiform gyri in children, but not in adults (Nath et al., 2011).

Given those findings, it could have thought that face circuitry would have been fully in place prior to reading acquisition, and that reading, which also involves a visual-to-auditory link, would compete with the same or nearby pathway. Favoring this interpretation, earlier studies on literate and illiterate adults reported that the growth of the VWFA is negatively correlated with left-hemispheric face responses (Dehaene et al., 2010). In a longitudinal study of 10 typically developing children during the first year of reading acquisition, however, we observed no direct competition or “pruning” of other visual categories by the growth of reading-related responses (Dehaene-Lambertz et al., 2018). Selecting the voxels that after a year of school were word-specific, it was possible to examine backward their specificity to other visual categories (tools, bodies, faces, and houses) before reading acquisition. These voxels actually had only a weak responsivity to objects, not faces, and this specificity did not change as their response to words increased (Dehaene-Lambertz et al., 2018). The present study, also based on typically developing children, similarly suggests a lack of direct competition between words and faces in the VWFA, but rather the existence of two parallel anterior-posterior axes of word- and face-selectivity, respectively at $x = -52$ to -42 and $x = -32$ (**Fig. 5**) (for converging results suggesting the presence of multiple parallel circuits in monkeys, see (Bao et al., 2020).

In contrast to Centanni et al (2018), we did not observe a negative correlation between the VWFA size and the left FFA size, which would have been suggestive of direct competition

or “pruning”. Rather, we found a positive shift of face responses towards the right FFA, congruent with previous reports showing a positive effect of reading performance on the extent of responses in the right FFA (Feng et al., 2020; Monzalvo et al., 2012). Thus, the “blocking” view of competition appears to be supported by our results: as previously suggested in our longitudinal study (Dehaene-Lambertz et al., 2018), the expansion of the VWFA with reading acquisition in the left hemisphere blocks that of the left FFA, and may force the further growth of face responses to occur in the right FFA.

4.4 Intense maturation of the fusiform gyri during school-age

What makes the ventral visual cortex capable of flexibly acquiring different category specificities throughout childhood, at the age of 6 or even 9-year-old? Weiner et al. (2016) investigated the cytoarchitectonic profiles of the ventral visual cortex and described at least four different areas in the fusiform gyri (FG1 to 4) but there was no single association between a cytoarchitectonic area and a unique visual category. For example, area FG4 comprises voxels responsive to bodies, faces and words. In a recent study, Gomez et al (2019b) explored the gene expression in visual cortices and discovered two series of genes with opposed hierarchical gradients, one ascending and one descending, from posterior to anterior areas comprising ~200 genes. The authors propose that these gradients signal changes in the distribution of subtypes of neurons synaptic regulation and myelination processes along the visual hierarchy. Age influences the magnitude of gene expression in low- and high-level visual areas along the two gradients, an adult-like pattern being reached around 5 years but with noticeable changes continuing to be present throughout childhood. Furthermore, Gomez et al (2017), by comparing 5-to-12-year-old children to young adults, showed that maturational changes were more intense in the face-selective regions than in the place-selective regions. These structural changes are consistent with what we observed here in a narrower age range (6- to 9-year-olds): responses to faces in the bilateral fusiform gyri increased with age whereas responses to houses were stable. As the task was similar in all blocks (detect the rare occurrence of a star), the differences between groups and visual categories cannot be related to the task, but must depend on the visual category. We could also exclude the possibility that

face responses were more dispersed in younger children, because the result remained similar when we considered the number of face-specific voxels in a ventral mask (**Fig. 4**).

Gomez et al (2017) also reported a decrease in T1 relaxation time between children and adults, in the FFA; it reflects microstructural proliferation, notably the growth of the dendritic arborization, that might increase the functional responses by pooling neurons over larger space and/or by refining the specificity of the response through lateral inhibition. All these results emphasize the magnitude of the maturational changes in the fusiform gyri at school-age, when new visual categories such as letters and numbers are intensively learned. They substantiate the neuronal recycling model (Dehaene and Cohen, 2007), according this architecture is at once prespecified for visual recognition and yet sufficiently flexible to acquire new culturally defined categories. As previously proposed (Dehaene-Lambertz et al., 2018), the newly acquired visual categories may take advantage of this plasticity to invade the ventral visual cortex at a moment where it is still weakly specialized cortex, without having to prune away previously stabilized cortical responses.

4.5 Functional connectivity of the VWFA and of the FFA

Why do specific and reliable subsectors of ventral visual cortex acquire a specialization for written words versus faces? One possibility is that those stimuli differ in ways that fit with pre-existing medial-lateral gradients of preference for features such as line junctions, curvature, foveal retinotopic bias, etc.(Hannagan et al., 2015; Hasson et al., 2002; Szwed et al., 2011). However, this view fell in disfavor when it was found that, when participants were trained to “read” words written in unusual fonts made of faces or houses, those non-letter-like reading stimuli continue to activate the VWFA during reading (Martin et al., 2019; Moore et al., 2014). More recently it was suggested that the connectivity to other brain regions might be an important factor (Hannagan et al., 2015; Saygin et al., 2016). Here indeed, confirming previous anatomical and functional reports (Bouhali et al., 2014; Saygin et al., 2012; Saygin et al., 2016), we observed that the FFA and the VWFA had very different functional correlations with other brain regions, even prior to reading acquisition. The ROIs the most affected by reading experience ($x = -48$, seed 3) had the strongest relation with the oral language network,

whereas the more internal seeds at $x = \pm 39$, i.e. those with face responses, were all correlated with the contralateral region and both amygdala. It is interesting to observe that in both cases, there was no difference between groups. Notably, the pre-readers who presented almost no selective activation in these ROIs, nevertheless exhibited similar “functional connectivity” as the older and more expert children, both in the case of the VWFA and of the FFA seeds. Those findings support the idea that connectivity comes first and drives the localization of functional specialization (Hannagan et al., 2015; Saygin et al., 2016).

Because structural connectivity is largely in place already at birth, a prediction of this view is that similar connectivity biases, predating the face and reading circuits, should already be observed in infants. The scarce data available so far support this view: lateral ventral occipito-temporal regions show a greater functional connectivity at rest with distal associative regions in the temporal and frontal lobes, where mesial regions are preferentially connected with ventral and internal areas, including the amygdala (Barttfeld et al., 2018; Li et al., 2020). All these results suggest that the connectivity to distant regions is an important factor in determining the computational role of ventral visual subregions.

5. Conclusions

The present cross-sectional study converges with the conclusions of Dehaene-Lambertz et al.’s (2018) longitudinal study, as well as many recent studies encompassing a larger age-range: the developing specialization of the human visual cortex is constrained by the connectivity to distant regions. The main contribution of the present research is to show that this growing specialization can occur at two very different time scales. On the one hand, the development of the reading circuit occurs rapidly, driven by a few months of schooling, and regardless of age, at least around six years of age. On the other hand, the development of the face circuit, in spite of six previous years of massive exposure to faces, is far from being finished at that age, and is primarily driven by age. In both cases, however, this development is made possible by the protracted plasticity of the fusiform regions, as elegantly shown through cyto-architectonic and gene expression analyses by Gomez et al (2019b). Reading

766 acquisition, and presumably other design features of our school system such as the rapid
767 acquisition of numerals and other mathematical symbols, takes advantage of this remarkable
768 window of plasticity.

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779

780 **Supplementary**

781 **Figures**

782

783 **Fig. S1. Number of voxels selectively responding to houses in the left and right ventral visual**
784 **cortex in each group.**

785

Fig. S2. Mosaic of preferences for different visual categories in ventral visual cortex. (A) Activation relative to fixation for the different categories in successive spheres of 6 mm regularly spaced at medial-lateral axis (± 57 to ± 27) in three groups of children (left: pre-readers; middle: beginning-readers, right: advanced readers). **(B)** Activation relative to fixation for different categories in successive cortical sites tracing a vertical line (y-axis) through the classical coordinates of the VWFA ($x = -48$) and FFA ($x = -39$).

Tables

Table S1

Regions of significant activations for each visual category vs. the three others across all participants (individual voxel $p=0.001$, cluster-level FWE corrected $p < 0.05$).

Region	MNI coordinates			No. of voxels in cluster	Cluster-level P value (FWE-corrected)	Z value at local maximum
Words > others						
Left middle temporal sulcus	-60	-33	6	474	<0.001	7.40
	-48	-39	0			6.381
	-54	-60	-12			6.324
Left precentral	-45	12	30	731	<0.001	6.42
Supplementary motor area	-3	12	54	295	<0.001	6.50
	0	-18	51			4.16
Posterior cingulate cortex	-3	-36	33	278	<0.001	6.34
	0	-33	21			5.47
Right middle temporal gyrus	54	-36	3	198	<0.001	5.93
Right angular gyrus	51	-69	33	174	<0.001	5.53
Left angular gyrus	-36	-66	30	689	<0.001	5.18
Left Middle frontal gyrus	-27	30	45	109	<0.001	4.45
Faces > others						
Right fusiform gyrus	42	-51	-21	121	<0.001	>8
Right amygdala/hippocampus	18	-9	-18	225	<0.001	>8
Left amygdala/hippocampus	-18	-9	-18	110	<0.001	>8
Left fusiform gyrus	-39	-51	-18	66	0.006	7.28

Houses > others						
Right fusiform gyrus	30	-42	-9	619	<0.001	>8
Left fusiform gyrus	-30	-45	-6	618	<0.001	>8
Left middle occipital gyrus	36	-87	15	125	<0.001	5.56
Medial superior frontal gyrus	-6	51	18	250	<0.001	4.72
Left angular gyrus	-42	-66	30	86	0.001	4.25
Checkerboard > others						
Left calcarine	0	-84	0	5442	<0.001	>8
	-6	-84	-6			>8
	-15	-93	21			>8
Right superior temporal gyrus	51	-39	15	198	<0.001	7.63
Right insular	33	21	-3	141	<0.001	6.55
Right inferior frontal gyrus	45	9	30	74	0.003	4.09

800

801 **Table S2**

802 **Regions of significant activations for each visual category vs. the three others in each group**
803 **(individual voxel p=0.001, cluster-level FWE corrected p < 0.05).**

Region	MNI coordinates			No. of voxels in cluster	Cluster-level P value (FWE-corrected)	Z value at local maximum
Pre-readers						
Words > others						
Inferior parietal lobule	-48	-60	45	108	<0.001	4.15
Faces > others						
Houses > others						
Left lingual	-30	-45	-6	64	0.001	4.73
Right middle occipital gyrus	30	-90	9	88	<0.001	4.40
Right fusiform gyrus	30	-48	-3	138	<0.001	4.11
Checkerboards > others						

Left calcarine	3	-87	0	2232	<0.001	6.67
Right superior temporal gyrus	48	-39	15	46	0.007	4.47
Left middle occipital gyrus	-39	-66	6	63	0.001	4.26
Beginning readers						
Words > others						
Right middle temporal gyrus	57	-42	-3	60	0.001	5.13
Left middle temporal gyrus	-42	-36	-6	106	<0.001	4.34
Left fusiform gyrus	-48	-57	-12			3.97
Middle cingulum cortex	6	-30	33	63	0.001	4.18
Left inferior parietal lobule	-30	-66	45	45	0.008	4.13
Inferior frontal gyrus	-60	18	15	34	0.029	3.83
Faces > others						
Right amygdala/ hippocampus	21	-9	-18	66	<0.001	5.35
Left amygdala/ hippocampus	-21	-9	-18	42	0.011	5.14
Right fusiform gyrus	39	-51	-21	64	<0.001	4.87
Houses > others						
Left fusiform gyrus	-30	-45	-3	97	<0.001	4.72
Right fusiform gyrus	30	-42	-12	80	<0.001	4.61
Checkerboards > others						
Left calcarine	6	-90	-6	2393	<0.001	6.52
Right hippocampus	24	-30	0	44	0.012	5.02
Advanced readers						
Words > others						
Left inferior frontal gyrus	-51	12	27	291	<0.001	5.22
Left fusiform gyrus	-45	-69	-12	118	<0.001	4.65
	-54	-57	-12			4.22
Right middle temporal gyrus	54	-33	3	98	<0.001	4.22
Left middle frontal gyrus	-30	30	48	59	0.002	4.07
Left middle temporal gyrus	-63	-33	6	62	0.001	3.92
Faces > others						
Right fusiform gyrus	39	-54	-18	201	<0.001	5.56
Left fusiform gyrus	-39	-51	-21	54	0.003	5.04
Right amygdala/ hippocampus	21	-9	-18	112	<0.001	4.75
Left amygdala/ hippocampus	-21	-6	-18	71	<0.001	4.56
Houses > others						
Right fusiform gyrus	33	-42	-9	323	<0.001	6.49
Left fusiform gyrus	-33	-39	-9	191	<0.001	6.19
Right middle occipital gyrus	33	-84	9	164	<0.001	5.35

Left middle occipital gyrus	-33	-90	21	108	<0.001	4.79
Left lingual	-27	-81	-12	39	0.022	4.80
Middle cingulum cortex	-9	-42	36	70	0.001	4.30
Checkerboards > others						
Left hippocampus	-21	-27	-6	35	0.029	7.17
Right lingual	9	-75	0	3461	<0.001	6.56
	-9	-75	0			6.42
Right middle temporal gyrus	45	-54	0	146	<0.001	5.41
Left superior temporal gyrus	48	-42	15	100	<0.001	4.51
Left superior parietal lobule	-27	-51	51	105	<0.001	4.37
Left middle occipital gyrus	-36	-63	6	59	0.002	4.34

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