Review

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Developmental neuroimaging of the human ventral visual cortex

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Here, we review recent results that investigate the development of the human ventral stream from childhood, through adolescence and into adulthood. Converging evidence suggests a differential developmental trajectory across ventral stream regions, in which face-selective regions show a particularly long developmental time course, taking more than a decade to become adult-like. We discuss the implications of these recent findings, how they relate to age-dependent improvements in recognition memory performance and propose possible neural mechanisms that might underlie this development. These results have important implications regarding the role of experience in shaping the ventral stream and the nature of the underlying representations.

Introduction

The human visual cortex has been extensively studied in adults. More than a dozen visual areas have been identified based on their retinotopic organization and functional selectivity [1,2]. The visual cortex includes many regions that are organized hierarchically, beginning with early visual areas, which are delineated on the basis of their retinotopic organization (see Glossary), then ascending into the high-level visual cortex, which displays weaker retinotopy [3,4] and higher stimulus selectivity (see Glossary) and includes regions selective to objects, faces and places [5–7] in the ventral (occipitotemporal) visual cortex. Functional magnetic resonance imaging (fMRI) studies in adults reveal that these retinotopic maps and selective regions can be reliably detected within individual subjects and are remarkably consistent across people in their spatial characteristics. However, several questions remain. It is unknown how the selectivity of visual regions comes about, when the visual cortex reaches maturity, and what the relationship is between cortical development and proficiency in various visual tasks.

Behavioral measurements have established that the visual system continues to develop postnatally for several years. Although substantial changes occur in the first year of life [8–10], some aspects of vision require many years to become adult-like. Until age six or seven years, there are significant improvements in visual proficiency in tasks involving second-order motion [11], form-from-motion [12], grating acuity discrimination [13] and orientation

discrimination [14]. Some aspects of vision develop more slowly. Spatio-chromatic processing of low-spatial frequency isoluminant stimuli takes ~12–13 years to reach an adult-like state [15]. Face perception and recognition memory reach the adult level only at an age of ~16 years [16–18] (Box 1). Similarly, event-related potentials (ERPs) to faces show a long developmental trajectory (Box 2).

Behavioral and ERP studies have revealed important clues regarding the developmental time course of visual processes in humans. Until recently, developmental changes in humans were not considered in the context of the underlying neural mechanisms in specific brain regions. Nevertheless, a substantial body of research in

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Glossary

Configural processing of faces: processing of the second-order relationship between face parts, such as spacing between eyes or spacing between mouth and nose.

DTI: Diffusion tensor imaging – a magnetic resonance imaging technique that enables the measurement of the restricted diffusion of water in tissue. DTI is used to measure the anisotropy of white matter structures and map white matter fiber tracks.

FIE: Face inversion effect – recognition of faces is disproportionately impaired on inverted faces. FIE is thought to impair both holistic and configural processing of faces.

Holistic processing of faces: reflects the idea that the perception of the whole is more than the perception of the sum of its parts. Tasks showing holistic processing of faces report that the recognition and memory of a face part (e.g. a nose) in isolation is worse than when it is in a face and that recognition of a part of the face (e.g. the top half of a face) is affected by the context (i.e. performance varies if the top and bottom parts are connected to form one face, or presented with a horizontal offset, in which the top and bottom parts are disjointed).

Recognition memory: describes a behavioral paradigm consisting of a study phase and a test phase. In the study phase a subject is shown a sequence of stimuli. Later (minutes or days) the subject participates in the test phase and is shown stimuli that he/she was presented with during the study phase mixed with new stimuli. The subject is asked to report whether each test stimulus is old (has seen it before) or new (has not seen it before).

Retinotopic map: a topographic map in which two adjacent points on the retina (or the visual field, if the subject maintains fixation) map into adjacent points on the cortex. The human visual cortex contains multiple retinotopic maps. For example, each of the lower visual areas, V1, V2, V3, V3a and hV4 contains a hemifield representation in each hemisphere. Thus, each of these areas contains a topographic map of the entire visual field. For a review see Ref. [1].

ROI: region of interest.

Selectivity: differential responses to specific visual stimuli. Selective regions as measured with fMRI refer to cortical regions that respond significantly more to some stimuli than to other stimuli, usually determined via a statistical criterion.

Ventral and dorsal processing streams: the visual cortex contains more than a dozen areas that are thought to be organized in two main processing streams. The ventral stream, thought to be involved in visual recognition, begins in V1 and extends ventrally into the occipitotemporal cortex. The dorsal stream, thought to be involved in visually guided actions and in determining where objects are located, begins in V1 and extends dorsally into the parietal cortex.

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Box 1. Behavioral investigations of the development of face perception

Faces contain rich visual information, including identity, emotion and intention. Adults often quickly perceive the complex information contained in a face and are able to remember the face later. Although there is evidence that newborn infants preferentially attend to faces [67], it is well documented that face recognition undergoes a prolonged development before reaching the adult level [17,18,68]. Face recognition memory increases markedly between 6 and 16 years of age (Figure I). Face recognition memory in 6–14 year-olds is 50–70% of the adult level, and there are slow gains until age 16 years [16]. Even in perceptual-matching tasks, performance improves markedly between four and 11 years of age [17,69]. What there is less agreement about is whether there is a qualitative difference in the way that children and adults recognize faces. One extensively studied marker of face processing is the face inversion effect (FIE) [70]. Inversion is thought to disrupt holistic processing (see Glossary) of faces. In their original study, Carey and Diamond [71] reported no FIE in children in contrast to adults. Therefore, they proposed a qualitative difference in face processing between children and adults,

in which children process face information in a more piecemeal manner than do adults who process faces holistically. However, in their subsequent studies, Cary and Diamond [72] and also other investigators found the FIE in children as young as four or five years [73–75]. Additional evidence for holistic processing of faces in children includes reports that children have better recognition of face parts when they are presented within a face rather than in isolation [74] and evidence that children's performance on composite faces is similar to that of adults [76]. Taken together, there is substantial evidence for holistic processing of faces in children, which suggests that the development of face processing involves quantitative, rather than qualitative, changes. Another debate surrounds differences in configural processing of faces (see Glossary) across development. One hypothesis suggests that children are particularly immature at configural processing but not at feature processing [75]. However, other research provides evidence for configural processing of faces even in four year-olds [77] and sensitivity to second-order relations in five-month-old babies [78].
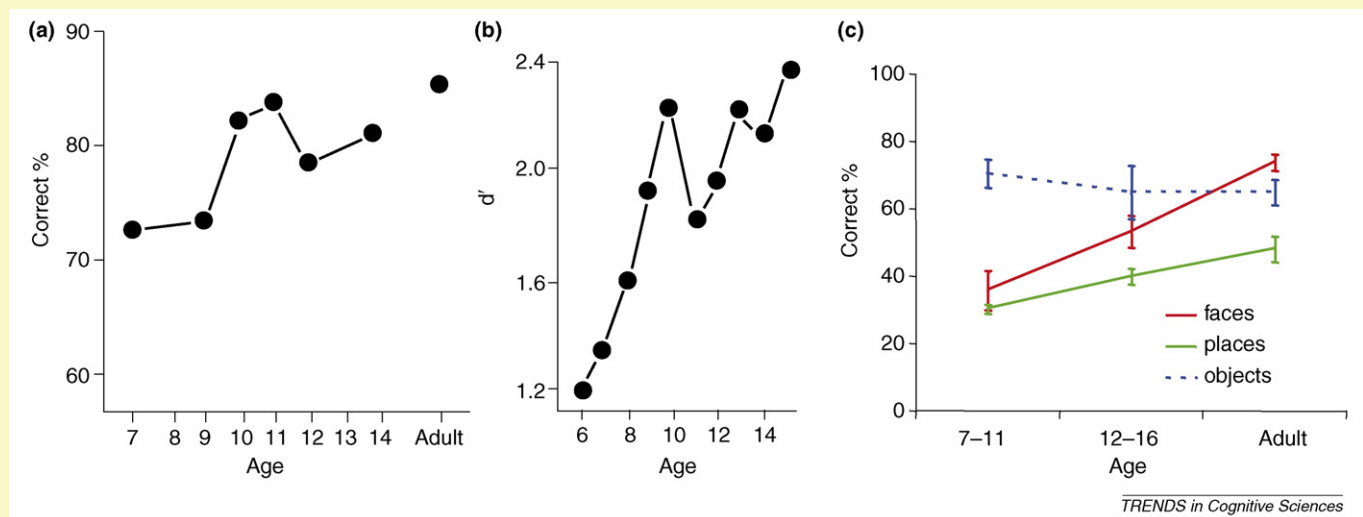

Figure I. Development of face and place recognition memory. Recognition memory performance for faces increases with age during middle childhood and adolescence. **(a)** Carey and colleagues [98] found a dip in performance at the onset of puberty. **(b)** Flin [99] found an increase in recognition memory for faces with age. **(c)** Golarai and colleagues [35] also found increases in place recognition memory with age (green) but no age-related changes in recognition memory for novel abstract objects (blue).

animals shows that experience in combination with genetic factors shape responses and functional organization in the visual cortex during crucial periods of development [19–22]. However, much less is known about the neural correlates of the development of the ventral cortex in humans and whether it involves critical temporal windows. Developmental neuroimaging is, therefore, crucial for understanding the neural substrates of this development, because it allows tracking of developmental changes in brain anatomy (with MRI) [23–25], function (with fMRI) and connectivity [26] (using diffusion tensor imaging (DTI), see Glossary) at a resolution of a few millimeters.

Using fMRI, researchers have started to examine the development of the visual system. fMRI of anesthetized infants who were presented with visual stimuli through closed eyes shows that the early visual cortex of infants activates in response to these stimuli [27–30]. Nevertheless, the pattern of blood-oxygen-level-dependent (BOLD) responses changes during the first year of life, probably because of changes in synaptic connections, oxygen consumption and vasculature. A few fMRI studies have investigated the development of the early visual cortex during

childhood. These studies suggest that retinotopic maps in V1, V2, V3, V3a [31] and contrast sensitivity in V1, V3a and MT (a motion-selective region in the posterior inferotemporal sulcus, ITS) [32] reach an adult-like state by age seven years. fMRI of high-level visual cortex, including face [33–37], place [35,36] and object-selective cortex [35,36] indicate that the face [33–37] and place-selective cortex [34,35] follow a much slower developmental trajectory and continue to develop after age seven years, in correlation with age-dependent improvements in recognition memory for faces [35] and places [35] and increased specialization in processing upright versus inverted faces [37,38]. These studies suggest that the ventral visual cortex might take longer to develop than early visual cortex.

This review will focus on recent findings of the development of the ventral visual cortex because of recent accumulating evidence of the characteristics of this development. We will (i) consider how functional selectivity might manifest with fMRI, (ii) review evidence for the development of functional selectivity in the ventral stream during mid-childhood and adolescence and (iii) discuss possible neural mechanisms underlying this development.

Box 2. Electrophysiological evidence for development of face processing in children

In adults, scalp recorded ERPs reveal that the N170 (a negativity observed 150–200 ms after stimulus onset) is a reliable marker of face processing [79,80]. The scalp N170 is significantly more negative when viewing human faces compared with objects or animal faces [79,81] and is more negative for inverted than for upright faces [82,83]. ERP recordings show that the N170 changes progressively with age towards the adult form [84]. In six-month-old infants an ERP component is evoked by faces but is substantially smaller in amplitude and longer in latency [85] (occurring at about 300 ms) compared with that of adults. Unlike adults, the N170 in six-month-olds is not modulated by face inversion; however, it is modulated by inversion in 12-month-olds [86]. In 5–14 year-olds, the N170 is delayed in onset, longer in duration and significantly smaller in amplitude (less negative) compared with that of adults [84,87] (Figure I). These developmental changes were observed for the N170, but not for object selective ERPs [84] (Figure I). The relationship between the development of N170 and behavioral improvements in face processing remains unknown. Furthermore, the cortical sources that generate the N170 are undetermined (but see Ref. [88]), as multiple brain sources might generate similar scalp ERPs. Intracranial recordings in epileptic adults suggest that face-selective ERPs are generated at multiple locations over the fusiform gyrus, the inferotemporal sulcus (ITS) and the superior temporal sulcus (STS) [89]. Development in any one of these foci might affect the N170 and might involve age-dependent increases in the selectivity of face responses and/or increases in synchrony of face-selective responses.
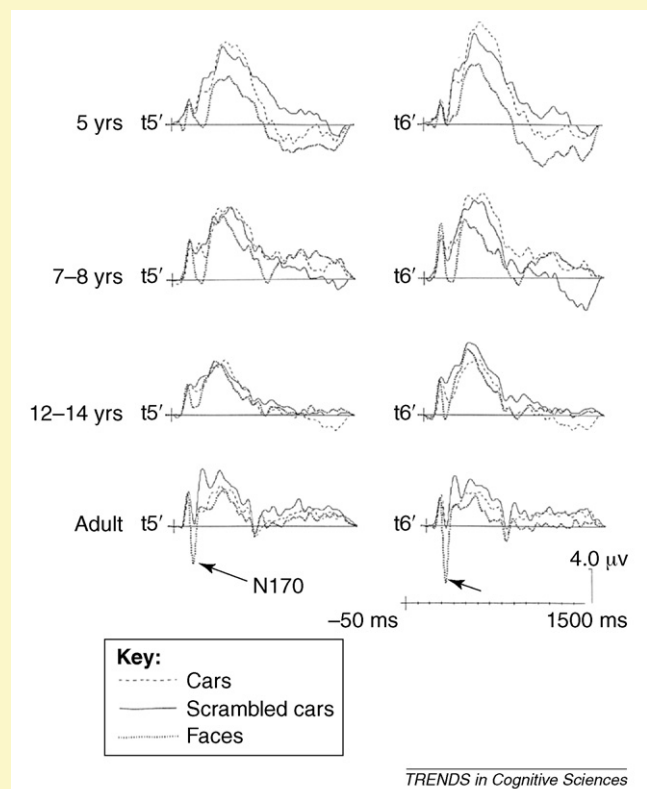

Figure I. ERP correlates of the development of the N170. Group averaged ERPs for faces (gray lines), cars (dashed lines) and scrambled (solid thin lines) from the T5 and T6 electrode sites. Adapted from Ref. [84]. The arrow marks the N170. The N170 is larger (more negative) and earlier in adults than in children.

fMRI measurements of the development of the ventral stream

When considering the development of the ventral stream, we hypothesize that functional specialization emerges

slowly during childhood with accumulated experience. Functional selectivity might manifest in several ways with fMRI. First, the spatial extent of functionally selective regions might change with development. Spatial changes might manifest as reductions in the extent of activations (e.g. broader extent of face-selective activations in children than in adults, because of a spatially spread-out and non-differentiated network in children) as suggested by the focalization model [39]. Alternatively, spatial changes might involve an increase in the size of functionally selective regions (e.g. the size of face-selective regions might be larger in adults than in children). An increase in the size of functionally selective regions might be associated with the development of functional specialization, as suggested by the experience-expectant model for face expertise [40,41], or with increased neural tuning to specific stimuli, as suggested by the interactive specialization model [42]. Second, development might change the magnitude of response (e.g. responses to faces might be higher in adults than in children). Third, development might be associated with changes in connectivity and/or interaction between regions (as suggested by the interactive specialization model [42,43]). These developmental changes are not mutually exclusive, as development might be associated with both increased cortical specialization and changes in connectivity.

Differential development of the human ventral stream
Functional organization of the adult ventral stream

The ventral visual stream in adults is characterized by several regions that respond preferentially to different stimuli (Figure 1a) and includes object-, face-, and place-selective regions. Object-selective regions in the lateral occipital cortex, occipitotemporal sulcus (OTS) and fusiform gyrus (together these regions make the lateral occipital complex, LOC) [5,44,45]) respond more strongly to objects than to scrambled objects [5,44,45] and are involved in object recognition [46]. Face-selective regions respond more strongly to faces than to objects and include a region in the fusiform gyrus (the fusiform face area, FFA) [6] that is involved in face perception [47,48], a region in the inferior occipital gyrus (sometimes referred to as OFA) and a region in the posterior superior temporal sulcus (STS). A region in the parahippocampal gyrus (the para-hippocampal place area, PPA) [7] responds more to places than to faces or objects and is involved in place perception [47] and memory [49].

Developmental neuroimaging of the face-selective cortex

Initial imaging studies of the development of face-selective regions in the occipitotemporal cortex reported various results. A positron emission tomography (PET) study found a region in the fusiform gyrus that responded more strongly to faces than to shapes in two-month-old infants [50]. Passarotti *et al.* [51] reported that during a face-matching task (versus blank) there was a larger extent of activation in 10–12 year-olds than in adults. However, others reported no face selective activations (versus objects or places) in the fusiform gyrus of five–eight year-olds [33] and a smaller extent of activations for faces
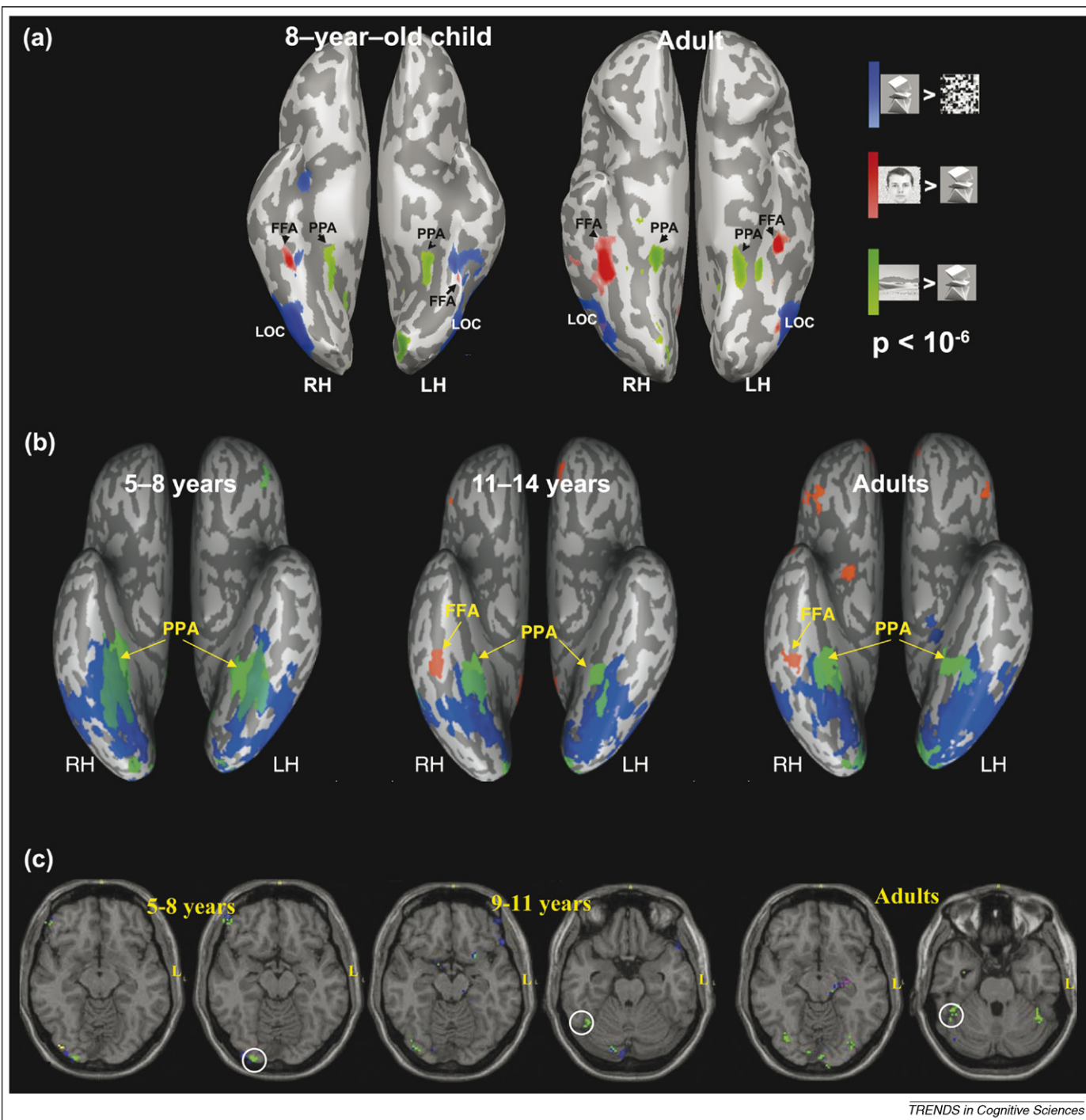
Figure 1. Face, place and object -selective regions in children, adolescents and adults. **(a)** Face, place and object-selective activations are shown for one representative child (eight years old) and one representative adult (adapted from Ref. [35]). Activation maps were generated by a voxel-by-voxel general linear model (GLM) (no spatial smoothing) in each subject and are shown on an inflated cortical surface of each of the individual subjects in the ventral view. Red: faces > abstract objects; green: scenes > abstract objects; blue: abstract objects > textures created by scrambling intact object images. The threshold for all contrasts was at the same significance level ($P < 10^{-6}$, voxel level, uncorrected). Abbreviations: FFA, fusiform face area; PPA, parahippocampal place area; LOC, lateral occipital complex. Only the ventral aspect of the LOC is visible in this view. **(b)** Group activations to faces, places and objects for children (five–eight year-old), adolescents (11–14 year-olds) and adults projected on to an inflated surface of an adult brain (adapted from Ref. [36]). Contrast maps from the group level random effects GLM ($P < 0.05$, corrected) for movie clip stimuli. Red: faces > objects + buildings + navigation; green: buildings + navigation > faces + objects; blue: objects > faces + buildings + navigation). The group analysis misses the left FFA in all age groups. **(c)** Group face-selective activations for young children (age five–eight years), older children (age 9–11 years) and adults on two axial slices for each group (adapted from Ref. [33]). Maps were generated from a group GLM analysis with a random effects model in which the data were transformed to the Montreal Neurological Institute (MNI, www.mni.mcgill.ca) adult template. Green: (faces > natural objects and natural objects > fixation) or (faces > manmade objects and manmade objects > fixation). Threshold for five–eight year-olds: $P < 0.05$; threshold for 9–11 year-olds and adults: $P < 0.001$. In this group analysis the adult lFFA is projected to the cerebellum. LH, left hemisphere; RH, right hemisphere.

than for houses in the fusiform gyrus in younger than in older children [34].

It is difficult to interpret these varied results. First, these studies used different tasks and criteria for

functionally defining face-selective activations. Second, results were based on group analyses. Thus, it was unclear whether the reported changes in the spatial extent of activations in children reflect developmental changes in

Box 3. Methodological issues in developmental neuroimaging

Interpretation of developmental fMRI data requires attention to several methodological issues [90,91].

Structural maturation

The brain reaches a relatively stable volume by age five years [92,93]. However, the gray and white matter volumes change well into early adulthood, with region-specific trajectories across the brain. Pre-adolescent increases in cortical gray matter (due to synaptogenesis) are followed by gray matter loss (due to synaptic pruning) during adolescence, maturing first in the early sensory–motor cortex and last in the prefrontal cortices [24,25]. Simultaneously, white matter volume increases until adulthood [23]. These structural changes might introduce confounds in the interpretation of results based on group analyses and those that involve transforming data to an adult template brain. Defining ROIs on an individual subject basis (Figure Ia) avoids the potential confounds introduced by a group analysis.

Many fMRI analyses are based on a general linear model (GLM) on which statistical thresholding is applied. Larger motion, higher variance in the BOLD responses and differences in the hemodynamic response across children and adults might lead to higher residual error of the GLM (reflecting worse fit of the GLM) in children than in adults [94] and this can compromise the detection of significant activations in children.

Motion control

Children might have difficulty staying still during the scan. Training children before and supporting their head during the scan (e.g. with a 'bite bar') are effective in limiting their motion. However, children's total motion during the scan tended to be higher than that of adults even with head support [35] (Figure Ia).

Developmental changes of the hemodynamic response function

In GLM-based fMRI analyses, experimental conditions are convolved with a hemodynamic response function (HRF). The HRF of infants differs from adults [95]. However, after age seven years, developmental changes in HRF are subtle [96].

Variance of BOLD responses

There might be age-dependent changes in the variance of the BOLD signal (even during rest periods). Golarai *et al.* [35] measured the coefficient of BOLD variance during the fixation baseline, which showed a (non-significant) trend to be higher in children than in adults (Figure I).
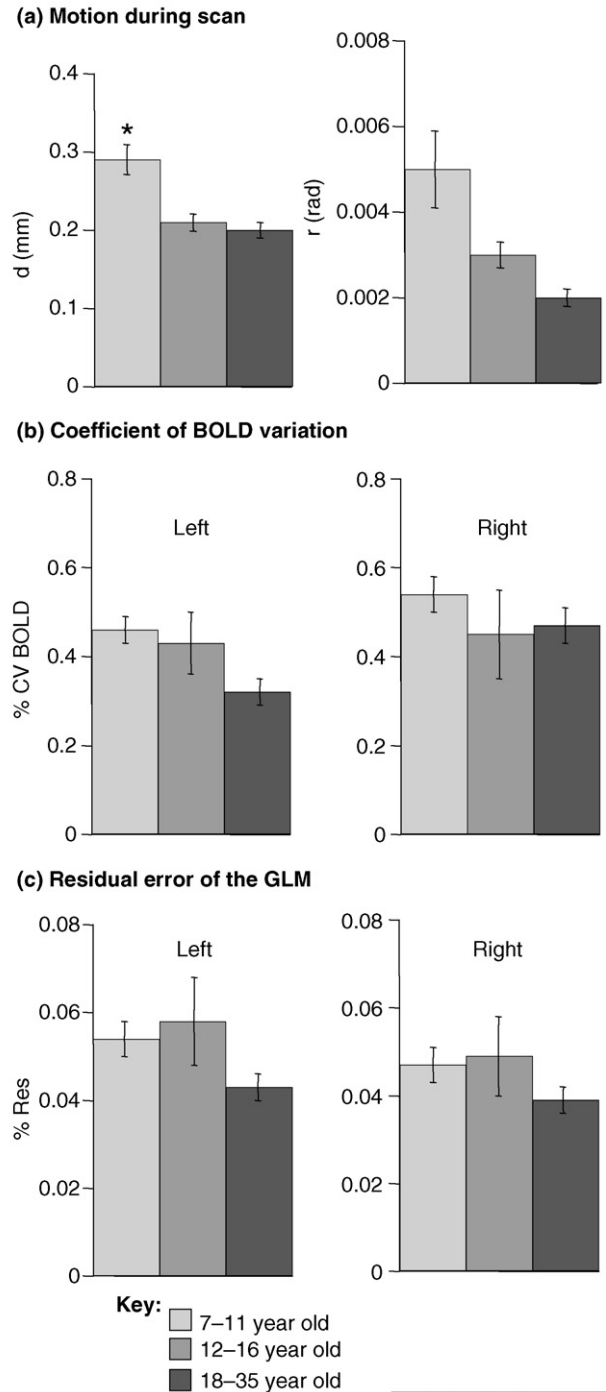

Figure I. BOLD-related confounds across age groups. Average measurements of BOLD-related confounds across age groups. Light gray: 20 children; medium gray: 10 adolescents; and dark gray: 15 adults. Asterisks: significantly different from that of adults ($P < 0.04$). **(a)** Motion during scan. Left: translation: $d[\text{mm}] = (x^2 + y^2 + z^2)^{1/2}$; right: rotation: $r[\text{radians}]$= pitch +roll+ yaw. **(b)** Coefficient of variation of BOLD responses during the blank baseline period: $\%cv\,BOLD = 100 \cdot \frac{1}{N}\sum_{i=1}^{N}\frac{\sigma_i}{\mu_i}$. **(c)** Variance of the residual error of the GLM: $\%Res = 100 \cdot \frac{\frac{1}{N}\sqrt{\sum_{i=1}^{N}ResMs(i)}}{Mean\,Amp}$. $\%cv\,BOLD$ and $\%Res$ were calculated over an anatomical region of the mid-fusiform gyrus. Figure based on supplemental data in Golarai *et al.* [35].

functional selectivity or greater variability in the location of face-selective activations across children. Furthermore, group analyses typically use adult templates, which might disproportionately affect the detection of functional regions in children (Box 3). Third, these studies did not examine anatomical maturation (e.g. the anatomical extent of the fusiform gyrus might be smaller in children than in adults). Fourth, these studies did not determine whether the observed developmental changes were specific to the face-selective cortex or were driven by nonspecific age-related differences that might generally affect BOLD responses in children (Box 3). Finally, these studies did not investigate the development of other regions in the ventral visual cortex.

Developmental neuroimaging of the face, place and object-selective cortex

To address these questions, Golarai *et al.* [35] identified face, place and object-selective regions in individual children (7–11 year-olds), adolescents (12–14 year-olds) and adult subjects while subjects fixated and performed a one-back task. The authors reported a prolonged development of the right FFA (rFFA) and left PPA (lPPA) that manifested as an expansion of the spatial extent of these regions across development from age seven years to adulthood (Figure 1a). The rFFA and lPPA were significantly larger in adults than in children, and these regions were of an intermediate size in adolescents. Notably, children's rFFA was about a third of the adult size but still evident in 85% of children. These developmental changes could not be explained by smaller anatomical volumes of the fusiform gyrus or parahippocampal gyrus [35], which were similar across children and adults, or higher BOLD-related

confounds in children [35] (Box 3), because results remained the same for a subset of subjects that were matched for BOLD-related confounds across ages. These developmental changes were specific to the rFFA and lPPA, as no differences were found across ages in the size of the LOC or the size of the STS face-selective region. Finally, within the functionally defined FFA, PPA and LOC, there were no differences in the level of response amplitudes to faces, objects and places across ages.

Golarai *et al.* [35] also measured recognition memory outside the scanner and found that face and place recognition memory increased from childhood to adulthood (Box 1, Fig. Ic). Furthermore, face recognition memory was significantly correlated with rFFA size in children and adolescents (Figure 2a), and place-recognition memory was significantly correlated with lPPA size in each of the age groups (Figure 2b). These data suggest that improvements in face and place recognition memory during childhood and adolescence are correlated with increases in the size of the rFFA and lPPA, respectively.

In another recent study, Scherf *et al.* [36] examined the development of the ventral stream in children (five–eight year-olds), adolescents (11–14 year-olds) and adults using movie clips containing faces, objects, buildings and navigation. Using group analysis methods, they reported the absence of face-selective activations (versus objects, buildings and navigation) in five–eight year-olds in both the fusiform gyrus and STS and a more variable location of face-selective activations in children than in adults (Figure 1b). In agreement with Golarai *et al.* [35], they found no difference in the spatial extent or level of response amplitudes to objects in the LOC (Figure 1b). However, in contrast to Golarai *et al.* [35], they reported no
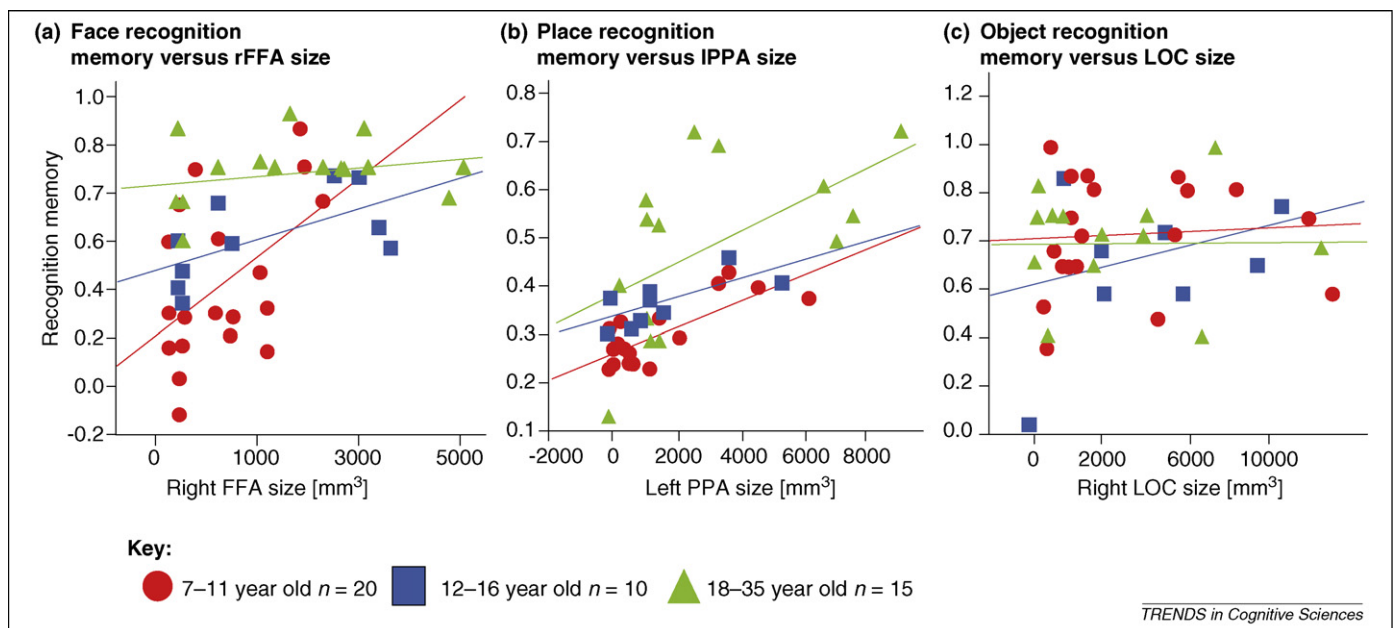

Figure 2. Recognition memory versus size of the rFFA, lPPA and LOC. Subjects participated in a behavioral study of recognition memory outside the scanner. In the study, subjects were shown a sequence of pictures of faces, places and abstract sculptures. About 15 min later they were shown another sequence of pictures (half of the pictures they had seen before) and were asked to report whether or not they had seen each picture previously. Recognition memory, as indicated in the *y*-axis, is measured as: $\frac{number(correct\ trials) - number(false\ alarms)}{total\ number\ of\ trials}$. 1 indicates 100% correct trials and no false alarms. Negative numbers indicate more false alarms than correct trials. Each point represents a single subject's region of interest (ROI) volume and recognition memory performance. **(a)** Recognition memory for faces versus FFA size; correlations are significant within children and adolescents (*r* > 0.49, *P* < 0.03), but not adults. **(b)** Recognition memory of places versus PPA size. Correlations are significant within each age group (*r* > 0.59, *P* < 0.03). **(c)** Recognition memory for objects versus LOC size. No correlations were significant (*P* > 0.4). Adapted from Ref [35].

developmental changes in the PPA. The variant results might be due to differences in stimuli, task and analysis methods across the two studies.

The absence of the FFA in five–eight year-olds reported in two studies [33,36] (Figure 1b,c) suggests that it might take at least seven–eight years for the FFA to emerge. Alternatively, the FFA might be smaller [35] and more variable [36] in young children, and thus less likely to be detected in group analyses. Furthermore, differences in fMRI results across young and older children might be related to nonspecific age-related differences (Box 3), rather than to differences in functional selectivity. Future research is necessary to resolve these possibilities by using individual subject analysis and controlling for nonspecific age-related BOLD and behavioral differences during fMRI scans.

Responses in the penumbral immature regions
What changes in the cortical selectivity underlie the spatial expansion of the rFFA and lPPA during development? This expansion might be due to (i) increased responses to faces (or places) around the initial 'hot spot', (ii) decreased responses to objects or (iii) generally lower response amplitudes in children.

To examine these possibilities, Golarai *et al.* [35] measured the response amplitudes in the FFA and PPA and surrounding cortex (Figure 3). They found that the penumbral regions surrounding children's nascent rFFA were characterized by adult-like response amplitudes to objects but lower responses to faces (Figure 3a). Similar effects were found in the lPPA penumbra (Figure 3b). These results suggest that specific increases in responses to faces (and places) in regions adjacent to the immature rFFA (and lPPA) resulted in the spatial expansion of these regions into the adjacent cortex.

Neural mechanisms underlying the development of cortical specialization
The neural correlates of these developmental changes are unknown and might involve sharpening of the neural tuning to faces or places (Figure 4b), increases in the

magnitude of responses to faces or places (Figure 4c) or increases in the number of face- or place-selective neurons (Figure 4d).

One possibility is that neurons initially respond broadly to many stimuli (Figure 4a). Experience might 'sharpen' the tuning of neural responses [42,52–55] in that their tuning width narrows around their preferred stimulus (Figure 4b). According to this model, face-preferring cells (shown in red in Figure 4a) initially respond to both faces and objects, but with development they become more narrowly tuned to faces (Figure 4b). Another possibility is that experience changes the magnitude of neural responses without changing the tuning width of neurons (Figure 4c). For example, the firing rate to faces might increase. Several studies report increases in the firing rates of monkey inferotemporal (IT) neurons after visual training [56–58], which supports this view. A third possibility is that experience changes the preferred responses of neurons resulting in an increase in the number of neurons that respond preferentially to trained stimuli [55,59] (e.g. more face-selective neurons). One study reported a substantial increase in the number of IT neurons that responded to stimuli that monkeys were trained with during one year [59].

These mechanisms are not mutually exclusive and any one or a combination of these mechanisms might yield increased selectivity with development as measured with fMRI (Figure 4, right column). Furthermore, different mechanisms might occur across different cortical regions and at different times during development. Future research with animal models [60,61] will be crucial for examining the relevance of these putative neural mechanisms during the development of the ventral stream.

Implications of differential development of the visual cortex
Overall, fMRI findings suggest differential developmental trajectories across the human ventral visual stream. The reasons for this differential development are unknown. Furthermore, it is difficult to disentangle maturational components (genetically programmed developmental
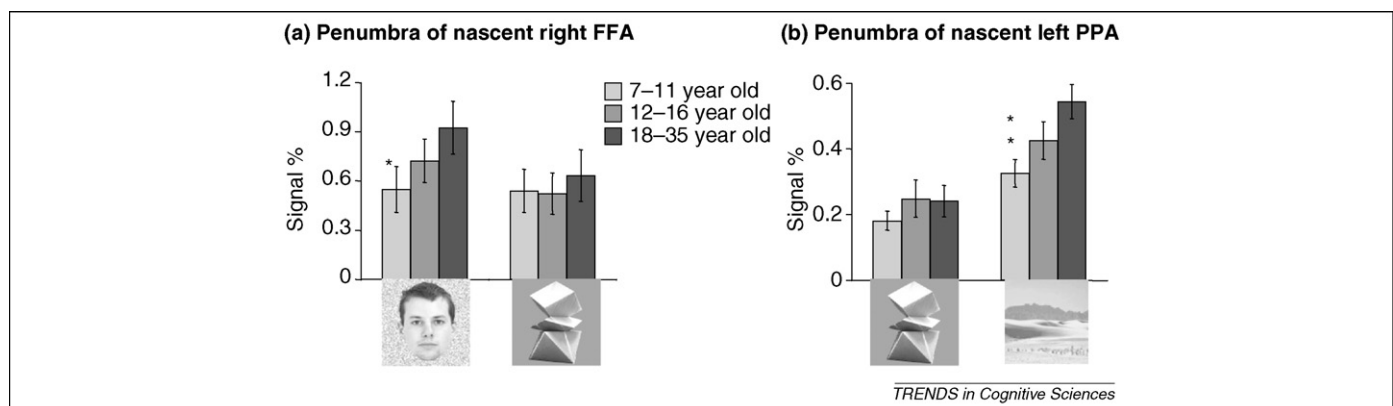

Figure 3. Response to stimuli in the penumbral region of the nascent rFFA and lPPA across children, adolescents and adults. **(a)** Mean BOLD responses to faces and objects were extracted from a penumbral region surrounding the immature child or adolescent rFFA grown to the size of the average adult rFFA. For adults we extracted responses from a region between each subject's rFFA and an ROI matched in size to the average child rFFA centered on the peak face-selective voxel. **(b)** Mean BOLD responses to places and objects from a penumbral region surrounding the immature child or adolescent lPPA until a region matched in size to the average adult lPPA. For adults, the region is between the adult lPPA and an ROI matched to the average child lPPA size centered on the peak place-selective voxel. Light gray: 7–11 year-olds; medium gray: 12–16 year-olds; black: 18–35 year-olds. Data include ten children, nine adolescents and 13 adult subjects that were matched for BOLD-related confounds (Box 3). Asterisks: significantly lower than adults (*P* < 0.05). Error bars indicate SEM across subjects. Adapted from Ref. [35].
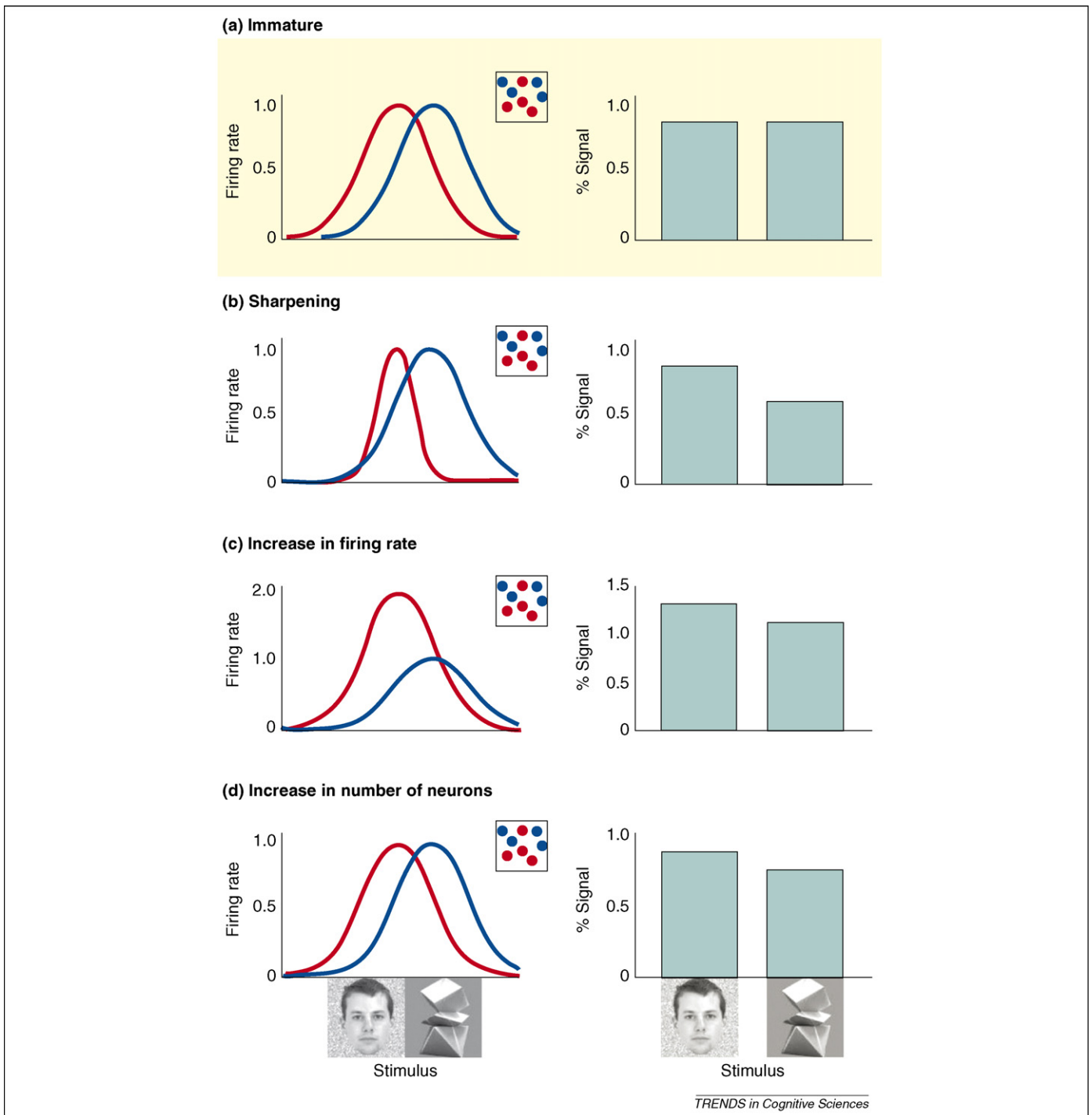
Figure 4. Possible neural mechanisms underlying increased functional selectivity with development. In this schematic, we consider how exposure to faces might change neural selectivity for faces and how it might manifest with fMRI. This figure illustrates responses in a putative voxel containing two neural populations – the red population, which prefers faces, and the blue population, which prefers objects. In all panels, the left column depicts neuronal firing rates; the inset illustrates the distribution of face (red) and object (blue) preferring neurons (represented by circles) in a voxel; and the right column illustrates the BOLD responses to faces and objects. Neural firing rates were modeled with a Gaussian with $\sigma = 1.5$ and were centered at two stimulus locations 1.5σ apart. The red curve reflects the firing rate for face-selective neurons, and the blue reflects the firing of object-selective neurons. In all panels (except **d**) half of the neurons in the voxel prefer faces and half prefer objects. BOLD responses (right column) were estimated for faces and objects as a sum of neural-population responses (i.e. firing rates) to each of these stimuli weighted by the proportion of each neural population in a voxel. **(a)** Immature region. The immature voxel contains an equal number of face and object neurons. Neural tuning to faces and objects is broad and overlapping. Because the sizes of the neural populations preferring faces and objects in the voxel are equal, the BOLD response to objects and faces is the same. **(b)** Sharpening: After exposure to faces, the tuning of face-selective neurons (red-left) becomes narrower around the preferred stimulus. This is modeled by a smaller σ (narrower tuning width) of the neural tuning curve for faces (in this example σ decreased by a factor of two). There is no change in the tuning to objects. As a consequence, the BOLD response to objects will decrease. If the initial tuning to faces and objects in (a) is not overlapping, sharpening at the neural level might not produce detectable changes with BOLD. **(c)** Increased firing rate: After exposure to faces, the magnitude of responses to faces increases (in this example the magnitude doubled), but there is no change in the tuning width. This will produce increased BOLD responses to both faces and objects and a larger increase for faces. **(d)** Increase in the number of selective neurons: after exposure to faces, more neurons in the voxel will respond preferentially to faces than to objects (more red neurons than blue in inset; in this example there are twice as many face-selective versus object-selective neurons in a voxel). As a consequence, BOLD responses will increase for faces and decrease for objects.

changes) from experience-related components, as both are likely to have a role during development. One possibility is that the type of representations and computations in the rFFA and lPPA might require more time and experience to mature than do those in the LOC. A second possibility is that different cortical regions might mature at different rates because of genetic factors. Alternatively, the FFA might retain more plasticity (even in adulthood) than does the LOC, as suggested by studies that show that FFA responses are modulated by expertise [56,62]. A fourth possibility is that different neural mechanisms might underlie experience-dependent changes in the LOC than in the FFA or PPA.

On the basis of the findings of prolonged development of the FFA and PPA and the correlation between their development and improvements in recognition memory, we propose the hypothesis that the differential development across the visual cortex underlies developmental improvements of specific visual abilities. Consistent with this hypothesis, a similar link between cortical development and visual proficiency might be evident in the early visual cortex. Adult-like retinotopic maps in the early visual cortex of seven year-olds [31] might be associated with adult-like visual acuity in six–seven year-olds, and adult-like responses in children's MT [32] might be related to adult-like processing of global motion in four–five year-olds [12]. Further research is necessary to determine the time course of development of the visual cortex more generally and the relationship between cortical development and improvements in specific visual tasks. Finally, it remains to be determined whether the prior maturation of the early visual cortex is a prerequisite for the later development of higher-level ventral stream regions.

Conclusions

An emerging picture from developmental neuroimaging studies of the ventral stream suggests a prolonged maturation process in which the spatial extent of face-selective regions continues to grow well into adolescence in correlation with improved proficiency in face-recognition memory. The prolonged development of face-selective regions sharply contrasts with adult-like spatial extent and responses of the LOC by age seven years. Less studied

to date is the development of place-selective regions, and there is some evidence for [35] and against [36] prolonged development.

Future studies are necessary for understanding the temporal characteristics of the development of the visual cortex more generally and the relationship between cortical development and the development of visual abilities (see Box 4 for outstanding questions). Research directions will include longitudinal studies [23], measurements of the development of connectivity [26] and changes in selectivity that might be evident with fMRI adaptation [63] and high-resolution fMRI [64–66]. Finally, animal models will be crucial for revealing the neural mechanisms underlying the development of the ventral visual cortex.

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Box 4. Outstanding questions

- How does the development of the human ventral stream relate to the development of the visual cortex more generally?
- How does the development of specific visual regions relate to development of proficiency in specific visual tasks?
- Face processing starts early after birth. Some studies suggest that lack of exposure to faces in early infancy leads to long-lasting deficits in face perception [97]. However, the role of early experience in shaping cortical selectivity is unknown. Furthermore, it is unknown whether early and late experience-dependent changes affect the same or different brain regions.
- What are the neural mechanisms underlying the development of the face- and place-selective cortex?
- In considering an appropriate animal model to study the underlying neural mechanisms, one promising direction is to investigate the development of the primate visual cortex. However, the time course of maturation of face-selective and object-selective regions in the primate inferotemporal cortex is not known.

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