

## Opinion

## Rethinking cortical recycling in ventral temporal cortex

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High-level visual areas in ventral temporal cortex (VTC) support recognition of important categories, such as faces and words. Word-selective regions are left lateralized and emerge at the onset of reading instruction. Face-selective regions are right lateralized and have been documented in infancy. Prevailing theories suggest that face-selective regions become right lateralized due to competition with word-selective regions in the left hemisphere. However, recent longitudinal studies examining face- and word-selective responses in childhood do not provide support for this theory. Instead, there is evidence that word representations recycle cortex previously involved in processing other stimuli, such as limbs. These findings call for more longitudinal investigations of cortical recycling and a new era of work that links visual experience and behavior with neural responses.

## Visual recognition offers insight into neural plasticity

Visual recognition is a key aspect of cognition. It allows us to recognize our friends and our foes, get lost in our favorite novels, and navigate through our daily lives. High-level visual regions located in **VTC** (see [Glossary](#)) are essential for these skills. **Word-** [1] and **face-** [2] **selective** regions are regions of the brain that contain neurons that respond more to words and faces, respectively, compared with other categories of visual stimuli. These regions can be identified in individuals using **fMRI** and are in close proximity (~1 cm apart). Category-selective regions in the brain contain neurons that preferentially respond to the stimuli of interest; however, fMRI measures activity in **voxels**, which contain 50 000–100 000 neurons. Luckily, we can leverage the fact that nearby neurons have similar response properties [3–6], which allows us to interpret responses at the voxel level measured by fMRI. For the purposes of this article, we discuss category-selective regions, which are clusters of neurons that share selectivity for a particular category. However, distributed responses across VTC also carry important category information [7,8], including information for visual categories for which there may not be a dedicated category-selective region.

The development of category-selective regions in VTC is a window into how the brain can change with experience. While face-selective regions can be identified in infancy [9] and continue to develop throughout childhood and adolescence [10–15], word-selective regions are not found before the onset of reading instruction, and start to develop as children learn to read, around 5–6 years of age [15–22]. In addition to different developmental trajectories, word- and face-selective regions also have different **lateralization** across hemispheres [23]; that is, both regions show a dominance in the extent of processing of their preferred stimulus in one hemisphere over the other: word-selective regions are left lateralized [24–28] and face-selective regions are right lateralized [29–33]. Word-selective regions are thought to be left lateralized because of their connections with language regions outside of visual cortex, which tend to be left lateralized [16,34–38]. The mechanism by which face-selective regions become right lateralized is less clear. The **theory of classical cultural recycling** and the **theory of graded hemispheric specialization**

## Highlights

Ventral temporal cortex supports visual processing of important categories, such as faces and words.

A predominant theory is that the development of word-selective cortex during the onset of reading instruction pushes face-selective responses to the right hemisphere.

Recent longitudinal measurements suggest that word-selective cortex is recycling cortical territory dedicated to processing limbs or tools rather than faces.

Future work should aim to link development measured with fMRI to the visual environment and behavior.

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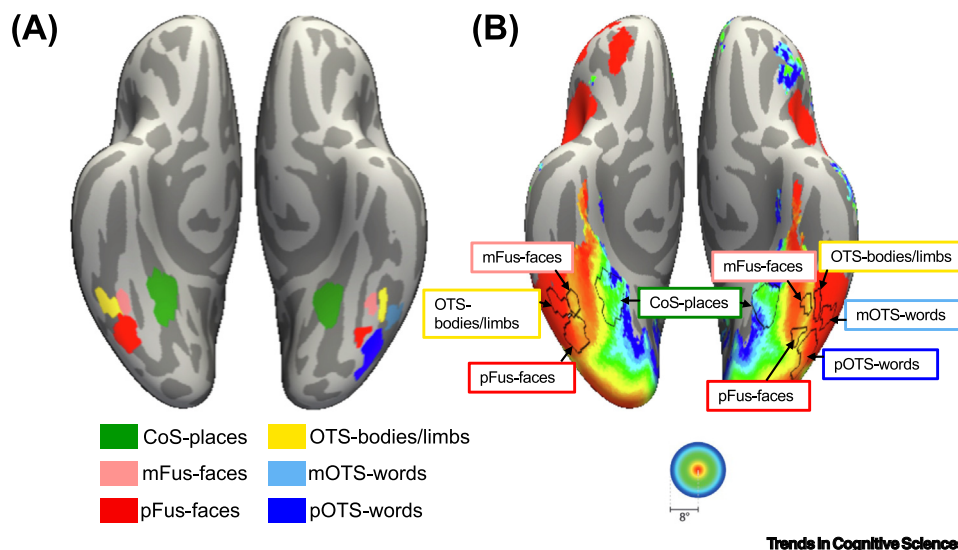
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suggest that word and face representations in VTC compete over development, leading to right lateralization of face-selective responses in adulthood. However, it was recently suggested that there is little evidence in support of these theories [39]. Importantly, word- and face-selective regions are surrounded by other category-selective regions in VTC, such as body- and limb-selective regions, which are located in between word- and face-selective regions (Figure 1A) [40,41]. Recent evidence showed that, as word selectivity increases in childhood, limb selectivity decreases, providing evidence for recycling of limb selectivity into word selectivity [15]. Moreover, these findings align with studies showing that **visual diet** and viewing behavior of children may favor hands earlier in development and words later in development [42,43]. Here, we argue that, to distinguish developmental theories, future studies should prioritize longitudinal measurements, include a wide range of stimulus categories, and link neural changes to children's visual experience and behavior.

### Theories on the development of word-selective regions

The theories of classical cultural recycling and graded hemispheric specialization provide a framework for thinking about how face- and word-selective regions emerge and become lateralized over development due to **cortical competition**. Here, we summarize the central aspects and predictions of each theory, together with two other theories of VTC development: the **revised theory of cultural recycling** [20] and the **theory of emergence**. To better illustrate the differences between these accounts, Figure 2 highlights the central mechanism



**Figure 1. Category-selective regions in ventral temporal cortex (VTC).** (A) Regions of interest (ROIs) of category-selective regions generated from maximum probability maps (MPMs) derived from individually defined ROIs in 29 adults from [37]. ROIs are defined using the contrast of the category of interest compared with eight other categories (voxel-level threshold:  $t > 3$ ). Probability maps are thresholded at 0.2 (probability maps are 1 at vertices where all subjects have the ROI, 0 at vertices where no subjects have the ROI, and 0.5 at vertices where half of subjects have the ROI). In a MPM, each vertex is colored by the category with the highest ('maximum') probability. Functional ROIs are named for their anatomical location and functional selectivity. CoS-places, collateral sulcus place-selective region (green); OTS-limbs/bodies, occipital temporal sulcus limb- and body-selective region (yellow); mFus-faces, mid fusiform gyrus face-selective region (pink); pFus-faces, posterior fusiform gyrus face-selective region (red); mOTS-words, mid occipital temporal sulcus word-selective region (light blue); pOTS-words, posterior occipital temporal sulcus word-selective region (dark blue). (B) The same category-selective regions based on MPMs [see (A)] are shown with respect to the average eccentricity maps of subjects from the Human Connectome Project from [74]. Eccentricity maps are thresholded at 10% variance explained. Maps range from 0 to 8 degrees of visual angle, where red represents the most foveal representations and blue represents the most peripheral.

### Glossary

**Bilateral:** when neural responses for a stimulus or task are distributed across both right and left hemispheres of the brain.

**Contralateral:** opposite side.

**Cortical competition:** the idea that there is a limited amount of cortical territory; thus, as some representations take up more cortical territory, there will be less cortical territory for other representations.

**Cortical recycling:** the idea that new representations repurpose cortical territory previously used for other representations.

**Face selective:** neurons in the brain that respond more strongly to faces than to other visual stimuli.

**fMRI:** neuroimaging technique that uses blood oxygenation to indirectly measure neural response with high spatial resolution.

**Fovea:** center of gaze.

**Lateralization:** dominance in the role and extent of neural processing associated with a stimulus or task in one of the hemispheres of the brain.

**Revised theory of cultural recycling:** a theory suggesting that the development of word selectivity in visual cortex does not impact pre-existing face representations, but instead blocks face representations from expanding in the left hemisphere.

**Theory of classical cultural recycling:** a theory suggesting that representations of recent cultural domains, such as reading, recycle cortical territory previously involved for other, evolutionary older, processes.

**Theory of emergence:** a theory suggesting that new category representations emerge in previously unspecified cortex without impacting existing representations.

**Theory of graded hemispheric specialization:** a theory suggesting that the emergence of word representations in VTC, predominantly in the left hemisphere and to an increase in face activations in the right hemisphere, leads to the right lateralization of face representations.

**Ventral temporal cortex (VTC):** the inferior part of temporal cortex where regions involved in processing visual

proposed by each theory in a simplified manner. However, not all aspects of these mechanisms are mutually exclusive.

The theory of classical cultural recycling proposes a mechanism by which new representations for recent cultural inventions, such as reading, writing, or arithmetic, develop upon evolutionarily older circuits that were previously used for other functions [44,45]. A central aspect of the theory is that the representation for the new cultural invention (e.g., reading) will form at the anatomical location that most closely meets the computational demands of the new task (for a recent computational account of cultural recycling, see [46]). A seminal study supporting the theory of classical cultural recycling compared neural responses in illiterate and literate adults. This study found that the region in left VTC that is typically selective to words in literate adults is selective to faces in illiterate adults [47]. The recycling hypothesis (Figure 2A) predicts that neurons that were once selective for one category (e.g., faces) change their selectivity to become selective for a different category (e.g., words) as individuals learn to read [48].

The theory of graded hemispheric specialization [49,50] proposes a mechanism of competition between word and face representations (Figure 2B). The theory suggests that face-selective regions start out **bilaterally** in the brain. As word-selective regions develop primarily in the left hemisphere to minimize connections to left-lateralized language regions, they compete with face-selective regions, causing face-selective regions to develop predominantly in the right hemisphere. A core aspect of this theory is that emerging word representations compete with pre-existing face representations for cortical territory because face and word recognition require high **visual acuity** to discriminate among items of their preferred category [51]. The neural resources that provide the best visual acuity are neurons with receptive fields that process information from the **fovea**. Indeed, in VTC, both face and word representations overlap with neurons representing the fovea [52–55] (Figure 1B). If there is limited cortical territory dedicated to foveal

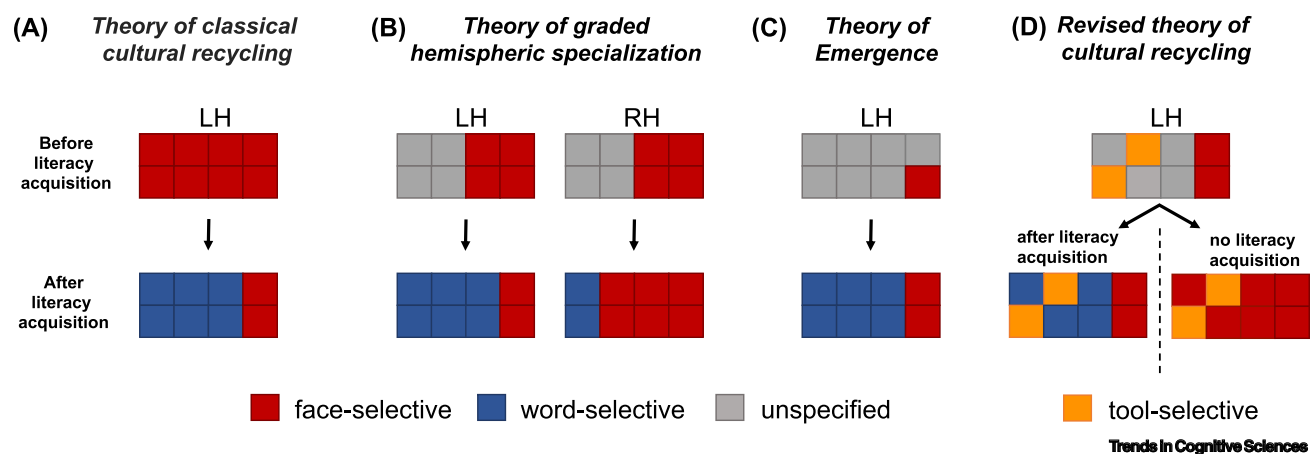
categories such as faces and words are located.

**Visual acuity:** sharpness of vision enabling perception of fine details and distinguishing between similar shapes, objects, and letters.

**Visual diet:** distribution of visual inputs that an individual sees during their daily life.

**Voxel:** a volume pixel. A 1-mm<sup>3</sup> voxel measured with MRI contains ~50 000–100 000 neurons.

**Word selective:** neurons in the brain that respond more strongly to words than other visual stimuli.



**Figure 2.** Theories proposed for the development of word-selective regions in ventral temporal cortex (VTC). Each row is a schematic of a section of VTC illustrating an idealized distribution of face- and word-selective neurons before and after literacy acquisition. Top row: before literacy acquisition. Bottom row: after literacy acquisition. (A) Theory of classical cultural recycling: cortex that was selective for one category (e.g., faces) before literacy acquisition becomes selective for words after literacy acquisition. (B) Theory of graded hemispheric specialization: as word-selective neurons develop during literacy acquisition in the left hemisphere (LH), face selectivity is pushed to the right hemisphere (RH). Given that this theory makes predictions about the lateralization of both faces (right) and words (left), the schematic shows both hemispheres. (C) Theory of emergence: with literacy acquisition, word-selective neurons develop over unspecified cortex that was not selective to any category earlier in childhood. (D) Revised theory of cultural recycling: as word-selective responses develop in individuals who learn to read, they block the expansion of face selectivity in the LH (bottom-left). In individuals who do not learn how to read, face selectivity expands in the LH (bottom-right). All panels: red, face-selective neurons; blue, word-selective neurons; orange, tool-selective neurons; gray, unspecified neurons. Adapted from [20].

processing, development of reading circuits may result in competition between word and face representations. Since this theory makes predictions about the lateralization of both face and word representations, the schematic in Figure 2B includes both hemispheres for this account.

The third theory, which we refer to here as the theory of emergence (Figure 2C), suggests that word representations emerge in previously unspecified cortex without impacting existing representations of other categories [12]. In line with this hypothesis, a longitudinal study in which illiterate adults were trained to read found that the development of word-selective responses with reading instruction was not coupled with a reduction in responses to other categories [56]. In addition, a recent longitudinal study during the first year of literacy acquisition found that word-selective cortex emerged as children underwent reading instruction, without changing other category representations [20]. Together, these studies suggest that the development of selectivity to words could emerge without impacting other categorical representations.

Recent longitudinal measurements in children led to the proposal of the revised theory of cultural recycling [20], which predicts different developmental outcomes depending on literacy acquisition (Figure 2D). In individuals who learn to read, the theory predicts that the emerging word-selective regions will take up increasing amounts of cortical territory and block the expansion of face-selective regions in the left hemisphere (Figure 2D, bottom-left). However, in individuals who do not learn how to read, the theory predicts that face-selective regions in the left hemisphere will continue to expand (Figure 2D, bottom-right). This theory suggests that competition between representations does not necessitate the destruction of prior representations.

Importantly, the schematic in Figure 2 illustrates that different developmental mechanisms can result in a similar pattern of left lateralization of word selectivity after literacy acquisition (Figure 2, compare lower row across A, B, and C). Given that cross-sectional studies only provide a window into a single time point, they are insufficient to distinguish between the possible developmental mechanisms underlying lateralization. Luckily, in recent years, several longitudinal studies examined development within the same children over time, allowing us to distinguish between different mechanisms for the first time. Here, we review recent findings and argue that there is not much evidence supporting the idea of competition between word and face representations over the same cortical territory over development (reviewed in [39]). Instead, new longitudinal measurements provide evidence of recycling of cortical territory that was previously selective to limbs or tools to both words and faces in both hemispheres.

### The sequence of lateralization over development

The theory of graded hemispheric specialization predicts that face-selective responses will be bilateral before the onset of reading instruction, and then increasingly right lateralized over development. This prediction is supported by cross-sectional studies comparing children and adults. One study leveraged the fact that processing of visual information in the two hemispheres is biased to the **contralateral** visual field. That is, images on the right side of the visual field are processed primarily in the left hemisphere (and vice versa). When the researchers presented faces to the right versus left visual field, they found that children and adolescents were equally good at recognizing faces in both visual fields, whereas adults had an advantage when faces were presented to the left visual field compared with the right visual field [57]. This study suggests that faces are processed equally well by both hemispheres early in childhood, and better by the right hemisphere in adulthood, supporting the idea that face processing is bilateral early in childhood and becomes right lateralized in adulthood.

Despite the predictions that face processing is bilateral until the onset of reading instruction, a study examining event-related potentials in infants aged 4–6 months found that face-selective

responses were already right lateralized in this age [58]. This finding suggests that right lateralization of face-selective responses pre-dates the onset of literacy instruction. In addition, another study found that decoding neural responses from the right hemisphere but not the left hemisphere can discriminate novel from familiar faces in infancy [59]. These studies call into question the idea that right lateralization of face responses is caused by literacy acquisition and suggest that a different mechanism occurring early in infancy leads to right lateralization of face-selective responses. However, evidence about the lateralization of face-selective responses in preschoolers is inconsistent [11,60], leading to the proposal that there may be a nonlinear development of lateralization of face-selective responses. However, more research is needed to precisely map the trajectory of lateralization of face responses during early childhood.

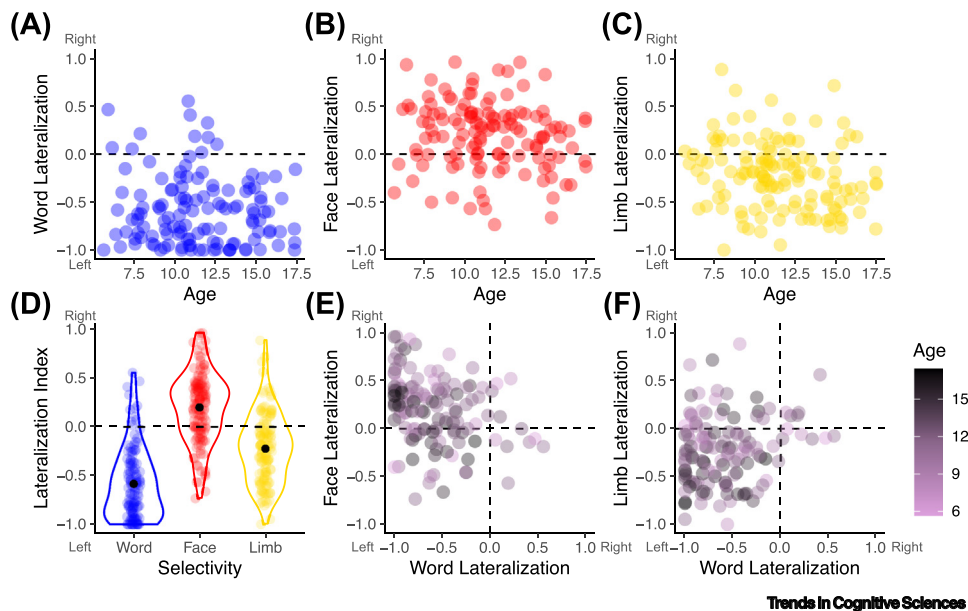
More recently, longitudinal studies have started to examine this question. A longitudinal investigation of children before and during the first year of reading instruction tested whether face-selective cortex was bilateral before reading instruction. They found that the volume of face-selective activation was greater in the right hemisphere both before and after reading instruction [20]. A second longitudinal study also found no evidence of change in the lateralization of either word-selective (Figure 3A) or face-selective (Figure 3B) responses from age 5 to 17 [15]. Together, these results call into question the idea that education is the catalyst by which face-selective responses become right lateralized. One note is that the study measuring children before and after reading instruction comprised a small sample (ten participants), and the longitudinal study of children and adolescents did not explicitly sample children before and after reading instruction. Therefore, studies that measure children longitudinally before and after reading instruction with a larger sample size will be essential to document the role of reading instruction in the lateralization of word- and face-selective responses.

### The relationship between the lateralization of face-selective regions and word-selective regions

A second prediction of the theories of graded hemispheric specialization and classical cultural recycling is that there will be an inverse relationship between the size and selectivity of word- and face-selective cortex in the left hemisphere. This prediction is supported by work that compared groups of adults with different levels of reading experience and found that there was a positive relationship between reading skill and the response to letter strings in the anatomical location corresponding to word-selective cortex, and a negative relationship between reading skill and face-selective responses in the anatomical location corresponding to word-selective cortex [47,48]. Similarly, a study in children and adolescents found a significant positive correlation between reading skill and lateralized neural response to faces [57]. An fMRI study in 5–6-year-old children also found that, in the left hemisphere, the size of the region selective for letters was negatively related to the size of the region selective to faces [61]. However, the results are mixed overall. One study in adults with variable language lateralization found that there was a significant negative correlation between language lateralization and face lateralization; however, there was no significant relationship between word and face lateralization [62]. Similarly, a recent study that tested the relationship between word and face lateralization in a large sample of adults also did not find evidence for a relationship between lateralization of face-selective and word-selective responses [63].

All the studies presented in this section thus far were cross-sectional. Recent longitudinal measurements find that cortical territory that is selective for faces expands in both hemispheres during childhood [15,21], while word-selective cortex primarily expands in the left hemisphere [15]. Moreover, the longitudinal data from [15] demonstrated that, while face-selective responses



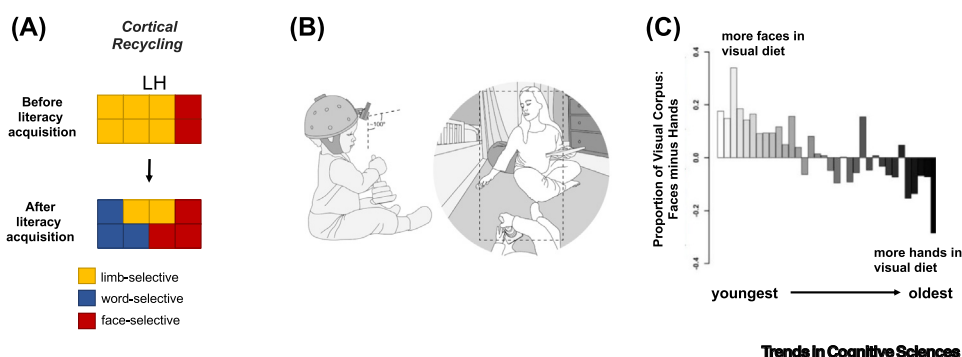


**Figure 3. Longitudinal analysis of word, face, and limb lateralization across childhood and adolescence.** Reanalysis of data from [15] that included 29 participants scanned longitudinally (initial age 5–12 years, mean  $\pm$  standard deviation,  $9.19 \pm 2.13$  years). Across all measures, the Lateralization Index examines the difference in number of voxels in lateral ventral temporal cortex (VTC) selective for faces (words or limbs) in right (RH) versus left hemisphere (LH) divided by the total:  $(RH - LH)/(RH + LH)$ . Lateralization index: 1 = right lateralized,  $-1$  = left lateralized, 0 = bilateral. (A) Word lateralization does not vary as a function of age [linear mixed model predicting word lateralization by age with a random intercept for subject:  $t(125.56) = -1.53$ ,  $P = 0.13$ ]. (B) Face lateralization does not vary as a function of age [linear mixed model predicting face lateralization by age with a random intercept for subject:  $t(124.78) = -0.64$ ,  $P = 0.52$ ]. (C) Limb lateralization does not vary as a function of age [linear mixed model predicting limb lateralization by age with a random intercept for subject:  $t(124.64) = -1.19$ ,  $P = 0.24$ ]. (D) Lateralization index of the number of word- (left, blue), face- (middle, red), and limb- (right, yellow) selective voxels in lateral VTC. One sample t-test comparing lateralization indices with zero (two-sided), word-selective responses are significantly left lateralized:  $t(127) = -18.17$ ,  $P < 2.2 \times 10^{-16}$ , face-selective responses are significantly right lateralized:  $t(127) = 6.30$ ,  $P = 4.5 \times 10^{-9}$ , and limb-selective responses are significantly left lateralized:  $t(127) = -7.12$ ,  $P = 7.03 \times 10^{-11}$ . (E) Relationship between word lateralization and face lateralization. Linear mixed model predicting face lateralization as a function of word lateralization and age with a random intercept of subject revealed no significant effect of word lateralization [ $t(123.41) = -1.00$ ,  $P = 0.32$ ] or age [ $t(124.70) = -0.80$ ,  $P = 0.43$ ]. (F) Relationship between word lateralization and limb lateralization. Linear mixed model predicting limb lateralization as a function of word lateralization and age with a random intercept of subject revealed no significant effect of word lateralization [ $t(122.67) = 0.51$ ,  $P = 0.61$ ] or age [ $t(124.26) = -1.11$ ,  $P = 0.27$ ]. (E,F) Darkness of points indicates the age of the participant at a given session.

are right lateralized and word-selective responses are left lateralized in children (Figure 3D), there is no evidence for a significant relationship between the lateralization of word- and face-selective cortex over development (Figure 3E). One concern in interpreting developmental data is that reading skill and age are often linked. That is, children who can read tend to be older than children who are unable to read. A recent study aimed to address this potential confound by scanning pre-reading 6-year-old children, beginning-reading 6-year-old children, and advanced-reading 9-year-old children. The idea was that the two groups of 6-year-old children were close in age, but differed in their reading ability, whereas the group of 9-year-olds differed from the 6-year-olds in both reading ability and age. The authors found that the growth of face-selective regions primarily in the right hemisphere was associated with age rather than with schooling, whereas growth of word-selective regions in the left hemisphere was associated with schooling rather than with age [21]. Together, these findings suggest that lateralization of word- and face-selective cortex may occur along independent developmental trajectories.

### Looking back in time: how longitudinal measurements can resolve changes in selectivity over development

One of the key predictions of the theories of classical cultural recycling and graded hemispheric specialization is that cortical territory that is selective for words after reading instruction was previously selective for faces. However, it is not possible to answer this question without longitudinal measurements (Figure 2). In recent years, the first longitudinal measurements have been made available that allow us to see the neural responses of word-selective cortex before reading instruction. A longitudinal study with first-graders [20] used fMRI to measure children's VTC before and after the onset of literacy instruction in school and found that cortex that became selective for words with schooling was previously 'weakly specified' for bodies and tools. Crucially, the authors found that face-selective responses did not change during the same time period and that initial weak selectivity to bodies and tools was retained, supporting the view that word-selective responses can emerge without impacting existing representations (Figure 2D). A recent longitudinal study also examined the development of functional responses to a wide range of categories in a sample of children initially aged 5–12. The authors found that word-selective regions grew significantly in the left hemisphere only. When they went back in time and examined the selectivity of the voxels that eventually became selective for words, the authors found that these voxels were previously selective for limbs not faces [15]. These data favor a **cortical recycling** hypothesis, although they suggest that limb selectivity is recycled to word selectivity (Figure 4A) instead of face selectivity, as previously proposed. While there was evidence for recycling of limb selectivity to word selectivity, there was no evidence of a relationship between lateralization of limb and word responses as predicted by a mechanism of competition (Figure 3F). These results raise new questions on the development of limb-selective regions. For instance, ventral limb-selective regions show a foveal bias in adulthood [64]. However, it is unknown whether the foveal bias of limb-selective regions changes across development, as found for word- and face-selective regions [65]. In addition, the development observed in [15] was specific to limb-selective cortex, while body-selective cortex remained largely stable, in line with prior findings [14]. The body-selective region in the fusiform gyrus was originally reported to be right lateralized [41], and reanalysis of data previously published in [15] replicates this finding, showing that body-selective cortex is right lateralized during childhood and adolescence [one sample t-test comparing lateralization index with zero (two-sided),  $t(127) = 4.09$ ,  $P = 7.58 \times 10^{-6}$ ]. By contrast, limb-selective cortex is left lateralized during childhood and adolescence (Figure 3C,D). These results highlight the



**Figure 4. Changes in neural representations may reflect changes in the visual environment.** (A) Schematic showing recent findings that voxels with a preference for limbs early in childhood are recycled to become word and face selective. (B) Schematic of head-mounted camera set up from [67]. (C) Quantification of how the visual diet changes across infancy from [42]. Bars depict individual infants ordered from youngest to oldest (ranging from 1 to 24 months). The y-axis depicts the proportion of the visual diet that is faces minus hands, where positive values represent more faces than hands in the visual diet, and negative values reflect more hands than faces.

importance of separating body and limb stimuli in future experiments. These findings also underscore the need to measure neural responses to a large range of stimuli rather than a few categories (e.g., faces and words), because if a category that a given population of neurons is selective for is not included in the experiment, then results might wrongly be interpreted as evidence for an emerging view when, in fact, neurons with a different selectivity are being recycled. In addition, it is important to consider the categories being compared when performing developmental analyses. If there are changes in neural response to a category that is used as a comparison, it can influence the interpretation of developmental results.

### Rethinking cortical recycling

Why would cortex recycle representations of limbs or tools instead of faces? Why does it matter? One possibility is that cortical recycling reflects changes in the visual environment and the behavioral tasks of the observer. Studies using head-mounted cameras (Figure 4B) provided new insights into the visual environment, also called visual diet, of infants and toddlers [42,66,67]. These studies found that, while infants initially spend a lot of time looking at faces, they increasingly look at hands over development [42,66] (Figure 4C). In addition, a recent eye-tracking study that compared gaze behavior in preschoolers and adults when viewing complex scenes revealed that the proportion of first fixations in a scene differed between the age groups. While preschoolers' first fixations were often directed toward hands, adults' first fixations were often directed toward text [43]. Together, these results suggest that changes in visual cortex could be driven by the relevance of different categories at different ages. For example, it is possible that toddlers and young children have large limb representations in VTC because they look at limbs when using gestures and gaining motor control. Then, once children go to school, they increasingly see text, leading to increased word representations in VTC. Future research could test these predictions by performing longitudinal measurements of children's visual diet (e.g., with a head-mounted camera) and cortical representations (e.g., with fMRI) to directly evaluate the relationship between neural changes and the visual environment.

Why might face-selective cortex not be a good candidate for recycling? While words and faces may be appealing candidates to be in competition given their similar computational demands, both word and face recognition are behaviorally relevant across development. In fact, studies have documented that both word and face recognition behavior continues to improve from adolescence to adulthood [12,68,69] and that reading ability may have positive effects on the recognition of objects, including faces [69]. We propose the hypothesis that, as more cortical territory in VTC becomes dedicated to word-selective and face-selective processing over development, word and face recognition behavior improves, respectively [12,15]. It might be that categories compete for cortical territory in VTC depending on their computational demands (e.g., need for foveal resources or connections to the rest of the brain) and behavioral relevance. In literate societies, both words and faces may take priority over other categories that are less relevant and, thus, do not cede cortical territory to one another. For example, one hypothesis is that processing visual information related to limbs or hands becomes less necessary as a child gains autonomy in their motor skills and develops spoken language. By contrast, in children who increasingly rely on their hands to communicate, such as children using sign language, we may expect that the cortical territory dedicated to hands would increase over development. Similarly, studies with participants with altered visual experience for certain visual categories due to their profession, such as hand surgeons, may be informative for investigating whether processes of recycling can still occur in adulthood [47] or whether these processes are limited to childhood due to higher malleability of VTC during that developmental period [70]. Future research can test these predictions to examine the links between recycling and behavioral relevance of visual categories (see Outstanding questions).



## Concluding remarks

Theories suggesting competition of word and face representations in the brain have enhanced our knowledge of the emergence of word representations and have been a useful framework for thinking about the development of category-selective representations [45,50]. Yet, recent evidence calls the competition between word and face representations into question [39], and instead suggests that word representations emerge in cortex with a prior preference for limbs or tools [15,20]. These results are in line with the idea of recycling of category selectivity in VTC [45], whereby cortex with an initial preference for limbs is recycled into cortex with a preference for words. However, we emphasize that additional research is needed to examine functional specialization in different contexts. For instance, it is possible that other mechanisms occur earlier in development, such as emergence of representations in infancy [9,58,71] or for different types of visual experience [47,72,73]. Future studies should prioritize longitudinal measurements, as well as linking neural responses to the visual diet and behavioral goals of children, to distinguish theories of the development of category-selective representations.

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## Declaration of interests

None declared by authors.

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## Outstanding questions

What is the developmental trajectory of the lateralization of face-selective responses from infancy to adulthood?

Does the recycling of limb selectivity have behavioral ramifications?

How does the 'visual diet' of a child affect the development of cortical selectivity to particular visual categories?

Is there a causal relationship between literacy acquisition and development of non-word (e.g., face, limb, or tool) category-selective representations in the brain?

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