

# A domain-relevant framework for the development of face processing

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## Abstract

Faces are thought to have a privileged status for processing relative to other visual images. Humans use faces to identify people, learn language, and to communicate and understand intentions, meaning and emotions. An enduring debate within the fields of developmental psychology and cognitive neuroscience is whether human face processing is specialized owing to domain-specific neural circuitry driven primarily by evolutionary mechanisms or whether it emerges from a domain-general architecture through experience. In this Perspective, we argue for an experience-based account based on associative and non-associative learning and supported by general neurobiological mechanisms. We posit that face-processing specialization emerges from activity-dependent, self-organizing processes where neuronal connectivity is shaped by the environment and constrained by intrinsic yet malleable neural architecture. This ‘domain-relevant’ framework for face processing reflects a dynamic interaction between the developing brain and the environmental input.

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## Introduction

Characterizing the extent to which development is domain-specific or domain-general has influenced our understanding of emerging behaviours and their underlying neural circuits. Domain-specific accounts posit that developmental processes are modular (distinct and encapsulated), dedicated to a singular, ethologically important function and specialized for specific types of stimuli, such as the perception of faces or sounds<sup>1–5</sup>. Domain-general accounts predict that developmental processes operate at a universal level within an environmental context, such that development in one domain can affect development in another domain and that neural processing is distributed across brain regions and primarily altered by experience<sup>6–10</sup>. Historically, domain-specific hypotheses ignore the importance of domain-general learning mechanisms and how they operate across species, ages, domains and brain regions<sup>11,12</sup>. Domain-general accounts include learning mechanisms, but often lack specific mechanistic explanations for how learning operates within the developing neural architecture to promote the emergence of specialized neural circuits localized similarly across individuals.

Theories regarding the development of face processing are entrenched within broader debates about whether human face-processing expertise arises from domain-specific or domain-general mechanisms as well as the relative roles of nature versus nurture. The importance of experience for shaping face processing is less controversial than the extent to which a modular and domain-specific face-processing system is present at birth. Domain-specificity is thought to arise from evolutionary pressures and results in innate (evolutionarily preserved and pre-determined) and modular face-processing mechanisms. Proponents of this dominant role of nature<sup>13–15</sup> infer innate and modular face-specific processing mechanisms from data showing the privileged status of face processing in adults<sup>16–19</sup>, specific deficits in face processing in patient populations<sup>13,20,21</sup>, genetic influences from twin studies<sup>22–25</sup>, domain-specific and modular-like neural responses to faces<sup>26,27</sup>, and early infant visual preferences or selective responses to faces or face-like stimuli<sup>28–30</sup>. Although some domain-specific accounts acknowledge a role for experience-based development<sup>15,31</sup>, all assume an intrinsic and evolution-based face-processing prototype that rigidly constrains the potential for postnatal specialization.

Conversely, domain-general accounts of the development of face processing posit that specialized neural circuits only emerge postnatally through environmental experience<sup>32–36</sup>. Data supporting a dominant role of nurture show that circuits critical for face processing are immature at birth<sup>28,37</sup>, develop<sup>38,39</sup> and require face experience to form<sup>40</sup>. This view emphasizes the interdependence of neural and cognitive systems during development and suggests that development in one domain affects development in other domains<sup>41</sup>. For example, one domain-general account suggests that the pattern of postnatal development of face processing narrows with (or is tuned by) experience and is directed by universal mechanisms critical for both sensory and cognitive development<sup>34,36</sup>.

In this Perspective, we do not argue that infants rely on a pre-specified face system, nor do we argue that the infant brain can be characterized as unconstrained. Instead, we propose that universal learning mechanisms mould the basic components of the visual system to represent the regularities present in the environment. First, we discuss how this learning-based ‘domain-relevant’ developmental account can explain early newborn face preferences and the developmental trajectory of face-discrimination and face-recognition abilities. Then we describe how associative and non-associative learning

mechanisms operate within a domain-relevant context and explain the development of face processing. Last, we discuss the subcortical and cortical regions involved in face processing as well as the emergence of specialized neural circuitry in response to experiences and expertise. Similar to other proposals<sup>42–44</sup>, we suggest that the development of face processing is dynamic and characterized by experience-dependent self-organization and re-organization during the acquisition of relevant developmental tasks.

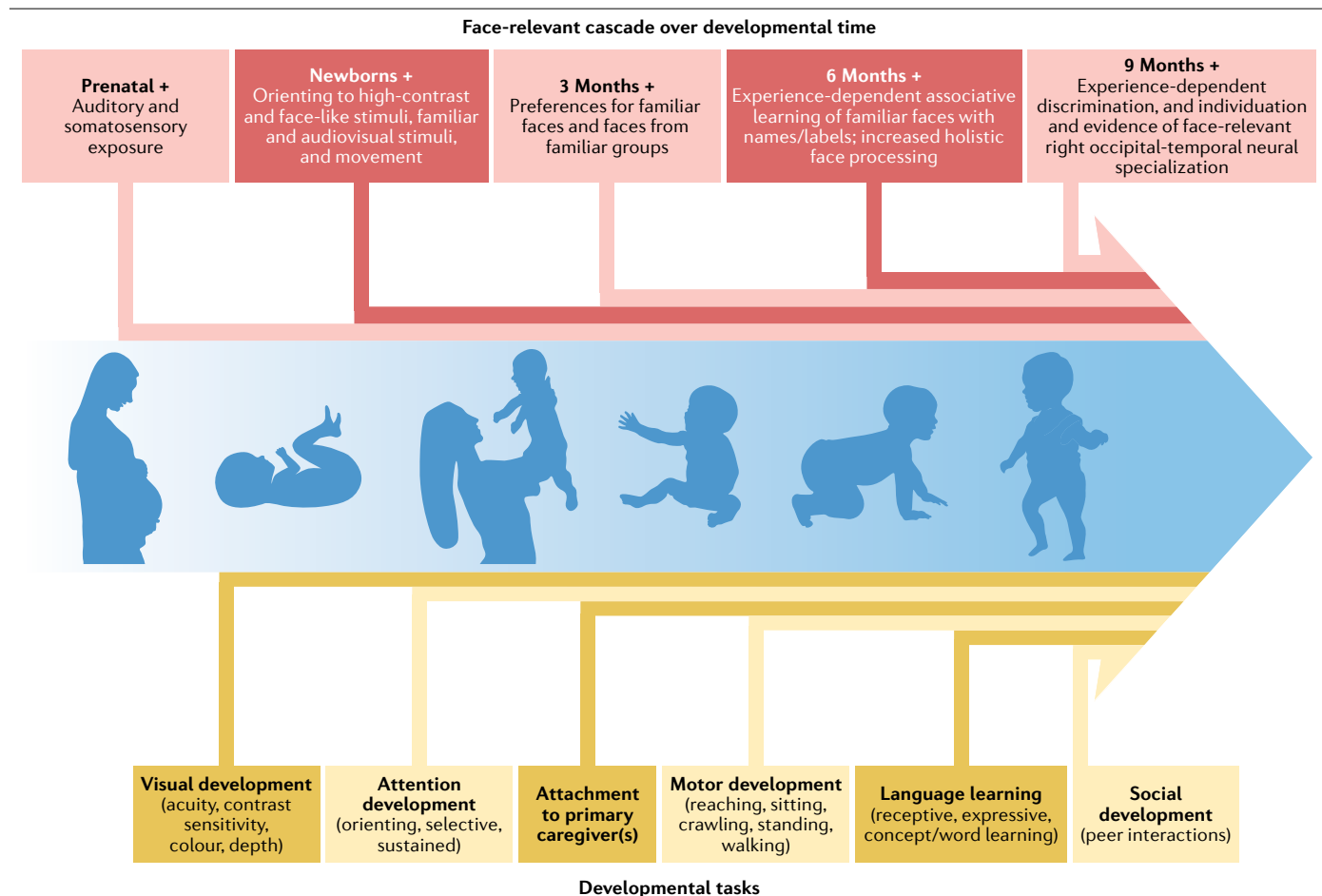
## A domain-relevant framework

A domain-relevant framework<sup>35,45,46</sup> can account for the emergence of specialized face processing<sup>35,47</sup>. This framework posits that the newborn brain has intrinsic architectural constraints relevant for, but not limited to the processing of specific kinds of input. Specialized processing emerges postnatally through general learning mechanisms (such as associative and non-associative learning) in response to changing experiential content<sup>48,49</sup> within an adaptable intrinsic brain architecture<sup>50–53</sup>.

This proposal is consistent with the notion that neural circuits develop in response to information ubiquitous in a given environment<sup>54</sup>. As a consequence, certain brain regions become more suitable for performing particular functions than others. However, we argue that such evolutionary mechanisms only operate at a broad level across individuals within a species (such as those that form/pattern vision)<sup>54</sup>, not on domain-specific processes (such as face recognition)<sup>55</sup>. Rather, such specificity requires learning from one’s environment. This capacity for plasticity, despite intrinsic constraints, is exemplified by animal work showing that after the auditory cortex has been rewired to receive retinal input it will respond to visual stimulation, exhibit typical primary visual cortex tuning properties, and, critically, support visual behaviour<sup>56,57</sup>. Rather than being endowed with rigid domain-specific modules, the brain learns from and adapts to the relevant aspects of the information it processes from the environment<sup>12,58</sup>. The evolution of such broad and adaptive mechanisms in the brain is not reflected in the development of specific specialized circuits, but rather in the brain’s increased capacity for learning and plasticity<sup>59</sup>. Although the developing visual system is wired to ‘expect’ visual input<sup>54</sup>, its functioning is shaped by the regularities in the sensory input from the environment. Thus, rather than pre-specification at birth, the primary constraint on face processing is the protracted development of visual acuity and other developmental systems that interact with and promote visual exploration and visual experience.

Face-processing skills emerge and self-organize around relevant developmental tasks across the first year of life (Fig. 1). These tasks include the cognitive, social, emotional and physical milestones that infants achieve given sociocultural expectations and environmental constraints<sup>60</sup>. For example, the development of the visual system, the presence (or absence) of caregivers, and the infant’s ability/desire to move around their environment can enhance or constrain face processing<sup>43</sup>. This proposal predicts that early experiences with familiar faces cascade and lead to continued attention to relevant and rewarding faces, associative pairing of faces with relevant features like names, high levels of face recognition and differentiation and the development of holistic processing. The acquisition of new developmental tasks impacts the stability of previously established neural systems, leading to both disruptions of previous competencies and new competencies that arise and cascade within and across domains<sup>61–63</sup>.

Central to our domain-relevant framework is the idea that face processing is a dynamic and iterative process that is limited by both



**Fig. 1 | A domain-relevant face-processing cascade.** The development of face-relevant processing skills emerges across the first year of life and cascades across development. Face processing self-organizes around relevant developmental

tasks, leading to domain-relevant learning within given sociocultural expectations and environmental constraints.

the environment and the developing visual system. Early visual processing is constrained by immature neural circuitry that affects how an infant engages with and experiences the environment. These early constraints gate postnatal experience which, in turn, modifies neural circuitry and subsequent visual behaviour, including early visual looking preferences.

## Early visual preferences

Newborns typically show visual preferences for face-like stimuli, a pattern that is often used to support nativist and domain-specific evolutionary accounts of face processing<sup>64–66</sup>. However, the neural mechanisms that support early visual preferences for face-like stimuli need not reflect a face-specific template, but instead might be due to the maturation of the visual system constraining what infants can see. For example, visual acuity is 12–25 times worse in newborns than in adults<sup>67</sup> and matures across the first 6 months of life<sup>68–70</sup>. Thus, the infant visual system is limited to processing high-contrast and low-spatial-frequency (few regions of contrast per unit distance) content, which is prevalent in face and face-like images<sup>71</sup>. However, infants also prefer to look at upright compared to inverted faces as well as images that contain more visual components in the top half<sup>35,72–74</sup>. Rather than

reflecting a face-specific template, a visual preference for faces or face-like images could simply reflect a preference for high-contrast information in the top half of images (for example, the eyes of a face). Beyond faces, symmetry is a prominent feature of the visual world and impacts visual behaviour<sup>75</sup>. The horizontal symmetry of faces<sup>76</sup>, in particular the eyes, provides an additional important feature for the visual system via binocular correlation<sup>77</sup>. Early constraints from the visual system contribute to visual preferences for face-like stimuli and lead to rapid face learning (reviewed previously<sup>35</sup>) without requiring a domain-specific template for face processing to be present at birth. In other words, early in development, infants prefer to look at things they can see best.

Newborns also prefer to look at their mother's face more than at other faces within hours after birth<sup>78–80</sup>. However, this preference is only shown after newborns have experienced the intermodal pairing of seeing their mother's face while hearing her voice<sup>80</sup>. In addition, experience appears to shape newborns' early preferential looking towards their mother's face: time spent looking is correlated with the amount of visual exposure during the first several postnatal hours<sup>78</sup>. Furthermore, extensive evidence suggests that young infants readily form associations between multimodal stimuli and can make arbitrary

visual–auditory associations with experience<sup>81–83</sup>. A newborn's preferences for his/her mother's face could result, in part, from an association formed from extensive in utero experience hearing the mother speaking coupled with limited postnatal visual experience<sup>80</sup>. Once newborns experience their mother's voice paired with seeing her face, they immediately identify the mother's face as familiar and distinguish it from other faces.

Together, studies examining neonate visual acuity and preferential looking illustrate that evidence of early visual face preferences in newborns does not necessitate a pre-specified template for face processing. Rather, our brains have maturational constraints and are wired to adapt to the regularities of our experience.

## Early visual experiences

Young infants spend a substantial amount of time attending to faces. This is attributable to newborns' initial visual preferences coupled with the experience of faces as ubiquitous and highly relevant. Faces are frequently present in the infant's field of view<sup>48,84</sup>, and are moving<sup>85</sup>, expressing emotions<sup>86</sup>, and talking or singing<sup>87</sup>. Recordings of infants' field of view during everyday activities show that faces are visually present for 15 min of every waking hour early in the first year of life but for only 5 min per hour towards the end of the first year<sup>48</sup>. For younger infants, relatively few individual faces appeared in their field of view but these faces were viewed at close distances and appeared large with both eyes visible<sup>48</sup>. In another study using recordings of the infant's field of view, faces were typically viewed close to the infant, in a frontal viewpoint, and 1-month-old and 3-month-old infants viewed upright faces more frequently (88%) than non-upright faces<sup>88</sup>.

The nature of early infant visual experiences with faces has been further quantified using parental report and video recordings. In Nevada (USA), parents report that when viewing faces, their infants see female faces 71% of the time and own-race-group faces 92% of the time<sup>89</sup>. Similarly, across the first 3 months of life, when infants in Toronto (Canada) see faces, they see female faces 70% of the time and faces from their own race group 96% of the time<sup>90</sup>. Although culture and context play an important part in what an infant sees during the first months of life, infants in China were reported to have similar experiences with faces (64% female; 99% own race group)<sup>91</sup>. These investigations further demonstrate that visual experience is heavily biased towards female and familiar-race faces during the first months of life.

Although it is difficult to experimentally manipulate face experiences in human infants, macaque monkeys raised in a laboratory without naturally experiencing monkey or human faces initially show no visual preference for one species or another<sup>92</sup>. Subsequent exposure to either monkey or human faces led to a preference to look at the exposed species.

Infants' visual experiences are structured by their behaviour and development<sup>63</sup>. Visual input depends on infant development and changes as a function of developmental task demands and context. Infant visual preferences at one point in development might only be optimal for that current state of infant learning<sup>93</sup>. For example, when infants shift from primarily lying on their backs to sitting upright at around 5–6 months of age, their new view of the world changes the nature of the perceptual scene and results in disruptions to face processing that are later resolved<sup>63</sup>. In addition, our framework suggests that early learning occurs by watching the relevant faces of others, especially caretakers. Extensive visual sampling of a few faces in younger infants could be an important feature of early visual experience for developing invariant representations that are critical for

robust visual recognition in older infants<sup>94–98</sup>. Consideration of the natural statistics of an infant's visual experience can provide important insights into how early learning enhances and constrains subsequent learning. In other words, faces are an important educational tool for learning during the first year of life.

## Perceptual narrowing

The development of face processing during the first year of life follows a trajectory known as 'perceptual narrowing' (also called perceptual tuning or attunement)<sup>36,39,42,99–103</sup>. Perceptual narrowing involves the tuning or maintenance of environmentally relevant perceptual distinctions and a decrease in sensitivity to perceptual distinctions that are less frequently experienced<sup>34</sup>. Faces from often-experienced and familiar groups appear to drive learning and tune face processing. For example, face differentiation (the ability to tell the difference between two individuals) does not differ for faces within familiar and unfamiliar race groups for ages 3–6 months<sup>104,105</sup>. Then, with development and experience, face processing becomes tuned to individuals within the race groups infants interact with most. By 9 months, infants show better differentiation of faces within a familiar race group than within a less familiar race group<sup>104–108</sup>. In addition, 9-month-old infants who are not exposed to individuals within other race groups also show difficulties in categorizing faces from unfamiliar race groups<sup>109,110</sup>. This disparity in face processing for familiar and unfamiliar race groups is negatively correlated with the amount of diversity in the infant's community<sup>111</sup> and the size of the community<sup>112</sup>. Finally, important face-processing skills such as emotion and gaze processing are also impaired for faces from unfamiliar groups relative to faces from familiar groups, suggesting that these biases cascade<sup>85,108,113,114</sup>.

Postnatal improvements in face-processing skills for faces from familiar groups occur across the first year, further illustrating how the regularities of experiences shape learning. The neural and behavioural mechanisms supporting perceptual narrowing of face processing are general and include associative and non-associative learning<sup>34,36,42,43</sup>. The similarity in the timeframes of perceptual narrowing for faces and perceptual narrowing in other domains<sup>34,36,101</sup> indicates that general learning mechanisms could drive perceptual narrowing and conform the brain and behaviour to the environment.

Infant face processing is constrained by both the immaturity of their visual system and the regularities of their visual environment. Starting at birth, faces of caregivers and those within familiar groups are disproportionately experienced relative to individuals within other groups. This biased sampling of faces results in face-processing impairments for faces within unfamiliar groups compared to familiar groups. These impairments, coupled with enhanced processing of faces within highly experienced groups can be accounted for by associative and non-associative learning mechanisms.

## Universal learning mechanisms

Associative and non-associative learning mechanisms are conserved across species and individual differences arise from variation in rates of learning, strength of associations, and frequency or probability of experiences<sup>115–117</sup>. Behavioural evidence of face processing in early infancy can be explained by associative and non-associative learning mechanisms, within the domain-relevant context of the maturation of the visual system, and without ascribing to a prespecified function (Box 1). Infants learn information that is available, repeated, relevant and rewarding<sup>61,118</sup> and this information changes over developmental time.



## Box 1

### Neurobiological mechanisms of learning

Both associative and non-associative learning mechanisms underlie domain-relevant and experience-dependent neural specialization. For example, activity-dependent changes in synaptic strength and long-term potentiation occur during eyeblink conditioning and operant learning (reviewed previously<sup>223</sup>). Statistical and conceptual learning have also been linked to neural changes across development in human infants<sup>128,130–132</sup> and in adults (reviewed elsewhere<sup>224</sup>). Finally, suppression, attenuation and/or adaptation in response to repeated stimuli could contribute to behavioural habituation in infants (reviewed previously<sup>225</sup>).

These complex adaptation effects, measured by single-cell recordings and neuroimaging in human and non-human animals, can be used to infer that a subpopulation of neurons responds to a repeated stimulus<sup>226,227</sup>. Occipitotemporal adaptation effects occur at a conceptual level in adults such that repetition of different images of the same object, of different examples of an object and of different but conceptually related words all result in decreased occipitotemporal responses<sup>228</sup>. Although adaptation effects are normally assessed by changes in sensitivity over short timescales (from milliseconds to minutes), there is increasing evidence that the visual system can adapt over hours and even days to produce long-term perceptual biases<sup>229</sup>. These include

distortions in the representation of face identity<sup>230</sup>, where the appearance of a face can change relative to a reference<sup>231</sup>, and such perceptual biases provide one way the brain can adapt to the sensory environment. Furthermore, electroencephalograph (EEG) synchronization and desynchronization could be important indices of learning for infants (reviewed previously<sup>232</sup>). In adults, increased demands of attention, alertness and task load are associated with decreases in alpha power (desynchronization)<sup>233</sup>. In infants, viewing novel objects during a joint attention and gaze-following task resulted in alpha desynchronization over the posterior occipital cortex<sup>234,235</sup>. Occipital gamma EEG activity in 6-month-old infants was also decreased with repetition of faces but not objects (toys) and this decreased neural response was associated with increased looking towards novel stimuli<sup>236</sup>. EEG studies in infants show learning by examining increases and changes in oscillatory power across frequency bands of interest and could index adaptation.

Together, these findings highlight just a few potential connections between neurobiological mechanisms of learning and likely neural specialization underlying domain-relevant and experience-dependent behaviours. Future investigations aiming to elucidate the development of neural processes underlying human associative and non-associative learning mechanisms are warranted.

#### Associative learning

For the purposes of this Perspective, associative learning includes classical and operant conditioning, statistical learning and conceptual learning. Classical conditioning occurs when a meaningful stimulus is paired with a neutral stimulus and a new association is formed that leads to predictive behaviours. Classical conditioning has been shown in infants as young as 10 days old using an eyeblink procedure<sup>119</sup>. Within the context of face processing, newborns have also been shown to make associations between their mother's face and voice, leading to a preference for looking at their mother's face within hours of birth<sup>80</sup>. Therefore, hearing their mother's voice before birth and then seeing her face associated with her voice after birth could be one of the first forms of associative learning by infants.

Operant conditioning involves learning the association between a behavioural response and a particular negative or positive outcome. For example, eye contact is thought to be one of the earliest behavioural responses in infants to be positively reinforced via operant conditioning, potentially contributing to later communicative skills<sup>120–122</sup>. Parents naturally reinforce sustained mutual eye contact with emotional expressions and touch, which might contribute to mastery of later developing or more complex tasks. In one study, infants showed increased eye contact, smiling and vocalizations when eye contact was reinforced by an adult smiling, cooing and rubbing the infants' legs or feet compared to when touch was omitted<sup>123</sup>. This finding suggests that parental touch reinforced infant–parent mutual eye contact. Sustained eye contact with a parent has also been shown to contribute to later joint attention abilities such as directing gaze toward the same object, which fosters subsequent development of social communication skills<sup>124</sup>.

Statistical learning, or learning the transitional probabilities and temporal contingencies within languages or visual scenes, is another relevant form of associative learning that contributes to how faces are processed<sup>125,126</sup>. In adults, face processing occurs in relation to the distribution of faces present within the environment and biases arise when any given face deviates from the cumulative learned distribution<sup>127</sup>. In infants, learning from a distribution of faces has also been shown to affect identity differentiation<sup>128,129</sup>. For instance, in one study two groups of 6.5-month-old infants were shown morphed female faces that moved from one identity to another using either a bimodal or unimodal distribution<sup>128</sup>. Infants were then shown pairs of faces that either matched or mismatched in identity. Those exposed to the bimodal distribution showed different neural responses for match and mismatch trials, whereas those exposed to the unimodal distribution showed similar responses<sup>128</sup>. These results suggest that infants formed either one or two identity categories depending on the learning distribution they were exposed to. These findings are also consistent with results showing that infant face processing is enhanced and constrained by the faces they see and interact with the most and suggests that infants use conditional probabilities to form representations of relevant faces.

Associative learning is also used to establish label–object or label–face associations during the first year of life<sup>107,130–132</sup>. Infants exhibit increased attention and increased perceptual learning and show more selective brain responses to faces and objects after parents read them books with specifically labelled (individual-level) names for faces or objects from 6 months to 9 months of age<sup>106,107,130–132</sup>. The specificity of the labels differentially directed infant attention and highlighted perceptual differences that then facilitated individuation<sup>133–135</sup>.

Furthermore, relative to faces from highly familiar groups, faces from less familiar groups might not be labelled at the same frequency or within the same context, causing faces from less familiar groups to be more readily categorized than individuated.

## Non-associative learning

Non-associative learning mechanisms include habituation and sensitization<sup>115,136</sup>. The dual-process model of infant attention posits that decreased responses (habituation) and increased responses (sensitization) to repeated stimuli are independent processes that interact to produce behaviour<sup>115,136–138</sup>. Models of infant attention also suggest the presence of age-related decreases in the amount of time it takes infants to habituate owing to increased rates of encoding and/or processing efficiency<sup>139</sup> or an increased ability to disengage from a stimulus<sup>140</sup>.

Habituation techniques are widely used to study infant development<sup>141–143</sup>, but habituation itself is not often cited as an important mechanism underlying infant learning<sup>142</sup> or face processing. Repeated experience can influence how an infant explores and interacts with their environment. For example, repeated exposure with familiar individuals in familiar contexts might lead to decreased looking at, or habituation to, the faces of those individuals, which could be an important factor for later perceptual processing. Similar to associative learning, individual differences in rates of habituation or dishabituation during non-associative learning can result in behavioural differences across infants<sup>144</sup>. For example, infant neural responses decreased with increased exposure to both familiar (mother's face) and unfamiliar female faces<sup>145</sup>, suggesting that repeated face exposure can result in a reduction in neural responses to faces in infants.

Although less is known about how sensitization (increased responding after stimuli repetition) influences face processing, 4-month-old infants showing sensitization to chequerboard patterns habituated more slowly than those who did not, suggesting that sensitization can affect individual differences in rates of habituation<sup>146</sup>. Although it has not yet been examined, sensitization might also be related to the perceptual narrowing and tuning effects described above. For example, increased sensitivity to detecting multiple types of face changes (replacing outer features or changing face feature spacing)

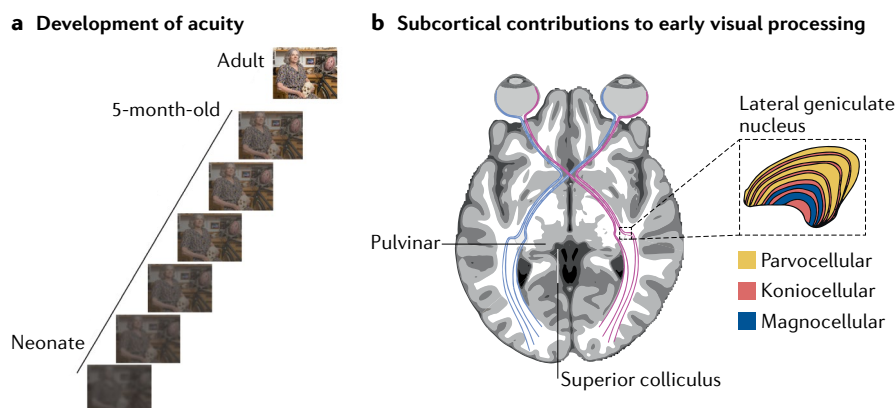
was shown in infants at 9–12 months of age compared to 4–6 months of age<sup>103</sup>. However, detection of face changes was best for human faces compared to monkey and sheep faces, consistent with experience-based tuning. In this example, it is possible that repeated attention and experience with face features could have increased sensitivity to those features, generally leading to the increased detection of face changes in faces from familiar groups.

The development of face processing is dependent on both associative and non-associative learning mechanisms that respond to relevant and repeated faces present in an infant's environment. This domain-relevant learning occurs within the context of the maturation of the visual system and is supported and constrained by an array of cortical and subcortical brain regions that serve unique functions and mature at different timescales.

## Development of neural specialization

In adults, the visual processing of faces is supported by 'face patches', or cortical brain regions that respond more to faces than to other visual input<sup>147–154</sup>. The stereotyped anatomical locations of face patches across individuals and their presence in multiple primate species<sup>147</sup> could be taken as evidence that the function of face patches is pre-specified<sup>155</sup>. However, face patches are not present in newborn monkeys<sup>37</sup> and do not develop without early visual experience with faces<sup>40</sup> (see ref. <sup>156</sup> for additional evidence on the role of experience in the formation of face patches). Computational modelling incorporating known biological constraints further demonstrates the sufficiency of visual experience for the emergence of specialized face processing<sup>157</sup>. Through domain-general associative and non-associative learning mechanisms, early experience drives the specialization of neural circuits for processing faces, including face patches, and is constrained only by the maturation of the visual system.

In utero, prior to substantial real-world experience, an intrinsic brain architecture develops through molecular guidance cues<sup>50,51</sup>, physical or mechanical pressures<sup>53</sup>, and activity-dependent processes<sup>158,159</sup> (see ref. <sup>160</sup> for a review of activity-dependent processes). This early intrinsic architecture includes broad anatomical connectivity linking brain networks<sup>161–163</sup>, cortical folding<sup>164</sup>, which influences laminar organization<sup>165</sup> and functional maps that facilitate communication



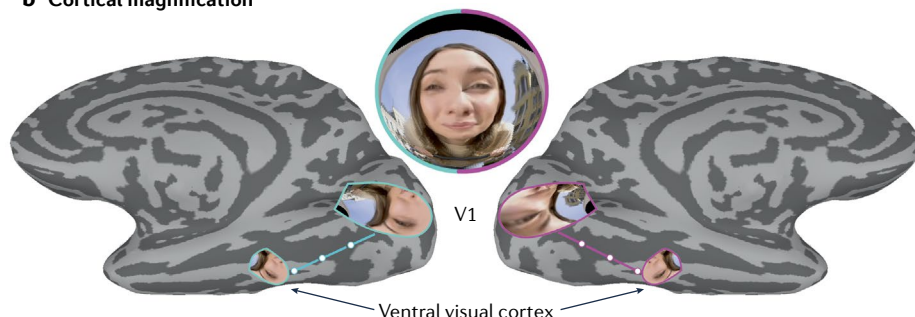
**Fig. 2 | Acuity constraints and neonate subcortical structures.** **a**, Infant visual acuity over the first 5 months in comparison to adult visual acuity. **b**, Visual pathways that route input from the retina to the cortex in the adult brain. Early processing is gated by the differential maturation of magnocellular and parvocellular pathways starting in the lateral geniculate nucleus. The pulvinar

and the superior colliculus are two subcortical structures whose response properties and connectivity in adults make them candidates for supporting visual behaviour in neonates, including preferential face looking. Images in panel a are courtesy of Anna Olivella and Reborn's BabySee App.

**a Foveated faces**



**b Cortical magnification**



**Fig. 3 | Foveated face processing.** **a**, The photo shows a typical baby's perspective with a mother's face occupying much of the visual field<sup>48,49</sup>. The heatmap illustrates the baby's foveation (centring of gaze) on the face. **b**, Foveated face input is relayed from the retina to visual area V1 through the

visual hierarchy and into the ventral visual cortex based on retinotopic connectivity. Given the regularity with which infants look at faces, face input will be relayed preferentially to regions of the ventral visual cortex representing foveal space, where face patches are typically found in adults.

within and across sensory systems<sup>166–168</sup>. We suggest that this early domain-relevant neural architecture then guides and constrains post-natal specialization such that the neonate visual system is capable of processing and detecting certain kinds of visual input over others without the need for pre-specified processing for any given function. Both subcortical and cortical mechanisms develop to support the emergence of cortical face patches during development.

## Subcortical mechanisms

Newborn humans preferentially look towards face-like images<sup>78,79</sup>, suggesting that there are brain circuits that preferentially process faces or face-like stimuli at birth. The neural structures mediating early face preferences do not need to respond to the fine features of a face (Fig. 2a). For instance, at a normal viewing distance, 1-month-old infants can discern only the outer contour of the face and vague dark regions around the eyes and mouth<sup>169</sup>. Given the low visual acuity of neonates<sup>68–70</sup>, a brain structure capable of orienting attention towards large, top-heavy, high-contrast features would be sufficient for driving early face-looking behaviour<sup>170–172</sup>. Indeed, 1-month-old infants exhibit preferential face-looking behaviour under visual tracking conditions<sup>64,65</sup>. Such visual sensitivity could be facilitated by magnocellular (in contrast to parvocellular) lateral geniculate nucleus (LGN) neurons that have higher contrast sensitivity and respond to lower spatial frequencies and higher temporal frequencies<sup>173,174</sup>. In addition, areas associated with magnocellular processing mature earlier than areas associated with parvocellular processing both anatomically<sup>52,175,176</sup> and functionally<sup>177</sup>, although see ref. <sup>178</sup> for the counter-argument that the parvocellular pathway develops first.

Although individual cortical neurons in macaque neonates respond preferentially to faces<sup>179</sup>, face-looking behaviour is unlikely to be driven by cortical circuits, given that neural responses<sup>180</sup>, metabolic activity<sup>181</sup>, macroscale selectivity<sup>37</sup>, and laminar organization<sup>175</sup> remain immature for the first several months postnatally. Instead, face-looking behaviour in human and non-human primate infants might be mediated by subcortical structures that are sensitive to salient features of faces perceivable under low visual acuity and that have response properties that can drive early face-looking behaviour (Fig. 2b). For example, the superior colliculus, an evolutionarily old brain structure that responds to salient visual input, is a good candidate<sup>178</sup>. It contains a retinotopic map of visual space that preferentially responds to input

in the upper half of the visual field, and could support topographically constrained, cross-modal learning<sup>182</sup> (reviewed elsewhere<sup>160</sup>). Another good subcortical candidate is the pulvinar, which contains neurons responsive to high-contrast, salient visual input<sup>183</sup>. The pulvinar is also interconnected with the superior colliculus<sup>184</sup> and has a critical role in the formation of cortical circuits promoting visuomotor behaviours<sup>185</sup>. Furthermore, neurons in both the pulvinar and superior colliculus contain coarse information about faces and face-like images in adult monkeys<sup>186</sup>. However, little is known about the functional development of either structure.

The involvement of subcortical structures for early face preferences in human infancy has classically been referred to as the CONSPEC system, because it contains information about the visual features of conspecifics<sup>31</sup>. In contrast with CONSPEC, here we argue that this system is not face-specific, but instead responds to visual input that is visible and salient to infants, which, based on the regularities of early visual experience, includes faces. Thus, the early functioning of these subcortical structures is in line with a domain-relevant framework of face processing.

## Cortical mechanisms

The localization of face patches to stereotyped locations in the cortex can be accounted for by the interaction between the regularities of early visual experience and the retinotopic maps of visual space<sup>187</sup>. Human infants as young as 4 months of age<sup>188</sup> and macaque neonates<sup>37</sup> preferentially fixate on faces in natural scenes, which leads to the selective input of facial information to the foveal regions of the ventral temporal cortex<sup>189–191</sup> (Fig. 3), where face patches develop postnatally<sup>166</sup>. Further, topographic maps provide an infrastructure for the selective input of facial information to the ventral temporal cortex across sensory modalities without ascribing to a pre-specification of function. Topographic links between the ventral temporal cortex and higher-order association cortices<sup>191–194</sup>, potentially mediated through subcortical structures<sup>195</sup> in combination with Hebbian-based learning<sup>196</sup>, can account for the findings of stereotyped localization of tactile<sup>197</sup> and auditory<sup>198</sup> facial information in the ventral temporal cortex. Thus, the presence of specialized brain regions such as face patches is not necessarily due to hardwired modules, but rather could reflect the regularities of experience within and across sensory modalities to enable flexible and dynamic learning through development.

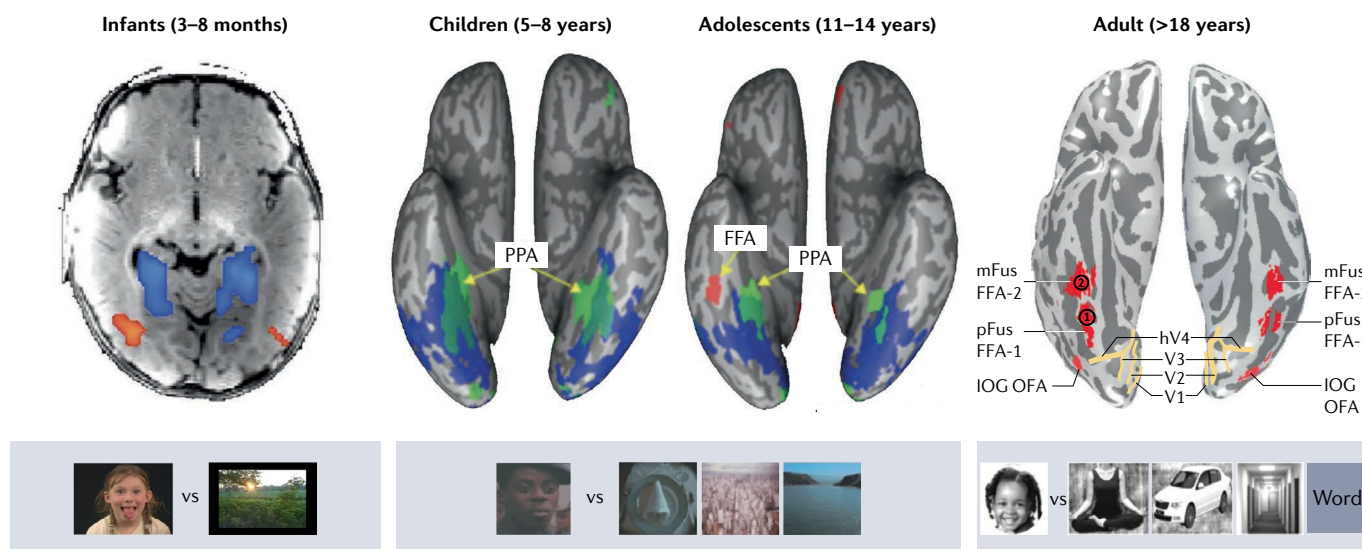


Face patches emerge within the first several months postnatally and mature throughout adolescence (Fig. 3). Although individual face-selective neurons have been identified by extracellular recordings in macaques as young as 5.5 weeks<sup>180</sup>, face patches were not identified using functional magnetic resonance imaging (fMRI) in macaques for the first several months<sup>37</sup>, indicating that, at the population level, face selectivity is not present at birth. In 2-month-old human infants, preferential responses to a woman's face compared to simple shapes were observed with positron emission tomography imaging in a region of ventral temporal cortex that corresponds to face patches in adults<sup>199</sup>. This result could be taken to indicate early neural responsiveness to faces. However, the limited stimuli tested were insufficient to evaluate face-specific responsiveness as evidenced by extensive activity throughout and outside the visual cortex. In addition, preferential responses to faces were also observed in cortical regions that typically do not exhibit face selectivity in adults, including cortical areas that eventually become part of the language network. Subsequent fMRI studies in 4–6-month-old human infants using dynamic movies reported preferential responses to faces compared to scenes<sup>28</sup> and objects<sup>29</sup> in the approximate region of face patches in older individuals. These preferential responses to faces highlight an early emergence of cortical face responsiveness, although the degree of selectivity and anatomical specificity differs markedly from face patches in adults. Rather than reflecting a mature selectivity to faces, this modest early preferential responsiveness is expected on the basis of non-face-specific processing of low-level visual features<sup>200,201</sup>, noncategorical shape selectivity<sup>202</sup> and/or retinotopic organization<sup>166</sup>, which co-vary with typical images of faces.

Face selectivity has also been reported in studies examining human infant neural responses to faces using event-related potentials (ERPs). In human adults, the N170 ERP component is greater in response

to faces compared to objects, a finding that has led this component to be referred to as face-selective or face-specific<sup>203–205</sup>. For infants, the N290 ERP component shows similar selectivity to faces. The N290 response is greater for faces than objects<sup>206,207</sup>, has been localized to regions where face patches are reported in adults<sup>206,207</sup>, is greater to own-species than to other-species faces<sup>208,209</sup>, is greater to own-race than to other-race faces by 9 months of age<sup>108,210</sup>, is greater to recently familiarized faces than to unfamiliar faces by 9 months of age<sup>211</sup>, and is greater to female compared to male faces in 7-month-old infants raised by a female caregiver<sup>212</sup>. Taken together, these studies indicate that cortical responses to faces are present in infants, are affected by experience, and develop gradually.

Face-selective cortical regions continue to develop throughout childhood and adolescence (Fig. 4 and Box 2). By the age of 6 years, the large-scale spatial organization of face-selective and other category-selective regions is present in the human ventral temporal cortex<sup>38,39</sup>. However, the spatial extent and magnitude of selectivity as well as finer differentiation (such as in the representation of one's own face versus other faces) continues to develop into adolescence<sup>38,213,214</sup>. In children, face patches might respond more to features of the face than to the whole face<sup>213</sup>. Increasing selectivity for faces through adolescence is due in part to decreasing responses to non-face images<sup>39,215</sup>. Indeed, the emergence of face patches could reflect an optimization of neural circuitry to build representations invariant to spatial transformations<sup>216</sup>. Consistent with this theoretical account, the anatomical extent of face patches continues to increase into adulthood and is associated with improvements in recognition memory for faces<sup>217</sup> and perceptual expertise<sup>218</sup>. Thus, this prolonged development of face-processing regions in the cortex parallels the development of face-recognition abilities is consistent with a domain-relevant framework<sup>219</sup>.



**Fig. 4 | Cortical development of human face processing.** Neuroimaging studies tracking the development of face patches in human ventral occipital-temporal cortex. In each panel, red colouring corresponds to regions that responded more strongly to faces than to other stimuli. In 3–8-month-old infants, greater responses to movies containing faces versus scenes were observed in the ventral temporal cortex<sup>28</sup>. In 5–8-year-old children, preferential responses to static faces compared to objects, buildings, and navigation scenes were not observed in the ventral temporal cortex<sup>39</sup>. In 11–14-year-old adolescents, face-selective

activity was observed using the same stimulus set<sup>39</sup>. In adults, several regions that preferentially respond to static images of faces more than to a variety of image categories are typically observed<sup>222</sup>. FFA, fusiform face area; hV4, human visual area V4; IOG, inferior occipital gyrus; mFus, middle fusiform; OFA, occipital face area; pFus, posterior fusiform; PPA, parahippocampal place area; V1, visual area V1; V2, visual area V2; V3, visual area V3. Left image adapted from ref. <sup>28</sup>, Springer Nature Ltd; middle images adapted with permission from ref. <sup>39</sup>, Wiley; right image adapted with permission from ref. <sup>222</sup>, Annual Reviews.



## Conclusion

In this Perspective, we argued that the infant brain at birth is not equipped with either a specific face-processing module or an immature system that has specific hardwired face-processing constraints. Assumptions of innate and evolution-driven specificity of face processing at birth are untestable and data purported to support this domain-specific perspective include a substantial amount of mechanistic speculation. This speculation has not led to advances in our understanding of child development and might ultimately interfere with scientific progress in the field of developmental psychology. Conversely, domain-general accounts need to incorporate constraints from intrinsic neural architecture and be better couched in mechanistic explanations of how learning operates within the developing brain.

As an alternative to both accounts, we argue for a domain-relevant framework for the emergence of face processing. Empirical work across the first year of life and into childhood and adolescence suggests that face processing and neural specialization is dynamic and experience-dependent, and that it self-organizes as developmental tasks and skills arise. Human and non-human primate research on the visual system in neonates and infants suggests that intrinsic subcortical and cortical architectural constraints do not rigidly limit certain neural circuits to face processing, but rather enable the infant visual system to capitalize on general learning mechanisms and to adapt to the domain-relevant features of the environment. Extensive work shows the importance of learning and experience in shaping behavioural and brain development that nurtures face processing in this manner. Moreover, these general learning mechanisms could be experimentally controlled and tested across ages, species and levels of analysis in future research.

The field would benefit greatly from a better understanding of the mechanisms underlying how experience enables infants to learn flexibly and regularly by self-organizing their behavioural and neural responses to domain-relevant features of the surrounding environment. To this end, neuroimaging of neonate and infant brains, biologically constrained computational modelling of their learning, and the use of animal models with controlled rearing paradigms should provide key insights into the role of experience in shaping the development of face processing. In addition, recording early infant visual experience, longitudinally and with high fidelity, should help to elucidate further the dynamic interplay between the developing brain and the changing environmental input. Finally, decades of research into general learning mechanisms support using associative and non-associative mechanisms for understanding and examining the behavioural and neurobiological basis of face processing. Future experimental investigations with neonates, infants and children could further probe the neural basis of learning and track developmental trajectories by implementing pre-learning and post-learning assessments of both their behaviour and brain state.

Beyond face processing, and across other domains of child development, a domain-relevant focus on learning from the environment will lead to more useful advances than will focusing on pre-specified innate mechanisms. Such advances will improve our understanding of the developing brain. In turn, they will also inform better preventative and intervention learning-support programmes<sup>220</sup> as well as policies that support the development of infants and children and their families<sup>221</sup>. For example, policies that provide families with access to paid parental leave and flexible childcare options could allow caregivers to implement a supportive home-learning environment that positively affects developmental trajectories<sup>221</sup>.

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## Box 2

### Lateralization

Although face patches (measured by functional magnetic resonance imaging (fMRI)) and face-specific responses (measured by electroencephalograph (EEG)) are typically identified bilaterally in human adults, the degree of selectivity to faces is greater over the right hemisphere than over the left hemisphere (measured with fMRI<sup>150,237</sup> and event-related potentials (ERPs)<sup>238,239</sup>). Such hemisphere differences in face processing are not apparent in macaques<sup>151</sup> and may emerge when human children learn to read, as a result of competition with nearby brain regions involved in the processing of words and language<sup>240–242</sup>. Lateralization of face patches in human ventral temporal cortex increases from childhood (7–9 years) to adulthood (24–45 years)<sup>243</sup>.

In human infants, lateralization is less consistently reported. ERP responses to featural and configural face changes showed lateralization between these two change conditions in 8-month-old but not in 4-month-old infants<sup>244</sup>. However, other studies report no significant ERP differences in how the right and left hemispheres respond to faces in infants<sup>245,246</sup>. The steady-state visual evoked potential EEG technique<sup>247</sup> can examine the development of the visuocortical processes underlying face processing in infancy and has the potential to provide greater sensitivity. Right lateralized face responses in infants as young as 4–6 months old, but more consistently after 9 months of age, are observed using steady-state visual evoked potentials<sup>248–251</sup>. These findings on the lateralization of face processing in human infants indicate that face-processing circuits in the brain do not develop in isolation, but rather reflect interactions with the development of other brain systems over different timescales, and as different developmental tasks arise<sup>42,43</sup>.

## References

1. Baillargeon, R. & Carey, S. in *Early Childhood Development and Later Outcome* (ed. Pauen, S. M.) 33–65 (Cambridge Univ. Press, 2012).
2. Carey, S. Précis of the origin of concepts. *Behav. Brain Sci.* **34**, 113–124 (2011).
3. Spelke, E. S. & Kinzler, K. D. Core knowledge. *Dev. Sci.* **10**, 89–96 (2007).
4. van der Lely, H. K. J. Domain-specific cognitive systems: insight from Grammatical-SLI. *Trends Cogn. Sci.* **9**, 53–59 (2005).
5. Coltheart, M. Modularity and cognition. *Trends Cogn. Sci.* **3**, 115–120 (1999).
6. Madole, K. L. & Oakes, L. M. Making sense of infant categorization: stable processes and changing representations. *Dev. Rev.* **19**, 263–296 (1999).
7. Quinn, P. C. & Eimas, P. D. A reexamination of the perceptual-to-conceptual shift in mental representations. *Rev. Gen. Psychol.* **1**, 271–287 (1997).
8. Rakison, D. H. & Lupyan, G. Developing object concepts in infancy: an associative learning perspective. VIII. General discussion. *Monogr. Soc. Res. Child Dev.* **73**, 85–100 (2008).
9. Rogers, T. T. & McClelland, J. L. *Semantic Cognition: A Parallel Distributed Processing Approach* (MIT Press, 2004).
10. Smith, L. B., Jones, S. S. & Landau, B. Naming in young children: a dumb attentional mechanism? *Cognition* **60**, 143–171 (1996).
11. Bates, J. E., Pettit, G. S., Dodge, K. A. & Ridge, B. Interaction of temperamental resistance to control and restrictive parenting in the development of externalizing behavior. *Dev. Psychol.* **34**, 982–995 (1998).
12. Karmiloff-Smith, A. An alternative to domain-general or domain-specific frameworks for theorizing about human evolution and ontogenesis. *AIMS Neurosci.* **2**, 91–104 (2015).
13. Farah, M. J., Rabinowitz, C., Quinn, G. E. & Liu, G. T. Early commitment of neural substrates for face recognition. *Cogn. Neuropsychol.* **17**, 117–123 (2000).
14. McKone, E., Crookes, K., Jeffery, L. & Dilks, D. D. A critical review of the development of face recognition: experience is less important than previously believed. *Cogn. Neuropsychol.* **29**, 174–212 (2012).

15. Sugita, Y. Innate face processing. *Curr. Opin. Neurobiol.* **19**, 39–44 (2009).
16. Hildebrandt, A., Wilhelm, O., Schmiedek, F., Herzmann, G. & Sommer, W. On the specificity of face cognition compared with general cognitive functioning across adult age. *Psychol. Aging* **26**, 701–715 (2011).
17. Tanaka, J. W. & Farah, M. J. Parts and wholes in face recognition. *Q. J. Exp. Psychol. A* **46**, 225–245 (1993).
18. Yin, R. K. Looking at upside-down faces. *J. Exp. Psychol.* **81**, 141–145 (1969).
19. Young, M. P. Objective analysis of the topological organization of the primate cortical visual system. *Nature* **358**, 152–155 (1992).
20. Barton, J. J. Structure and function in acquired prosopagnosia: lessons from a series of 10 patients with brain damage. *J. Neuropsychol.* **2**, 197–225 (2008).
21. Takahashi, N. et al. Prosopagnosia: a clinical and anatomical study of four patients. *Cortex* **31**, 317–329 (1995).
22. Polk, T. A., Park, J., Smith, M. R. & Park, D. C. Nature versus nurture in ventral visual cortex: a functional magnetic resonance imaging study of twins. *J. Neurosci.* **27**, 13921–13925 (2007).
23. Wilmer, J. B. et al. Human face recognition ability is specific and highly heritable. *Proc. Natl Acad. Sci. USA* **107**, 5238–5241 (2010).
24. Zhu, Q. et al. Heritability of the specific cognitive ability of face perception. *Curr. Biol.* **20**, 137–142 (2010).
25. Quinones Sanchez, J. F., Liu, X., Zhou, C. & Hildebrandt, A. Nature and nurture shape structural connectivity in the face processing brain network. *Neuroimage* **229**, 117736 (2021).
26. Kanwisher, N. Domain specificity in face perception. *Nat. Neurosci.* **3**, 759–763 (2000).
27. Yovel, G. & Kanwisher, N. The neural basis of the behavioral face-inversion effect. *Curr. Biol.* **15**, 2256–2262 (2005).
28. Deen, B. et al. Organization of high-level visual cortex in human infants. *Nat. Commun.* **8**, 13995 (2017).
29. Kosakowski, H. L. et al. Selective responses to faces, scenes, and bodies in the ventral visual pathway of infants. *Curr. Biol.* **32**, 265–274.e5 (2022).
30. Park, J., Newman, L. I. & Polk, T. A. Face processing: the interplay of nature and nurture. *Neuroscientist* **15**, 445–449 (2009).
31. Morton, J. & Johnson, M. H. CONSPEC and CONLERN: a two-process theory of infant face recognition. *Psychol. Rev.* **98**, 164–181 (1991).
32. Gauthier, I. & Nelson, C. A. The development of face expertise. *Curr. Opin. Neurobiol.* **11**, 219–224 (2001).
33. Nelson, C. A. in *The Development of Face Processing in Infancy and Early Childhood: Current Perspectives* (eds Pascalis, O. & Slater, A.) 79–97 (Nova Science, 2003).
34. Scott, L. S., Pascalis, O. & Nelson, C. A. A domain-general theory of the development of perceptual discrimination. *Curr. Dir. Psychol. Sci.* **16**, 197–201 (2007).
35. Simion, F. & Giorgio, E. D. Face perception and processing in early infancy: inborn predispositions and developmental changes. *Front. Psychol.* **6**, 969 (2015).
36. Hadley, H., Rost, G., Fava, E. & Scott, L. A mechanistic approach to cross-domain perceptual narrowing in the first year of life. *Brain Sci.* **4**, 613–634 (2014).
37. Livingstone, M. S. et al. Development of the macaque face-patch system. *Nat. Commun.* **8**, 14897 (2017).
38. Golarai, G., Ghahremani, D. G., Eberhardt, J. L. & Gabrieli, J. D. E. Distinct representations of configural and part information across multiple face-selective regions of the human brain. *Front. Psychol.* **6**, 1710 (2015).
39. Scherf, K. S., Behrmann, M., Humphreys, K. & Luna, B. Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. *Dev. Sci.* **10**, F15–F30 (2007).
40. Arcaro, M. J., Schade, P. F., Vincent, J. L., Ponce, C. R. & Livingstone, M. S. Seeing faces is necessary for face-domain formation. *Nat. Neurosci.* **20**, 1404–1412 (2017).
41. Smith, L. B., Colunga, E. & Yoshida, H. Knowledge as process: contextually-cued attention and early word learning. *Cogn. Sci.* **34**, 1287–1314 (2010).
42. Markant, J. & Scott, L. S. Attention and perceptual learning interact in the development of the other-race effect. *Curr. Dir. Psychol. Sci.* **27**, 163–169 (2018).
43. Scherf, K. S. & Scott, L. S. Connecting developmental trajectories: biases in face processing from infancy to adulthood. *Dev. Psychobiol.* **54**, 643–663 (2012).
44. Jayaraman, S. & Smith, L. B. in *The Cambridge Handbook of Infant Development: Brain, Behavior, and Cultural Context* (eds Lockman, J. J. & Tamis-LeMonda, C. S.) 553–579 (Cambridge Univ. Press, 2020).
45. Bates, E. et al. in *A Companion to Cognitive Science* Ch. 46 (eds Bechtel, W. & Graham, G.) 590–601 (Blackwell, 1998).
46. Karmiloff-Smith, A. An alternative to domain-general or domain-specific frameworks for theorizing about human evolution and ontogenesis. *AIMS Neurosci.* **2**, 91–104 (2015).
47. Farroni, T. et al. Newborns' preference for face-relevant stimuli: effects of contrast polarity. *Proc. Natl Acad. Sci. USA* **102**, 17245–17250 (2005).
48. Jayaraman, S., Fausey, C. M. & Smith, L. B. The faces in infant-perspective scenes change over the first year of life. *PLoS ONE* **10**, e0123780 (2015).
49. Jayaraman, S., Fausey, C. M. & Smith, L. B. Why are faces denser in the visual experiences of younger than older infants? *Dev. Psychol.* **53**, 38–49 (2017).
50. Flanagan, J. G. Neural map specification by gradients. *Curr. Opin. Neurobiol.* **16**, 59–66 (2006).
51. O'Leary, D. D. M., Yates, P. A. & McLaughlin, T. Molecular development of sensory maps. *Cell* **96**, 255–269 (1999).
52. Rakic, P. Prenatal development of the visual system in rhesus monkey. *Phil. Trans. R. Soc. Lond. B* **278**, 245–260 (1977).
53. Van Essen, D. A tension-based theory of morphogenesis and compact wiring in the central nervous system. *Nature* **385**, 313–318 (1997).
54. Greenough, W. T., Black, J. E. & Wallace, C. S. Experience and brain development. *Child Dev.* **58**, 539–559 (2022).
55. McKone, E., Kanwisher, N. & Duchaine, B. C. Can generic expertise explain special processing for faces? *Trends Cogn. Sci.* **11**, 8–15 (2007).
56. Sur, M., Garraghty, P. E. & Roe, A. W. Experimentally induced visual projections into auditory thalamus and cortex. *Science* **242**, 1437–1441 (1988).
57. von Melchner, L., Pallas, S. L. & Sur, M. Visual behaviour mediated by retinal projections directed to the auditory pathway. *Nature* **404**, 871–876 (2000).
58. Finlay, B. L. Endless minds most beautiful. *Dev. Sci.* **10**, 30–34 (2007).
59. Gomez-Robles, A., Hopkins, W. D. & Sherwood, C. C. Increased morphological asymmetry, evolvability and plasticity in human brain evolution. *Proc. Biol. Sci.* **280**, 20130575 (2013).
60. Havighurst, R. J. *Developmental Tasks and Education* (Univ. Chicago Press, 1948).
61. Oakes, L. M. & Rakison, D. H. *Developmental Cascades: Building The Infant Mind* (Oxford Univ. Press, 2020).
62. Smith, L. B. & Thelen, E. Development as a dynamic system. *Trends Cogn. Sci.* **7**, 343–348 (2003).
63. Cashion, C. H., Ha, O. R., Allen, C. L. & Barna, A. C. A U-shaped relation between sitting ability and upright face processing in infants. *Child Dev.* **84**, 802–809 (2013).
64. Goren, C. C., Sarty, M. & Wu, P. Y. Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics* **56**, 544–549 (1975).
65. Johnson, M. H., Dziurawiec, S., Ellis, H. & Morton, J. Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition* **40**, 1–19 (1991).
66. Valenza, E., Simion, F., Cassia, V. M. & Umiltà, C. Face preference at birth. *J. Exp. Psychol. Hum. Percept. Perform.* **22**, 892–903 (1996).
67. Dobson, V. & Teller, D. Y. Visual acuity in human infants: a review and comparison of behavioral and electrophysiological studies. *Vis. Res.* **18**, 1469–1483 (1978).
68. Atkinson, J., Braddick, O. & Braddick, F. Acuity and contrast sensitivity of infant vision. *Nature* **247**, 403–404 (1974).
69. Kiorpes, L. The puzzle of visual development: behavior and neural limits. *J. Neurosci.* **36**, 11384–11393 (2016).
70. Kiorpes, L. & Movshon, J. in *The New Visual Neurosciences* Ch. 12 (eds Chalupa, L. & Werner, J. S.) 1423–1431 (MIT Press, 2003).
71. Kleiner, K. A. & Banks, M. S. Stimulus energy does not account for 2-month-olds' face preferences. *J. Exp. Psychol. Hum. Percept. Perform.* **13**, 594–600 (1987).
72. Morton, J., Johnson, M. H. & Maurer, D. On the reasons for newborns' responses to faces. *Infant Behav. Dev.* **13**, 99–103 (1990).
73. Macchi Cassia, V., Turati, C. & Simion, F. Can a nonspecific bias toward top-heavy patterns explain newborns' face preference? *Psychol. Sci.* **15**, 379–383 (2004).
74. Simion, F., Macchi Cassia, V., Turati, C. & Valenza, E. The origins of face perception: specific versus non-specific mechanisms. *Infant Child Dev.* **10**, 59–65 (2001).
75. Wagemans, J. Detection of visual symmetries. *Spat. Vis.* **9**, 9–32 (1995).
76. Slater, A. & Sykes, M. Newborn infants' visual responses to square wave gratings. *Child Dev.* **48**, 545–554 (1977).
77. Wilkinson, N., Paikan, A., Gredebäck, G., Rea, F. & Metta, G. Staring us in the face? An embodied theory of innate face preference. *Dev. Sci.* **17**, 809–825 (2014).
78. Bushnell, I. W. R. Mother's face recognition in newborn infants: learning and memory. *Infant Child Dev.* **10**, 67–74 (2001).
79. Pascalis, O., de Schonen, S., Morton, J., Deruelle, C. & Fabre-Grenet, M. Mother's face recognition by neonates: a replication and an extension. *Infant Behav. Dev.* **18**, 79–85 (1995).
80. Sai, F. Z. The role of the mother's voice in developing mother's face preference: evidence for intermodal perception at birth. *Infant Child Dev.* **14**, 29–50 (2005).
81. Lewkowicz, D. J. Infant perception of audio-visual speech synchrony. *Dev. Psychol.* **46**, 66–77 (2010).
82. Lewkowicz, D. J. & Lickliter, R. The development of intersensory perception: comparative perspectives. *J. Cogn. Neurosci.* **8**, 185–187 (1996).
83. Slater, A., Brown, E. & Badcock, M. Intermodal perception at birth: newborn infants' memory for arbitrary auditory-visual pairings. *Early Dev. Parent.* **6**, 99–104 (1997).
84. Fausey, C. M., Jayaraman, S. & Smith, L. B. From faces to hands: changing visual input in the first two years. *Cognition* **152**, 101–107 (2016).
85. Xiao, N. G. et al. Eye tracking reveals a crucial role for facial motion in recognition of faces by infants. *Dev. Psychol.* **51**, 744–757 (2015).
86. Eisenberg, N., Cumberland, A. & Spinrad, T. L. Parental socialization of emotion. *Psychol. Inq.* **9**, 241–273 (1998).
87. Dissanayake, E. Motherese is but one part of a ritualized, multimodal, temporally organized, affiliative interaction. *Behav. Brain Sci.* **27**, 491–503 (2004).
88. Sugden, N. A. & Moulson, M. C. Hey baby, what's "up"? One- and 3-month-olds experience faces primarily upright but non-upright faces offer the best views. *Q. J. Exp. Psychol.* **70**, 959–969 (2017).
89. Rennels, J. L. & Davis, R. E. Facial experience during the first year. *Infant Behav. Dev.* **31**, 665–678 (2008).
90. Sugden, N. A., Mohamed-Ali, M. I. & Moulson, M. C. I spy with my little eye: typical, daily exposure to faces documented from a first-person infant perspective: infants' daily exposure to faces. *Dev. Psychobiol.* **56**, 249–261 (2014).
91. Liu, S. et al. Asian infants show preference for own-race but not other-race female faces: the role of infant caregiving arrangements. *Front. Psychol.* **6**, 593 (2015).
92. Sugita, Y. Face perception in monkeys reared with no exposure to faces. *Proc. Natl Acad. Sci. USA* **105**, 394–398 (2008).

93. Smith, L. B. & Slone, L. K. A developmental approach to machine learning? *Front. Psychol.* **8**, 2124 (2017).
94. Abudarham, N., Grosbard, I. & Yovel, G. Face recognition depends on specialized mechanisms tuned to view-invariant facial features: insights from deep neural networks optimized for face or object recognition. *Cogn. Sci.* **45**, e13031 (2021).
95. Földiák, P. Learning invariance from transformation sequences. *Neural Comput.* **3**, 194–200 (1991).
96. Li, N. & DiCarlo, J. J. Unsupervised natural experience rapidly alters invariant object representation in visual cortex. *Science* **321**, 1502–1507 (2008).
97. Wiskott, L. & Sejnowski, T. J. Slow feature analysis: unsupervised learning of invariances. *Neural Comput.* **14**, 715–770 (2002).
98. Wood, J. N. & Wood, S. M. W. The development of newborn object recognition in fast and slow visual worlds. *Proc. R. Soc. B* **283**, 20160166 (2016).
99. Flom, R. Perceptual narrowing: retrospect and prospect: perceptual narrowing. *Dev. Psychobiol.* **56**, 1442–1453 (2014).
100. Lewkowicz, D. J. & Ghazanfar, A. A. The emergence of multisensory systems through perceptual narrowing. *Trends Cogn. Sci.* **13**, 470–478 (2009).
101. Maurer, D. & Werker, J. F. Perceptual narrowing during infancy: a comparison of language and faces: language and faces. *Dev. Psychobiol.* **56**, 154–178 (2014).
102. Pascalis, O. et al. On the links among face processing, language processing, and narrowing during development. *Child Dev. Perspect.* **8**, 65–70 (2014).
103. Simpson, E. A., Jakobsen, K. V., Frigaszy, D. M., Okada, K. & Frick, J. E. The development of facial identity discrimination through learned attention. *Dev. Psychobiol.* **56**, 1083–1101 (2014).
104. Kelly, D. J. et al. Development of the other-race effect during infancy: evidence toward universality? *J. Exp. Child Psychol.* **104**, 105–114 (2009).
105. Kelly, D. J. et al. The other-race effect develops during infancy: evidence of perceptual narrowing. *Psychol. Sci.* **18**, 1084–1089 (2007).
106. Pascalis, O. et al. Plasticity of face processing in infancy. *Proc. Natl Acad. Sci. USA* **102**, 5297–5300 (2005).
107. Scott, L. S. & Monesson, A. The origin of biases in face perception. *Psychol. Sci.* **20**, 676–680 (2009).
108. Vogel, M., Monesson, A. & Scott, L. S. Building biases in infancy: the influence of race on face and voice emotion matching. *Dev. Sci.* **15**, 359–372 (2012).
109. Anzures, G., Quinn, P. C., Pascalis, O., Slater, A. M. & Lee, K. Development of own-race biases. *Vis. Cogn.* **21**, 1165–1182 (2013).
110. Quinn, P. C., Lee, K., Pascalis, O. & Tanaka, J. W. Narrowing in categorical responding to other-race face classes by infants. *Dev. Sci.* **19**, 362–371 (2016).
111. Bar-Haim, Y., Ziv, T., Lamy, D. & Hodes, R. M. Nature and nurture in own-race face processing. *Psychol. Sci.* **17**, 159–163 (2006).
112. Balas, B. & Saville, A. Hometown size affects the processing of naturalistic face variability. *Vis. Res.* **141**, 228–236 (2017).
113. Pickron, C. B., Fava, E. & Scott, L. S. Follow my gaze: face race and sex influence gaze-cued attention in infancy. *Infancy* **22**, 626–644 (2017).
114. Xiao, N. G. et al. Older but not younger infants associate own-race faces with happy music and other-race faces with sad music. *Dev. Sci.* **21**, e12537 (2018).
115. Groves, P. M. & Thompson, R. F. Habituation: a dual-process theory. *Psychol. Rev.* **77**, 419–450 (1970).
116. Morand-Ferron, J. Why learn? The adaptive value of associative learning in wild populations. *Curr. Opin. Behav. Sci.* **16**, 73–79 (2017).
117. Rakison, D. H. & Yermolayeva, Y. How to identify a domain-general learning mechanism when you see one. *J. Cogn. Dev.* **12**, 134–153 (2011).
118. Thelen, E. & Smith, L. B. *A Dynamic Systems Approach to The Development of Cognition and Action* (MIT Press, 1994).
119. Little, A. H., Lipsitt, L. P. & Rovee-Collier, C. Classical conditioning and retention of the infant's eyelid response: effects of age and interstimulus interval. *J. Exp. Child Psychol.* **37**, 512–524 (1984).
120. Mundy, P. & Newell, L. Attention, joint attention, and social cognition. *Curr. Dir. Psychol. Sci.* **16**, 269–274 (2007).
121. Pelaez, M. & Monlux, K. Operant conditioning methodologies to investigate infant learning. *Eur. J. Behav. Anal.* **18**, 212–241 (2017).
122. Pelaez, M. & Monlux, K. Development of communication in infants: implications for stimulus relations research. *Perspect. Behav. Sci.* **41**, 175–188 (2018).
123. Peláez-Nogueras, M. et al. Infants' preference for touch stimulation in face-to-face interactions. *J. Appl. Dev. Psychol.* **17**, 199–213 (1996).
124. Suarez-Rivera, C., Smith, L. B. & Yu, C. Multimodal parent behaviors within joint attention support sustained attention in infants. *Dev. Psychol.* **55**, 96–109 (2019).
125. Aslin, R. N. Statistical learning: a powerful mechanism that operates by mere exposure. *Wiley Interdiscip. Rev. Cogn. Sci.* **8**, e1373 (2017).
126. Fiser, J. & Aslin, R. N. Statistical learning of new visual feature combinations by infants. *Proc. Natl Acad. Sci. USA* **99**, 15822–15826 (2002).
127. Dotsch, R., Hassin, R. & Todorov, A. Statistical learning shapes face evaluation. *Nat. Hum. Behav.* **1**, 0001 (2016).
128. Altvater-Mackensen, N., Jessen, S. & Grossmann, T. Brain responses reveal that infants' face discrimination is guided by statistical learning from distributional information. *Dev. Sci.* **20**, e12393 (2017).
129. Jessen, S. & Grossmann, T. Exploring the role of spatial frequency information during neural emotion processing in human infants. *Front. Hum. Neurosci.* **11**, 486 (2017).
130. Pickron, C. B., Iyer, A., Fava, E. & Scott, L. S. Learning to individuate: the specificity of labels differentially impacts infant visual attention. *Child Dev.* **89**, 698–710 (2018).
131. Scott, L. S. Mechanisms underlying the emergence of object representations during infancy. *J. Cogn. Neurosci.* **23**, 2935–2944 (2011).
132. Scott, L. S. & Monesson, A. Experience-dependent neural specialization during infancy. *Neuropsychologia* **48**, 1857–1861 (2010).
133. Dewar, K. & Xu, F. Do 9-month-old infants expect distinct words to refer to kinds? *Dev. Psychol.* **43**, 1227–1238 (2007).
134. Halberda, J., Mazocco, M. M. M. & Feigenson, L. Individual differences in non-verbal number acuity correlate with maths achievement. *Nature* **455**, 665–668 (2008).
135. Xu, Y. et al. Functional consequences of a CK1δ mutation causing familial advanced sleep phase syndrome. *Nature* **434**, 640–644 (2005).
136. Rankin, C. H. et al. Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. *Neurobiol. Learn. Mem.* **92**, 135–138 (2009).
137. Kaplan, P. S. & Werner, J. S. Habituation, response to novelty, and dishabituation in human infants: tests of a dual-process theory of visual attention. *J. Exp. Child Psychol.* **42**, 199–217 (1986).
138. Kaplan, P., Werner, J. & Rudy, J. Habituation, sensitization, and infant visual attention. *Adv. Infancy Res.* **6**, 61–109 (1990).
139. Kavšek, M. The comparator model of infant visual habituation and dishabituation: recent insights: infant visual habituation and dishabituation. *Dev. Psychobiol.* **55**, 793–808 (2013).
140. Colombo, J. Infant attention grows up: the emergence of a developmental cognitive neuroscience perspective. *Curr. Dir. Psychol. Sci.* **11**, 196–200 (2002).
141. Aslin, R. N. What's in a look? *Dev. Sci.* **10**, 48–53 (2007).
142. Colombo, J. & Mitchell, D. W. Infant visual habituation. *Neurobiol. Learn. Mem.* **92**, 225–234 (2009).
143. Lipsitt, L. P. Learning, habituation, and classical conditioning processes in the human newborn: sensitization. *Ann. NY Acad. Sci.* **608**, 113–127 (1990).
144. Kavšek, M. & Bornstein, M. H. Visual habituation and dishabituation in preterm infants: a review and meta-analysis. *Res. Dev. Disabil.* **31**, 951–975 (2010).
145. Snyder, K., Webb, S. J. & Nelson, C. A. Theoretical and methodological implications of variability in infant brain response during a recognition memory paradigm. *Infant Behav. Dev.* **25**, 466–494 (2002).
146. Colombo, J., Frick, J. E. & Gorman, S. A. Sensitization during visual habituation sequences: procedural effects and individual differences. *J. Exp. Child Psychol.* **67**, 223–235 (1997).
147. Bell, A. H., Hadj-Bouziane, F., Frihauf, J. B., Tootell, R. B. & Ungerleider, L. G. Object representations in the temporal cortex of monkeys and humans as revealed by functional magnetic resonance imaging. *J. Neurophysiol.* **101**, 688–700 (2009).
148. Clark, V. P. et al. Functional magnetic resonance imaging of human visual cortex during face matching: a comparison with positron emission tomography. *Neuroimage* **4**, 1–15 (1996).
149. Jacques, C. et al. Corresponding ECoG and fMRI category-selective signals in human ventral temporal cortex. *Neuropsychologia* **83**, 14–28 (2016).
150. Kanwisher, N., McDermott, J. & Chun, M. M. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* **17**, 4302–4311 (1997).
151. Pinsk, M. A. et al. Neural representations of faces and body parts in macaque and human cortex: a comparative fMRI study. *J. Neurophysiol.* **101**, 2581–2600 (2009).
152. Puce, A., Allison, T., Asgari, M., Gore, J. C. & McCarthy, G. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *J. Neurosci.* **16**, 5205–5215 (1996).
153. Tsao, D. Y., Freiwald, W. A., Knutsen, T. A., Mandeville, J. B. & Tootell, R. B. H. Faces and objects in macaque cerebral cortex. *Nat. Neurosci.* **6**, 989–995 (2003).
154. Tsao, D. Y., Freiwald, W. A., Tootell, R. B. H. & Livingstone, M. S. A cortical region consisting entirely of face-selective cells. *Science* **311**, 670–674 (2006).
155. Powell, L. J., Kosakowski, H. L. & Saxe, R. Social origins of cortical face areas. *Trends Cogn. Sci.* **22**, 752–763 (2018).
156. Huber, E. et al. A lack of experience-dependent plasticity after more than a decade of recovered sight. *Psychol. Sci.* **26**, 393–401 (2015).
157. Blauch, N. M., Behrmann, M. & Plaut, D. A connectivity-constrained computational account of topographic organization in primate high-level visual cortex. *Proc. Natl Acad. Sci. USA* **119**, 1–12 (2022).
158. Butts, D. A. Retinal waves: implications for synaptic learning rules during development. *Neuroscientist* **8**, 243–253 (2002).
159. Hebb, D. O. The organization of behavior: a neuropsychological theory (John Wiley and Sons, 1949). *Sci. Educ.* **34**, 336–337 (1950).
160. Arcaro, M. J., Schade, P. F. & Livingstone, M. S. Universal mechanisms and the development of the face network: what you see is what you get. *Annu. Rev. Vis. Sci.* **5**, 341–372 (2019).
161. Dubois, J. et al. The early development of brain white matter: a review of imaging studies in fetuses, newborns and infants. *Neuroscience* **276**, 48–71 (2014).
162. Li, J., Osher, D. E., Hansen, H. A. & Saygin, Z. M. Innate connectivity patterns drive the development of the visual word form area. *Sci. Rep.* **10**, 18039 (2020).
163. Goldman-Rakic, P. S. Development of cortical circuitry and cognitive function. *Child Dev.* **58**, 601–622 (1987).
164. Garcia, K. E. et al. Dynamic patterns of cortical expansion during folding of the preterm human brain. *Proc. Natl Acad. Sci. USA* **115**, 3156–3161 (2018).



165. Hilgetag, C. C. & Barbas, H. Developmental mechanics of the primate cerebral cortex. *Anat. Embryol.* **210**, 411–417 (2005).
166. Arcaro, M. J. & Livingstone, M. S. A hierarchical, retinotopic proto-organization of the primate visual system at birth. *eLife* **6**, e26196 (2017).
167. Arcaro, M. J., Schade, P. F. & Livingstone, M. S. Body map proto-organization in newborn macaques. *Proc. Natl Acad. Sci. USA* **116**, 24861–24871 (2019).
168. Ellis, C. T. et al. Retinotopic organization of visual cortex in human infants. *Neuron* **109**, 2616–2626.e6 (2021).
169. Souther, A., & Banks, M. The human face: a view from the infant's eye. Presented at the meeting of the Society for Research in Child Development (1979).
170. Kleiner, K. A. & Banks, M. S. Stimulus energy does not account for 2-month-olds' face preferences. *J. Exp. Psychol. Hum. Percept. Perform.* **13**, 594–600 (1987).
171. Simion, F., Valenza, E., Cassia, V. M., Turati, C. & Umiltà, C. Newborns' preference for up-down asymmetrical configurations. *Dev. Sci.* **5**, 427–434 (2002).
172. Turati, C., Simion, F., Milani, I. & Umiltà, C. Newborns' preference for faces: what is crucial? *Dev. Psychol.* **38**, 875–882 (2002).
173. Derrington, A. M. & Lennie, P. Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *J. Physiol.* **357**, 219–240 (1984).
174. Liu, C.-S. J. et al. Magnocellular and parvocellular visual pathways have different blood oxygen level-dependent signal time courses in human primary visual cortex. *Am. J. Neuroradiol.* **27**, 1628–1634 (2006).
175. Bourne, J. A. & Rosa, M. G. P. Hierarchical development of the primate visual cortex, as revealed by neurofilament immunoreactivity: early maturation of the middle temporal area (MT). *Cereb. Cortex* **16**, 405–414 (2006).
176. Rakic, P. Genesis of the dorsal lateral geniculate nucleus in the rhesus monkey: site and time of origin, kinetics of proliferation, routes of migration and pattern of distribution of neurons. *J. Comp. Neurol.* **176**, 23–52 (1977).
177. Hammarenger, B. et al. Magnocellular and parvocellular developmental course in infants during the first year of life. *Doc. Ophthalmol.* **107**, 225–233 (2003).
178. Atkinson, J. Early visual development: differential functioning of parvocellular and magnocellular pathways. *Eye* **6**, 129–135 (1992).
179. Rodman, H. R., Skelly, J. P. & Gross, C. G. Stimulus selectivity and state dependence of activity in inferior temporal cortex of infant monkeys. *Proc. Natl Acad. Sci. USA* **88**, 7572–7575 (1991).
180. Rodman, H. R., Scalaidhe, S. P. & Gross, C. G. Response properties of neurons in temporal cortical visual areas of infant monkeys. *J. Neurophysiol.* **70**, 1115–1136 (1993).
181. Distler, C., Bachevalier, J., Kennedy, C., Mishkin, M. & Ungerleider, L. G. Functional development of the corticocortical pathway for motion analysis in the macaque monkey: a <sup>14</sup>C-2-deoxyglucose study. *Cereb. Cortex* **6**, 184–195 (1996).
182. Pitti, A., Kuniyoshi, Y., Quoy, M. & Gaussier, P. Modeling the minimal newborn's intersubjective mind: the visuotopic-somatotopic alignment hypothesis in the superior colliculus. *PLoS ONE* **8**, e69474 (2013).
183. Robinson, D. L. & Petersen, S. E. The pulvinar and visual salience. *Trends Neurosci.* **15**, 127–132 (1992).
184. Stepniewska, I., Qi, H.-X. & Kaas, J. H. Projections of the superior colliculus to subdivisions of the inferior pulvinar in New World and Old World monkeys. *Vis. Neurosci.* **17**, 529–549 (2000).
185. Homman-Ludie, J., Kwan, W. C., de Souza, M. J. & Bourne, J. A. Full: Ontogenesis and development of the nonhuman primate pulvinar. *J. Comp. Neurol.* **526**, 2870–2883 (2018).
186. Nguyen, M. N. et al. Population coding of facial information in the monkey superior colliculus and pulvinar. *Front. Neurosci.* **10**, 583 (2016).
187. Arcaro, M. J. & Livingstone, M. S. On the relationship between maps and domains in inferotemporal cortex. *Nat. Rev. Neurosci.* **22**, 573–583 (2021).
188. Kwon, M.-K., Setoodehnia, M., Baek, J., Luck, S. J. & Oakes, L. M. The development of visual search in infancy: attention to faces versus salience. *Dev. Psychol.* **52**, 537–555 (2016).
189. Hasson, U., Levy, I., Behrmann, M., Hendler, T. & Malach, R. Eccentricity bias as an organizing principle for human high-order object areas. *Neuron* **34**, 479–490 (2002).
190. Lafer-Sousa, R. & Conway, B. R. Parallel, multi-stage processing of colors, faces and shapes in macaque inferior temporal cortex. *Nat. Neurosci.* **16**, 1870–1878 (2013).
191. Kamps, F. S., Hendrix, C. L., Brennan, P. A. & Dilks, D. D. Connectivity at the origins of domain specificity in the cortical face and place networks. *Proc. Natl Acad. Sci. USA* **117**, 6163–6169 (2020).
192. Xu, R., Bichot, N. P., Takahashi, A. & Desimone, R. The cortical connectome of primate lateral prefrontal cortex. *Neuron* **110**, 312–327.e7 (2022).
193. Yeo, B. T. et al. The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *J. Neurophysiol.* **106**, 1125–1165 (2011).
194. Groen, I. I. A., Dekker, T. M., Knapen, T. & Silson, E. H. Visuospatial coding as ubiquitous scaffolding for human cognition. *Trends Cogn. Sci.* **26**, 81–96 (2022).
195. Triplett, J. W., Phan, A., Yamada, J. & Feldheim, D. A. Alignment of multimodal sensory input in the superior colliculus through a gradient-matching mechanism. *J. Neurosci.* **32**, 5264–5271 (2012).
196. Tomasello, R., Wennekers, T., Garagnani, M. & Pulvermüller, F. Visual cortex recruitment during language processing in blind individuals is explained by Hebbian learning. *Sci. Rep.* **9**, 3579 (2019).
197. Murty, R. N. A. et al. Visual experience is not necessary for the development of face-selectivity in the lateral fusiform gyrus. *Proc. Natl Acad. Sci. USA* **117**, 23011–23020 (2020).
198. van den Hurk, J., Van Baelen, M. & Op de Beeck, H. P. Development of visual category selectivity in ventral visual cortex does not require visual experience. *Proc. Natl Acad. Sci. USA* **114**, E4501–E4510 (2017).
199. Tzourio-Mazoyer, N. et al. Neural correlates of woman face processing by 2-month-old infants. *Neuroimage* **15**, 454–461 (2002).
200. Srihasam, K., Vincent, J. L. & Livingstone, M. S. Novel domain formation reveals proto-architecture in inferotemporal cortex. *Nat. Neurosci.* **17**, 1776–1783 (2014).
201. Yue, X., Robert, S. & Ungerleider, L. G. Curvature processing in human visual cortical areas. *Neuroimage* **222**, 117295 (2020).
202. Long, B., Yu, C.-P. & Konkle, T. Mid-level visual features underlie the high-level categorical organization of the ventral stream. *Proc. Natl Acad. Sci. USA* **115**, E9015–E9024 (2018).
203. Bentin, S., Allison, T., Puce, A., Perez, E. & McCarthy, G. Electrophysiological studies of face perception in humans. *J. Cogn. Neurosci.* **8**, 551–565 (1996).
204. Caldara, R. et al. Face versus non-face object perception and the 'other-race' effect: a spatio-temporal event-related potential study. *Clin. Neurophysiol.* **114**, 515–528 (2003).
205. Itier, R. J., Latinus, M. & Taylor, M. J. Face, eye and object early processing: what is the face specificity? *Neuroimage* **29**, 667–676 (2006).
206. Conte, S., Richards, J. E., Guy, M. W., Xie, W. & Roberts, J. E. Face-sensitive brain responses in the first year of life. *Neuroimage* **211**, 116602 (2020).
207. Guy, M. W., Zieber, N. & Richards, J. E. The cortical development of specialized face processing in infancy. *Child Dev.* **87**, 1581–1600 (2016).
208. de Haan, M., Pascalis, O. & Johnson, M. H. Specialization of neural mechanisms underlying face recognition in human infants. *J. Cogn. Neurosci.* **14**, 199–209 (2002).
209. Halit, H., de Haan, M. & Johnson, M. H. Cortical specialisation for face processing: face-sensitive event-related potential components in 3- and 12-month-old infants. *Neuroimage* **19**, 1180–1193 (2003).
210. Balas, B., Westerlund, A., Hung, K. & Nelson Iii, C. A. Shape, color and the other-race effect in the infant brain. *Dev. Sci.* **14**, 892–900 (2011).
211. Scott, L. S. & Nelson, C. A. Featural and configural face processing in adults and infants: a behavioral and electrophysiological investigation. *Perception* **35**, 1107–1128 (2006).
212. Righi, G., Westerlund, A., Congdon, E. L., Troller-Renfree, S. & Nelson, C. A. Infants' experience-dependent processing of male and female faces: insights from eye tracking and event-related potentials. *Dev. Cogn. Neurosci.* **8**, 144–152 (2014).
213. Aylward, E. H. et al. Brain activation during face perception: evidence of a developmental change. *J. Cogn. Neurosci.* **17**, 308–319 (2005).
214. Passarotti, A. M. et al. The development of face and location processing: an fMRI study. *Dev. Sci.* **6**, 100–117 (2003).
215. Cantlon, J. F., Pined, P., Dehaene, S. & Pelphrey, K. A. Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cereb. Cortex* **21**, 191–199 (2011).
216. Leibo, J. Z., Liao, Q., Anselmi, F. & Poggio, T. The invariance hypothesis implies domain-specific regions in visual cortex. *PLoS Comput. Biol.* **11**, e1004390 (2015).
217. Golarai, G. et al. Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nat. Neurosci.* **10**, 512–522 (2007).
218. Bukach, C. M., Gauthier, I. & Tarr, M. J. Beyond faces and modularity: the power of an expertise framework. *Trends Cogn. Sci.* **10**, 159–166 (2006).
219. Carey, S. & Diamond, R. Are faces perceived as configurations more by adults than by children? *Vis. Cogn.* **1**, 253–274 (1994).
220. Bate, S. & Bennetts, R. J. The rehabilitation of face recognition impairments: a critical review and future directions. *Front. Hum. Neurosci.* **8**, 491 (2014).
221. Scott, L. S. & Brito, N. H. Supporting healthy brain and behavioral development during infancy. *Policy Insights Behav. Brain Sci.* **9**, 129–136 (2022).
222. Grill-Spector, K., Weiner, K. S., Kay, K. & Gomez, J. The functional neuroanatomy of human face perception. *Annu. Rev. Vis. Sci.* **3**, 167–196 (2017).
223. Gruart, A., Leal-Campanario, R., López-Ramos, J. C. & Delgado-García, J. M. Functional basis of associative learning and its relationships with long-term potentiation evoked in the involved neural circuits: lessons from studies in behaving mammals. *Neurobiol. Learn. Mem.* **124**, 3–18 (2015).
224. Zeithamova, D. et al. Brain mechanisms of concept learning. *J. Neurosci.* **39**, 8259–8266 (2019).
225. Turk-Browne, N. B., Scholl, B. J. & Chun, M. M. Babies and brains: habituation in infant cognition and functional neuroimaging. *Front. Hum. Neurosci.* **2**, 16 (2008).
226. Grill-Spector, K., Henson, R. & Martin, A. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* **10**, 14–23 (2006).
227. Krekelberg, B., Boynton, G. M. & van Wezel, R. J. A. Adaptation: from single cells to BOLD signals. *Trends Neurosci.* **29**, 250–256 (2006).
228. Wheatley, T., Weisberg, J., Beauchamp, M. S. & Martin, A. Automatic priming of semantically related words reduces activity in the fusiform gyrus. *J. Cogn. Neurosci.* **17**, 1871–1885 (2005).
229. Webster, M. A. & MacLeod, D. I. A. Visual adaptation and face perception. *Phil. Trans. R. Soc. B* **366**, 1702–1725 (2011).
230. Jiang, F., Blanz, V. & O'Toole, A. J. Three-dimensional information in face representations revealed by identity aftereffects. *Psychol. Sci.* **20**, 318–325 (2009).
231. Leopold, D. A., O'Toole, A. J., Vetter, T. & Blanz, V. Prototype-referenced shape encoding revealed by high-level aftereffects. *Nat. Neurosci.* **4**, 89–94 (2001).
232. Barry-Anwar, R., Riggins, T. & Scott, L. S. In *The Oxford Handbook of Developmental Cognitive Neuroscience* (ed. Cohen Kadosh, K.) (Oxford Univ. Press, 2020).
233. Klimesch, W. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* **16**, 606–617 (2012).



234. Hoehl, S., Michel, C., Reid, V. M., Parise, E. & Striano, T. Eye contact during live social interaction modulates infants' oscillatory brain activity. *Soc. Neurosci.* **9**, 300–308 (2014).
235. Michel, C. et al. Theta- and alpha-band EEG activity in response to eye gaze cues in early infancy. *Neuroimage* **118**, 576–583 (2015).
236. Snyder, K. A. & Keil, A. Repetition suppression of induced gamma activity predicts enhanced orienting toward a novel stimulus in 6-month-old infants. *J. Cogn. Neurosci.* **20**, 2137–2152 (2008).
237. McCarthy, G., Puce, A., Gore, J. C. & Allison, T. Face-specific processing in the human fusiform gyrus. *J. Cogn. Neurosci.* **9**, 605–610 (1997).
238. Allison, T. Electrophysiological studies of human face perception. I: Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cereb. Cortex* **9**, 415–430 (1999).
239. Rossion, B. et al. A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain* **126**, 2381–2395 (2003).
240. Behrmann, M. & Plaut, D. C. A vision of graded hemispheric specialization. *Ann. NY Acad. Sci.* **1359**, 30–46 (2015).
241. Dehaene, S. & Cohen, L. The unique role of the visual word form area in reading. *Trends Cogn. Sci.* **15**, 254–262 (2011).
242. Dundas, E. M., Plaut, D. C. & Behrmann, M. The joint development of hemispheric lateralization for words and faces. *J. Exp. Psychol. Gen.* **142**, 348–358 (2013).
243. Hildesheim, F. E. et al. The trajectory of hemispheric lateralization in the core system of face processing: a cross-sectional functional magnetic resonance imaging pilot study. *Front. Psychol.* **11**, 507199 (2020).
244. Scott, L. S., Shannon, R. W. & Nelson, C. A. Neural correlates of human and monkey face processing in 9-month-old infants. *Infancy* **10**, 171–186 (2006).
245. de Haan, M. & Nelson, C. A. Brain activity differentiates face and object processing in 6-month-old infants. *Dev. Psychol.* **35**, 1113–1121 (1999).
246. Gliga, T. & Dehaene-Lambertz, G. Development of a view-invariant representation of the human head. *Cognition* **102**, 261–288 (2007).
247. Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottareau, B. R. & Rossion, B. The steady-state visual evoked potential in vision research: a review. *J. Vis.* **15**, 4 (2015).
248. Barry-Anwar, R., Hadley, H., Conte, S., Keil, A. & Scott, L. S. The developmental time course and topographic distribution of individual-level monkey face discrimination in the infant brain. *Neuropsychologia* **108**, 25–31 (2018).
249. de Heering, A. & Rossion, B. Rapid categorization of natural face images in the infant right hemisphere. *eLife* **4**, e06564 (2015).
250. Farzin, F., Hou, C. & Norcia, A. M. Piecing it together: infants' neural responses to face and object structure. *J. Vis.* **12**, 6–6 (2012).
251. Peykarjou, S., Hoehl, S., Pauen, S. & Rossion, B. Rapid categorization of human and ape faces in 9-month-old infants revealed by fast periodic visual stimulation. *Sci. Rep.* **7**, 12526 (2017).

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## Author contributions

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## Competing interests

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