

Opinion

Social Origins of Cortical Face Areas

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Recently acquired fMRI data from human and macaque infants provide novel insights into the origins of cortical networks specialized for perceiving faces. Data from both species converge: cortical regions responding preferentially to faces are present and spatially organized early in infancy, although fully selective face areas emerge much later. What explains the earliest cortical responses to faces? We review two proposed mechanisms: proto-organization for simple shapes in visual cortex, and an innate subcortical schematic face template. In addition, we propose a third mechanism: infants choose to look at faces to engage in positively valenced, contingent social interactions. Activity in medial prefrontal cortex during social interactions may, directly or indirectly, guide the organization of cortical face areas.

Functional Neuroimaging of Infants

Humans spend a lot of time looking at other human faces. Seeing faces helps the perceiver engage appropriately in social interactions, because faces contain information about others' identities, attention, and intentions. After decades of experience, human adults are thus expert perceivers of human faces. Correspondingly, there are multiple regions of the human brain that are **face selective** (see [Glossary](#)), highly active while viewing faces compared with viewing images of anything else [1–3]. Similar regions exist in macaques [4–6] and chimpanzees (e.g., [7]). How do adult brains come to have this functional organization? How do innate architectural biases interact with experience of the visual world to create an adult face-expert brain?

An obvious way to address this question would be to directly study the brain in infancy, to see when and how functionally selective regions emerge. However, studying infant brains is challenging because infants are less compliant and attentive than adults. In 2017, the first studies were published that used **fMRI** to measure cortical responses to faces in infants: one study of human infants [8] and two studies of rhesus macaque infants [9,10]. These new results provide exciting, converging descriptions of the earliest stages of the functional development of face regions in human and macaque cortex. Here, we describe neural mechanisms that contribute to the origins of cortical faces areas in these infants. In particular, we argue that faces are not just salient visual patterns during infancy, but are perceived in the context of infant-directed **social interaction**. Thus, preferences for social interactions, possibly represented in **medial prefrontal cortex (mPFC)**, likely guide the organization of cortical face areas.

Cortical Face Responses in Adulthood and Infancy

In humans (*Homo sapiens*), face selective regions are located in ventral occipital and temporal cortex [e.g., the occipital face area (OFA) and fusiform face area (FFA)] and the **superior temporal sulcus (STS)**. In rhesus macaques (*Macaca mulatta*), five face selective regions are found in the STS [4–6]. In both species, the locations of these regions are stable within individuals and stereotyped across individuals. Face selective regions are also reliably

Highlights

Adult primates have highly stereotyped cortical regions for perceiving faces.

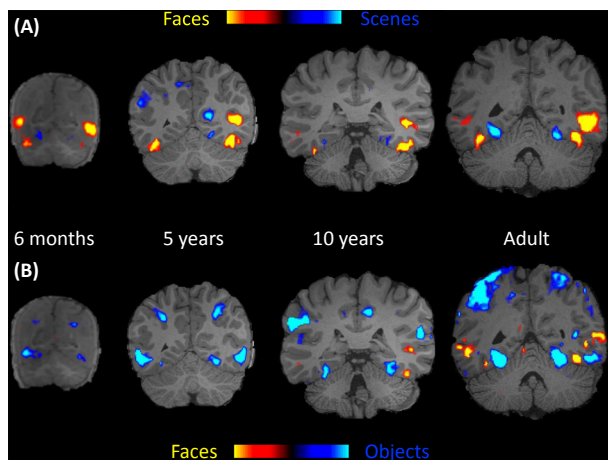
New fMRI data from infant primates show early preferential responses to faces with an organization similar to adult face areas, but do not answer the question of how this organization arises.

Recent neuroimaging data also indicate that medial prefrontal cortex (mPFC) responds to positive, contingent social interaction beginning in early infancy.

Given that faces have a key role in early social interaction, biased connectivity with mPFC may have a role in scaffolding the development of face selective regions.

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Figure 1. Face Preferring Regions across Human Development. fMRI reveals a similar location for regions that preferentially respond to faces (hot colors) when contrasted with scenes (cool colors), across development (A). Selective responses to faces (hot colors) when contrasted with objects (cool colors) emerge later during development, with the size and selectivity of these regions increasing through adolescence (B). Peak clusters are displayed on exemplar subjects for illustrative purposes. Data from 5- and 10-year-old children were provided by Michael Cohen and Nancy Kanwisher; infant and adult data were reported in [8].

positioned within a broader functional organization, spatially interleaved with scene selective and color selective regions in ventral temporal cortex [11,12]. Disrupting function in face selective regions produces specific face recognition deficits in both species [13,14]. In humans, stimulating FFA can even produce an illusory perception of a face [15]. Thus, activity in face selective regions appears to play a causal and necessary role in adult face perception.

Are these regions present in infancy? Direct fMRI experiments in infants revealed that cortical regions that would be face selective in adulthood show a **face preference** in the earliest scans acquired. Dynamic movies of faces elicited greater activity in both ventral temporal and STS regions of 4- to 6-month-old human infants, compared with dynamic movies of natural environments [8] (Figure 1). Similarly, at 30 days of age, macaque infants, which mature more quickly than human infants [16], displayed greater activation to dynamic movies of monkeys than to movies of environmental scenes in precisely the cortical regions that went on to develop face selectivity in the ensuing months [9]. Thus, the spatial organization of later face selective responses is already present in very young macaque and human infants.

These fMRI findings of early preferential responses to faces converge with extensive evidence from other neuroimaging methods, such as **functional near infrared spectroscopy (fNIRS)** and **electroencephalography (EEG)**. In human infants 3–9 months of age, these studies have observed preferential responses [i.e., increased oxygenated blood flow or differential event-related potential (ERP) components] to faces relative to other categories over temporo-occipital regions and STS [17–22]. These methods have also provided evidence of other signatures of face processing in infant cortex, including individuation and differential responses to upright versus inverted faces [20–22], although the specific ERP components indicating face sensitivity and the age at which they are observed vary across experiments (Box 1).

At the same time, the fMRI data suggest that both fusiform and STS regions are less selective for faces in infancy than in adulthood. In both human infants [8] and rhesus macaque infants [9], responses to objects (e.g., chairs or toys) were just as high as responses to faces throughout the relevant regions of cortex. Longitudinal data from rhesus macaque infants indicate that face selectivity (i.e., low responses to all other objects in face preferring regions) emerges only after extensive visual experience with faces. In three macaques scanned multiple times during their first year, cortical regions first responded more to monkey faces than to object control photos

Glossary

Electroencephalography (EEG): a method to record electrical activity from the scalp as a measure of neural activity. This method has high temporal and low spatial resolution.

Face preference: a neuron, or neural population, responding more to faces than some (but not all) other categories of visual images (e.g., environmental scenes).

Face selective: a neuron, or neural population, responding more to faces than any other visual category. Face selective cortical regions are often identified by contrasting responses to faces and objects.

fMRI: measures blood oxygenated level-dependent (BOLD) signals to track blood flow in the brain in response to neural activity.

Functional near-infrared spectroscopy (fNIRS): similar to fMRI, fNIRS measures hemodynamic responses to neural activity, but it does so by tracking changes in the absorption of near-infrared light as the light travels through the brain from an emitter placed on the participant's scalp to a nearby detector.

Medial prefrontal cortex (mPFC): the medial surface of the prefrontal cortex anterior to the cingulate sulcus (the medial parts of Brodmann's areas 9, 10, and 11). Functions associated with regions in mPFC include social attention, self-referential processing, reward evaluation, and affective theory of mind.

Retinotopy: the mapping of visual responses across the cortical surface, preserving the spatial relations of the sensory receptors of the retina.

Social interaction: infants are sensitive to many different cues of an attentive caregiver, including high-pitched prosody, stroking or rocking, and direct gaze. One critical cue is likely contingency (e.g., alternation or imitation) between the infant and the partner in vocalizations, gestures, or expressions.

Subcortical template: a rough visual feature map that resides in a subcortical structure and allows rapid recognition of an important stimulus class.

Superior temporal sulcus (STS): the sulcus between the middle and

Box 1. Conflicting Evidence of Face Selectivity in Human Infants

fMRI studies of macaque and human infants find early preferential responses to faces relative to environmental scenes in future face selective cortical areas, but slow development of face selectivity [8,9]. In particular, responses to objects were as high as responses to faces in both ventral temporal and STS regions. Selective responses to faces in typical face areas appeared later, after months (in macaques) or years (in humans) of experience [10,23,24]. While these fMRI findings are consistent with one another, they are not consistent with evidence for face versus object responses in young human infants from studies using EEG and fNIRS [17–22]. What might explain the conflicting evidence from different neuroimaging modalities?

One possibility is that hemodynamic (i.e., fMRI) measures are insufficiently sensitive to early cortical response properties. In neonatal macaques, electrophysiological measures detect stimulus-evoked activity in visual cortex that is not apparent in hemodynamic or deoxyglucose measurements [90–92]. Thus, electrophysiological (i.e., EEG) measurements may be more sensitive than hemodynamic measurements to true early face selective responses in infant cortex.

Alternatively, responses to faces in infant EEG may not in fact be face selective. Many EEG studies investigate the face-inversion effect (e.g., [93–95]), but differential responses to upright and inverted faces might reflect general perceptual learning rather than face selective processing [96]. Differences in evoked responses to faces versus objects in young infants are inconsistent across studies (e.g., [17,95,96]). The distinct processing of faces versus objects detected by the steady-state visually evoked potential (SSVEP) method [19] may reflect online categorization of face images rather than persistent selectivity [97]. Thus, it remains possible that neither fMRI nor EEG find evidence for face selective responses in human infants.

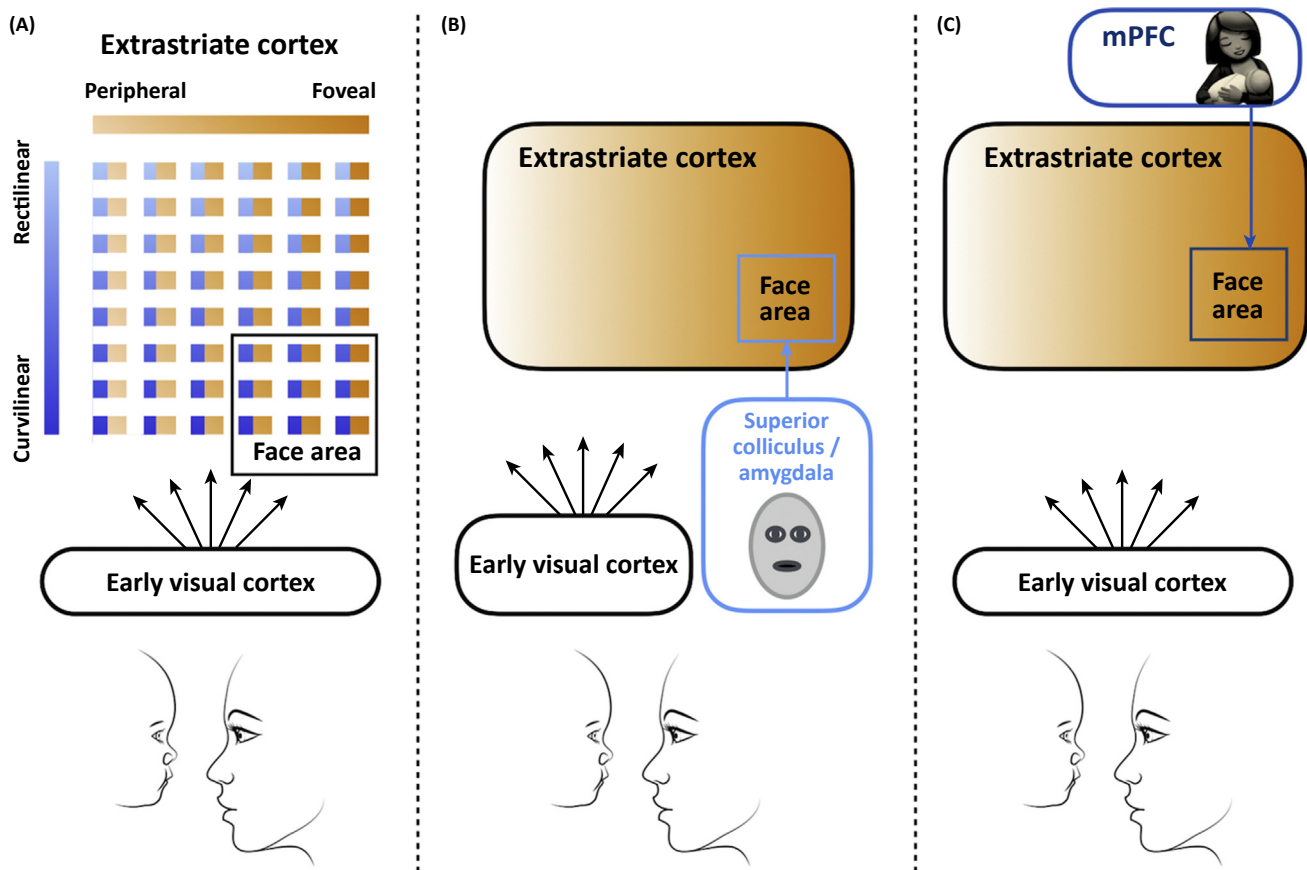
Reconciling contradictory findings from fMRI and fNIRS is more difficult. Both methods measure the same hemodynamic signals and have employed similar dynamic videos of faces and objects. Yet, multiple fNIRS studies found face selective responses in temporal cortex of human infants between 0 and 6 months of age [20,22,47,98]. One possible explanation for the discrepancy is that standard fMRI viewing conditions (i.e., a small mirror-mediated view of a projection screen) dampen face responses compared with more natural fNIRS viewing conditions. Another possibility is that fNIRS experiments have not adequately ruled out potential confounding differences in vascular blood flow when viewing socially engaging faces [99]. Recent advances for both methods should allow researchers to tease apart these factors [100,101] and hopefully arrive at converging conclusions about when face selectivity emerges in cortical face areas.

superior temporal gyri. In humans, regions of STS show preferential responses to faces, voices, biological motion, and other social stimuli. In macaques, multiple regions of the STS respond to faces. In the current context, we mostly refer to the region of STS responding preferentially to faces in both species.

when the monkeys were 200 days old [9]. The emergence of selectivity may be even later in humans: face selective responses in the fusiform gyrus are measured around age 5 years (comparable to ~450 days for macaques) and continue to increase in size throughout adolescence [23,24] (Figure 1; but see Box 1 for conflicting evidence from other neuroimaging methods). This late development of face selective regions requires visual experience with faces, at least in macaques. Unlike human infants, it was possible to raise infant macaques without any visual experience of faces; human researchers fed and played with the infants while wearing welder's masks. In three infant macaques raised without visual experience of faces, face selective cortical regions were not observed at the typical age of 200 days, or even at 400 days old, the oldest age tested [10].

One question that remains is how either the early preferential or later selective cortical responses to faces are related to infants' behavioral face-processing abilities. Since human and macaque infants show many behavioral signatures of face perception, including average face preferences [25,26], recognition of specific individuals [27–30] and better recognition of upright than inverted faces [31,32], a face selective cortical area may not be required for many aspects of face perception (see Outstanding Questions).

In sum, direct neuroimaging of infants suggests that face selective areas in cortex emerge from two sources. Early in infancy, systematic regions of cortex are already biased to respond preferentially to images of faces. Learning from visual experience builds on this pre-existing scaffold by increasing selectivity and reducing responses to other visual categories, thus canalizing a species-typical profile of face selective cortical regions. Here, we ask: what is



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Figure 2. Three Mechanisms Guiding the Development of Cortical Face Areas. (A) Extrastriate cortex is organized according to overlapping low-level feature dimensions (e.g., the eccentricity and shape dimensions represented orthogonally along the x and y axes [33]. Preferential responses to faces may arise in the part of extrastriate cortex ('Face Area', outlined) that combines their particular low-level properties (e.g., frequent foveation and curvilinearity). (B) An innate subcortical template may facilitate the detection of face-like images. The template could influence face areas either by directing infants' visual attention or through direct connectivity (shown here). Biased connectivity from this template could potentiate responses to faces in specific regions of extrastriate cortex (i.e., the 'Face Area' box in this panel). (C) Infants' preferential interest in social interaction, and the brain systems that support such interactions, may also influence face area development either by directing infants' visual attention or through direct connectivity (shown here). In particular, biased connectivity from medial prefrontal cortex (mPFC) regions that respond to prosocial interaction could potentiate responses to faces in specific regions of extrastriate cortex (i.e., the 'Face Area' box in this panel).

the nature and mechanism of the early bias? What prepares certain patches of cortex to develop into 'face areas'? At least three distinct mechanisms may contribute (Figure 2).

'Proto-organization' of Simple Visual Features

First, the organization of face areas may arise from the fact that extrastriate visual cortex is 'proto-organized': neurons respond to simple visual statistics, and are spatially grouped by preferences for these features [33,34]. At birth, no patch of high-level cortex need be specifically pre-disposed to respond to faces, or any other behaviorally meaningful category. Instead, higher order visual regions initially inherit the visual features that drive early visual regions. These include preferential responses to parts of the visual field (i.e., **retinotopic** organization of responses to stimulation in the fovea or periphery) as well as responses to visual features, such as high- versus low-spatial frequencies, and square versus curved edges (i.e., rectilinearity versus curvilinearity). In extrastriate cortex, responses to these different visual

features may self-organize into a map, such that a preference for each combination of features occurs independently [35]. Thus, innately, neural responses are spatially organized along low-level dimensions of visual image statistics.

Critically, the statistics of infants' actual visual experiences are highly nonrandom. For example, human and macaque mothers frequently position their infants face-to-face [36–39]. Thus, human and macaque infants have extensive experience with face images on their fovea at a typical distance. Such images co-activate neurons with preferences for foveal input, curvilinearity, or low spatial frequency. Thus, patches of cortex in which responses to all of these low-level features overlap will be frequently co-activated. Repeated co-activation, over months and years of experience, could then lead these neurons to learn selective responses to faces.

Strengths of this hypothesis include that it relies only on well-documented mechanisms of cortical organization, and established patterns of connectivity from early to higher order visual regions. We agree that patterning of low-level visual statistics is likely one part of the early scaffold of face areas in macaques and in humans. However, this mechanism is unlikely to be the whole story. For example, if infants' experience of low-level visual statistics fully explains their subsequent cortical organization, any class of stimuli could become preferred by 'face areas', if it was curvilinear and frequently foveated. This hypothesis can be tested. The three infant macaques with no visual experience of faces fixated hands as much as typical macaque infants fixate faces [10]. Responses to hands, in extrastriate cortex, were bigger and more robust in these macaque infants, but the hand responses were not in foveal-biased regions (unlike typical face areas) and did not simply take over typical face patches [10]. Thus, frequent fixation of hands (and no experience of faces) alone is insufficient to convert face areas into hand areas. (However, other differences in the shape of faces and hands, such as spatial frequency, could explain the failure of face areas to become hand areas.) Another weakness of this hypothesis is that human infants' early cortical responses to faces are stronger in the right hemisphere [19,22,40], although the 'proto-organization' of visual cortex by simple features is bilaterally symmetric [33].

More critically missing is an explanation of infants' intrinsic motivation to look at faces. Infants do not only receive passive visual experiences; rather, they actively prefer to look at face-like images within hours of birth, and possibly before [41–43]. One-day-old human infants prefer to look at schematic faces with black dots placed on white ovals, rather than white dots placed on black ovals, in the eye region [42]. What drives these early preferences, and what role do they have in cortical specialization?

Innate Subcortical Face Template

In addition to proto-organization in cortex, there may be a second neural system underlying macaque and human infants' early detection of, and preference for, faces [42,44–48]. Infants' sensitivity to a specific set of visual features (curvilinear, symmetric, enclosed, lower frequency in the bottom half, etc.) could reflect an innate, subcortical 'face template' that directs an infant's attention to face-like shapes [45,46]. This proposal is modeled on the detailed example of imprinting in domestic chickens. Chicks are born with two innate mechanisms that jointly operate to ensure imprinting on the mother hen, in typical environments. First, the optic tectum contains a rough visual template of a hen (a bird head on a body) that directs the chicks' attention to objects that match the template. Second, a mechanism in the mesopallium forms a strong and irreversible memory of, and attachment to, any object to which the chick attends, regardless of its match to the template [46,49].

The primate visual system may have an analogous mechanism for guiding early social attention. Primates may have a subcortical region in the superior colliculum, pallidum, and/or amygdala that contains an innate template of a face, and that directs neonates' attention to matching stimuli. A **subcortical template** could guide the early and stereotypical spatial organization of face preferring responses in cortex either directly or indirectly [45,50]. If the influence is indirect (as it is in the chick model), the innate subcortical template would explain infants' looking to faces, and then cortical regions could learn face preferences based only on the visual statistics of experience. Alternatively, if the influence is direct, the subcortical template may have biased direct connectivity to parts of extrastriate cortex, potentiating responses to images that match the innate template. This direct input could facilitate and accelerate acquisition of cortical face selectivity (Figure 2B).

These alternatives could be tested by using fMRI in human or macaque infants. For example, do subcortical responses to faces predict neonatal orienting to faces? Is there biased connectivity between face preferring subcortical regions and parts of extrastriate cortex early in infancy? To date, however, direct neural evidence for a subcortical face template is lacking in primates. For example, in infant macaques, no preferential responses to faces were observed in the pallidum or amygdala [9], although negative results in fMRI of infants must be interpreted with caution [33].

So far, we have described two visual mechanisms that could support human and macaque infants' earliest neural responses to faces. First, the earliest cortical face preferences may reflect low-level visual statistics; infants' frequent experience foveating the curvilinear features of faces then causes the category-specific cortical specialization for faces per se [9,10]. Second, face images may match an innate, subcortical visual template that attracts and guides infants' attention, and shapes (directly or indirectly) the response of cortical face areas [51]. These mechanisms are not incompatible and may operate in concert. Still, both mechanisms operate over faces as a pattern of bottom-up visual input.

Strikingly, however, bottom-up visual input does not appear to be necessary to establish the typical spatial layout of preferential face responses in the human visual system. In humans who are born blind, 'face areas' show preferential responses to facial sounds, including laughing, chewing, blowing a kiss, and whistling [52,53]. The spatial pattern of responses to facial versus environmental sounds in blind humans can be used to identify responses to movies of faces versus scenes in sighted humans. These patterns were present in humans born without eyes, whose fusiform and STS regions were deprived of visual input from conception. Thus, the pattern of bottom-up visual input cannot be the only source of face-preferential organization in human cortex.

Instead, a key factor driving infants' early behavioral and cortical responses to faces is the functional role of faces in meaningful social interactions.

Social Factors Drive Early Looking Towards Faces

Neonatal looking to faces is likely driven by a perceptual template, but quickly after birth both macaque and human infants' attention to faces is not explained solely by the presence or absence of a schematic face. Within weeks, infants choose to look at faces in order to engage in positively valenced, contingent social interactions.

Within the first few weeks of life, both macaque and human infants' attention to schematic faces declines [48,54] as they develop a preference for dynamic rather than static faces. If a

responsive social partner suddenly adopts a static and unresponsive expression (an experimental paradigm referred to as the 'still face'), human infants look away from the partner's face and express less positive affect [55–57]. Young human infants even disengage from dynamic, speaking faces when contingency between the partner's face and their own behavior is disrupted (i.e., by switching from a live face-to-face interaction to a prerecorded video of the same person [58]). Macaque and human infants who consistently experience less responsive face-to-face interactions are subsequently less likely to spontaneously look at new faces [59,60]. Thus, within the first few months of life, macaque and human infants' attention to faces is dependent upon immediate and accumulated evidence that the face represents a responsive social partner.

Human infants' attention to faces is also driven by multimodal cues to social value. From the first weeks of life, infants prefer infant-directed speech to adult-directed speech [61,62]. By 5 months of age, human infants preferentially attend to faces previously associated with infant-directed speech [63] or other kinds of prosocial behavior, such as helping and comforting [64,65]. At the same age, human infants also orient preferentially to another cue of a social interaction: their own name [66]. Social touch can also enhance human infants' attention to faces [67].

Thus, infants recognize faces not only as specific patterns of low-level input, but also as social interaction partners. Infants' social experiences with faces affect later social behavior. When human researchers raised infant macaques with the same amount of physical handling but differential exposure to mutual gaze and lip-smacking (a macaque affiliation gesture), affiliative face-to-face interaction promoted the infants' later social interest and approach [59]. Similar differences in early human infants' exposure to contingent interaction with faces are related to later engagement in contingent social behavior, as well as infants' attachment [68,69].

Indirect Influence of Social Interaction on Face Area Development

The motivation to engage in contingent social interactions could influence the development of cortical face areas indirectly. As described above, neonatal orienting to face images may be driven by a subcortical face template, but infants soon shift attention particularly to the faces of social partners. Thus, both a subcortical template (in neonates) and social preferences (throughout infancy) could promote foveating faces, and maintain high levels of correlated responses in the proto-organized regions of extrastriate cortex.

What are the candidate neural regions or systems for representing social value that might direct infants' attention to the faces of social partners? One possibility is mPFC, particularly regions associated with recognition of social value and self-relevant social interactions in adults [70–75]. Previously, researchers thought that, in human infants, the prefrontal cortex lacked well-organized function, but more recent evidence suggests that mPFC is engaged by valued social interactions even in young human infants [76]. In the fMRI data, human infants showed clear mPFC activation at both the group and individual level while viewing dynamic faces [8] (see Box 2 for a comparison with infant macaques). fNIRS studies observed responses in infant mPFC to many cues of infant-directed social interactions, including faces, infant-directed speech, and infants' own names [77–79], even in neonatal infants [78]. mPFC responses to faces and voices are strongest when presented with cues of positive social attention toward the infant, including direct gaze and smiling [77,80,81]; when social partners respond contingently by following the infants' own gaze shifts [82]; and in response to a familiar and highly valued social partner (i.e., the infant's mother, [81,83,84]).

Box 2. mPFC Responses in Infants: Species Similarity or Difference?

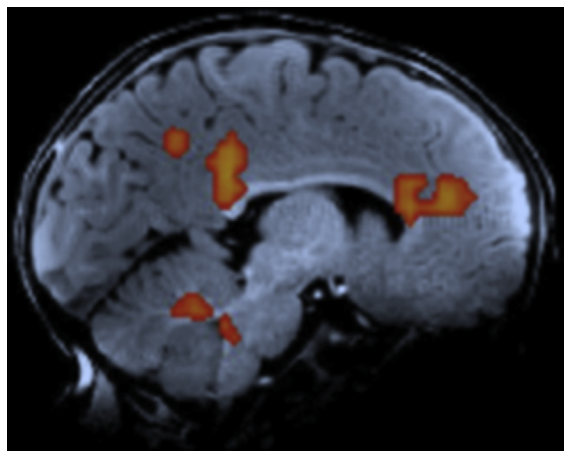
In human infants, viewing faces evoked activity in mPFC (Figure 1) [8]. However, an mPFC response to faces was not observed in the fMRI study of infant macaques [9]. What could account for this difference?

First, the results may reveal a true species difference: human infants could have a distinct area of the mPFC for recognizing and responding to social interactions that is not present in macaque infants. Human social cognition is more sophisticated than that of other primates [102,103]. Also, the connectivity fingerprint of mPFC is distinct in human and macaque brains, consistent with divergent functional roles [104]. On the other hand, in adult macaques, face areas do show functional connectivity to medial prefrontal regions associated with social interaction [105,106], and macaque infants appear to value and depend on social interaction during development [28,36,59].

Second, the results might derive from the geometry of the custom-built MRI coils used for infant scanning. The human infant 32-channel array included four surface coils positioned over the forehead to directly measure mPFC [107], whereas the monkey infant four-channel array was positioned over the back of the head to prioritize visual cortex [9].

Third, mPFC activation may reflect the specific stimuli used in each study. In human infants (and adults), mPFC responses are observed for dynamic faces, including cues of attention (direct gaze, communicative mouth movements, and play gestures) and positive valence (smiling, children's faces, and infant-directed prosody [8,21,81,83]). By contrast, macaque infants were presented still photographs of unfamiliar adult monkey faces [9,10]. Only the youngest monkeys (30 days) saw movies; these movies showed unfamiliar adults interacting with each other and did not present cues of positive interaction towards the infant observer. Thus, it is possible that mPFC responses in macaque infants would be observed in experiments presenting more ecologically valid dynamic stimuli.

In sum, it remains unclear whether the social function of mPFC is similar, or dissimilar, in human and macaque infant development. Addressing this question will be important for understanding whether an mPFC-based mechanism for recognizing social value could have a similar role in the development of cortical face networks in both species.



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Figure 1. Medial Prefrontal Cortex (mPFC) Response to Dynamic Faces in Human Infants.

The functional role of mPFC in recognizing valued social interactions may promote the development of cortical face areas by sustaining attention on faces throughout infancy and early childhood. This mechanism could operate alongside both a subcortical face-template and proto-organized visual maps, yet makes specific, testable predictions. First, reliable mPFC responses to social interaction with conspecifics should begin very early in infancy, perhaps as early as the first cortical responses to faces (see Outstanding Questions). Second, it should be possible to measure infants' mPFC responses during social interactions and predict the infants' subsequent attention to the faces involved.

Direct Influence of mPFC on Face Area Development?

The functional role of faces in social interactions might even be reflected in the innate architecture of the infant brain. That is, the proto-organization of infant visual areas may reflect not only bottom-up connectivity (mapping visual features and simple shapes), but also top-down connectivity. For example, regions of fusiform gyrus and STS may have pre-existing connectivity with mPFC regions that respond to positively valenced, contingent social interactions. Face areas would develop at the confluence of both sources of input. Top-down signals of social value from nonvisual sources, such as contingency [58], affiliative touch [67], or infant-directed speech [61,62], would strengthen responses to faces when they co-occur, as when parents hold infants face-to-face while stroking or talking to them.

Connectivity between face areas and mPFC does exist in adults, measured functionally in humans [85] and macaques [86], and by direct anatomical tracing in macaques [87]. Within human adults, the location of the FFA can be predicted by connectivity to plausible 'higher order' social regions [88]. Top-down influences on responses to socially relevant stimuli could also explain some aspects of face area organization. First, laterally biased top-down connectivity could account for evidence of an early right lateralized bias for face processing [19,40], much as pre-existing connectivity to higher order language regions explains the left lateralized development of the visual word form area [89]. Second, top-down activation during social interaction could explain how facial sounds can evoke activity in 'face areas' even in congenitally blind adults [52,53].

Our hypothesis has implications for the spatially organized face preference observed in infant fMRI experiments described above. If innate extrastriate cortex is proto-organized only by simple visual features, then face preferences in infant cortex reflect only the combination of visual features in the stimulus. By contrast, if biased connectivity to mPFC also shapes the location of early face responses, then face-preference responses in infant cortex incorporate the social function of faces ontogenetically and even phylogenetically.

This direct version of mPFC influence on face area organization makes some additional predictions. First, effective connectivity from mPFC to developing face areas should be directly observable in infancy. Second, this account makes strong predictions about the kind of experience necessary for face area development. Infants that experience salient face images in the environment but separated from social interaction (e.g., still photographs associated with juice) should develop atypical face areas. Conversely, if social partners were associated with some other contingently responsive visual display, even one with different visual features, face areas could become specialized for processing this novel category instead.

Concluding Remarks

In sum, new fMRI evidence collected in human and macaque infants has raised a new puzzle: what accounts for the early spatial organization of species-typical face networks, reflected in preferential face responses during the first months of life, long before complete face selectivity? We propose that three mechanisms could work together during the development of cortical face areas: (i) bottom-up statistical learning of biased input; (ii) a subcortical template for detecting face shapes; and (iii) mPFC responses to the social value associated with contingent face-to-face interaction. Thus, the process of cortical face specialization interacts with early systems for recognizing and responding to signals of social value. Future research can test this hypothesis by investigating the structural and functional interactions between regions involved in perceiving faces and social interaction in human and macaque infants.

Outstanding Questions

How plastic is the function of cortical face areas when developing in different environments? On the one hand, face deprivation prevents cortical face specialization and fails to encourage face regions to adopt responses to other frequently foveated categories, including hands. On the other, there is some evidence that face areas respond to social and emotional sounds in blind individuals. In the absence of face exposure, could other visual stimuli colonize face areas if they had a similar role in contingent social interaction? Would typical face areas develop given visual but not social experience with faces?

Is mPFC responsible for human infants' earliest responses to social interaction? Tracts to mPFC myelinate slowly in humans, and are immature during early infancy. Also, most evidence for mPFC responses to social cues comes from infants 4 months of age or older, but infants' responses to social interaction and to specific social partners begin to emerge weeks or months earlier. If mPFC activity does not underlie social preferences in 2–3-month-olds, what other brain regions are involved?

How do preferential or selective cortical responses to faces relate to behavioral measures of face processing? Do early preferential responses play a role in learning to recognize specific individuals? Does subsequent specialization either support or result from distinctive signatures of face processing, such as inversion sensitivity and holistic recognition? How do preferential or selective responses relate to the ability to extract socially relevant cues, such as emotion or gaze direction, from faces?

What are the species-specific differences between humans and macaques that support the higher level social cognitive capacities of humans? The behavior and neural data reviewed here from human and macaque inferences contain mostly homologous patterns. Yet, human social cognitive capacities surpass those of macaques by the time humans are toddlers. What neural mechanisms support and drive these differences?

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