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Letter

# Cortex Is Cortex: Ubiquitous Principles Drive Face-Domain Development

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Powell, Kosakowski, and Saxe [1] argued in a recent review that two bottom-up models previously proposed to account for the development of face domains in inferotemporal cortex (IT) [2,3] are insufficient to explain the existing data. They proposed instead that face domains are predisposed to process faces via selective connectivity to social information in medial prefrontal cortex. Here we explain why activity-dependent mechanisms acting on a retinotopic proto-architecture provide a sufficient explanation for the development of face, and other category, domains.

In the review, the proto-architecture model is shown with curvature and eccentricity being independent. However, crucial to the protoarchitecture model is the extensive evidence [4] that these two features are correlated. Central visual field prefers high curvature and peripheral prefers straighter contours, and this likely reflects an intrinsic relationship between retinotopy, receptive field size, and curvature tuning throughout the visual system. This organization, which is present at birth [5], would therefore bias central representations to prefer faces over scenes without any innate bias specific to faces.

The review argues against the retinotopic protoarchitecture model on the grounds that both monkey [6] and human [7] infants show face-versus-scene selectivity. However, both studies failed to find selectivity for faces over objects. Deen *et al.* [7] interpreted the lack of face-versus-object selectivity as an indication of immaturity in face domains, but we think it represents selectivity for low-level features intrinsic to a retinotopic proto-architecture.

The second argument against the proto-architecture model is that hand patches in face-deprived monkeys did not 'convert face areas into hand areas'. This reflects a different interpretation of our wording than what we meant to convey. We found no faces > object selectivity in what should be face domains. We found hands > object selectivity in this region, but greater hand selectivity further in the fundus of the superior temporal sulcus (STS), as in controls. So, in one sense the face domains did convert to hand domains since hands were the preferred category in the usual face region of the STS of face-deprived monkeys, but we were emphasizing the similarity in hand selectivity between deprived and controls. A major shift in hand responsiveness would not be expected since hand experience was not manipulated between groups.

The third argument presented against the retinotopic proto-architecture model was that it cannot account for preferential face looking in neonatal humans and monkeys. That is correct: the model does not speak to what drives early preferential looking. We proposed that infants learn to look at faces because they discover that faces are important sources of information. Box 1 suggests a possible low-level explanation for very early face looking.

Lastly, the finding that adult congenitally blind humans show 'face' activations to whistling illustrates the massive potential of post-birth experience-driven plasticity but does not prove that face domains require top-down influences; instead it may reflect general map-based brain connectivity below semantic or social relevance [8].

In contrast to Powell *et al.*, we think IT domains could arise solely by the same kind of activity-dependent self-organizing mechanisms that are widely accepted as sufficient to account for the exquisite organization and complex receptive field properties of V1. Such a model is based on experimentally established mechanisms: visually driven activity-dependent plasticity (synaptic selection, refinement, and clustering) acting on a retinotopic proto-architecture (trophic molecules and sorting rules). The model does not require a heretofore undiscovered and mechanistically unclear face template and does not require selective connectivity between face patches and medial prefrontal cortex as proposed in the review (connectivity to medial prefrontal cortex is actually weaker from face patches than from the surrounding non-face IT [9]). The protoarchitecture model is based on principles ubiquitous to all primates, and indeed mammals, fish, and amphibians. While behavioral and neural differences in face processing between humans and monkeys undoubtedly exist and are important areas of research, we do not believe such factors play a major role in determining whether face domains develop. We agree that social interactions are undoubtedly a prominent aspect of typical primate experience and that experience plays an important role in development. However, we do not think that social brain areas themselves directly mold face domains, but instead that social experience has an indirect influence on face domain development by reinforcing behavior, which in turn affects activity-dependent self-organizing mechanisms. As such, social experience is one of many environmental factors that influence the fundamental, ubiquitous principles guiding cortical organization and experience-driven plasticity.

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## Box 1. Why Do Newborns Look at Faces?

A number of studies report that infant humans and infant monkeys look preferentially at faces within a few days or hours of birth. Infants tend to look more at schematic faces with two eye-like dark spots above a single dark curve or spot, compared with the inverted configuration or a scrambled configuration [3]. Infants will also look preferentially at two or four dots above a smaller number of dots compared with stimuli with the smaller number above [10], suggesting that at least one component of this early 'face' preference may reflect simply a 'top-heavy' bias for high-contrast things in the upper visual field. Infants also prefer dark eyes surrounded by light [11], suggesting a bias towards the unique form of a human face under natural lighting conditions. However, the conclusion that this reflects an eye-specific template versus low-level contrast saliency been challenged [12]. Also, the degree and sign of eye-to-face contrast vary across ethnicities and non-human primate species, further challenging any face-template evolutionary explanation. Early biases may have emerged from environmental pressures ubiquitous across species since, in many situations, what is going on above the horizon may be critical for survival. Further, many of the infant looking experiments were biased to elicit reflexive looking by using moving or flashed stimuli. Both reflexive looking and an upper-field bias could involve the evolutionarily old subcortical structure, the superior colliculus, which generates automatic saccades towards salient stimuli and has upper (vs lower) visual field biases in evoked activity and contrast sensitivity [13]. Johnson and colleagues [3] proposed that early face looking was driven by subcortical processes, which were then supplanted by cortical mechanisms. We are therefore supportive of Johnson and colleagues' model, although we reject the idea of an actual face template.

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