The evolution of face processing networks

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Recent studies in marmosets, macaques, and humans have begun to show commonalities and differences in the evolution of face processing networks. Despite differences in brain size and gyrification across species, myelination and motion may be key anatomical and functional features contributing to the surprising similarity of face networks across species.

Faces are crucial for social communication in primates. Examination into the evolution of cortical networks specialized for face processing has largely relied on comparisons between macaques and humans [1] (Figure 1). A recent paper [2] adds another species to the mix, the common marmoset, whose evolutionary origin is about 10 million years prior to macaques. In combination with recent studies in macaques examining the location of face patches relative to retinotopic areas [3] and natural face motion [4], we are beginning to understand the anatomical and functional features contributing to similarities and differences of the face network across species.

The brains of marmosets, macaques, and humans are vastly different in size and gyrification [5]. On average, the marmoset brain (7.5 g) is approximately 12 times smaller than the macaque brain (88 g) and approximately 180 times smaller than the human brain (about 1350 g). Likewise, the marmoset brain is extremely smooth and lacks the extensive cortical folding of the human brain. This difference has been quantified by calculating gyrification indices (GIs) across species: macaque brains are about 1.5 times as gyrified as marmoset brains, whereas human brains are about 2.2 times as gyrified as marmoset brains [5]. Greater GIs indicate the presence of gyri and sulci that are missing in species with lower GIs. Thus, marmosets lack gyri and sulci that are present in macaques and humans, and macaques lack gyri and sulci that are present in humans.

These differences in the outer appearance of the cerebrum across species make the consistency of the topology of face networks all the more impressive (Figure 1A). Specifically, using both electrocorticography (ECoG) and fMRI, Hung and colleagues [2] found that the face network in marmosets consists of six distributed face patches. The anatomical topology of these patches was consistent across methodologies and individual marmosets. Strikingly, the distribution of these patches resembles two parallel streams, which is consistent with the organization of the face network in macaques [1] and humans [6]. Although

the number of patches may differ across species, and face patches in humans are more ventral due to areal expansion and increased gyrification, the similarity in the gross topological structure into two parallel streams is astounding considering there are around 35 million years separating marmosets and humans.

Insights into the similarities and differences of face networks across species may be gleaned from their positioning relative to other cortical areas that are considered to be homologous across species [7]. One such area is MT/V5, which is heavily myelinated in primates. Interestingly, some face patches neighbor MT in marmosets [2], macaques [3], and humans [6]. This consistency across all three species may be partly constrained by myelination differences between MT and neighboring cortex. Using MT as an anchor also reveals key differences across species. For example, face patches on the superior temporal sulcus (STS) in marmosets and macaques are ventral to MT, whereas the STS face patches in humans are situated dorsally above MT. This difference in cortical location relative to MT may be a consequence of areal expansion of the temporal lobe [7] and increased gyrification in humans [5]. This increased cortical territory may also accommodate additional functions such as processing the complex mouth movement repertoire associated with language in humans as compared to macaques and marmosets.

Despite these differences in cortical location, recent evidence also shows that it is likely that face patches across species may share a common preference for particular aspects of motion processing. For example, in humans, STS regions are more easily localized using dynamic movies of facial motion as opposed to static images [8]. Similarly, in macaques, dorsal face patches have a preference for natural motion such as mouth movements (Figure 1B, [4]), whereas the ventral patches do not show this preference. Interestingly, stimuli depicting natural face motion also identify an additional face patch in macaques that is not localized with static images (MD in Figure 1B). These results make two predictions. First, natural face motion may contribute to the consistency of the dorsal face patches across species. Second, the segregation of processing of natural face motion versus computations associated with static form such as identity may contribute to the separation of face patches into parallel streams across species.

Additional functional factors also likely contribute to the similar topological layout of the face network across species. Shape [9] and position biases [10] likely play important roles. In further support of the latter, recent findings show that face patches across species (PL in macaques and IOG-faces/OFA in humans) overlap a
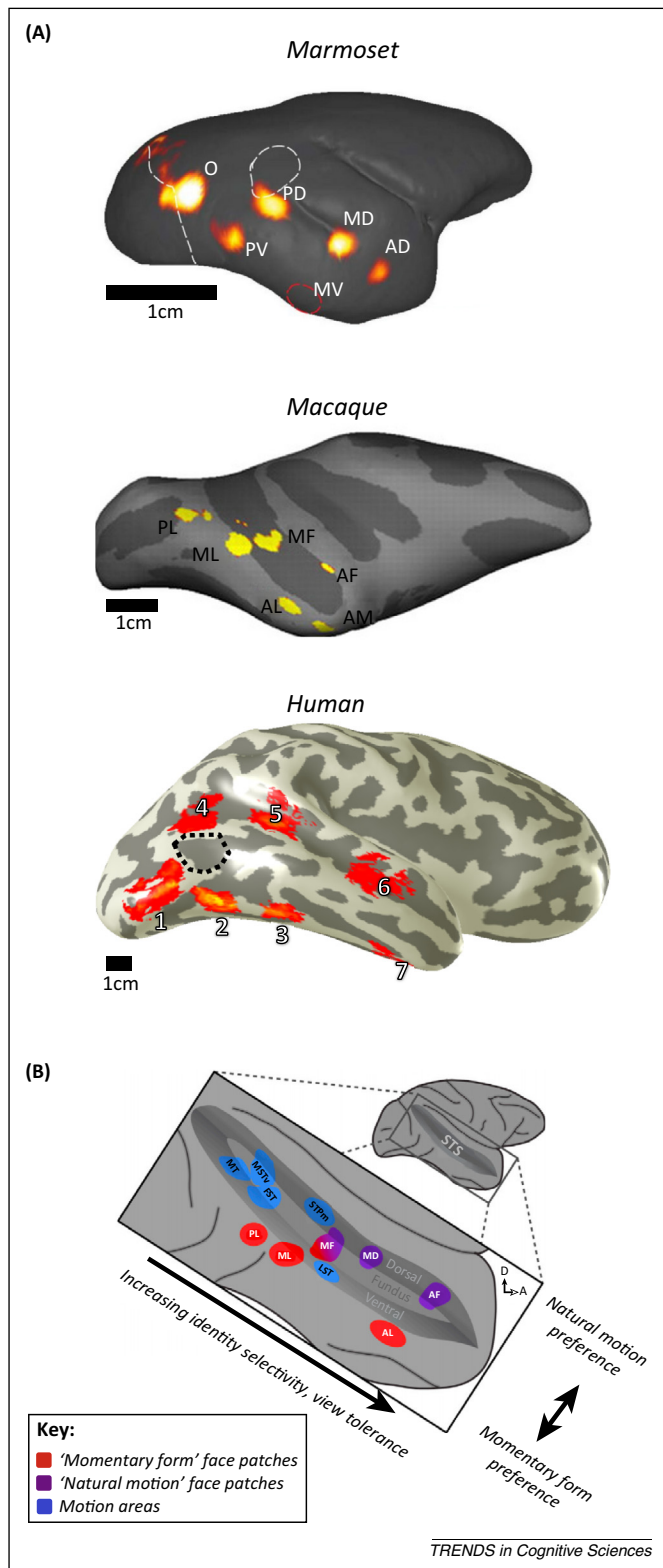
Figure 1. The evolution of face processing networks. **(A)** Cortical surface of a marmoset (from [2]), a macaque (from [1]), and a human. Warm colors indicate face-selective regions for each species. Dotted circular outline indicates the location of area MT in marmosets and the hMT+ complex in humans. Human data are from our laboratory and represent known face patches identified in our previous work [6], as well as others [1,8]. 1, IOG-faces/OFA; 2, pFus-faces/FFA-1; 3, mFus-faces/FFA-2; 4, pSTS-faces; 5, mSTS-faces; 6, aSTS-faces; 7, AT-faces. Marmoset brain image reproduced with permission from the Society for Neuroscience. Macaque brain image reproduced with permission, Copyright (2008) National Academy of Sciences, U.S.A. **(B)** A proposed model illustrating the relationship between face- and motion-selective areas relative to aspects of face and motion processing in the macaque. Processing axes occur in both dorsal–ventral, as well as anterior–posterior, axes. Dorsal face patches process aspects of natural face motion, whereas ventral face patches process momentary form preference likely encapsulated in static images (from [4]). Of note is the fact that an additional face patch (MD) is identifiable using natural face motion, but not static images used to typically localize the face network. All authors approved the use of their images for the present article.

retinotopic map considered to be homologous across species [3]. This suggests the possibility that retinotopy may further constrain the positioning of some of the patches of the face network.

In summary, recent advances in neuroimaging now incorporate marmosets into the discussion of face networks. Likewise, recent advances in our understanding of the location of face patches in macaques and humans relative to retinotopic areas and motion-selective regions shows a striking similarity in the cortical layout and topology of these networks. Due to the vast difference in brain size and gyrification across species, there are dissimilarities in the precise anatomical location of these regions. Nevertheless, anatomical factors such as myelination and perhaps white matter connectivity are likely common drivers for the organizational similarity across species. Additional functional features that are ecologically relevant such as natural motion of faces, position biases, and shape sensitivity, may also contribute. Altogether, the door is now open to examine the complexity of face processing in species that are phylogenetically farther away from humans, but phylogenetically closer to macaques. Both the similarities and differences across species offer an exciting opportunity to further understand the anatomical, functional, and evolutionary mechanisms underlying face perception, as well as aspects that are uniquely human.

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