

Face recognition systems in monkey and human: are they the same thing?

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Abstract

Primate societies are based on face recognition. Face recognition mechanisms have been studied most extensively in humans and macaque monkeys. In both species, multiple brain areas specialized for face processing have been found, and their functional properties are characterized with increasing detail, so we can now begin to address questions about similarities and differences of face-recognition systems across species with 25 million years of separate evolution. Both systems are organized into multiple face-selective cortical areas in spatial arrangements and with functional specializations, implying both hierarchical and parallel modes of information processing. Yet open questions about homologies remain. To address these, future studies employing similar techniques and experimental designs across multiple species are needed to identify a putative core primate face processing system and to understand its differentiations into the multiple branches of the primate order.

Introduction

Faces are special: we encounter them more frequently than almost any other type of object, and they provide a rich source of diverse social information [1]. This is the case for virtually all primate species. If this is so, then even the first living primate's brain should have contained machinery for face recognition. We should therefore expect to find remnants of this system in the evolved face processing systems of living primates today. But what is the evidence for this? Specialization of brain areas for face processing have, to date, only been studied extensively in two primate species, humans and macaque monkeys, which belong to the catarrhine group of primates. This group is thought to have split some 25 million years ago into the old world monkeys, which macaques belong to, and hominoids, which humans belong to [2,3]. What properties do the macaque and human face-processing systems share? And can we infer homology from these commonalities? Recent investigations into the human and macaque face-processing systems allow us to begin answering these questions.

They further offer insights into mechanisms of object recognition, principles of brain organization, and the evolution of social brains. The better we understand homologies between the systems, the better we can use data available from only one species to understand the other. Research into face-recognition systems will deepen our understanding of the evolution of social perceptual abilities. Here, we review selected findings on human and macaque face processing systems in order to highlight similarities and differences between the two species and delineate directions for future research.

Face-selective brain areas in humans and macaque monkeys

Faces activate special areas within those parts of the visual system that are dedicated to object recognition [4-9]. In humans, numerous functional magnetic resonance imaging (fMRI) studies have reported three occipito-temporal areas that respond significantly more strongly to faces than any other non-face objects. These face-selected areas were found in the lateral

occipital cortex, the occipital face area (OFA) of the mid fusiform gyrus [10], the fusiform face area (FFA) [7], and one within the posterior part of the superior temporal sulcus (STS), the STS-FA [11] (Fig. 1A, right). As imaging technology has improved and more diverse stimulus sets have been used, further areas and subdivisions have been found: the FFA can be subdivided into an anterior and a posterior part [12,13]; it is accompanied by one or two more anterior face areas [13-15]; similarly, the STS-FA appears to be only one of multiple face areas inside the STS [16,17]; and a face-selective prefrontal region was found in or close to the inferior frontal gyrus (IFG) [14,17,18]. Thus, it appears that face processing in humans is supported by an array of specialized face areas (see Table 1). In macaque monkeys, fMRI and electrophysiological recording studies have revealed five face areas inside the STS (Fig. 1A, left), one in anterior inferotemporal cortex on the ventral surface of the temporal lobe [14] (Table 1B), and three in the frontal lobe [19]. A further face-selective region might exist on or outside the dorsal lip of the STS [13], and a recent study reported three further areas on the ventral surface of the temporal lobe [20] (see Table 1B). Thus, in both human and macaque monkey, using the same technique, multiple face-selective areas are found to exist; they are found primarily in the temporal lobe, with lower frequency in the frontal lobe; they reside within object-selective cortex; and, while there are still some uncertainties, the numbers of face areas might match exactly in both species. This match is not trivial given the huge difference in absolute size of macaque and human brain and the variation in the number of cortical fields across species [21]. If there is a one-to-one mapping between human and macaque face areas, then how could it have been established?

Similarities and differences between human and macaque face-processing systems

Homology of brain areas is classically established with a set of criteria including (i) relative location, (ii) cytoarchitecture/immunohistochemistry/gene expression profiles, (iii) connectivity, and (iv) functional similarity [22-25]. Below, we review existing evidence for each of these four criteria and discuss the mappings between human and macaque face areas they suggest.

Relative location

The location of face areas, relative to other cortical areas and relative to each other, provides a first constraint on homologies. Temporal lobe face areas in both species are organized along an occipitotemporal axis [14], embedded in the larger organization of the entire visual system that progresses from early visual areas occipitally to more high-level, object-selective areas temporally [26-28]. It is, thus,

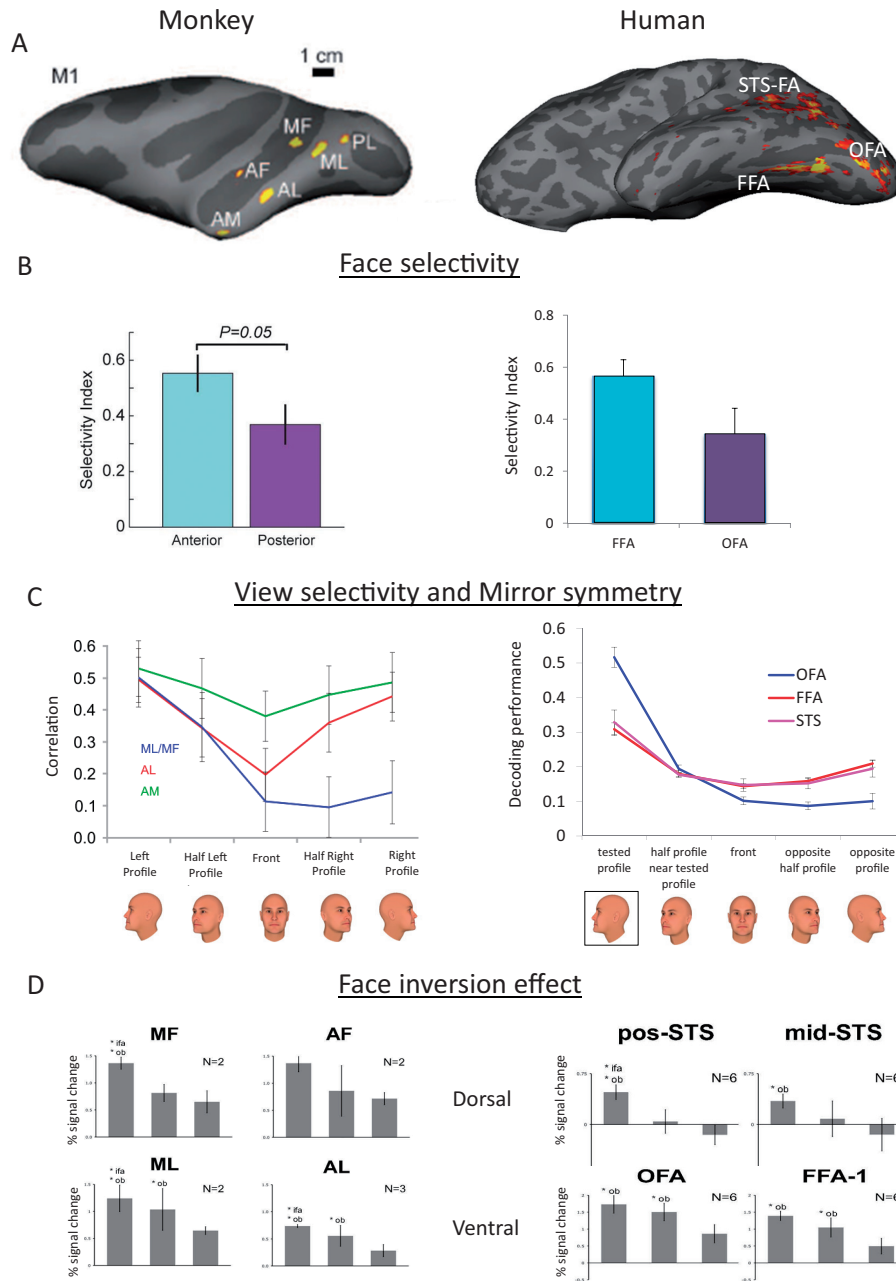
most parsimonious to assume that homologies between face areas conform to this pattern. Similarly, in both species, face areas are found at more ventral and at more dorsal locations, and it appears most plausible to assume that ordering of areas along this dorso-ventral axis would be preserved across species. These considerations lead to a first scenario (Table 2, Scenario 1).

However, human and macaque face-processing systems also exhibit a striking difference in spatial location [14]: while most of the macaque face areas are located inside or close to the STS, the majority of human areas are located at more ventral locations. A recent report on additional, more ventrally located macaque face areas [20], thus, raises the possibility, in agreement with the above interpretative scheme, that human and macaque STS face areas might correspond, as do the more ventral areas of the temporal lobe (Table 2, Scenario 2). However, in this scenario, a stunning mismatch between the numbers of face areas across species inside/around the STS and along the ventral part of inferotemporal cortex remains unexplained.

Understanding the organization of face-processing systems requires not only understanding of the relative position of face areas towards each other but also their embedding into the rest of the brain. Systematic mapping of macaque and human visual cortices onto each other reveals an overall shift of areas ventrally from the STS in humans compared to macaque monkeys [29], corresponding to overall areal expansion in this region [30]. Thus, the fact that human face areas are found on the ventral surface of the temporal lobe, while macaque face areas are mostly found on the lateral surface is consistent with this overall pattern. In agreement with this interpretation, landmark-based cross-species warping of the macaque onto the human brain, estimates that macaque middle face patches in the STS correspond to human FFA [8,15], and macaque anterior area AM map onto human AFP [15] (Table 2, Scenario 1).

Our understanding of the organization of the human face areas has been greatly advanced recently by investigations of their relative location to body- and motion-selective areas [12,31,32]. In humans, a systematic pattern of alternating face- and body-selective areas, some surrounding motion-selective area MT in an alternating pattern was found. Similarly, the macaque face- and limb-selective areas have been found to be located in the same neighborhood as each other [8,13,33] and as motion-selective areas in the STS [34]. However, in contrast to the human brain, no face area has been found dorsal to area MT in the macaque brain, no circular arrangements of face- and body-areas have been

Figure 1. Functional correspondence between human and monkey face areas



(A) **Left:** In the macaque temporal lobe, six face patches have been consistently found by fMRI. They have been referred to, from posterior to anterior, as the posterior lateral (PL), medial lateral (ML, medial fundus (MF), anterior lateral (AL), anterior fundus (AF), and anterior medial (AM) face patch. **Right:** In the human temporal lobe, three face-selective brain regions have been frequently described: the fusiform face area (FFA), the occipital face area (OFA), and the STS face area (STS-FA). (B) **Left:** Anterior face areas in monkeys show higher face selectivity than posterior areas (modified from ref [47]). **Right:** The human FFA shows higher face selectivity than the OFA (based on data collected by Erez & Yovel, submitted). (C) **Left:** Tuning to head orientation in ML/MF, AL, and AM. Correlation coefficients between population activity vectors to twenty five faces at five different head orientations were computed based on data from ref [49]. Only cross-individual correlations were computed. Error bars indicate one standard deviation. Head orientation coding is strongly mirror-symmetrical in AL, weakly in AM, and not mirror-symmetrical in MF/ML. **Right:** Evidence for mirror-symmetric coding of head orientation in human FFA and STS-FA, but not OFA was found using multivoxel-pattern analysis [51]. (D) Inversion effect is larger in the dorsal (monkey MF/AF and human STS) than the ventral face areas (monkey ML/AL and human OFA/FFA). Inverted faces show similar response to upright objects in the dorsal areas but higher response than upright objects in the ventral areas (reconstructed from Pinsk [13]).

Table 1A. Approximate correspondence of human face-selective areas (defined by contrast faces>objects) across studies

Study	Face-selective areas							
Haxby et al [60]	Inferior Occipital Gyrus	Lateral Fusiform Gyrus						STS
Kanwisher & Yovel [59]	OFA	FFA						fSTS
Tsao et al [14]	OFA	FFA			AFPI	AFP2		STS-FA
Pinsk et al [13]	OFA	FFA1		FFA2		AT		postSTS/midSTS
Rajimehr et al [15]	OFA/IOG		FFA			ATFP		STS
Weiner and Grill-Spector [31]	IOG-face	posFus-face		midFus-face				pSTS ¹
Pitcher et al [17]	OFA		FFA					pSTS ² aSTS ³

¹the STS face areas reported in the other studies are anterior to this one

²also reported pcSTS, which may correspond to postSTS in Pinsk et al., [13] and pSTS in Weiner and Grill-Spector, [31]

³was found only with dynamic stimuli

OFA – Occipital Face Area, FFA – Fusiform Face Area, AFP – Anterior Face Patch, STS-FA – superior temporal sulcus- face area, fSTS – face superior temporal sulcus, pSTS – posterior STS, aSTS – anterior STS

Table 1B. Approximate correspondence of macaque face-selective areas (defined by contrast faces>objects) across studies

Study	Face-selective areas							
Tsao et al [14]	PL	ML		MF	AL		AF	AM
Pinsk et al [13]		ML		MF	AL		AF	AD
Rajimehr et al [15]			Posterior temporal face patch (PTFP)			Anterior temporal face patch (AFTP)		
Bell et al [47]			Posterior face-selective region			Anterior face-selective region		
Ku et al ¹ [20]	pSTS	mSTS			aSTS/TEad			AMTS
Issa et al [64]	PL	ML			AL			AM

¹Ku et al. further report on vV4, TEpd, TF and EC in the temporal lobe (see Table 2)

IOG – Inferior Occipital Gyrus, AFTP – Anterior Temporal Face patch

posFus – posterior Fusiform; midFus – middle Fusiform; TEad – anterior dorsal portion of temporal area “E” of von Economo and Koskinas. AMTS – anterior medial temporal sulcus

Table 2. Correspondence between human and monkey face areas based on relative and absolute anatomical location and connectivity

Scenario 1						
Posterior-anterior axis						Species
Dorso-Ventral Axis	dorsal			MF	AF	Macaque
	ventral	PL		pSTS	aSTS	Human
		OFA		ML	AL	Macaque
				pFFA	mFFA	Human
					AM	
					AFP	
Scenario 2						
Posterior-anterior axis						Species
Dorso-Ventral Axis	dorsal			mSTS	aSTS	Macaque
	ventral		vV4	pSTS	aSTS	Human
		OFA		TF	AMTS	Macaque
				FFA	AFP	Human
Scenario 3						
Posterior-anterior axis						Species
Dorso-Ventral Axis	dorsal			-		Macaque
	ventral			STS-FA(s)		Human
				PL-ML/MF-AL/AF-AM		Macaque
				OFA - FFA - AFP		Human

Three scenarios indicating putative correspondences between macaque and human face areas along the posterior-anterior and dorso-ventral anatomical axis

demonstrated, and fewer body areas (two) have been found [33]. Further comparative studies are necessary to gain a complete understanding of how the spatial maps of functional specializations [35] that embed face area maps between human and macaque.

Differences in cytoarchitecture, immunohistochemistry and gene expression

While cytoarchitectonic, immunohistochemical, and gene expression differences across brain areas provide, arguably, the strongest clues for homology, these important pieces of information are only beginning to be used to identify putative anatomical specializations of face areas in humans and macaque monkeys. Cytoarchitectonic differences across the cortex [36] have, together with connectivity data, been used to parcel the STS of macaque monkeys [37] into subdivisions, which correlate with functional specializations [38]. Thus, it is important to know where exactly inside the STS macaque face patches are located (and especially where they are located relative to cytoarchitectonically defined STS subregions) in order to establish each area's identity and allow for thorough comparisons with human areas. Human STS is cytoarchitecturally subdivided as well [39], as are the ventral portions of the temporal lobe in which the fusiform face areas reside [40]. Correlating functional specializations with cytoarchitecture should be a major future research focus, as difficult as it is, with cytoarchitecture typically performed post-mortem. But the development of neuroimaging correlates of the cyto- and myeloarchitecture [41,42] might provide new tools to allow for these structure/function correlations.

Connectivity

Connectivity among brain areas constitutes an important third anatomical criterion for establishing homology across species. In macaque monkeys, using electrical stimulation with fMRI, strong connections have been found between the majority of face areas [43], notably also along the dorsoventral axis. In humans, diffusion tensor imaging (DTI) studies suggest strong connections between the OFA and FFA, but weak connections between these areas and the STS [44]. Studies of functional connectivity also report strong linkage of OFA and FFA [45,46]. These findings suggest that, in humans, two face-processing streams might exist, a dorsal and a ventral one, with only weak connections between them. In this scenario (Table 2, Scenario 3), the ventral human face-processing system would find a homolog in the entire macaque face-processing system, both richly interconnected; yet the STS face area(s) would constitute an evolutionarily new development of humans or hominoids, without correspondence in the macaque brain. This scenario is independently supported by the finding of a face area

directly dorsal to the MT/MST complex [12], which does not appear to have a counterpart in the macaque.

Functional specializations

Functional specializations of face areas, currently, provide the richest source of information for a cross-species comparison of face-processing systems (Table 3). Of particular relevance are experiments demonstrating clear functional dissociations between face areas.

Face selectivity

The most basic feature of a face-selective area is how much more strongly it responds to faces than to non-face stimuli. Bell et al. [47] reported greater face-selectivity in the anterior than posterior face areas in the monkey (Fig. 2B, left). Similarly, human fMRI studies reveal greater selectivity in the more anterior area FFA than in the posterior area OFA (e.g. [17]) (Fig. 2B, right).

Hierarchical organization

Hierarchical object recognition systems are characterized by increasing object selectivity from one processing level to the next and concomitantly increasing abstraction from (invariance to) accidental image features like position, size or object orientation [48]. In macaque monkeys, receptive field sizes increase from posterior to anterior face areas, and face-selective responses grow more and more position-invariant [49]. Similarly, in humans, the OFA shows stronger responses to contralateral than ipsilateral faces, whereas the FFA shows similar responses to faces in both visual fields [50].

As position invariance increases along the face-processing hierarchy, so does invariance to head orientation. Cells in the middle face areas (MF and ML) are tuned to the orientation of face stimuli, firing maximally for one particular head orientation; cells in more anterior area AL showed a mirror-symmetric tuning to head orientation; and cells in the most anterior area AM were highly

Table 3. Organization principles for establishing homologies between the human and monkey face processing systems

Posterior-Anterior Organization
Relative Location of Areas
Hierarchy Receptive Field Size ^{49,50}
Magnitude of Face Selectivity ^{17,47}
Mirror Symmetry ^{49,51-52}
Individual Selectivity ^{49,53-54}
Dorso-Ventral Organization
Relative Location of Areas
Face Inversion Effect ¹³
Motion Sensitivity ^{17-18,34}

Correspondence between human and monkey face areas based on functional similarities suggests two organization principles along the posterior-anterior and dorso-ventral anatomical axis.

invariant to head orientation [49]. In humans, fMRI data indicate that the representation of view in the OFA was similar to early visual areas and consistent with view-selectivity and a mirror symmetric representation in the FFA [51,52] (Fig. 1C).

With increasing invariance to position and head orientation, a higher specificity for facial identity is built up from the middle face areas, via AL to AM in the macaque brain [49]. In humans, facial identity selectivity (but not invariance to head orientation) was reported anterior to the FFA in one study [53] and inside and anterior to the FFA (invariant to facial expressions) in another [54]. Future studies establishing the relationship of this selectivity to the anterior face areas will be necessary to confirm the now suggestive functional similarity to macaque area AM.

A hierarchical organization of face areas predicts increasing response latencies from posterior to anterior areas. In the macaque, response latencies, as gathered from single neuron firing rates (and the local field potential's first face-selective component), increase from 88 ms (126 ms) in the middle face areas to 104 ms (133 ms) in AL and to 124 ms (145 ms) in AM [49]. In humans, a transcranial magnetic stimulation study suggests that the OFA is maximally engaged in face processing at 100-110 ms after stimulus onset [55,56], consistent with the results of a simultaneous electroencephalogram-fMRI study that found that the OFA face-selectivity is correlated with face-selectivity at 110 ms. The FFA in this latter EEG-fMRI study was correlated with the face-selective N170 event-related potential component [57], indicating later processing time of about 60 ms.

Taken together, both human and macaque face-processing systems are organized along the occipito-temporal axis (OFA-FFA-aFA and PL-ML/MF-AL/AF-AM) [14] in a processing hierarchy. Mirror-symmetry of head orientation tuning in monkey area AL and human FFA and STS suggest homology, but correspondences between the other face areas remain unclear (Table 1, Scenario 1).

Face inversion

Recognition of upside down relative to upright stimuli drops more severely for faces than non-face objects [58]. A larger face inversion effect was found in anterior than in posterior face areas in macaques [47], and in FFA and STS-FA compared with the OFA in humans [59]. Pinsk et al. [13] reported a smaller inversion effect in ventral (probably ML and AL) than in dorsal (probably MF and AF) macaque face areas. Furthermore, the response to inverted faces did not differ from upright objects in the monkey dorsal face areas, similar to the human STS-FA,

whereas the response to inverted faces was higher than the response to upright objects in the monkey ventral face areas, similar to the human OFA and FFA (Figure 1D). These findings suggest a correspondence between the monkey dorsal face areas (MF and AF) and the human STS-FA and the ventral monkey face (ML and AL) areas and the human OFA and FFA (Table 2, Scenario 2).

Selectivity for facial motion

A similar division of labor between dorsal and ventral face-processing areas, proposed early on [60,61], is suggested by studies of facial motion. In macaque monkeys, selectivity for facial motion is found more dorsally inside the STS or even dorsally to it [34]. In humans, the STS-FA is exquisitely tuned to facial motion, while the OFA and the FFA respond similarly to static and moving faces [17,18]. Thus, in addition to an occipitotemporal axis of hierarchical organization, both human and macaque face-processing systems are also organized along a dorso-ventral axis characterized by functional differentiation (face inversion and facial motion) and indicating parallel organization of face-processing systems (Table 2, Scenario 2)

Conclusions and outlook

Comparing face areas across two primate species has provided us with important insights into the neural mechanisms of face recognition. Yet, in trying to establish homologies between the systems, we still need to consider several very different models seriously. The model most consistent with current data is one of two face-processing streams, a dorsal and a ventral one, each organized in a hierarchical fashion (Table 2, Scenario 1, Table 3). Yet, more needs to be learned about functional specializations within and outside face areas, their connections and anatomical underpinnings to reach certainty about the evolution of face-recognition systems in primates. This will also require insights into the brains of additional primate species, in particular the great apes [62], new-world monkeys, and non-primate species (e.g. sheep [63]) for in- and out-group comparisons. Future research into functional specializations of face areas should utilize, as much as possible, common stimulus designs, behavioral paradigms, and experimental techniques.

Abbreviations

AF, anterior fundus; AFP, anterior face patch; AL, anterior lateral; AM, anterior medial; DTI, diffusion tensor imaging; FFA, fusiform face area; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; MF, medial fundus; ML, medial lateral; MST, medial superior temporal; MT, middle temporal; OFA, occipital face area; PL, posterior lateral; STS, superior temporal sulcus.

Disclosure

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