

Cortical face processing systems

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Key points

- The primate brain contains face cells, face areas, connected into face-processing networks.
- Face-processing systems in primate species separated by tens of millions of years of evolution, are surprisingly similar.
- Faces contain a multitude of social information that need to be extracted, starting with the detection of the presence of the face and proceeding to the ability to recognize a familiar individual's face.
- Face cells exhibit properties that can explain major property of face perception.
- Impairments of face processing, either due to developmental factors or acquired through brain damage, have been highly informative about the functional organization of face-processing circuits and neural mechanisms of face processing.
- Facial shape information can be integrated with other sources of information, even non-visual information, aiding the processing of dynamic person information.
- One major goal of face processing is the recognition of familiar individuals, and major neural systems and mechanisms supporting this link between social perception and memory have been identified.

Abstract

Faces are visual stimuli of high social importance. Facial information is extracted within visual cortex by a network of interlinked face-selective areas, each with unique functional properties. Neurons within face areas exhibit central properties of face perception like face detection by coarse facial features, holistic processing, or generation of a physical face space, and their activity has been causally linked to face perception. Some face cells combine selectivity for faces with non-visual information like familiarity. At the intersection of high-level vision and social cognition, the domain of face-processing has proven fertile ground for uncovering principles of complex information processing.

Introduction

Faces are a special category of visual objects, characterized by a common overall structure, a common first-order composition of facial parts, with variation of these features and their relative position. As such, face processing is a form of visual information processing. Face-processing is supported by a network of cortical areas, integrated within the many cortical regions that process visual objects. This is not to say that face processing is a purely cortical affair. It relies, of course, on visual inputs, which are most frequently considered to not be face-specific. Furthermore, proposals for sub-cortical processing that is face-specific have been put forward (Johnson, 2005; Morris et al., 1999). In particular, a pathway including the superior colliculus, pulvinar, and amygdala has been proposed, and evidence for face-responsive and face-selective in these brain areas, in particular in the amygdala, has been found (Gothard et al., 2007; Hoffman et al., 2007; Mosher et al., 2014; Nguyen et al., 2013, 2014). Here we will focus on cortical face processing, simply because our understanding of the areas and networks involved and the neural mechanisms employed, are in a much more mature state.

Faces are a special category of visual objects not only for their physical properties, but also because of their high social relevance. Faces transmit a great variety of socially relevant information (Willis and Todorov, 2006), and as such visual face-processing is serving subsequent social functions. Some of these are known and studied well. For example, the visual analysis of eye gaze directs the gaze of a perceiver and its attentional state (“gaze following” (Deaner and Platt, 2003)). A facial expression like a smile can elicit a reciprocating response (“facial mimicry” (Dimberg, 1982; Shepherd and Freiwald, 2018)). The analysis of the face of a familiar person can activate memories and knowledge of that person (Jenkins et al., 2018). And, especially in interactions with others, we make inferences from the face about internal, unobservable states. All of these and more processes link visual face processing to motor, emotional, mnemonic, and cognitive systems. Some of these links have been explored, and we know some of the networks involved (Livneh et al., 2012; Marciniak et al., 2014; Shepherd and Freiwald, 2018; Shepherd et al., 2009). But here we will focus on the visual processing systems for faces, again, because they are best understood.

Face recognition, from a computational point of view, is a daunting task. But for most of us detecting a face in a scene, recognizing a friend, and noticing even minute changes in facial expression are effortless. How is that possible? The brief answer is that primate brain contains specialized cells and circuitry that support face recognition, and some of the computational mechanisms these circuits implement are now becoming clear. Here, we provide a comprehensive overview of primate face processing systems from single cells to circuits and their links to behavior.

The functional organization of face-processing circuits

One of the greatest surprises in systems neuroscience was the discovery that there are cells in the brain tuned to a meaningful complex stimulus, faces. Charles Gross’ discovery of these cells, while providing evidence for earlier ideas about single-unit codes of person identity, which Lettvin had famously coined “grandmother cells” (Gross, 2002), seemed unbelievable. And Gross’ finding called for an explanation: how can such complex shape-selectivity arise from simpler representations in early visual cortex (Hubel, 1982)? The natural answer was, and has remained, hierarchies that transform visual information through multiple levels of processing (LeCun and Bengio, 1995; Riesenhuber and Poggio, 1999). What the discovery of face cells did for the concept of hierarchy, the discovery of entire face areas by functional MRI (Kanwisher et al., 1997; McCarthy et al., 1997) did for the concept of modularity: it reinvigorated debates on local versus distributed information processing (Haxby et al., 2001; Kanwisher, 2000). Face-processing systems in primates, as we understand them today, instantiate multiple organizational features, including some that had been thought of as mutually exclusive: face-processing systems are modular and distributed and face-processing appears to proceed in parallel *and* through hierarchies.

Distributed and modular organization

Face cells (Fig. 1A) have been found in temporal (Perrett et al., 1992) and prefrontal cortex (Ó Scalaidhe et al., 1997; Rolls et al., 2006) of the macaque monkey brain, which was taken to suggest that faces are represented in a distributed fashion. Local clustering of face cells (Perrett et al., 1984) (Fig. 1B) and intrinsic imaging suggested an organization of columns (Fujita et al., 1992) (Fig. 1C). Later neuroimaging studies revealed a large-scale organizational feature, face patches several millimeters in diameter (Pinsk et al., 2009; Tsao et al., 2003, 2008a) (Fig. 1D), resembling the earlier discovery of face areas in humans (Kanwisher et al., 1997) (Fig. 2A and B). These patches are primarily located laterally in the lower bank of the superior temporal sulcus (STS) and medio-dorsally in the fundus. Face patches contain very high fractions of face-selective neurons (typically 90% or more of visually responsive cells, depending on criterion) (Freiwald and Tsao, 2010; Issa et al., 2013; Tsao et al., 2006). Whatever the computational reason for local grouping of face cells (Dobs et al., 2022), they constitute domain-specific specialized hardware, possibly implementing functional modules (Kanwisher, 2010). As multiple face areas have been found across temporal and prefrontal cortex (Tsao et al., 2008a,b), it has become clear that modular organization goes hand in hand with distributed processing.

Face networks, parallel pathways, and hierarchies

Distributed face areas do not operate in isolation, but are interconnected into a face-processing network through selective long-distance connections. This has been directly shown in macaque monkeys through targeted electrical stimulation of single face areas eliciting selective activations of the other face areas (Moeller et al., 2008) (Fig. 1E) and through tracer injections into face areas showing direct and selective connections to the other face areas (Crimaldi et al., 2016). Subsequent resting state connectivity

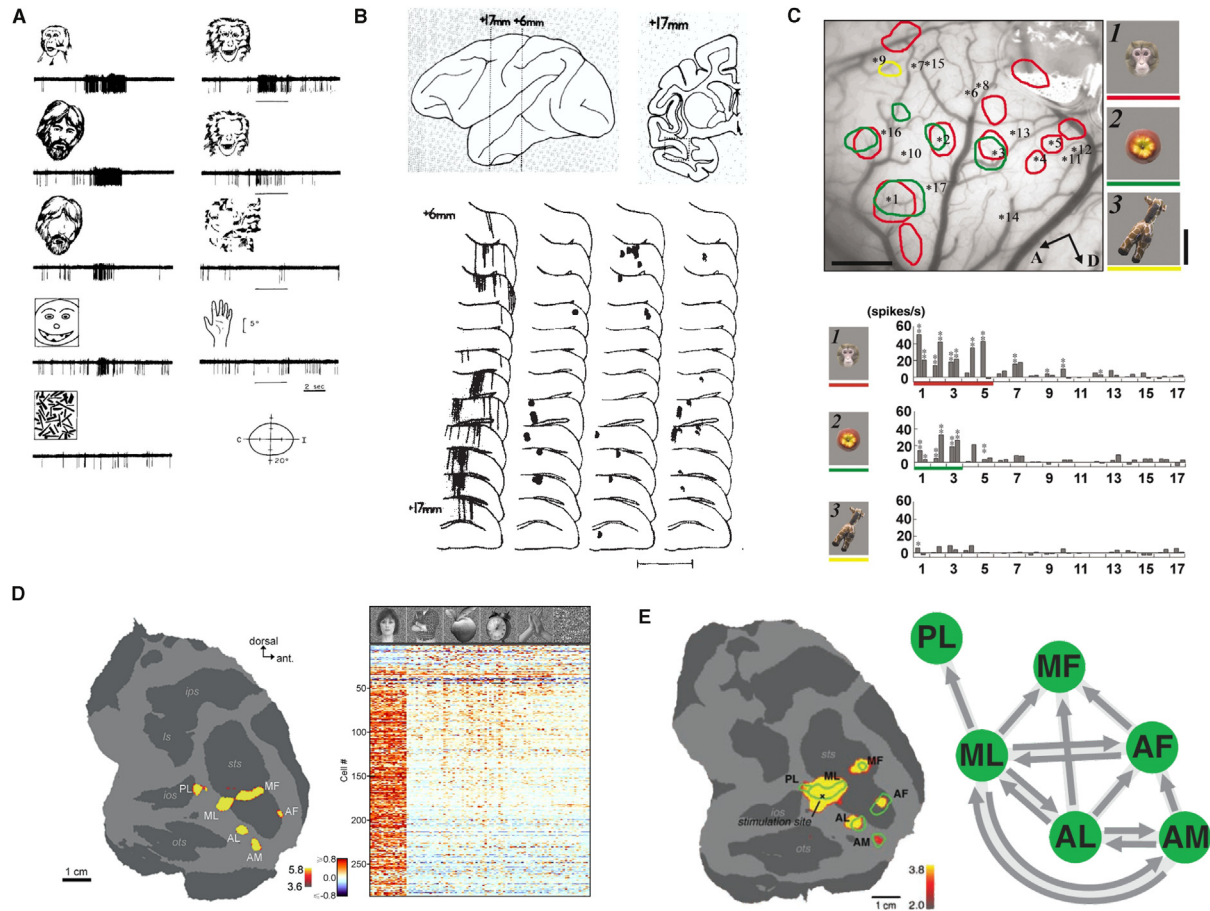


Fig. 1 (A) A face-selective neuron recorded in the superior temporal sulcus (STS) of the macaque monkey (Bruce et al., 1981). Vertical lines depict action potentials. Intact or reduced monkey and human faces, but not a scrambled face or a collection of oriented elements elicit responses. (B) Top: schematic of macaque monkey brain from the side and coronal slice 17 mm anterior to interaural line. Bottom: coronal slices through the STS (scale bar: 5 mm) showing recording tracts (left), and locations of front (circle), profile (half circle), and head motion (arrow) selective neurons. Neurons with like properties tend to cluster together (Perrett et al., 1987). (C) Top: Intrinsic optical imaging revealed spatially-specific activations for faces (red) and other object categories at a size of under 1 mm (scale bar: 1 mm) (Tsunoda et al., 2001), interpreted as feature columns. Bottom: Targeted electrophysiological recordings at 17 locations inside and outside these columns demonstrate degree of selectivity. (D) Left: fMRI in the macaque monkey revealed multiple face-selective regions (shown as thresholded activations (color bar depicts log significance values) on a computer-flattened surface with dark regions depicting sulci) of a few millimeters diameter (scale bar: 1 cm). Face areas occur at repeating anatomical locations in and around the STS (“sts”): posterior lateral (PL), mediolateral (ML), medial-fundus (MF), anterior lateral (AL), anterior fundus (AF), and anterior medial (AM) face area (Freiwald et al., 2009). Right: Matrix of normalized response magnitudes (red: response enhancement, blue: suppression) of all visually responsive cells (vertical axis) recorded from ML and MF during the presentation of 96 stimuli (horizontal axis) shows 97% of cells significantly modulated by faces (Tsao et al., 2006). (E) Left: Electrical stimulation inside face area ML (x) produced significant activations in ML and all other face areas (green outlines, otherwise conventions as in D), indicating strong and direct connections. Right: compiling results from all stimulation experiments, shows that face areas are wired into a face-processing network (Moeller et al., 2008).

measurements of selective connectivity between face areas (Schwiedrzik et al., 2015) extended this knowledge into the domain of metrics that can be used in human brains. Here, fiber tract tracing has provided yet further support that human face areas are also directly interconnected (Grill-Spector et al., 2017; Gschwind et al., 2012). Thus, facial information processing is integrated not only locally, but also across the larger distances separating face-selective areas.

The spatial arrangement of face areas, relative timing of activation, and functional characteristics highlight two organizational principles within the network. The most direct measures have been made in the macaque face-processing system, which we will focus on first. First, face areas are organized along a posterior-anterior axis and response latencies systematically progress from early to late areas, suggesting hierarchical organization. Facial information appears to be systematically transformed from early view-specific representations into late identity-specific representations (Freiwald and Tsao, 2010; Meyers et al., 2015). In the most posterior area, PL, selectivity for a single feature, the eye, seems to dominate (Issa and DiCarlo, 2012), at the next level, in areas MF and ML, a wide range of features are represented, and this selectivity is modulated by the embedding of features into the facial whole (Freiwald et al., 2009). While face representations in MF and ML are view-selective, this dependence is reduced at the next level, AL, through construction of a mirror-symmetric invariance to head orientation, and reduced even further in AM, where representations

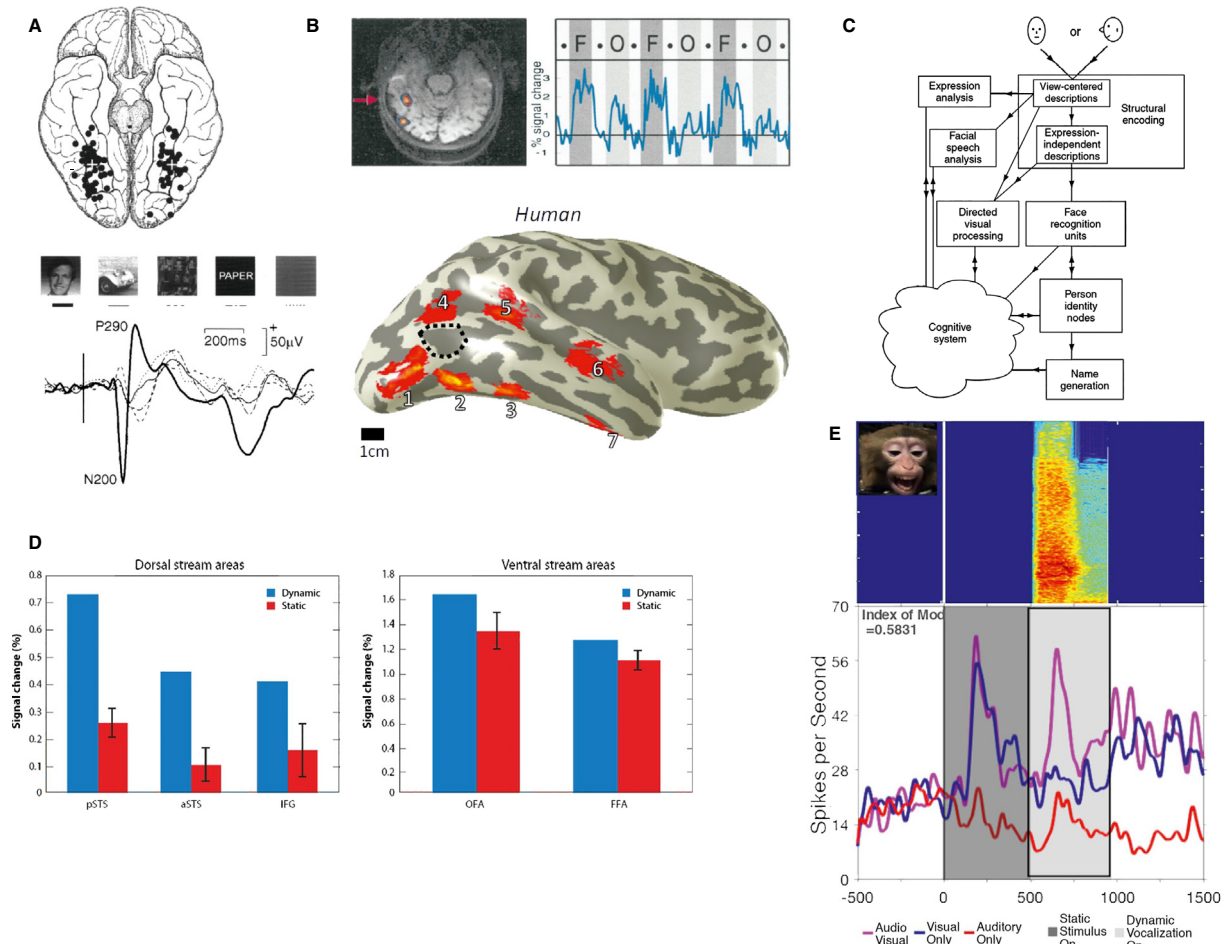


Fig. 2 (A) Top: Epicortical recordings from the ventral surface of the human brain revealed face-selective locations (black dots). Bottom: Recording traces from one location show a high degree of face selectivity early (~200 ms) and late (~900 ms) after stimulus onset (Allison et al., 1999). (B) Top: fMRI in the human brain found spatially-specific face activations (left: activations on anatomical surface through occipitotemporal cortex, right: BOLD response during presentation of blocks of faces (F) and objects (O) (Kanwisher et al., 1997)). Bottom: Face areas on the surface of the human brain (1: OFA, 2: posterior FFA; 3: medial FFA; 4: posterior STS; 5: middle STS; 6: anterior STS; 7: anterior temporal face area) (Weiner and Grill-Spector, 2015). (C) Functional schematic of face-processing systems as proposed by Bruce & Young suggested different functional pathways and interactions with cognitive and mnemonic systems (Bruce and Young, 1986). (D) BOLD responses to dynamic (blue) and static (red) faces in dorsal stream human face areas and inferior frontal gyrus (IFG) and ventral face areas, shows a clear functional dichotomy (Duchaine and Yovel, 2015). (E) Face area AF contains cells that respond to images of faces (blue), but are modulated by the simultaneous onset of a vocalization (pink) (Khandhadia et al., 2021).

for facial identity are robust against variation in head orientation (Dubois et al., 2015; Freiwald and Tsao, 2010; Meyers et al., 2015). Concomitantly, tolerance for stimulus position and size is increased as well. Orthogonal to this hierarchical principle of information processing, a second functional distinction between face areas along the ventral-dorsal axis exists. Face areas located in the fundus of the STS (dorsal) exhibit a pronounced preference for natural facial motion that face areas located laterally in the lower bank (ventral) lack (Fisher and Freiwald, 2015a). These results suggest different kinds of facial information are processed through two parallel streams. These results resemble earlier findings in the human face-processing system discussed below.

The spatial distribution of face patches requires long-distance connections for them to interact, thus raising the question why the system is organized in this seemingly non-economical manner. The answer may be that the anatomical location of face patches is governed by another organizing principle, their belonging to multiple separate larger-scale object-processing maps. Such a scenario appears plausible given the curious co-localization of color patches directly ventral to some face areas (Lafer-Sousa and Conway, 2013). Face and color processing share a foveal bias (Hasson et al., 2002), and such retinotopic bias might explain their co-localization (Rajimehr et al., 2014). Also abutting many face areas are body areas (Pinsk et al., 2009; Popivanov et al., 2012; Tsao et al., 2003), whose co-localization with face areas may serve to support person perception. Furthermore, areas of expertise for non-facial shapes have been found in close proximity to face areas (Srihasam et al., 2014). This spatial pattern of functional specialization parallels a pattern of connectivity whose discovery had given rise to the distinction of posterior, middle, and anterior parts of inferotemporal cortex (Felleman and van Essen, 1991). That there is a repeating pattern of interconnected shape-processing

circuits, including, but not limited to faces and bodies has been shown directly (Bao et al., 2020). Thus it appears that there is common logic to this entire region of cortex (Yamins and DiCarlo, 2016), including face-selective areas, though at least one exception has been documented of an inferotemporal area close to two face areas with functional properties closer to and direct connections with parietal and prefrontal cortex (Sani et al., 2019, 2021; Stemmann and Freiwald, 2018, 2019).

Evolutionary roots: Human and non-human primate face-processing systems

Despite an estimated 25 million years of separate evolution (Stewart and Disotell, 1998), human and macaque face processing systems bear remarkable similarities (Freiwald et al., 2016; Tsao et al., 2008a; Yovel and Freiwald, 2013) (but also see (Ku et al., 2011)), and some of these similarities might extend to the evolutionarily more distant New World monkeys (Hung et al., 2015; Weiner and Grill-Spector, 2015). In the human temporal and frontal lobes, multiple, spatially separate face areas have been found (for a review, see (Duchaine and Yovel, 2015)). Like macaques, human ventral face areas are adjacent to body-selective areas (Peelen and Downing, 2005; Schwarzlose et al., 2005). The overall number of face areas is similar to that in macaques, and so is their spatial arrangement in the temporal lobe with two occipito-temporal series of areas, one in ventral temporal cortex and the other, dorsal one, in the STS (Yovel and Freiwald, 2013). Functional specializations along the ventral series of face areas follow a progression similar to that in the macaque monkey, suggesting a hierarchical organization: in the occipito-temporal direction face selectivity increases (Bell et al., 2009), position dependence decreases (Hemond et al., 2007), mirror-symmetric confusion of facial profile views emerges (Axelrod and Yovel, 2012; Kietzmann et al., 2012), and facial identity selectivity grows stronger (Yang et al., 2016). Similarly, in both macaque and human face areas, the response to faces is augmented by the presence of an anatomically correctly placed body, and this augmentation grows stronger from posterior to anterior face areas (Bernstein et al., 2014; Fisher and Freiwald, 2015b; Song et al., 2013). Furthermore selectivity for facial motion is highly pronounced in dorsal areas, but not in ventral ones (Bernstein et al., 2018; Fisher and Freiwald, 2015a; Fox et al., 2009b; Pitcher et al., 2011a, 2019). Similar to the macaque, the ventral face areas appear to be interconnected, while connectivity of the two streams appears limited (Gschwind et al., 2012) and is still the subject of active research (Yeatman et al., 2014). Similarities between the systems extend beyond the temporal lobe. Face-selective neurons and areas have been found in the macaque in three major parts of prefrontal cortex (PFC) (Barat et al., 2018; Ó Scalaidhe et al., 1997; Rolls et al., 2006; Tsao et al., 2008b), and later fMRI work confirmed the presence of face-selective areas in the human PFC (Axelrod and Yovel, 2013; Chan and Downing, 2011; Pitcher et al., 2011a; Tsao et al., 2008a). Thus, human and macaque face-processing systems, according to at least two sets of criteria, anatomical location and functional specialization, appear to be homologous.

Neuroanatomical investigations of cytoarchitectonic features and white matter connections of the human face processing system provide further insights about the anatomical-functional correspondence (for review, see (Grill-Spector et al., 2017)). Alignment of functional MRI data with anatomical data from postmortem individuals revealed that the posterior and anterior face areas in the human fusiform gyrus are located in regions with distinct cytoarchitecture properties. This suggests that the two areas have different functional roles in face processing. Furthermore, investigation of white matter tracts indicate direct hierarchical connections between the OFA, the posterior and middle FFA. However these regions are not only connected in a hierarchical manner but also have direct connections with other regions including retinotopic visual areas, the dorsal face areas in the STS, and the intraparietal sulcus (Grill-Spector et al., 2017).

The functional significance of the anatomical properties of the face areas is evident in studies that revealed that properties of different parts of white matter tracts are associated with performance on face or scene recognition tasks. For example, face recognition was associated with the fractional anisotropy (FA) of the anterior part of the ILF in the right hemisphere, whereas scene recognition was strongly correlated with the FA of the posterior and middle but not the anterior part of the ILF bilaterally (Gomez et al., 2015; Tavor et al., 2014). Furthermore, developmental prosopagnosics show atypical white matter properties adjacent to face areas but not place areas (Gomez et al., 2015; Song et al., 2015). A study using quantitative MRI (qMRI) (Mezer et al., 2013) also revealed that gray matter properties in the fusiform face areas, which are thought to reflect cellular properties of cortical neurons, were correlated with performance on face processing tasks (Gomez et al., 2017).

Taken together, the correspondence between the neuroanatomical and functional properties of the face processing network and their association with performance on face recognition tasks indicate a sophisticated, multi-part machinery that works in concert to allow proficient face recognition.

From neural processes to behavior

Face detection & eye movements

For facial information to be extracted, the face must first be detected in a scene. Face detection has been proposed, based on psychophysical and computational work, to rely on coarse contrast relationships between the different parts of the face (Sinha, 2002). Due to the three-dimensional structure of the face, e.g., with the eyes set back relative to the forehead, the forehead will be brighter than the eyes under most illumination conditions. Since change of appearance due to change of illumination is among the most difficult problems for object recognition, heuristics that are robust against this non-affine transformation are of great use. Furthermore, coarse contrast features do not require facial detail and thus should be easy to compute and relatively independent of facial identity. Humans indeed use twelve contrast-pairs (e.g., forehead brighter than left eye) to detect faces (Sinha, 2002). This behavioral characteristic finds a clear correspondence at the single cell level. Half of the neurons in ML and MF, when probed with coarse-contrast face stimuli, showed sensitivity to contrast relationships between pairs of facial parts (e.g., nose and left eye) (Ohayon et al., 2012).

Cells exhibited highly consistent preferences for a specific polarity of each pair (e.g., nose brighter than left eye region). Importantly, the population preferences for contrast included all of the twelve pairs found to be important in human detection behavior, and the population's polarity preferences matched that of human observers in all twelve cases.

Another approach that has been used to study the mechanisms of face detection is face pareidolia. Face pareidolia refers to the tendency to perceive a face in non-face object stimuli. Out of 12 features that were examined, only the presence of eyes and mouth-like features were shown to strongly predict a percept of a face. Removal of these features reduced "faceness" ratings as well as face-induced attentional biases (Omer et al., 2019; Palmer and Clifford, 2020). Studies with humans and monkeys show that face pareidolia stimuli generate similar behavioral and neural effects as real faces. This includes face-generated attentional biases (Palmer and Clifford, 2020; Takahashi and Watanabe, 2013), patterns of eye movements (Taubert et al., 2017), and face-selective fMRI and electrophysiological responses (Liu et al., 2014; Taubert et al., 2017; Wardle et al., 2020). The electrophysiological responses to face pareidolia stimuli are found at early latencies, similar to real faces, which indicates that they reflect perceptual rather than high-level cognitive re-interpretation (Wardle et al., 2020). Face-selective brain areas in humans and monkeys show higher responses to face pareidolia stimuli than similar objects that do not generate a percept of a face. Overall, this robust phenomenon indicates that face detection mechanisms are broadly tuned to face-like stimuli to not miss a face, even at the cost of false detection of non-face objects.

Following detection of a face in the visual field, the visual system must shift fixation onto the face, and in the initial fixation, most of the information necessary to judge identity, expression, and other fine-grained characteristics can be obtained (Hsiao and Cottrell, 2008). Fixation patterns will impact visual processing within the network. While it is frequently assumed that because of the large receptive fields within inferotemporal cortex, it might not, it has been shown that some face cells at least have rather small receptive fields (Issa and DiCarlo, 2012), whose activity will thus depend critically on the point of fixation. Work over the last decade has demonstrated that individual observers reliably direct their initial fixation to an idiosyncratic position on the face, known as the preferred fixation location (PFL) (Peterson and Eckstein, 2013; Peterson et al., 2016). PFLs are centered on the midline of the face, and most PFLs are located in the information-rich zone between the eyebrows and the mouth (Fig. 3A and B). PFLs estimated in daily life using mobile eye-tracking are remarkably consistent with lab-based measurements ($r = 0.91$) (Peterson et al., 2016) and facial fixations are consistent across at least 18 months (Mehouder et al., 2014). Fixating the same location on the face reduces differences in the retinal position of faces and thus standardizes representations delivered to cortical face processing mechanisms.

Behavioral studies have demonstrated that PFLs are tightly linked to the position on the face where performance for an individual is best (Fig. 3B). Further evidence for retinotopic encoding of faces comes from a study demonstrating that performance with the eyes is better when they are presented above fixation than below fixation, whereas the opposite is true for mouths (de Haas et al., 2016) and from a demonstration that face discrimination from EEG responses is strongest when observers fixate their PFL (Stacchi et al., 2019). Although performance is best when observers fixate their sweet spot, observers with widely divergent fixation patterns show comparable face identity memory when allowed to freely fixate (Arizpe et al., 2017).

Holistic face representations

A key characteristic of human face recognition is the holistic nature of upright-face processing relative to the more part-based nature of object processing and inverted face processing (Tanaka and Farah, 1993). The face-inversion effect is the robust observation that humans perceive face information far less precisely in inverted than in upright faces (Yin, 1969), and there is ample evidence to suggest that subjects use a more holistic strategy with upright than with inverted faces (Farah et al., 1995; Young et al., 1987). In the middle face patches, the response to inverted faces is, on average, delayed, more transient and overall reduced (Perrett et al., 1982; Tsao et al., 2006). This neural face-inversion effect may be confined to the face patches as it was found to be much weaker for face-cells located outside the face patches (Taubert et al., 2015a). How might face inversion affect the processing of facial features? Cells in ML/MF, when probed with cartoon stimuli, were tuned to more features in the upright than the inverted face (Freiwald et al., 2009). Furthermore, tuning to one feature, eyebrows, was lost entirely under inversion, while tuning to the mouth was generated de novo. This pattern of results can be explained with a holistic template matching hypothesis that proposes incoming facial features in both upright and inverted faces are matched against an upright face template. The account also explains how the shape of feature tuning can be preserved upon face inversion, as was observed for features that do not change shape and do not markedly change position when faces are inverted. Second, the part-whole effects reported in human psychophysical studies, demonstrate that features are better recognized within a face than in isolation (Tanaka and Farah, 1993). ML/MF cells exhibit tuning to isolated facial features, but tuning is greatly augmented, when features are part of the entire face (Freiwald et al., 2009). Third, maybe the most striking expression of the context dependence of facial features, is the so-called Thatcher illusion (Thompson, 1980). Inversion of local features like the eyes or the mouth, which are easily noticed as grotesque distortions in the upright face, are hardly recognizable in the inverted face. A single-unit correlate of this effect has been reported in ML (Taubert et al., 2015b), where inversion of the eyes reduced the response in the upright, but not the inverted face and similar effects are reported in human electrophysiological studies (Carbon et al., 2005). Notably, a study that used an individual differences approach revealed no correlations across human participants between the magnitude of the part-whole effect and the composite face effect (Rezlescu et al., 2017), concluding that they reflect different mechanisms. Nevertheless, whereas the magnitudes of these effects may not be correlated across individuals, misaligned faces in the composite task, face parts in the part-whole task, and inverted faces in a face inversion task all diverge from the template of the whole upright face. Thus, each of these effects may be the outcome of the

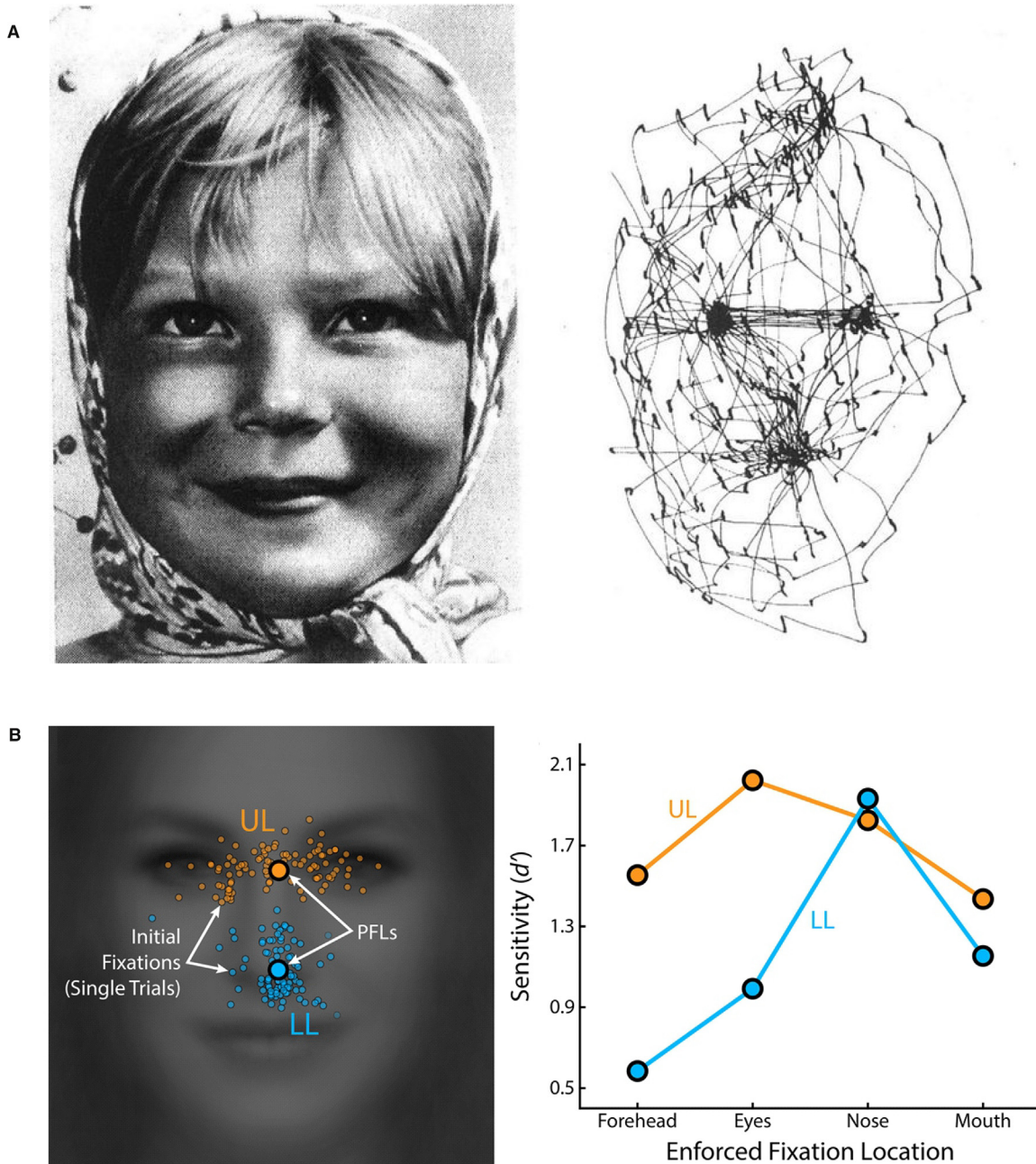


Fig. 3 (A) Humans scan faces in a typical triangular fashion across eyes, nose, and mouth (Yarbus, 1967). (B) Preferred fixation location and matched tuning. The left panel shows the position of first fixations on a face for two participants. Participants in a celebrity identification task fixated on the side of a display and then saccaded to a centrally-presented face. Fixations for an Upper Looker (UL) landed at the level of the eyes while fixations for a Lower Looker (LL) landed lower on the face. The large circles display the average position of fixations for each participant, labeled as the preferred fixation location (PFL). The right panel demonstrates the match between each participant's PFL and performance in a sequential same/different task. Face perception ability was measured at four retinotopic positions with enforced fixations at the forehead, eyes, nose, and mouth. Performance profiles show that the two individuals differ in the tuning of their retinotopic face encoding, with the upper looker doing best when fixating high on the faces (UL, orange) while the lower looker (LL, blue) does better when fixating lower down the faces.

optimization of the face processing system for the classification of upright whole faces of different identities, which requires tuning to fine details, and therefore do not transfer well to any modification of this face template.

Face space

We have emphasized the complexity of faces and of the social information they represent. We have also discussed a great variety of tuning properties in face cells and highlighted that many brain areas appear to be necessary to process faces. In light of this

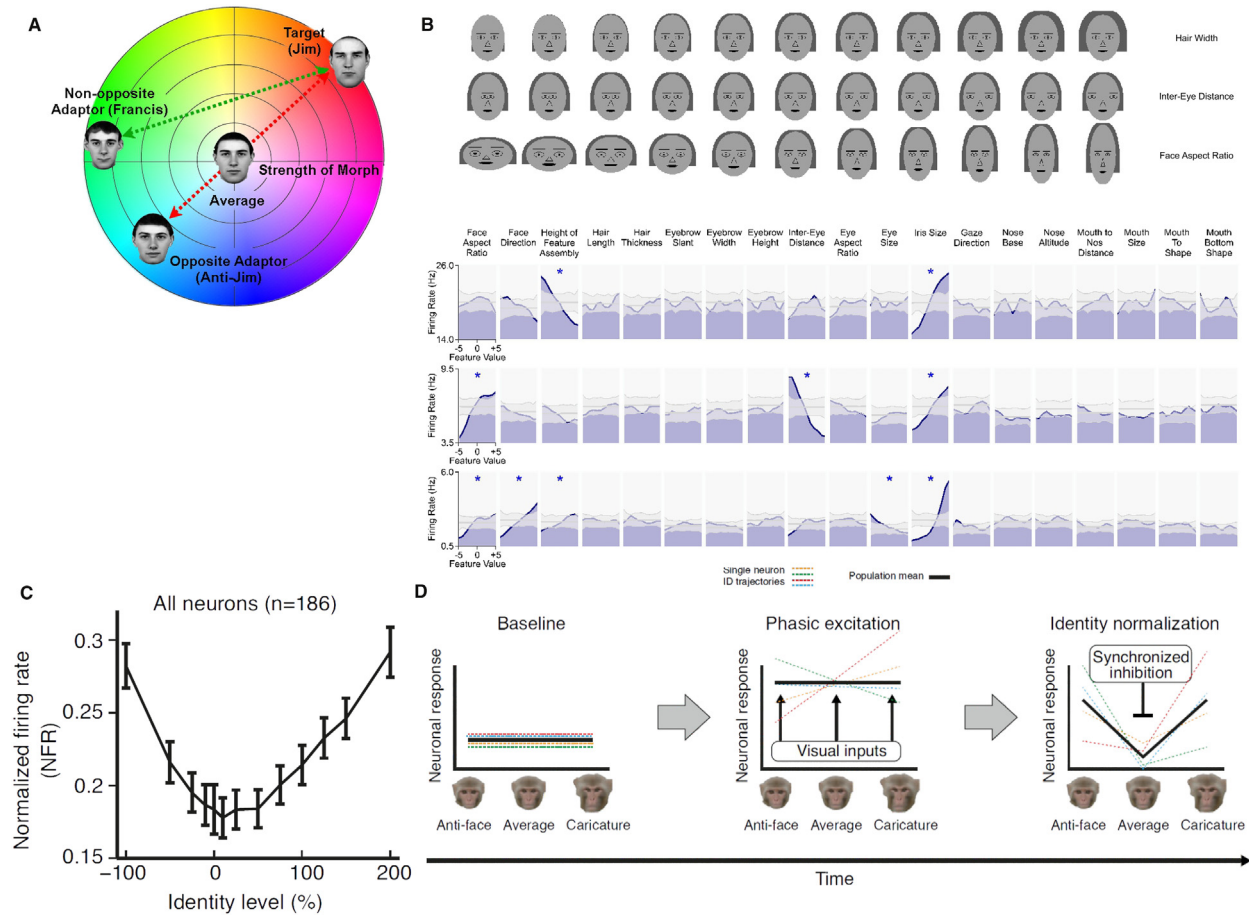


Fig. 4 (A) Schematic of the concept of face space. Adaptation to a specific face was shown to bias face perception towards the opposite direction in face space. Aftereffects were greater for face/anti-face pairs than for non-opposite face pairs (pairs whose trajectories do not cross the center of face space), even though the pairs were matched for perceptual dissimilarity (Rhodes and Jeffrey, 2006; Tsao and Freiwald, 2006). (B) Recordings from face areas ML and MF showed tuning of cells to facial features (Freiwald et al., 2009). Example cartoon stimuli used in this study, varying along three dimensions are shown at top, tuning curves for three example neurons to all nineteen stimulus dimensions at bottom from left to right. Significant tuning (*) typically took the form of ramp-shaped tuning across the entire range of feature variation. (C) Another study found V-shaped tuning in three face areas with minimal responses occurring in the center of face space (identity level 0) (Koyano et al., 2021). (D) A temporal analysis of this effect shows that in the initial phasic response neurons exhibited ramp-shaped axis-coding, while later this tuning combined with norm-based coding as a result of population normalization by synchronous inhibition (Koyano et al., 2021).

complexity, it might be surprising that there is actually something simple about the visual processing of shapes as complex as faces. This simplicity is captured by the concept of faces space, which has become central to the understanding of face representations. Faces are organized, perceptually and neurally, according to their physical properties (Leopold et al., 2001; Turk and Pentland, 1991; Valentine, 1991): representations of physically similar faces occupy neighboring regions of face space. Because there are many features, this space is high-dimensional. So face-space is a multi-dimensional space in which each face occupies a unique position based on its combination of features (Leopold et al., 2001; Turk and Pentland, 1991; Valentine, 1991). Beyond this local scale, the brain organizes representations, and it does so in ways similar to the lower-dimensional color space: The space is thought to be organized by two properties: it is organized around a center occupied by the average face, around which facial identities are located along trajectories that reflect how each face's characteristics deviate from the average face. The distance of a face along a trajectory is determined by the similarity of a face to the average face (Fig. 4A) (Tsao and Freiwald, 2006). Distinctive faces, therefore, occupy the fringes of the space.

There are several ways such a high-dimensional space with these two main properties could be generated neurally. The first distinction that has been discussed (Rhodes and Leopold, 2011) is the question of tuning width: broad tuning curves spanning entire axes of face space, i.e., ramp-shaped tuning curves of opposite polarity, can efficiently encode the position of a face feature along an axis. Alternatively, an axis could be tiled by narrow tuning curves, in which each cell functions as a channel and coding is exemplar-based. Psychophysical results suggest broad tuning: when one adapts to one identity, subsequent perception of the "anti"-identity is enhanced (Leopold et al., 2001). This is very similar to color-adaptation. This effect is compatible with the broad tuning model, not the exemplar-based model. These adaptation studies also speak to a second main question about the organization of

face space, and that is whether the center occupies a special role or not: it was found that this long—distance adaptation effect occurs more strongly around the center of face space, i.e., for face and anti-face, than for an equidistant pair of control identities whose direct connection does not pass through the center of face space (Rhodes and Jeffrey, 2006) (Fig. 4A).

Consistent with psychophysics, broad tuning curves have indeed been found in macaque face areas. In MF/ML, feature tuning is predominantly ramp-shaped yielding a maximal response to one extreme and a minimal response to the opposite extreme (Fig. 4B), and for almost all feature dimensions, opponent polarities were found across cells (Freiwald et al., 2009). Subsequently, ramp-shape tuning was also found in face areas AM (Chang and Tsao, 2017) and AF (Koyano et al., 2021), suggesting they might be a common feature to all face areas. Recent investigations of vastly different computational models supporting face-processing have found ramp-shaped tuning across very different architectures (Hosoya and Hyvarinen, 2017; Raman and Hosoya, 2020). It thus appeared that as long as a system is trained and effective at discriminating faces, would generate this property. It is thus plausible that ramp-shape tuning arises not from properties of the network like network design or learning rules, but from stimulus geometry or statistics, though this has not been proven mathematically (Freiwald and Hosoya, 2021).

Axis coding might thus be the answer to how neurons generate one of the main perceptual characteristics of face space. More distinct response patterns to extreme faces compared to average faces might, furthermore, explain why identity has been found in some studies to be perceived more easily in caricatures than the original face (Rhodes et al., 1997). But what about the other, the potential for the center of face space to play a special role? The first study on the neural basis of face space focused on this question and described broad tuning curves whose minimal or maximal response occurred at the center of face space (Leopold et al., 2006) (see also Fig. 4C). This finding suggests that incoming visual information is compared against the average face (norm-based coding). Whatever the mechanism for such a comparison might be, the existence of so-called V-shape neural tuning curves implies a special role for face space, yet comes with the surprising property that physically very different faces would elicit very similar responses—the cells effectively measure the distance from the center of face space, not its direction. Given that V-shape tuning was found along with the dominant ramp-shaped tuning in another study (Freiwald et al., 2009), raises the possibility that the two coexist scattered across the neural population. However, a recent study investigating this question directly and across three face areas, ML, AF, and AM, came to a different conclusion (Fig. 4D). Ramp-shape tuning emerged early and persisted throughout the neural response, while norm-based coding emerged later (Koyano et al., 2021), suggesting that it may result from normalization by the activity of the entire cell population. Thus, axis coding and norm-based coding might result from entirely different neural mechanisms.

Faces as sources of dynamic social information

Faces convey rich social information including race, expression, gender, attractiveness as well as inferred social traits such as trustworthiness and dominance (Todorov, 2008). Correspondingly, face-selective cells have been found that are tuned to very different aspects of faces: some face cells are tuned to head orientation or gaze (De Souza et al., 2005; Desimone et al., 1984; Perrett et al., 1985), others to facial expressions (Gothard et al., 2007; Sugase et al., 1999), to physical characteristics of the face including facial features and identity (Freiwald et al., 2009; Young and Yamane, 1992), or to familiarity (Eifuku et al., 2011; Young and Yamane, 1992). Thus specializations of face cells exist that are plausible neural mechanisms supporting the different social dimensions of face recognition.

This diversity of tuning to different aspects has long been thought to follow an inherent logic and to be organized into two major processing pathways. Functional and structural connectivity findings support the idea of a separation between the STS, which contains multiple face-selective regions, dorsally and the OFA and FFA ventrally (Bernstein and Yovel, 2015; Duchaine and Yovel, 2015; Pitcher and Ungerleider, 2021). Models mainly differ according to what the main distinguishing feature is between pathways—and to what extent the division of labor is complete or partial (Calder and Young, 2005; Young and Bruce, 2011). Earlier functional models of face perception suggested a division of labor between the processing of invariant aspects of facial information such as identity, gender, and race in the ventral face-selective areas (OFA, FFA) and the processing of changeable aspects such as gaze and expression in the dorsal face-selective regions in the STS (Haxby et al., 2000; Hoffman and Haxby, 2000). In this model, the OFA, which is thought to process facial features, projects to both the FFA, extracting those invariant aspects of faces necessary for face identification, and the STS processing changeable aspects of faces like eye gaze, lip movements, and facial expressions. Note that the distinction is between two classes of static information being processed by two different pathways.

However, more recent studies have shown that a major distinction between the ventral face areas (OFA and FFA) and the STS face area is their sensitivity to dynamic information: whereas the OFA and FFA show similar responses to dynamic and static faces, the STS shows a much stronger response to dynamic than static faces (Fox et al., 2009a; Pitcher et al., 2011a, 2019) (Fig. 2D). This is consistent with an earlier model that proposed a central role to the STS in the processing of dynamic information from faces (O'Toole et al., 2002). Similarly, the macaque dorsal and ventral face areas are also affected differently by dynamic information, with dorsal areas exhibiting a larger response increment for dynamic over static faces than ventral areas (Polosecki et al., 2013). Dorsal areas were further shown to be selective for natural facial movement (Fisher and Freiwald, 2015a). In this fMRI study of facial motion selectivity, a new face-motion selective area was discovered in the upper STS, named middle dorsal area (MD). Thus, MD is clearly selective for dynamic face information. However, when MD was targeted for electrophysiological recordings and probed for selectivity to static images, it was shown to exhibit a face selectivity as high as that of previously recorded ventral face areas and tuning to a wide variety of facial features, including gaze direction, head orientation (robustly against changes in expression and identity), expression (robustly against changes in head orientation and identity), and even for identity (robustly against changes

in head orientation and expression) (Yang and Freiwald, 2021). Hence, MD appears to encode both changing and changeable features of faces, as well as structural ones. These findings support both major models of face processing pathways and suggest that the functional separation between the dorsal and the ventral pathway is not absolute.

It is important to note that there is one very fundamental difference between dorsal and ventral face areas. The dorsal ones reside in parts of the STS that are not exclusively visual. In fact, it has even been shown that selectivity for dynamic faces, biological motion, and voices overlaps spatially within the posterior STS face area (Deen et al., 2015, 2020). And a recent single-cell study in an anterior STS face area, AF, directly showed that about three quarters of cells in this area were influenced by auditory stimulus components (Khandhadia et al., 2021) (Fig. 2E). Findings like these show that parts of the human and macaque STS may represent faces in a format that is integrated with other sensory properties. Specifically, it has been suggested that these representations play a role in dynamic person perception (Yovel and O'Toole, 2016). Furthermore, recent studies have also demonstrated a special role of the posterior STS in the processing of dynamic social interactions: a region that is selective to social interaction depicted by humans as well as interactive objects has been identified and partially overlaps with the face-selective STS (Isik et al., 2017; Sliwa and Freiwald, 2017). Thus, the face-selective STS may be part of a general system for the processing of dynamic social information from faces, voices, and bodies. Based on these and other findings, a third pathway has recently been proposed to lie between the “what” (ventral) and “where” (dorsal) pathways in both the monkey and the human brain (Pitcher and Ungerleider, 2021). This pathway would originate in primary visual cortex (V1), include the generally motion-selective middle temporal area MT, and extend through the STS. The pathway is thought to be specialized for the processing of dynamic social stimuli. Accordingly, it has been suggested that the third pathway integrates sensory information from different modalities “to enable primates to understand and interpret actions of others” (Pitcher and Ungerleider, 2021).

Causal links between face-processing systems and behavior

We have discussed links between neural processes and behavior above. These are correlational. This leaves open the question whether these processes contribute to face recognition. Several findings suggest that activity inside face areas, but not in nearby areas that are not selective to faces, is behaviorally relevant. To determine the behavioral relevance of a neural mechanism, behavior must be assessed while that process is disrupted. Until the advent of neuroimaging, the study of patients with face processing deficits following brain damage was the primary evidence about the neural basis of human face processing (Bodamer, 1947; De Renzi, 1986). The location of lesions in these patients as well as their associated deficits (e.g., left visual field loss) provided early insight into the neural regions contributing to face processing (Bornstein and Kidron, 1959; De Renzi, 1986). Behavioral testing with individuals with acquired prosopagnosia has also shed light on the computations supporting face processing (Barton et al., 2021; Bruce and Young, 1986; Rossion, 2014). Over the last decades, work on acquired prosopagnosia has been supplemented by other types of causal evidence.

Acquired prosopagnosia

Acquired prosopagnosia clearly demonstrates the importance of face processing for our daily lives. At age 47, Faith underwent a resection to remove a right temporal tumor. During her recovery, Faith was confused by the large number of different nurses who visited her room and had the sense that the appearance of her friends and family wasn't right. Six days after surgery, a woman entered Faith's room and approached her in a friendly manner. Faith assumed it was a physician, but Faith's husband greeted the woman warmly and when she spoke Faith immediately recognized the voice of a childhood friend. Faith could see her friend's distinctive long eyelashes and straight teeth but could not perceive her friend's entire face in a glance. This realization stunned Faith, and in the days that followed, she noticed that she also couldn't judge age, gender, expression, gaze direction, or attractiveness from the face. Faith's voice perception however was normal (Jiahui et al., 2017), and she was also able to recognize people's bodies from a distance. Faith's difficulties with face perception have persisted, and they create numerous difficulties for her in social settings. Neuroimaging has shown that her face deficits result from the typical cause of prosopagnosia—damage to the posterior right hemisphere face-selective areas (Susilo et al., 2015).

In addition to providing the first indication of the critical role that ventral occipital and temporal regions play in face processing (Hecaen and Angelergues, 1962; Whiteley and Warrington, 1977), cases like Faith's have also highlighted hemispheric differences in face recognition. Numerous cases have resulted from unilateral lesions to the right hemisphere (Busigny et al., 2014; Dalrymple et al., 2011; De Renzi, 1986; Susilo et al., 2015). In contrast, only a handful of cases have been reported following lesions limited to the left hemisphere. fMRI and EEG responses to faces are also right lateralized in right-handed neurotypical participants (Bentin et al., 1996; Bukowski et al., 2013; Eimer, 2011) and stimulation to right-hemisphere face areas is far more likely to produce face distortions than stimulation to left-hemisphere face areas (Rangarajan et al., 2014). Right lateralization in right and left handers is comparable for OFA and pSTS, but right FFA tends to be larger than left FFA in right handers but this relationship is reversed in some left handers (Bukowski et al., 2013). Accordingly, most prosopagnosia cases resulting from left hemisphere lesions are left handed (Rossion, 2014). Interestingly, the macaque face network, with the exception of an orbitofrontal face area, does not appear to be right lateralized (Tsao et al., 2008a,b).

Studies of visual recognition following brain damage have suggested face processing depends, at least in part, on mechanisms different from those used for object recognition. Acquired prosopagnosics often have deficits with object recognition (Dalrymple et al., 2011; Damasio et al., 1982), but spared object recognition has been demonstrated in a number of thoroughly tested cases (Busigny et al., 2014; McNeil and Warrington, 1993; Rezlescu et al., 2012, 2014; Riddoch et al., 2008). For example, following a right

occipito-temporal lesion, Patient R.M. could no longer recognize his face in the mirror and had great difficulty with judgments of age, sex, and expression (Sergent and Signoret, 1992). Nevertheless, he scored substantially better than all control participants on a task in which participants were presented with 210 photographs of cars and asked to report the car make, model, and model year. The opposite condition—spared face recognition with object agnosia—has also been documented (Assal et al., 1984; McMullen et al., 2008). The most in-depth investigation of this condition involved Mr. C.K. who suffered a closed head injury after being struck by a car while jogging (Gauthier et al., 2004; Moscovitch and Moscovitch, 2000; Moscovitch et al., 1997; Rivest et al., 2009). Mr. C.K.'s object recognition and word recognition were severely impaired; he struggled to recognize objects at even the basic level (e.g., a car, a chair). His recognition of upright faces, however, was comparable to controls (Moscovitch and Moscovitch, 2000; Moscovitch et al., 1997; Rivest et al., 2009).

Developmental prosopagnosia

Acquired prosopagnosia has been studied for many decades, but more recently it has become apparent that many people have great difficulty recognizing facial identity due to developmental problems rather than brain damage (Bentin et al., 1999; Duchaine, 2000; Hasson et al., 2003; Nunn et al., 2001). This form of prosopagnosia is known as *developmental prosopagnosia* (DP) (McConachie, 1976; Susilo and Duchaine, 2013) or *congenital prosopagnosia* (Behrmann and Avidan, 2005). Deficits with facial identity in DP can be as severe as those seen in acquired prosopagnosia. For example, one DP who contacted our laboratory (www.faceblind.org) told us: “I wasn’t sure who the groom was at my wedding and grabbed a similarly-built groomsman for the cake cutting.” DP sometimes runs in families (De Haan, 1999; Duchaine et al., 2007; Duchaine, 2008), consistent with twin studies that have revealed that differences in face recognition are driven primarily by genetic differences (Shakeshaft and Plomin, 2015; Wilmer et al., 2010; Zhu et al., 2010). Several findings indicate face processing in DP depends on qualitatively similar mechanisms as it does in individuals with normal face processing (Abudarham et al., 2021a; Jiahui et al., 2018; Tardif et al., 2019). Thus, it appears that DPs represent the extreme lower tail of the normal distribution (Barton and Corrow, 2016), with super recognizers occupying the opposite end of the distribution (Bobak et al., 2016; Ramon, 2021; Russell et al., 2009). Like acquired prosopagnosia cases, individuals with DP are more likely to have trouble with aspects of face perception other than identity such as detection (Garrido et al., 2008), expression (Biotti and Cook, 2016), and sex (Marsh et al., 2019).

Not surprisingly, DP is associated with neural differences in regions similar to those that produce acquired prosopagnosia. While fMRI studies have found that the locations of face-selective areas in DPs and neurotypical individuals are comparable (Jiahui et al., 2018), the responses in these areas in DPs are reduced (Dinkelacker et al., 2011; Furl et al., 2011; Jiahui et al., 2018; Zhao et al., 2016) as is connectivity between face areas (Lohse et al., 2016; Rosenthal et al., 2017; Song et al., 2015; Zhao et al., 2016). Examination of the time course of DP face processing with EEG has shown abnormal responses are present across a broad range of time points over the temporal lobe (Eimer et al., 2012; Fisher et al., 2016), with the first differences emerging within 200 ms of stimulus presentation (Fisher et al., 2016; Towler et al., 2012). Structural differences in the vicinity of face-selective areas have been detected in both gray matter (Behrmann et al., 2007; Garrido et al., 2009) and white matter (Gomez et al., 2015; Song et al., 2015).

Experimental disruption of face processing

Experimental disruption during behavioral performance provides a controlled means to demonstrate a causal link between neural mechanisms and behavior, and studies using these methods in both humans and monkeys have demonstrated clear links between particular neural regions and face recognition. Transcranial magnetic stimulation (TMS) provides a non-invasive means to examine the functional role of brain regions in humans. Because of TMS’s limited ability to target regions not close to the scalp, most studies have targeted superficial face areas OFA and pSTS-FA. TMS to the right OFA impairs face shape discrimination but not object or body shape discrimination (Pitcher et al., 2007, 2009, 2012). Similarly, TMS to the extrastriate body area (EBA) selectively disrupts body discrimination while TMS over the lateral occipital complex (LO), an area implicated in object recognition, selectively disrupts object discrimination (Pitcher et al., 2009). The three category-selective areas targeted in these studies all responded substantially to non-preferred categories (e.g., objects and bodies for OFA) (Schwarzlose et al., 2008), so the category-selectivity of these impairments indicates (i) the presence of a response within a region does not imply behavioral relevance (see also Dilks et al. (2013), Pitcher et al. (2011b)), and (ii) supports a modular view of high-level visual recognition. Consistent with results from acquired prosopagnosics, TMS over both OFA and pSTS-FA has been found to disrupt expression perception (Pitcher et al., 2008; Sliwinska et al., 2020), but the effective time window for pSTS-FA disruption is longer than the OFA window (Pitcher et al., 2008) consistent with the notion of hierarchical processing.

Intracranial stimulation has a long history in human neuroscience, and researchers have applied it to investigate the neural basis of face processing (Allison et al., 1994; Puce et al., 1999), particularly in the last decade (Jonas et al., 2012, 2014, 2015; Rangarajan et al., 2014; Rangarajan and Parvizi, 2016; Schalk et al., 2017; Schrouff et al., 2020). After mapping the category-selectivity of regions in right middle and posterior fusiform gyrus, Parvizi et al. (2012) electrically stimulated face-selective areas. These stimulations caused pronounced distortions to face percepts (Parvizi et al., 2012). Consistent with a modular view, the patient reported only subtle distortions when the face regions were stimulated while he was viewing non-face objects. Evidence for functional lateralization of face-processing was provided by another study from this group which found stimulation to the right hemisphere face areas caused face-selective distortions, but comparable stimulation in the left hemisphere did not distort face percepts but led only to non-face, elementary distortions like phosphenes (Rangarajan et al., 2014). Similarly, Jonas et al. (2014) stimulated right OFA, severely disrupting the ability to discriminate simultaneously presented faces (see also Jonas et al. (2012)). Thus, electrical stimulation demonstrates a causal role of right hemisphere face-selective areas for face processing. Moreover, the absence of face

distortions following stimulation to left hemisphere face areas in combination with the rarity of acquired prosopagnosia after unilateral left hemisphere lesions raise questions about what role left hemisphere areas make to face processing in humans (but see (Sliwinska and Pitcher, 2018)).

Even closer causal links between face activity and behavior have been established in macaque monkey. Afraz et al. (2006) electrically stimulated clusters of face-selective neurons in anterior inferotemporal cortex. Subjects were more likely to detect a face when face clusters were electrically stimulated, whereas stimulation of clusters that were not face-selective did not affect behavior. Electrical stimulation in anterior inferotemporal face area AM altered face identification and also the perception of some non-face objects (Moeller et al., 2017). Similarly, causal manipulations inside or close to medial face areas also changed performance on different face-processing tasks. Sadagopan et al. (2017) inactivated face area ML in one hemisphere with muscimol, a GABA_A agonist, while subjects had to detect a target stimulus inside a cluttered stimulus array. Inactivation decreased detected likelihood in a psychometric fashion, as if target stimulus contrast had been perceptually reduced, only for face, but not control stimuli like bodies or shoes. Afraz et al. (2015) used optogenetics and muscimol in separate experiments to selectively suppress activity in face-selective clusters in the lower bank of the STS, likely in the vicinity of ML. During face gender decisions, suppression in face clusters, but not outside them, weakly disrupted performance. Together, these causal studies demonstrate that face-selective neurons and face-selective areas play critical roles in primate face processing.

Recognition of familiar and unfamiliar faces

The primary goal of the face identity processing is to recognize the faces of familiar people. This is because the need to identify unfamiliar faces is quite rare in real-life settings. Nevertheless, most research on face recognition has used unfamiliar faces to investigate the mechanisms of face recognition, under the explicit or implicit assumption that the perceptual representation of unfamiliar faces can inform us about the representation of familiar faces as well. Indeed, there are many phenomena in face recognition that are common to both familiar and unfamiliar faces (for review see (Johnston and Edmonds, 2009)). These include the face-inversion effect (Yarmey, 2013; Yin, 1969, but see Megreya and Burton, 2006), measures of holistic processing such as the composite face effect (Le Grand et al., 2004; Young et al., 1987), and the Thatcher illusion (Thompson, 1980). Furthermore, contrast negation impairs (Kemp et al., 1996), and distinctiveness enhances recognition of both familiar and unfamiliar faces (Bruce et al., 1987). Also, prosopagnosic individuals almost always have difficulty both in recognizing familiar faces and perceptually matching unfamiliar faces (Dalrymple et al., 2011; Duchaine et al., 2007; Van Belle et al., 2010), and super recognizers, show superb performance both for familiar faces (Russell et al., 2009) as well as on unfamiliar face perception and recognition tasks (Bobak et al., 2016).

Despite these similarities, empirical findings and theoretical models of face recognition have, at the same time, emphasized significant differences between the representations of familiar and unfamiliar faces (Bruce and Young, 1986; Hancock et al., 2000; Johnston and Edmonds, 2009; Kramer et al., 2018; Young and Burton, 2018). This is primarily motivated by the better performance in perceptual matching and old-new memory tasks for familiar than unfamiliar faces, in particular when different images of the same identity are used (e.g., Bruce (1982), Jenkins et al. (2011), Ritchie et al. (2015)). These findings have led to the suggestion that unfamiliar faces are represented by a pictorial code and familiar faces are represented by a view-invariant, structural code, therefore suggesting qualitatively different perceptual representations for familiar and unfamiliar faces. However, recent neuroimaging, computational, and behavioral studies suggest that the perceptual representation of familiar and unfamiliar faces are similar and that differences emerge at post perceptual stages (Abudarham et al., 2019, 2021b; Blauch et al., 2021; Landi and Freiwald, 2017).

An fMRI study in macaque monkeys showed that all face areas respond more strongly to familiar than to unfamiliar faces (Landi and Freiwald, 2017). This increased response was found in two paradigms, one in which sequences of images of personally familiar and unfamiliar faces and objects were shown, and one in which personally familiar and unfamiliar stimuli were revealed slowly over the course of 32 s by adding increasing amounts of high spatial frequency information. Responses to personally familiar and unfamiliar faces differed quantitatively, but not qualitatively: the response to the former appeared to be a scaled-up version of the latter (Landi and Freiwald, 2017). How these overall activity effects, manifesting at the level of entire areas, are reflected at the level of neural populations, remains unknown. It is possible that more neurons are tuned to personally familiar faces than to unfamiliar ones, a coding mechanism that would maintain face space representations (as discussed above) for both familiar and unfamiliar faces, but other scenarios are possible as well. These findings are consistent with human neuroimaging studies that showed similar responses to familiar and unfamiliar faces in posterior perceptual face areas (Natu and O'Toole, 2011; Ramon and Gobbini, 2017).

Electrophysiological and neuroimaging findings are overall consistent with the proposal that differences between the representation of familiar and unfamiliar faces take place at post-perceptual stages. ERP studies in humans report that differences between familiar and unfamiliar faces are typically found at 250 and 400 ms after stimulus onset (for review see (Ramon and Gobbini, 2017)). Human fMRI studies reveal differences between familiar and unfamiliar faces in anterior temporal areas or in social brain regions (Collins and Olson, 2014; Gobbini et al., 2007; Natu and O'Toole, 2011; Ramon and Gobbini, 2017) rather than in the more posterior visual face areas. In the aforementioned fMRI study in macaque monkeys (Landi and Freiwald, 2017), two additional face areas were found that had not been noticed in prior studies with unfamiliar faces and were particularly strongly modulated by personal face familiarity. One of these areas was located in perirhinal cortex (called PR), the other in the temporal pole region (called TP). When tested with the 32-s slow reveal paradigm, these areas exhibited a qualitative difference in response between personally familiar and unfamiliar faces. They exhibited a non-linear response increase akin to the moment of recognition, but did not show this response during the presentation of unfamiliar faces or objects (Landi and Freiwald, 2017). This stands in

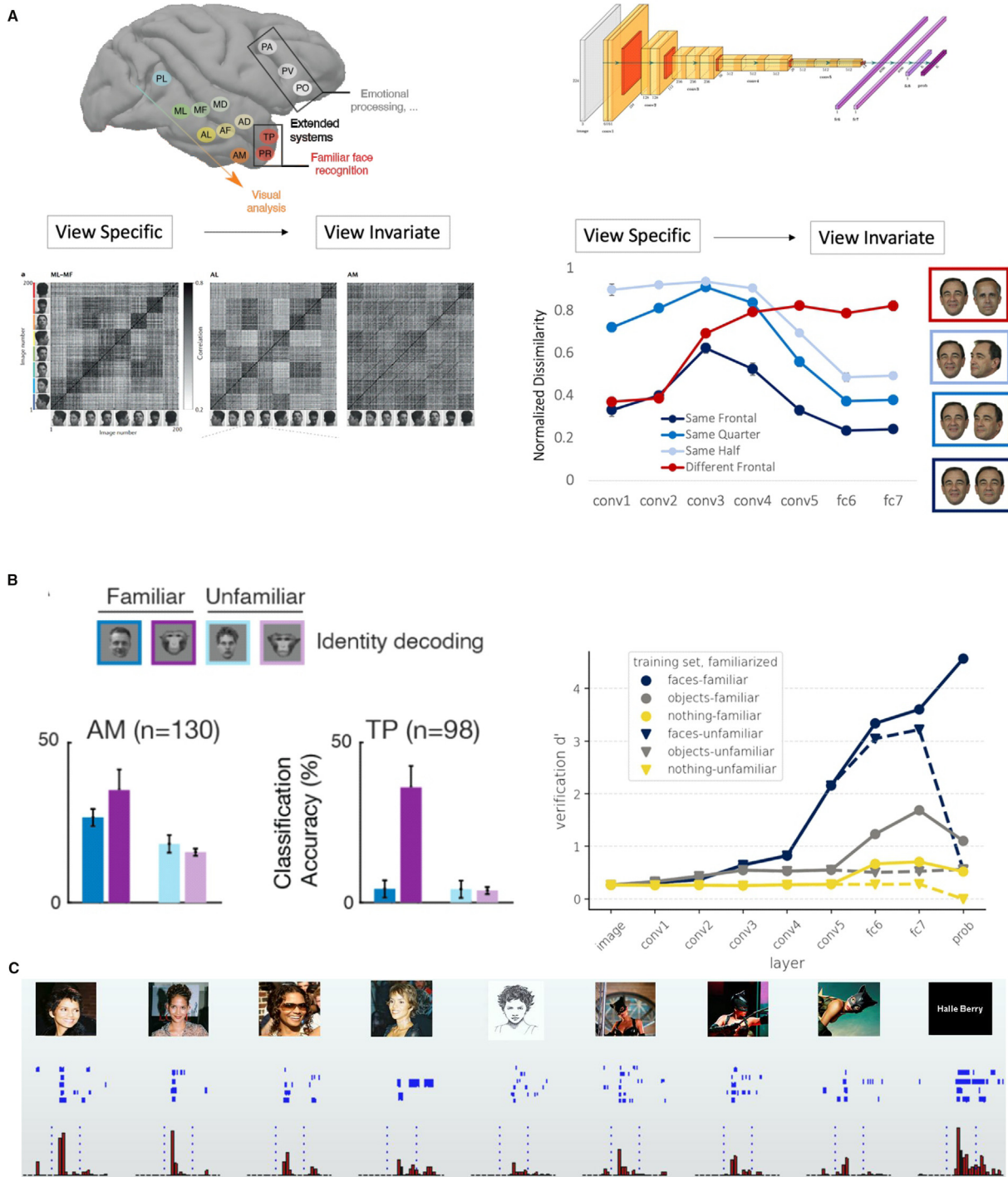


Fig. 5 (A) Left: Faces are processed in a hierarchical manner from a view-selective representation in posterior face patches (ML/MF) to a view-invariant representation in the anterior face patch (AM) (Freiwald and Tsao, 2010; Landi and Freiwald, 2017). Right: Similar hierarchical representation is also found in DCNN (shown for VGG-16) optimized for face recognition. Normalized dissimilarity was computed based on the distance between feature vectors for pairs of same identity faces across different views (blue) or different identity faces from the same view (red) for each layer of a DCNN. Results indicate a view-specific representation in low-level layers and a view-invariant representation in high-level layers of the network (Abudarham et al., 2021b; Blaich et al., 2021). (B) Left: The high-level perceptual area, AM, can classify both familiar and unfamiliar faces, whereas TP can classify only personally familiar faces (Landi et al., 2021). Right: Performance for familiar (trained) and unfamiliar (untrained) faces in a face-trained DCNN, object-trained DCNN and untrained DCNN (Blaich et al., 2021). Performance for familiar and unfamiliar faces is similar in the high-level perceptual layer, fc7. An additional increase in performance for familiar faces is found in the output/identity-based layer that classifies the representation that is generated by fc7 to the trained identities. Thus, performance for unfamiliar faces is mediated by the perceptual system, whereas

stark contrast to the core face-processing network, in which even the most high-level area AM did not exhibit this effect. Electrophysiological recordings targeted to AM and TP confirmed and extended these differences at the single-cell level (Landi et al., 2021). They also showed that, surprisingly, population responses and coding latencies were similar in AM and TP, suggesting (but not demonstrating) parallel rather than serial processing in these areas (as suggested by the classical Bruce and Young model (1986) (Fig. 2C) and subsequent models that built on it). One implication of this result is that differences between neural responses to familiar and unfamiliar faces found at short latencies in the human brain (Dobs et al., 2019; Visconti di Oleggio Castello and Gobbini, 2015), may not necessarily reflect differences at perceptual stages of processing, but could as well reflect differences in the visual representation at subsequent memory stages.

The finding that differences between the representation of familiar and unfamiliar faces emerge at post-perceptual stages is also consistent with a recent computational model of familiar face recognition that compared performance levels for trained (familiar) and untrained (unfamiliar) faces in face-trained, object-trained, and untrained deep convolutional neural networks (DCNNs) (Blauch et al., 2021) (Fig. 5A). Findings show that performance at the final perceptual (penultimate) layer, which corresponds to high-level perceptual representation, is similar for trained and untrained identities (Fig. 5C). An advantage in identification for familiar faces is found in the output layer, where the trained faces are classified to different identities based on their perceptual representations. Thus, performance for familiar and unfamiliar faces is determined by different parts of the system. Familiar face matching is based on classifying faces to identity-based representations of the trained identities. This finding is similar to TP which classifies only personally familiar faces but not unfamiliar faces (Fig. 5B). Unfamiliar face matching is based on the perceptual distance between their representations in the preceding, perceptual layer of the network. This high-level perceptual representation is not fully pictorial but similar to AM, enables generalization across different head-views also for unfamiliar faces (Fig. 5A). Consistent with these findings, it has been recently suggested that this generalization across different head-views is enabled by a subset of critical, view-invariant facial features that are used for identification of both familiar and unfamiliar faces in humans as well as in the penultimate layer of DCNNs optimized for face recognition (Abudarham et al., 2019, 2021b). This view-invariant representation and sensitivity to these critical facial features depends on specific experience with faces and is not found in a DCNN that was optimized for object recognition (Abudarham et al., 2021b).

Another important distinction that is revealed in both the monkey and human studies is the difference between visually familiar and personally familiar faces. Visually familiar faces are face images that were shown repeatedly visually, typically in the context of a lab experiment. Personally familiar faces are not only visually familiar but are also associated with unique semantic information. Landi and Freiwald (2017) found a clear difference between these two types of familiarizations. Only personally familiar faces but not visually familiar faces showed the non-linear response increase in PR and TP. These findings may be similar to human neuro-imaging studies that also found differences in neural response to visually and personally familiar faces (Natu and O'Toole, 2011). Personally familiar faces differ from lab-based visual familiarization in the amount of visual exposure, which is more extensive to the former, but are also strongly associated with semantic information that visually familiar faces lack. How can we tell if the differences between visually familiar and personally familiar faces is due to visual or semantic differences between them? To study the relative contribution of visual and conceptual exposure during the process of familiarization, while matching the amount of visual exposure, recent studies have presented faces with person-related labels such as names or occupations, with person-unrelated labels such as object names, or with no labels (Schwartz and Yovel, 2016). Person-related labels improved recognition, whereas person-unrelated labels did not improve recognition relative to non-labels. Similarly, social-evaluations of faces during encoding (e.g., how intelligent does the face look?) improves face recognition, whereas perceptual-evaluations during encoding (e.g., how round does the face look?) does not improve recognition, relative to faces that were learned with no evaluations (Schwartz and Yovel, 2019a,b). Furthermore, a recent fMRI study showed that faces that were evaluated socially but not perceptually during encoding activated the social brain network during retrieval (Shoham et al., 2021). Thus, the process by which faces become personally familiar is not purely visual but involves semantic and social processing mechanisms that convert a visually meaningless representation of an unfamiliar face image to a socially meaningful representation of a familiar person.

Taken together, the perceptual and conceptual experience that primates have with familiar faces enables the system to learn faces in a supervised manner, linking different appearances of the same identity to an identity-based representation. Single-cell recordings from one face-familiarity area in the temporal pole shows that these representations are still face, and not person selective (Landi et al., 2021), thus matching the prediction of specific face recognition units by Bruce and Young (1986). Bruce and Young proposed that a subsequent stage of processing would contain person identity representations. The cells with properties closest to what one might expect at such a processing stage are the so-called "concept cells", which have been found in medio-temporal lobe areas, including hippocampus and perirhinal cortex, in humans (Quiroga et al., 2005). These cells demonstrate robustness to very different pictures of a known individual (Fig. 5C). And some of these cells have been shown to respond also to the written name of a person or even an auditory signal revealing their identity, showing that these are not simply face, but a conceptual person-selective cells (Quiroga, 2012). This representation thus reflects invariance beyond purely visual information about the

performance for familiar faces is mediated by an identity-based representation of familiar faces. (C) Single unit recordings in humans' hippocampus and perirhinal cortex revealed neurons, known as "concept neurons", that show an identity-selective response to highly variable images of familiar identities. This representation is based on person knowledge indicating that conceptual information links different visual appearances of the same identity to an identity-based representation. In this example, the response to different images of the actress Halle Barry (including image in which her face is masked and another displaying her name) is based on person knowledge rather than perceptual information of her identity (Quiroga et al., 2005).

face that must be based on person knowledge. Thus, combinations of visual and conceptual factors are likely to contribute to the invariant representation of familiar faces and people.

Conclusion/summary/outlook

Primates possess specialized machinery within the visual system to process the socially important stimulus category of faces. The system is organized at multiple levels, from single cells, through clusters or columns, areas, to networks. Within the network, there is functional specialization, which can often be linked in a meaningful manner to specific perceptual phenomena or computational steps in face processing. Some of these links have been established closely, though frequently more coarsely than correlational studies, through causal manipulations. Compared to other high-level visual processes or to other computations within the social brain, links between neural processes and behavior in the face-processing system, due to many decades of study, are very close. Yet these links will need to become even closer if we are to gain a full understanding of the system's operation. We are briefly highlighting four areas of future development.

The neural mechanisms of face processing have been explored in great detail, but a deeper understanding is still necessary. Cortex consists of many different cell types wired together into intricate local circuits, which then connect to each other at larger scales. We lack a deeper understanding of what the functions are that each level of organization affords, and how these functional properties at different levels of organization interact to generate overall face-recognition behavior. For example, there is evidence for feedback in the form of prediction signals passed from higher-level to lower-level areas (Issa et al., 2018; Schwiedrzik and Freiwald, 2017). Yet how the supposed inter-areal interactions take place or interact with local processes is currently unknown. Resolving these questions will be of relevance for understanding the operations of large brains in general beyond the domain of face recognition.

Some computational principles of the system's operation have been worked out, lifting the understanding of the system beyond a descriptive level. We now have theories for why ramp-shape tuning might emerge across all face-selective areas (Hosoya and Hyvarinen, 2017), why mirror-symmetric tuning might arise specifically at the hierarchical level of face area AL (Leibo et al., 2017), or why it might have a modular dimension to its functional organization (Dobs et al., 2022). And the increased use of computational modeling, sometimes very closely integrated to combine it with stimulus generation (Ponce et al., 2019), raises new possibilities for understanding the selectivity of face cells. This work needs to be moved ahead, in close conjunction with increasing mechanistic understanding, to gain a deep understanding of why the system is organized and why it works the way it does.

Relatively little attention has been paid to understanding the computational goals of the face-processing system. Typically, assumptions are made about the kinds of discriminations a particular area should be capable of or of the capabilities a deep network model of a particular processing hierarchy should have. This is not untypical for visual neuroscience at large. But given the rich sets of information faces provide and the advanced understanding that, in many cases, psychophysics has provided about how these are processed, more effort will need to be made to better understand these computational goals and their implementation. A case in point is recent modeling of the face-processing system as an analysis-by-synthesis system (Yildirim et al., 2020), in which incoming visual information is not simply used to infer the facial identity, but to fit the latent variables of an internal face model. This very different conceptualization of what it is the system is trying to achieve was more successful in explaining its physiology and psychophysics, highlighting that we might still be missing some of the fundamentals of organization and function of these systems.

To achieve a deeper level of understanding, we will need to better appreciate how different parts of the face-processing network feed into and interact with other parts of the brain. Understanding what is read out and how will be critical to appreciating the computational goals within the system as much as elaborating its role for behavior. In the Introduction, we highlighted how closely face processing is integrated with behaviors like gaze-following, facial mimicry, person knowledge, or social cognition. We can already see some of the links between networks, but none have been analyzed with the precision or depth that has been achieved inside face-processing systems. Faces will present both a challenge and an opportunity. The challenge are the multiple social dimensions of faces, providing a multitude of pieces of information. The opportunity is that there are dedicated circuits for face processing, greatly simplifying the analytic process in large primate brains.

Conflict of interest

None to disclose.

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Relevant websites

<https://facetest.psy.unsw.edu.au>.
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