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# Face Processing Systems: From Neurons to Real-World Social Perception

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Annu. Rev. Neurosci. 2016. 39:325–46

The *Annual Review of Neuroscience* is online at [neuro.annualreviews.org](http://neuro.annualreviews.org)

This article's doi:

10.1146/annurev-neuro-070815-013934

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## Keywords

face recognition, functional brain organization, neural mechanisms of behavior, social brain function

## Abstract

Primate face processing depends on a distributed network of interlinked face-selective areas composed of face-selective neurons. In both humans and macaques, the network is divided into a ventral stream and a dorsal stream, and the functional similarities of the areas in humans and macaques indicate they are homologous. Neural correlates for face detection, holistic processing, face space, and other key properties of human face processing have been identified at the single neuron level, and studies providing causal evidence have established firmly that face-selective brain areas are central to face processing. These mechanisms give rise to our highly accurate familiar face recognition but also to our error-prone performance with unfamiliar faces. This limitation of the face system has important implications for consequential situations such as eyewitness identification and policing.

## Contents

NEURAL SYSTEMS FOR FACE PROCESSING .....	326
Distributed and Modular Organization .....	327
Face Networks: Parallel and Hierarchical Pathways.....	327
Human and Nonhuman Primate Face-Processing Systems.....	329
FACE PROCESSING: FROM CELLS TO BEHAVIOR.....	330
Face Detection .....	330
Holistic Face Representations .....	330
Face Space .....	331
Faces as Sources of Social Information.....	334
CAUSAL LINKS BETWEEN FACE-PROCESSING	
SYSTEMS AND BEHAVIOR.....	334
Acquired Prosopagnosia .....	334
Experimental Disruption of Face Processing .....	335
RECOGNITION OF FAMILIAR AND UNFAMILIAR FACES .....	337
FACE RECOGNITION IN THE REAL WORLD: CHALLENGES	
AND POSSIBLE SOLUTIONS.....	339
CONCLUSION .....	340

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 is effortless. How is that possible? The 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 link to behavior. We highlight the surprising limitations of unfamiliar face recognition and discuss their implications for real-world situations such as eyewitness testimony.

## NEURAL SYSTEMS FOR FACE PROCESSING

Gross's discovery of cells selective for faces provided the first evidence consistent with earlier ideas about single-unit coding of person identity, which Lettvin had famously referred to as grandmother cells (Gross 2002). Gross's 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 & Bengio 1995, Riesenhuber & Poggio 1999). What the discovery of face cells did for the concept of hierarchy, the discovery of entire face areas by functional magnetic resonance imaging (fMRI) (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

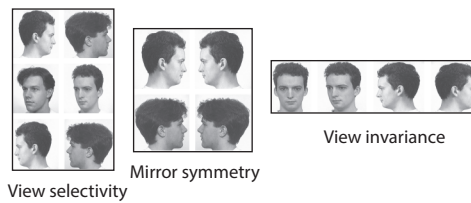
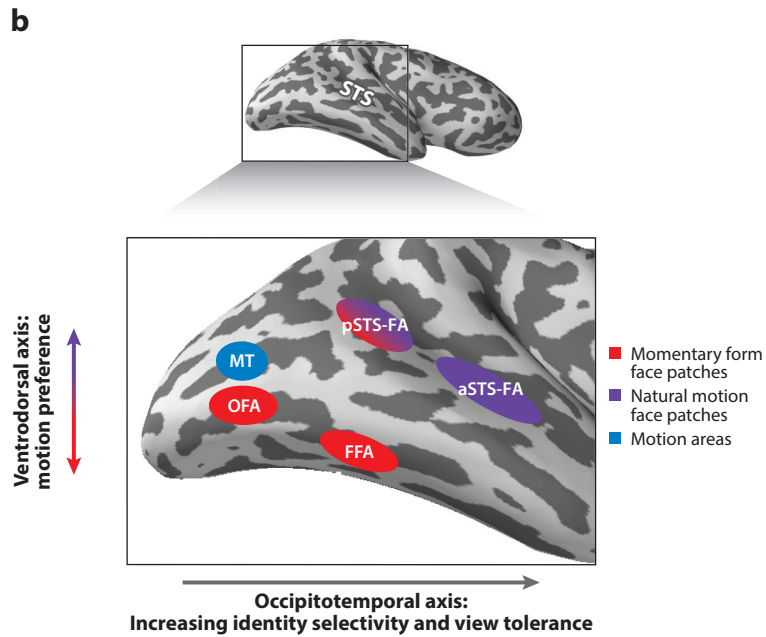
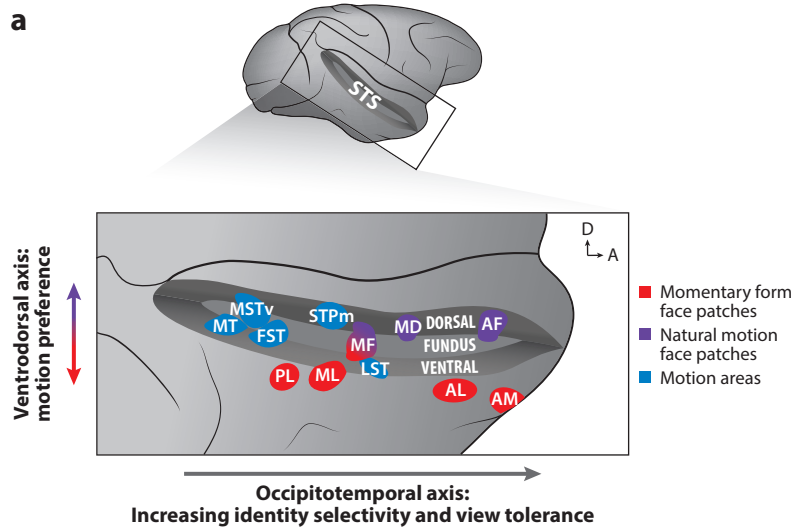
Face cells have been found across temporal (Perrett et al. 1992) and prefrontal cortex (PFC) (Ó Scalaidhe et al. 1997, Rolls et al. 2006) of the macaque monkey brain, suggesting that faces are represented in a distributed fashion. Local clustering of face cells (Perrett et al. 1984) suggested the organization of columns that was later found (Fujita et al. 1992). Subsequent neuroimaging studies revealed a large-scale organizational feature: face patches several millimeters in diameter (Pinsk et al. 2009; Tsao et al. 2003, 2008a). These patches are primarily located laterally in the lower bank of the superior temporal sulcus (STS) and mediodorsally in the fundus (see **Figure 1a**). Face patches contain very high fractions of face-selective neurons (Freiwald & Tsao 2010, Issa et al. 2013, Tsao et al. 2006). Whatever the computational reason for local grouping of face cells, they constitute domain-specific specialized hardware, possibly implementing functional modules (Kanwisher 2010). As multiple face areas have been found across temporal cortex and PFC (Tsao et al. 2008a,b), it has become clear that modular organization goes hand in hand with distributed processing.

## Face Networks: Parallel and Hierarchical Pathways

Distributed face areas do not operate in isolation but are interconnected into a face-processing network through selective long-distance connections (Moeller et al. 2008). 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 (Freiwald & Tsao 2010). 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 & Tsao 2010, Meyers et al. 2015). In the most posterior area, the posterior lateral face patch (PL), selectivity for a single feature, the contralateral eye, seems to dominate (Issa & DiCarlo 2012); at the next level, in areas the middle fundus (MF) and middle lateral (ML) face patches, 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). Although face representations in the MF and ML are view selective, this dependence is reduced at the next level, the anterior lateral face patch (AL), through construction of a representation with mirror-symmetric invariance to head orientation, and reduced even further in the anterior medial face patch (AM), where representations for facial identity are robust against variation in head orientation (Dubois et al. 2015, Freiwald & 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 ventrodorsal 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 & Freiwald 2015a). These results suggest different kinds of facial information are processed through two parallel streams. However, given the complex connectivity between face areas (Moeller et al. 2008) and the fact that information processed in either stream is likely informative for computations in the other, the parallelism is likely not one of functional isolation between streams.

The spatial distribution of face patches requires long-distance connections for them to interact, thus raising the question of why the system is organized in this seemingly noneconomical 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 colocalization of color patches directly ventral to some face areas (Lafer-Sousa & Conway 2013). Face and color processing share a foveal bias (Halgren et al. 1999), and because retinotopic organization is carried from early- into high-level visual areas (Levy et al. 2001), a retinotopic bias for color and faces might play a role in their colocalization (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 colocalization with face areas may serve to support person perception.

## Human and Nonhuman Primate Face-Processing Systems

Despite an estimated 25 million years of separate evolution (Stewart & Disotell 1998), human and macaque face processing systems bear remarkable similarities, and some of these similarities might extend to the evolutionarily more distant New World monkeys (Hung et al. 2015). In the human temporal and frontal lobes, researchers have found multiple, spatially separate face areas (for a recent review, see Duchaine & Yovel 2015) (**Figure 1b**). Like macaques, human ventral face areas are adjacent to body-selective areas (Peelen & Downing 2005, Schwarzlose et al. 2005), and they are similarly accompanied, ventrally, by color areas (Lafer-Sousa et al. 2016). The overall number of face areas is similar to that in macaques, and so is their spatial arrangement in the temporal lobe with two occipitotemporal streams, one in ventral temporal cortex and the other, dorsal stream in the STS (Yovel & Freiwald 2013). Functional specializations along the ventral stream of face areas follow a progression similar to that in the macaque monkey, suggesting a hierarchical organization: In the occipitotemporal direction, face selectivity increases (Bell et al. 2009), position dependence decreases (Hemond et al. 2007), mirror symmetric confusion of facial

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### Figure 1

Organization of face processing systems in the macaque and human brain. (a) Face patches in the macaque STS, shown here opened on a lateral view of the brain (*top*), are organized functionally along an occipitotemporal (posterior-anterior) axis and a ventrodorsal axis (expanded view, *bottom*). Arrows in the upper right corner indicate dorsal (D) and anterior (A) directions. General motion areas (*blue*) and face areas (*red* and *purple*) are shown. Ventral areas (in the ventral bank of the STS and further ventrally) are selective for momentary form of faces (*red*), whereas areas at more mediodorsal locations in the STS (fundus and dorsal bank) are selective for natural facial motion (*purple*). Hierarchical processing from view-selective to view-invariant representation is manifested in the posterior-anterior axis: Representations are transformed from view-specific into increasingly view-tolerant and identity-selective ones. (b) Face and motion areas (colors as in panel a) in the human brain are found ventrally in the lateral occipital cortex and the fusiform gyrus and dorsally in the STS. A functional organization of hierarchical processing along the posterior-anterior axis and sensitivity to motion along the ventrodorsal axis is found, similar to the one in the macaque brain. The ventral areas (*red*) show no sensitivity to motion, whereas face areas in the STS are highly sensitive to moving faces. As in the macaque brain, the transformation along the occipitotemporal axis progresses via an intermediate representation that does not differentiate between left and right profile views (*bottom*). View selectivity was found in the lateral occipital cortex and mirror symmetry in the fusiform gyrus and pSTS. Abbreviations: AF, anterior fundus face patch; AL, anterior lateral face patch; AM, anterior medial face patch; aSTS, anterior STS; FA, face area; FFA, fusiform face area; FST, fundus of the superior temporal motion area; LST, lower superior temporal motion region (Nelissen et al. 2006); MD, middle dorsal face patch; MF, middle fundus face patch; ML, middle lateral face patch; MSTv, ventral medial superior temporal area; MT, middle temporal motion area; OFA, occipital face area; PL, posterior lateral face patch; pSTS, posterior STS; STPm, middle part of the superior temporal polysensory region; STS, superior temporal sulcus.

profile views emerges (Axelrod & 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 in the presence of an anatomically correctly placed body, and this augmentation grows stronger from posterior to anterior face areas (Bernstein et al. 2014, Fisher & Freiwald 2015b, Song et al. 2013). Furthermore, selectivity for facial motion is highly pronounced in dorsal areas but not in ventral ones (Fox et al. 2009, Pitcher et al. 2011a). Similar to the macaque, the ventral face areas appear to be interconnected, whereas 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 PFC (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 & Yovel 2013, Chan & Downing 2011, Pitcher et al. 2011a). Thus, human and macaque face-processing systems, according to at least two sets of criteria, anatomical location and functional specialization, appear to be homologous.

## FACE PROCESSING: FROM CELLS TO BEHAVIOR

### Face Detection

For facial information to be extracted, the presence and location of 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, with the eyes set back relative to the forehead, the forehead will be brighter than the eyes under most illumination conditions. Because change of appearance owing to illumination variation is among the most difficult problems for object recognition, heuristics that are robust against this nonaffine 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 use at least 12 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 the 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) (**Figure 2a**) (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 12 pairs found to be important in human detection behavior, and the population's polarity preferences matched those of human observers in all 12 cases.

### 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 & 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 reduced overall (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 the ML and 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, whereas 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 (Freiwald et al. 2009). 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 change position markedly 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 & 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, the most striking expression of the context dependence of facial features may be the so-called Thatcher illusion (Thompson 1980). Inversion of local features such as the eyes or the mouth, which are noticed easily 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) (**Figure 2b**).

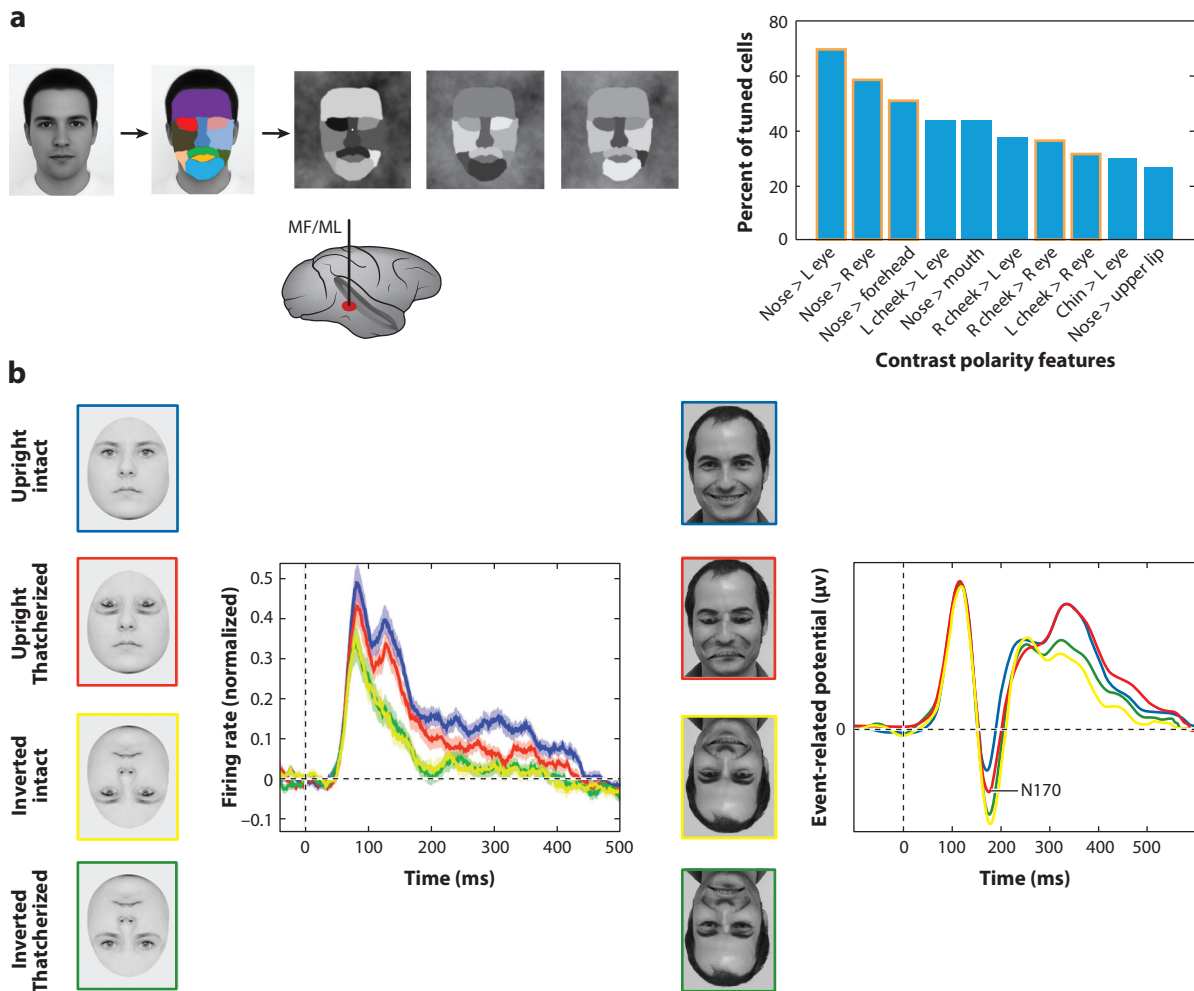
## Face Space

Many productive investigations of face processing have utilized the concept of face space: a multidimensional space in which each face occupies a unique position based on its combination of features (Leopold et al. 2001, Turk & Pentland 1991, Valentine 1991). The space is thought to be 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 (**Figure 2c**). The distance of a face along a trajectory is determined by the similarity of a face to the average face, so distinctive faces occupy the fringes of the space.

Two main models have been considered in discussions of how dimensions in face space are coded (Rhodes & Leopold 2011). One possibility is broad tuning curves spanning entire axes of face space. Such ramp-shaped tuning curves of opposite polarity can encode the position of a face feature along an axis efficiently. Second, 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 that the center of face space occupies a special position such that identities located in opposite directions are related to each other even though they are perceptually dissimilar: When one adapts to one identity, subsequent perception of the anti-identity, but not that of an equidistant control identity, is enhanced (Leopold et al. 2001). This effect is compatible with the broad tuning model, not the exemplar-based model. Moreover, these aftereffects are stronger than aftereffects found when faces matched in similarity to face/antiface pairs are used to create a morph continuum (Rhodes & Jeffery 2006). Consistent with these psychophysical findings, broad tuning was indeed found in two macaque face areas.

In the ML and MF, the aforementioned feature tuning is predominantly ramp-shaped, yielding a maximal response to one extreme and a minimal response to the opposite extreme (**Figure 2c**), and for almost all feature dimensions, opponent polarities were found across cells (Freiwald et al. 2009). More anteriorly, likely in AM, broad tuning curves have also been found in response to facial identities (Leopold et al. 2006). Unlike tuning curves of cells in the ML and MF, these tuning curves exhibited increased firing as a function of distance from the center of face space

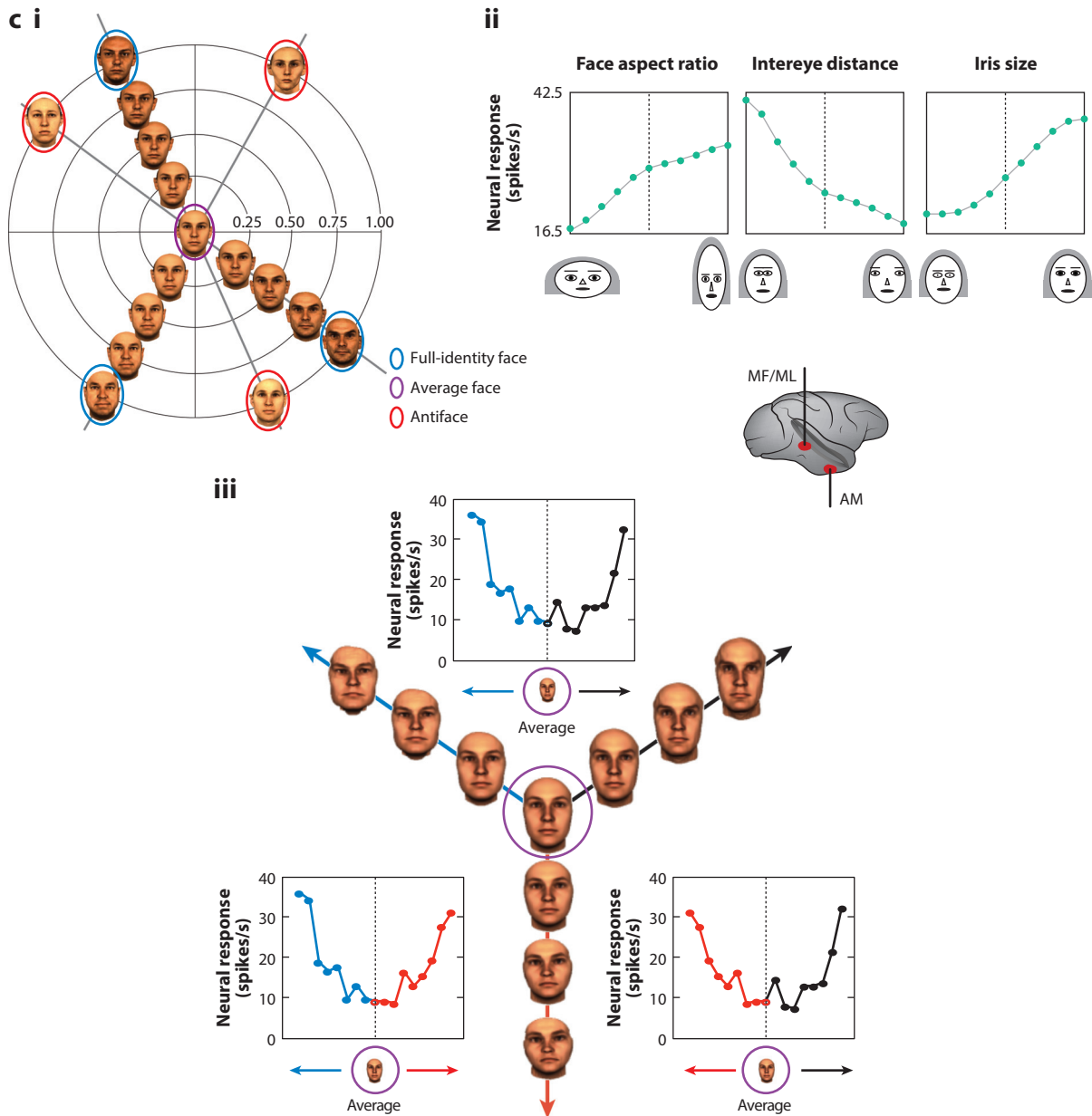




**Figure 2**

Mechanisms for face detection, holistic face processing, and face space. (a) (Left) To generate stimuli that probe selectivity for coarse-contrast face stimuli, a front-view picture of a face was segmented into 11 areas, to which 11 luminance values were then assigned randomly (Ohayon et al. 2012). Recordings from the middle face patches (MF/ML, bottom) during stimulus presentation revealed selectivity of cells to the polarity of a large fraction of all possible contrast pairs and dominance of a single polarity for each pair. (Right) Histogram of the 10 most common contrast polarity features and their relative proportion in the cell population. The top two contrast polarity features express higher luminance for the nose region than left and right eyes, respectively. Five of these contrast features and their polarities were predicted by human psychophysics (columns outlined in orange). (b) Effects of Thatcherizing faces on face-selective responses in single units from face area ML (left) and the evoked potential from the right occipitotemporal electrode in humans (right). (Left) Face cells in ML differentiate between intact and Thatcherized upright faces (blue and red) but not between intact and Thatcherized inverted faces (green and yellow) (Taubert et al. 2015b). This is consistent with the behavioral Thatcher illusion first reported by Thompson (Thompson 1980). (Right) Event-related potentials to Thatcherized and intact upright and inverted faces recorded from a right occipitotemporal EEG electrode in humans also show a difference in the amplitude of the N170 between intact and Thatcherized upright faces but no difference for inverted faces (Carbon et al. 2005). (c, i) Two-dimensional depiction of perceptual face space (Leopold et al. 2001). The space is centered on an average face. Each face occupies a particular location in face space based on its deviation from the average face along many dimensions. Faces along the same trajectory originating at the average face all have the same identity, but faces further from the average face have greater identity strength and are therefore more distinctive. An antiface is a face on the opposite side of the average face from a face with an equal identity strength. Aftereffects for opposite adaptor pairs are greater than aftereffects for nonopposite faces matched for perceptual similarity. (ii) Facial feature selectivity of a middle face patch





**Figure 2 (Continued)**

neuron (Freiwald et al. 2009). Macaques viewed cartoon faces that varied randomly along 19 dimensions, each with feature values ranging from one extreme (−5) to another (+5) (valence arbitrary). Typical cells were tuned to small subsets of feature dimensions (here, four) and exhibited ramp-shape tuning curves with minimal responses elicited by one feature extreme and maximal responses by the opposite feature extreme. Thus, tuning curves spanned face space. The sample neuron shown here was modulated by face aspect ratio (preferring narrow faces), intereye distance (preferring narrowly spaced eyes), eye aspect ratio (preferring wide eye shapes), and iris size (preferring large irises). (iii) Response of a face-responsive cell, likely recorded in AM to stimulus trajectories originating in the average face. The center face illustrates stimuli shown and their organization along three trajectories (*red, blue, and black*) originating in the center of face space. For all trajectories, the neuron’s firing rate increased with distance from the center of face space. Abbreviations: AM, anterior medial face patch; L, left; MF, middle fundus face patch; ML, middle lateral face patch; R, right.

(Figure 2c), which provides neurophysiological evidence for the special role of the center of face space. More distinct response patterns of ML and MF neurons to extreme faces compared to average faces might, furthermore, explain why some studies have found identity to be perceived more easily in caricatures than the original face (Rhodes et al. 1997).

### **Faces as Sources of Social Information**

A multitude of social information can be extracted from fine variations across faces, including gender, age, attractiveness, changing mental states such as social attention and mood (Haxby et al. 2000), and even inferred character attributes such as trustworthiness (Todorov 2008). Many face cells have tuning properties that suggest an involvement in some of these social inferences. Some face cells are tuned to head orientation or gaze (De Souza et al. 2005, Desimone et al. 1984, Perrett et al. 1985), and similar selectivity has been reported in the STS of the human brain (Carlin et al. 2011). This selectivity may support an analysis of the direction of social attention in the dorsal face pathways. Researchers have also found similar head-view selectivity in the parallel, ventral face pathway, but there it may reflect an initial view-dependent step preceding a view-invariant face representation. Other face cells appear to be tuned to facial expressions (Gothard et al. 2007, Sugase et al. 1999) and yet others to physical characteristics of the face, including facial features and identity (Freiwald et al. 2009, Young & Yamane 1992). Mechanisms for the processing of expression and identity may overlap in common neural systems (Bernstein & Yovel 2015, Calder & Young 2005). Yet other studies have reported neural population codes to reflect another social quality: familiarity (Eifuku et al. 2011, Young & Yamane 1992). Thus, specializations of face cells exist that are plausible neural mechanisms supporting the different social dimensions of face recognition.

### **CAUSAL LINKS BETWEEN FACE-PROCESSING SYSTEMS AND BEHAVIOR**

The links between particular neural processes and behavior discussed above are correlational, leaving open the question of whether these neural processes actually contribute to face recognition. Many regions in extrastriate cortex show a response to faces that is well above baseline, but as we discuss below, several findings suggest the response to faces is behaviorally relevant in face-selective but not in nearby areas that are not selective to faces. To determine the behavioral relevance of a neural mechanism, behavior must be assessed while that neural process is disrupted.

### **Acquired Prosopagnosia**

The earliest evidence causally linking neural regions and face processing was provided by patients who acquired face-processing deficits due to brain damage. Prosopagnosia can result from lesions extending from the ventral occipital lobe (Bouvier & Engel 2006, Dalrymple et al. 2011, Rossion et al. 2003) to the anterior temporal lobe (Busigny et al. 2014, Dalrymple et al. 2011) in the right hemisphere, whereas unilateral left hemisphere lesions produce prosopagnosia rarely (Barton et al. 2002, De Renzi et al. 1994; see Rossion 2014 for discussion of these cases). Thus, consistent with lateralization of face processing in human fMRI and event-related potentials (Bentin et al. 1996, Bukowski et al. 2013), this pattern indicates face processing in humans is strongly right lateralized.

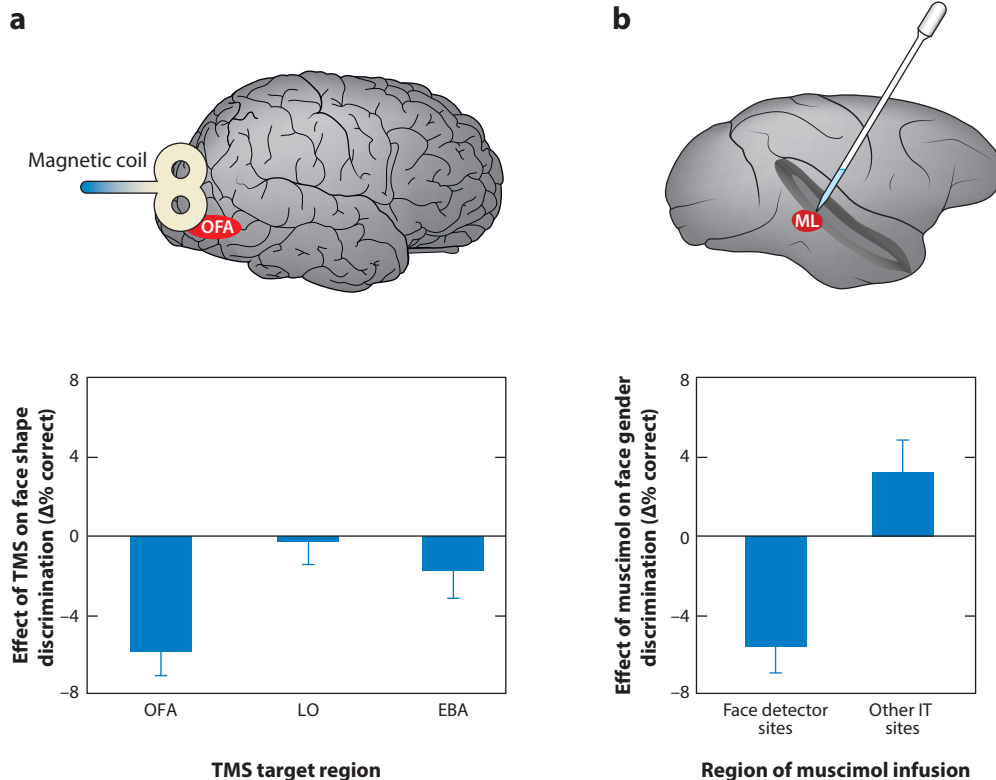
Functional imaging has allowed researchers to assess the status of face-selective areas in individuals with acquired prosopagnosia. Patient P.S. suffered from dense prosopagnosia following a

closed-head injury, and fMRI revealed the damage overlapped with her right occipital face area (OFA) while leaving the right fusiform face area (FFA) intact (Rossion et al. 2003, Sorger et al. 2007). Findings from other prosopagnosics have provided further evidence that right hemisphere posterior face-selective areas are critical to face recognition (Dalrymple et al. 2011, Fox et al. 2011). However, prosopagnosia following damage to anterior temporal regions that spare posterior face-selective regions has been reported in several cases (Busigny et al. 2014, Dalrymple et al. 2011, Fox et al. 2011). Thus, face-selective regions along the entire ventral pathway appear to contribute causally to face recognition. Less is known about the areas supporting face perception for aspects of faces other than identity. R-ST1, one of the few cases with lesions to the face network restricted to the STS (Fox et al. 2011), exhibited deficits with facial expression recognition consistent with the role of STS face areas in the processing of changeable facial information (Haxby et al. 2000). Importantly, in identity-matching tasks, R-ST1 performed normally when expression was held constant but had pronounced deficits when expression differed in the images to be matched, suggesting STS face areas contribute to identity computations carried out in ventral stream areas when expression variation is present.

### 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) is a noninvasive means to examine the functional role of brain regions in humans. Most TMS studies have targeted the OFA and the posterior STS face area (pSTS-FA), which are both located close to the scalp and thus can be disrupted by TMS. TMS to the right OFA impairs face shape discrimination but not object or body shape discrimination (**Figure 3**) (Pitcher et al. 2007, 2009, 2012). Similarly, TMS to the extrastriate body area (EBA) disrupts body discrimination selectively, whereas TMS over the lateral occipital complex (LOC), an area implicated in object recognition, disrupts object discrimination selectively (Pitcher et al. 2009). The three category-selective areas targeted in these studies all responded substantially to nonpreferred categories (e.g., objects and bodies for the OFA) (Schwarzlose et al. 2008), so the category selectivity of these impairments indicates (*a*) the presence of a response within a region does not imply behavioral relevance (see also Dilks et al. 2013, Pitcher et al. 2011b) and (*b*) supports a modular view of high-level visual recognition. Consistent with results from acquired prosopagnosics, TMS over both the OFA and pSTS-FA has been found to disrupt expression perception, but the effective time window for pSTS-FA disruption is longer than the OFA window (Pitcher 2014), consistent with the notion of hierarchical processing.

Intracranial stimulation has a long history in human neuroscience, and researchers have applied it recently to investigate the neural basis of face processing. After mapping the category selectivity of regions in right middle and posterior fusiform gyri, Parvizi et al. (2012) stimulated face-selective areas electrically. These stimulations caused pronounced distortions to face percepts. Consistent with a modular view, the patient reported only subtle distortions when the face regions were stimulated while he was viewing nonface 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 nonface, elementary distortions such as phosphenes (Rangarajan et al. 2014). Similarly, Jonas et al. (2014) stimulated the 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



**Figure 3**

Causal studies of face processing. (a) Effect of TMS over three right hemisphere category-selective areas on sequential face discrimination (Pitcher et al. 2009). The behavioral effect was computed by subtracting percent correct in the absence of TMS from percent correct when TMS was delivered over a given area. TMS over the OFA disrupted face discrimination, whereas TMS over the LO object area and EBA had no significant effect on face discrimination. Similar category-selective effects were found for object discrimination at in the LO object area and body discrimination in the EBA (not shown). (b) Effect of muscimol microinjection on face gender discrimination (Afraz et al. 2015). The behavioral effect was calculated by subtracting percent correct when faces were presented in the ipsilateral VF from percent correct in the contralateral VF. Sites had been categorized as face detector sites or other inferotemporal sites based on the response to briefly presented images of faces and nonface objects prior to muscimol injection. Inactivation of face detector sites, but not control sites, caused a deficit in face gender discrimination. Abbreviations: EBA, extrastriate body area; LO, lateral occipital; ML, middle lateral face patch; OFA, occipital face area; TMS, transcranial magnetic stimulation; VF, visual field.

hemisphere face areas, in combination with the rarity of acquired prosopagnosia after unilateral left hemisphere lesions, raises questions about what role, if any, left hemisphere areas make to face processing in humans.

Researchers have conducted surprisingly few experiments disrupting face processing in the macaque. Afraz et al. (2006) stimulated clusters of face-selective neurons electrically while macaques made face/nonface decisions on briefly presented stimuli. The macaques were more likely to report the presence of a face when face clusters were stimulated, whereas stimulation of clusters that were not face selective did not affect behavior. Recently, Afraz et al. (2015) used optogenetics and muscimol in separate experiments to suppress activity selectively in face-selective clusters in the lower bank of the STS, likely inside or in the vicinity of the ML.

During face gender decisions, suppression in face clusters, but not outside them, disrupted performance weakly (**Figure 3a**). These effects were restricted to contralaterally presented faces, likely reflecting the position of the inactivated neurons' receptive fields. Together, the causal studies described above demonstrate that face-selective neurons and face-selective areas play critical roles in primate face processing and suggest that these areas play a much more prominent role than areas that are face responsive but not face selective.

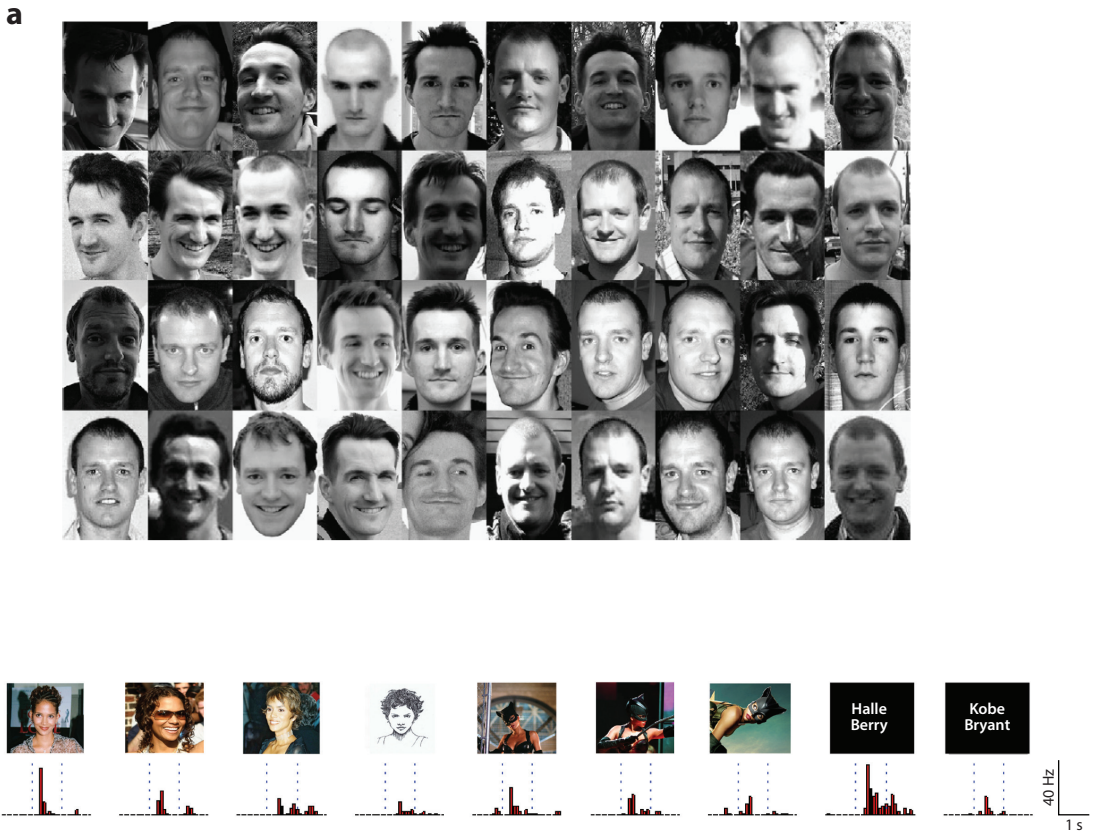
## RECOGNITION OF FAMILIAR AND UNFAMILIAR FACES

Most studies on face processing use unfamiliar faces. Unfamiliar faces are ideal stimuli to isolate the contribution of the visual system to face recognition because they are associated with far less semantic and emotional information than familiar faces. Nevertheless, the primary goal of face recognition for social creatures is to recognize familiar individuals. Many of the basic phenomena of face recognition are common to familiar and unfamiliar faces (for a review, see Johnston & Edmonds 2009), including the face inversion effect (Yarmey 1971, Yin 1969; but see Megreya & Burton 2006), the composite face effect (Le Grand et al. 2004, Young et al. 1987), and the Thatcher illusion (Thompson 1980). Contrast negation impairs recognition of both familiar and unfamiliar faces (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 recognizing both familiar and unfamiliar faces (Dalrymple et al. 2011, Duchaine et al. 2007, Van Belle et al. 2010). Despite these similarities, the processing of familiar and unfamiliar faces differs in important ways. First, familiar faces are better recognized across different images based on their internal rather than external features, whereas no such difference is found for unfamiliar faces (Clutterbuck & Johnston 2005, Ellis et al. 1979, Young et al. 1985). A second difference is that matching of unfamiliar faces across different illuminations (Johnston et al. 1992), head orientations (Hill et al. 1997, O'Toole et al. 1998), and expressions (Bruce 1982) is prone to error, whereas comparable tasks with familiar faces are effortless (**Figure 4a**).

How is this invariance for familiar faces generated? The original Bruce & Young (1986) model proposed that unfamiliar face representation involves a pictorial code, which is primarily image based, whereas the representation of familiar faces relies on a structural code, which is more abstract and less susceptible to changes in view, expression, and lighting. Burton, Jenkins, and colleagues (Burton et al. 2005; Jenkins & Burton 2006, 2011) suggested that this representation may be generated by averaging the various images of the same person that an observer encounters, separately for multiple views. These averaged representations will then include the essential, diagnostic features of a given identity. Consistent with this view, averaged faces made from many face exemplars of a given individual are better recognized than averaged faces made from fewer exemplars (Burton et al. 2005). Thus, representations of familiar faces benefit from rich perceptual exposure to the same individuals. In contrast, when we see an image of an unfamiliar face, it can be difficult to disentangle superficial pictorial information from information about the stable characteristics of the face.

Familiar faces are rich not only in perceptual information but also in semantic, emotional, and social information, which can enhance face recognition. For example, participants better remember a face when asked to make a personality judgment (e.g., "Does the face look intelligent?") than when they make a perceptual judgment (e.g., "Does the face have a large nose?") (Curtois & Mueller 1979). Similarly, associating new faces with unique labels (i.e., each face with a different letter) increases face recognition compared to associations with similar labels (e.g., all faces are associated with the same letter) (McGugin et al. 2011). These findings suggest that social, emotional, and higher-level categorizations all play a role in face recognition abilities. The





**Figure 4**

From unfamiliar face recognition to person knowledge. (a) Subjects were asked to sort 40 face images by identity (Jenkins & Burton 2011). Although the array included 20 images of two individuals each, subjects who were unfamiliar with the faces sorted them into an average of seven identities. Subjects familiar with the two individuals successfully sorted the images to two identities. These results demonstrate the challenge of generalizing across different images of the same person for unfamiliar faces. (b) A single neuron in the medial temporal lobe of an epilepsy patient exhibiting robust responses to a wide variety of images of actress Halle Barry, including images in which her face is completely masked, and even her name written in letters (Quiroga et al. 2005). The response profile demonstrates that nonface-related knowledge (i.e., knowledge about the movie she appeared in with this mask, knowledge of her name) shaped the response of this neuron, thus generating a highly invariant person representation beyond the representations that can be obtained from vision alone.

contribution of conceptual information to the invariant representation that we have for familiar faces is also evident in the response of the so-called concept cells (Quiroga et al. 2005) that demonstrate robustness to very different pictures of a known individual, even when the face is largely hidden in the image (see **Figure 4b**). This type of representation thus reflects invariance beyond purely visual information about the face and must be based on person knowledge. Thus, combinations of visual and conceptual factors are likely to contribute to the invariant representation of familiar faces.

In summary, recognition of familiar faces is robust to many different variations in the image of a given person. By contrast, recognition of different images of unfamiliar people is challenging owing to the limited amount of information available.



## FACE RECOGNITION IN THE REAL WORLD: CHALLENGES AND POSSIBLE SOLUTIONS

The limitations of unfamiliar face recognition have substantial effects in many consequential situations. Eyewitness identification is highly accurate for familiar faces, but when identification of unfamiliar faces is required, errors are frequent (Wells et al. 2002) and an important factor in miscarriages of justice (Rattner 1988). In fact, eyewitness misidentification accounts for more than 70% of convictions overturned by DNA testing in the USA (<http://www.innocenceproject.org/free-innocent/improve-the-law/fact-sheets/dna-exonerations-nationwide>; Natl. Res. Council. Natl. Acad. 2014). Another factor often limiting eyewitness identification of unfamiliar faces is the other-race effect: Identification is substantially worse for faces of races a subject has had little contact with in daily life (Hugenberg et al. 2010, Malpass & Kravitz 1969, Meissner & Brigham 2001). Face recognition is also used at border crossings where simultaneous matching of a live person to a passport photo is required. Although simultaneous matching is easier than eyewitness identification, a recent study conducted with passport officers found these highly experienced individuals incorrectly accepted 14% of the passports that did not match their bearers (White et al. 2014). Furthermore, the officers' performance was no better than that of student participants. Notably, the passport officers showed great individual differences (errors ranged from 0% to 30%), and these differences were not associated with years of experience in their job.

In the past decade, it has become apparent that great individual differences in face processing exist (for a review, see Yovel et al. 2014). In developmental prosopagnosia, individuals with no history of brain damage or general impairments have difficulty recognizing the faces of family and friends (Susilo & Duchaine 2013). On the opposite end of the spectrum are super-recognizers; they rarely forget the faces of people they interact with and regularly recognize faces encountered only briefly years before (Russell et al. 2009, 2012). The majority of the population lies somewhere between these extremes, and differences among them are stable (Bowles et al. 2009, Wilhelm et al. 2010) and strongly heritable (Wilmer et al. 2010, Zhu et al. 2010). Lab-based face identity tests not only are correlated with other lab-based face recognition tests (Germine et al. 2012) but also predict performance in more ecologically valid identification situations such as eyewitness identification (Andersen et al. 2014). Modest relationships have been found between face recognition ability and some known face-processing effects such as the composite face effect (DeGutis et al. 2013) and face aftereffects (Dennett et al. 2012), but the neurocognitive sources of most variance in face processing abilities is unknown.

The reliable and stable individual differences across lab-based and real-life face recognition tasks suggest that when face recognition plays a role in consequential situations, individual ability should be considered. In courts, awareness of an eyewitness' face recognition skill would allow the judge and jury to better assess the weight they should place on the eyewitness' testimony. Selection for occupations such as passport officers and police officers would benefit from consideration of face recognition ability, and the London Metropolitan Police have applied this suggestion successfully (Davis et al. 2013, Robertson et al. 2016). In collaboration with face researchers, the organization has identified officers and staff with especially good face recognition. These super-recognizers used their skills to identify hundreds of suspects from low-resolution surveillance videos taken during the large-scale riots in London in 2011, and a team of super-recognizers have watched live video during large festivals to identify and then capture suspects wanted for previously committed crimes.

In summary, the belief that all humans are experts in face recognition has led to the assumption that face recognition can be relied on in real-life settings. However, although this assumption is, by and large, true for identification of familiar faces, it has detrimental effects on criminal justice,

border control, and policing because we are far from perfect when it comes to identification of unfamiliar faces (Burton & Jenkins 2011).

## CONCLUSION

The dedicated system for face processing in the primate brain has been the focus of intensive basic and applied research in recent decades. The findings discussed here provide an overview of attempts to bridge the gap between levels of organization from single cells to networks of areas and behavior as well as between lab-based and real-life face recognition. This work shows the promise of these approaches but also makes clear that these are only the initial steps toward a comprehensive understanding of the operations required for successful face recognition.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

The authors are grateful to Arash Afraz, David Leopold, Jess Taubert, and Stefan Schweinberger for discussion and an anonymous reviewer for valuable suggestions on an earlier version of the manuscript. W.F. was supported by grants from the National Eye Institute (R01 EY021594-02); the National Institute of Mental Health (R01 MH105397-02); the Human Frontier Science Program (RGP0015/2013); the National Science Foundation Science and Technology Center for Brains, Minds, and Machines (CCF-1231216/5710003506); the New York Stem Cell Foundation (NYSCF-R-NI23); and the Simons Foundation through the Simons Collaboration on the Global Brain (365002). W.F. is a New York Stem Cell Foundation Robertson Investigator. G.Y. was supported by a grant from the Israeli National Foundation (ISF-446/12).

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# Contents

Beyond the CB1 Receptor: Is Cannabidiol the Answer for Disorders of Motivation? <i>Natalie E. Zlebnik and Joseph F. Cheer</i> .....	1
Ten Years of Grid Cells <i>David C. Rowland, Yasser Roudi, May-Britt Moser, and Edvard I. Moser</i> .....	19
Ant Genetics: Reproductive Physiology, Worker Morphology, and Behavior <i>D.A. Friedman and D.M. Gordon</i> .....	41
Alzheimer's Disease Mechanisms and Emerging Roads to Novel Therapeutics <i>Carlo Sala Frigerio and Bart De Strooper</i> .....	57
Human Spinal Motor Control <i>Jens Bo Nielsen</i> .....	81
Clarifying Human White Matter <i>Brian A. Wandell</i> .....	103
Neuronal Mechanisms of Visual Categorization: An Abstract View on Decision Making <i>David J. Freedman and John A. Assad</i> .....	129
Dorsal Anterior Cingulate Cortex: A Bottom-Up View <i>Sarah R. Heilbronner and Benjamin Y. Hayden</i> .....	149
3-D Maps and Compasses in the Brain <i>Arseny Finkelstein, Liora Las, and Nachum Ulanovsky</i> .....	171
From Cajal to Connectome and Beyond <i>Larry W. Swanson and Jeff W. Lichtman</i> .....	197
Computational Analysis of Behavior <i>S.E. Roian Egnor and Kristin Branson</i> .....	217
Correlations and Neuronal Population Information <i>Adam Kohn, Ruben Coen-Cagli, Ingmar Kanitscheider, and Alexandre Pouget</i> .....	237
The Emergence of a Circuit Model for Addiction <i>Christian Lüscher</i> .....	257

Brain Disorders Due to Lysosomal Dysfunction <i>Alessandro Fraldi, Andrés D. Klein, Diego L. Medina, and Carmine Settembre</i> .....	277
Reward and Aversion <i>Hailan Hu</i> .....	297
Face Processing Systems: From Neurons to Real-World Social Perception <i>Winrich Freiwald, Bradley Duchaine, and Galit Yovel</i> .....	325
New Perspectives on Genomic Imprinting, an Essential and Multifaceted Mode of Epigenetic Control in the Developing and Adult Brain <i>Julio D. Perez, Nimrod D. Rubinstein, and Catherine Dulac</i> .....	347
Maps of the Auditory Cortex <i>Alyssa A. Brewer and Brian Barton</i> .....	385
The Genetic Basis of Hydrocephalus <i>Maria Kousi and Nicholas Katsanis</i> .....	409

## Indexes

Cumulative Index of Contributing Authors, Volumes 30–39 .....	437
---	-----

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#### TABLE OF CONTENTS FOR VOLUME 1:

- *Adaptive Optics Ophthalmoscopy*, Austin Roorda, Jacque L. Duncan
- *Angiogenesis in Eye Disease*, Yoshihiko Usui, Peter D. Westenskow, Salome Murinello, Michael I. Dorrell, Leah Schepke, Felicitas Bucher, Susumu Sakimoto, Liliana P Paris, Edith Aguilar, Martin Friedlander
- *Color and the Cone Mosaic*, David H. Brainard
- *Control and Functions of Fixational Eye Movements*, Michele Rucci, Martina Poletti
- *Deep Neural Networks A New Framework for Modeling Biological Vision and Brain Information Processing*, Nikolaus Kriegeskorte
- *Development of Three-Dimensional Perception in Human Infants*, Anthony M. Norcia, Holly E. Gerhard
- *Functional Circuitry of the Retina*, Jonathan B. Demb, Joshua H. Singer
- *Image Formation in the Living Human Eye*, Pablo Artal
- *Imaging Glaucoma*, Donald C. Hood
- *Mitochondria and Optic Neuropathy*, Janey L. Wiggs
- *Neuronal Mechanisms of Visual Attention*, John Maunsell
- *Optogenetic Approaches to Restoring Vision*, Zhuo-Hua Pan, Qi Lu, Anding Bi, Alexander M. Dizhoor, Gary W. Abrams
- *Organization of the Central Visual Pathways Following Field Defects Arising from Congenital, Inherited, and Acquired Eye Disease*, Antony B. Morland
- *Contributions of Retinal Ganglion Cells to Subcortical Visual Processing and Behaviors*, Onkar S. Dhande, Benjamin K. Stafford, Jung-Hwan A. Lim, Andrew D. Huberman
- *Ribbon Synapses and Visual Processing in the Retina*, Leon Lagnado, Frank Schmitz
- *The Determination of Rod and Cone Photoreceptor Fate*, Constance L. Cepko
- *A Revised Neural Framework for Face Processing*, Brad Duchaine, Galit Yovel
- *Visual Adaptation*, Michael A. Webster
- *Visual Functions of the Thalamus*, W. Martin Usrey, Henry J. Aliitto
- *Visual Guidance of Smooth Pursuit Eye Movements*, Stephen Lisberger
- *Visuomotor Functions in the Frontal Lobe*, Jeffrey D. Schall
- *What Does Genetics Tell Us About Age-Related Macular Degeneration?* Felix Grassmann, Thomas Ach, Caroline Brandl, Iris M. Heid, Bernhard H.F. Weber
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