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A Comparative View of Face Perception

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Abstract

Face perception serves as the basis for much of human social exchange. Diverse information can be extracted about an individual from a single glance at their face, including their identity, emotional state, and direction of attention. Neuropsychological and fMRI experiments reveal a complex network of specialized areas in the human brain supporting these face-reading skills. Here we consider the evolutionary roots of human face perception by exploring the manner in which different animal species view and respond to faces. We focus on behavioral experiments collected from both primates and non-primates, assessing the types of information that animals are able to extract from the faces of their conspecifics, human experimenters, and natural predators. These experiments reveal that faces are an important category of visual stimuli for animals in all major vertebrate taxa, possibly reflecting the early emergence of neural specialization for faces in vertebrate evolution. At the same time, some aspects of facial perception are only evident in primates and a few other social mammals, and may therefore have evolved to suit the needs of complex social communication. Since the human brain likely utilizes both primitive and recently evolved neural specializations for the processing of faces, comparative studies may hold the key to understanding how these parallel circuits emerged during human evolution.

For humans, faces are among the most important visual stimuli, a fact that becomes apparent in social settings – as a species we are constantly, almost obsessively, monitoring each other's faces, paying close attention to subtle details that can give some insight into the emotional state, level of engagement, or object of attention of our associates. Fluency with faces offers great social advantages, allowing one to glean aspects of another's internal thought processes and to predict their behavior. But how did humans come to place so much emphasis upon this particular aspect of personal appearance? Is the capacity to read faces a product of our society, finely tuned to meet the needs of human culture? Already in the nineteenth century, Darwin suggested that this is not the case, and that human facial expressions share much in common with those of many animals (Darwin, 1872). For Darwin the study of faces fell naturally into a comparative and evolutionary context, a perspective adopted by only a small group of contemporary researchers (e.g. Parr, Waller, & Fugate, 2005; Pascalis & Kelly, 2009).

Here we take a first step in exploring the evolution of face perception by reviewing a wide range of behavioral studies that provide insight into the following questions: (1) To what extent do faces constitute a “special” category of visual stimuli for nonhuman primates as well as other mammalian and vertebrate species? That is, to what extent are they important

stimuli, eliciting specific behavioral and neural responses? (2) What types of information are various animals able to extract from a face? (3) How and when might have different aspects of face perception emerged during evolution? Our review covers behavioral experiments conducted in animals from many taxa related to visual individual recognition, predator detection, gaze following, and reaction to emotional expressions. While avoiding detailed descriptions of brain anatomy and physiology, we do refer to relevant neurophysiological data where available. In the first section, we set the stage by breaking down face perception, based on data from human studies, into several dissociable components that provide a conceptual framework to guide our review of animal face perception and social vision more generally.

Components of face perception

What kinds of information can be extracted from a face? Numerous studies have demonstrated that face perception is multi-faceted: not only do we recognize individuals, but also monitor their faces to obtain a continuous stream of social information, ranging from communicative gestures to emotional and attentive states (for reviews see Bruce & Young, 1998; Kanwisher & Yovel, 2006; Peterson & Rhodes, 2003; Tsao & Livingstone, 2008). In our comparative review, we separately analyze different aspects of face perception, described briefly here for humans:

1) Identity

The recognition of individual faces is in some ways the pinnacle of human visual performance. Since all faces have the same basic configural appearance (e.g. two eyes above a nose and mouth, some times called the *first-order* configuration), individuals must be identified by subtle deviations from this prototypic pattern, sometimes referred to as *second-order* relational information or configuration (Diamond & Carey, 1986). Human face recognition is highly efficient, involving a parallel integration of information over the entire face (for reviews, see Farah, Wilson, Drain, & Tanaka, 1998; McKone, Kanwisher, & Duchaine, 2007). This form of recognition appears to rely on specialized areas in the brain that are selectively engaged by faces that are upright and of normal contrast polarity (Kanwisher, 2000; Rossion & Gauthier, 2002; Thompson, 1980; Tsao & Livingstone, 2008; Yin, 1969).

2) Emotional Expression

Humans communicate their emotional states to others through the stereotypic posturing of facial elements. Elaborated facial musculature contributes to a large repertoire of expressions involving the display of the teeth, the furrowing of the brow, and the closure of the eyes, some of which are uniquely human and some not (Darwin, 1872). The appearance of an emotional expression can directly influence the observer's own emotional state. The appearance of the eyes serves as a particularly salient emotional cue (Adolphs et al., 2005; Whalen et al., 2004). Some basic facial expressions seem to be consistent across human populations (Ekman, Sorenson, & Friesen, 1969), possibly owing to their adaptive value in evolution (Schmidt & Cohn, 2001).

3) Gaze

In addition to its role in signaling emotional state, the appearance of the eyes also provides insight into an individual's attentive state, including their level of engagement, intentions, or focus of interest. This aspect of face perception may be particularly well developed in humans, since the sclera of the human eye is more visible than in other primates (Kobayashi & Kohshima, 1997). Indeed, human infants primarily use the orientation of the eyes, rather than the head, to determine another's direction of gaze (Tomasello, Hare, Lehmann, & Call,

2007). Gaze interplay is a salient feature of social interaction and is abnormal in a number of psychiatric conditions, in which patients typically avoid looking into the eyes of others (Coss, 1978b; Johnson et al., 2005).

4) Attraction

Faces play an important role in human sexual attraction, which has been linked to face averageness, symmetry, and sexual dimorphism (masculinity in male faces, femininity in female faces) (Rhodes & Simmons, 2007). These attributes may in turn be related to mate quality, so that our preferences for them could have been sexually selected (Rhodes, 2006). Similarly, subtle coloration of the face affects perceived health, which is important in attractiveness (Stephen, Coetzee, Law, & Perrett, 2009).

5) Development

The developmental trajectory of face perception is complex and only partly understood. Newborn infants detect and visually orient to face-like patterns in preference to other complex patterns (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991; for a review see Johnson, 2005), and form a preference for their mother's face within days of birth (Bushnell, Sai, & Mullin, 1989; Pascalis, de Schonen, Morton, Deruelle, & Fabre-Grenet, 1995). They are also able to discriminate and imitate a few basic facial expressions in the hours after birth (Meltzoff & Moore, 1983). During the first year of life, face processing mechanisms are “tuned” by exposure to faces (Kelly et al., 2007; Pascalis, de Haan, & Nelson, 2002; Pascalis et al., 2005), and recognition performance continues to improve through childhood and adolescence (Carey, 1992; Carey, Diamond, & Woods, 1980; Mondloch, Geldart, Maurer, & Le Grand, 2003; Mondloch, Le Grand, & Maurer, 2002). The basis of this improvement remains controversial, with some arguing that sensitivity to second-order configuration improves throughout childhood (Mondloch et al., 2003) and others attributing it to the development of domain-general skills in attention and executive functions (Crookes & McKone, 2009).

6) Neural Specialization

Different circuits in the brain support the perception of different kinds of information, a principle that is evident in both brain damaged patients and functional imaging studies (Adolphs, Tranel, & Damasio, 1998; Calder & Young, 2005; Hoffman & Haxby, 2000; Humphreys, Donnelly, & Riddoch, 1993). The most prominent face-specialized area in the human brain is on the fusiform gyrus, where responses are stronger to faces than to any other category of stimuli (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006). This region may receive basic perceptual representations of faces from a more posterior occipital face-selective area (Fairhall & Ishai, 2007), and damage in the vicinity of these areas can lead to the inability to recognize individual faces (Bouvier & Engel, 2006; Damasio, Damasio, & Van Hoesen, 1982). Some neurons in the medial temporal lobe are thought to represent people at a very general, abstract level, and respond robustly and selectively to faces (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005). By contrast, the superior temporal sulcus (STS) appears sensitive to changeable aspects of the face, as it responds selectively to emotional expression and eye gaze (Allison, Puce, & McCarthy, 2000; Engell & Haxby, 2007; Hoffman & Haxby, 2000). Eye gaze perception additionally activates the intraparietal sulcus, and its coding can be dissociated from that of identity and expression (Pelphrey & Vander Wyk, 2010). Other neural structures respond to specific emotional expressions. For example, the amygdala responds selectively to fearful or unhappy facial expressions (Morris et al., 1996), whereas the orbitofrontal cortex responds to angry facial expressions (Blair, Morris, Frith, Perrett, & Dolan, 1999).

Thus research in humans has shown that face perception entails a diverse set of skills that are supported by multiple specialized neural circuits and that require years to fully develop. Based on this framework we now turn to face perception by nonhuman species, reviewing the extent to which different animals look at faces to extract different types of information, and referring to the developmental course and neural basis of face processing where information is available. We ask to what extent faces are a special category of visual stimuli for nonhuman primates, other mammals, and other vertebrates. We survey a wide range of experiments investigating the specific types of visual information various animals are and are not able to extract from faces. Then, based on the shared capacities of different animals, we speculate on the evolutionary history of different aspects of face perception, and how this history might be informative about our own face perception.

Nonhuman primates

Like humans, other primates are highly developed in their use of faces for social purposes, such as recognition, communication, and mate selection. Primates have been tested extensively on how they perceive faces, primarily because of their evolutionary proximity to humans and human-like capacity to read faces, but also because they can be easily trained to respond to images and videos in a laboratory setting (see Figure 1A)

Identity

All primate species tested experimentally are able to recognize familiar individuals by the appearance of their faces. Nonetheless, careful testing has revealed some differences between species. Chimp face perception seems to be most similar to humans. They are able to readily discriminate photos of unfamiliar conspecifics, and when doing so rely primarily on the eyes (Parr, Heintz, & Akamagwuna, 2006; Parr, Winslow, Hopkins, & de Waal, 2000; Tomonaga, Itakura, & Matsuzawa, 1993). Chimps are also sensitive to familial similarity in unfamiliar faces (Parr & de Waal, 1999) (Figure 2A). In fact, a number of experiments indicate that chimps use configural processing in a manner similar to humans, since their recognition is sensitive to the same manipulations that disrupt face recognition in humans, such as rotational inversion (Parr, Dove, & Hopkins, 1998; Tomonaga, 2007), and second-order spatial distortions (Parr et al., 2006).

Rhesus macaques also recognize each other by their faces, with individual recognition being an important feature of their dominance hierarchy (Bovet & Washburn, 2003; Deaner, Khera, & Platt, 2005; Parr et al., 2000). They also appear sensitive to familial resemblance, as they spend more time looking at their kin than at other conspecifics, even when lacking previous visual experience with them due to early postnatal separation (Wu, Holmes, Medina, & Sackett, 1980) (testing apparatus shown in Figure 1B). Compared to chimps, macaques pay more attention to the component parts of a face and their first-order, rather than second-order, spatial relations (Parr, Heintz, & Pradhan, 2008; Parron & Fagot, 2007). Also, the effect of rotational inversion on face recognition in monkeys has been mixed (Gothard, Brooks, & Peterson, 2009; Parr et al., 2008; Parr, Winslow, & Hopkins, 1999; Phelps & Roberts, 1994; Tomonaga, 1994; Weiss, Kralik, & Hauser, 2001; Wright & Roberts, 1996), suggesting that if they do use configural processing, it is to a lesser degree than humans and chimps.

The primates that have been tested also appear to exhibit a *conspecific advantage*; that is, they recognize and discriminate members of their own species more readily than other species. This advantage has been likened to the human *other-race effect*, where faces from one's own race are more easily recognized than faces from another race (Malpass & Kravitz, 1969; Meissner & Brigham, 2001). One comparative behavioral study used viewing preferences as a measure of face recognition in humans, Tonkean macaques (Old World

monkeys), and capuchins (New World monkeys). Each species was shown photographs of a large number of faces, from their own species and from 2-3 other primate species. New faces from the same-species engendered reliably longer looking times than new faces from other species, suggesting better individual recognition of conspecific than heterospecific faces (Dufour, Pascalis, & Petit, 2006) (Figure 2B). A similar advantage for conspecifics was also demonstrated in rhesus macaques (Fujita, 1987, 1993; Pascalis & Bachevalier, 1998). Interestingly, the reduced recognition of heterospecifics may involve a change in the way faces are analyzed. For example, rhesus macaques, while showing some signs of configural analysis for conspecific faces, appear to switch to a feature-based mode of analysis when viewing human faces (Gothard et al., 2009).

The capacity to efficiently recognize heterospecific faces appears to be, at least in part, shaped by experience. Chimps raised in a human environment, having more exposure to human than chimp faces, were better at discriminating pictures of unknown human faces than unknown chimp faces (Martin-Malivel & Okada, 2007). Similarly, rhesus macaques explicitly trained for several months to discriminate between four human faces with reduced identity cues scored nearly as well as humans performing the same task (Leopold & Bondar, 2005). Under normal conditions, experience may determine which categories of faces will be analyzed in a configural manner and which will not (Pascalis et al., 2002; Sugita, 2008) (see **Development** section below).

Finally, tests of self-recognition in a mirror can be used to assess individual recognition to some extent. This paradigm allows for testing in a wide range of species, and typically involves observing whether or not an animal, upon observing a mark on its face in the mirror, attempts to remove it by touching its own face. Using this test, many (but not all) chimps are able to recognize themselves in the mirror (Gallup, 1970; Povinelli, Rulf, Landau, & Bierschwale, 1993). While this appears to be a shared cognitive capability of the great apes (Swartz, 1997), there is minimal evidence for self-recognition in other primate species (Gallup, 1977; Hauser, Miller, Liu, & Gupta, 2001).

Emotional Expression

Facial expression in primates is a difficult topic to summarize. Whereas some universal facial gestures appear to be shared across a broad range of primate species (see Figure 2C), others are distinctly species-specific and highly stereotyped (Gaspar, 2006; Preuschoft & van Hooff, 1995). Similarly, whereas aspects of facial expression perception may be inborn, others can be learned socially. In an example of inborn expression recognition, rhesus macaques raised in isolation of their conspecifics respond immediately to facial threats without any prior experience with faces (Sackett, 1966).

Emotional expressions are tightly linked to the mobility of the face, which increased during primate evolution, possibly reflecting the increasing importance of social exchange (Andrew, 1963; Burrows, 2008; Huber, 1931). To communicate anything, faces must be configurable into a range of postures. Primates, including apes, Old World monkeys and New World monkeys, are endowed with a broad repertoire of facial expressions involving the lips and eyes (Hauser, 1993; Maestripieri & Wallen, 1997; Preuschoft & van Hooff, 1995; Thierry, Demaria, Preuschoft, & Desportes, 1989; Tomonaga et al., 2004; van Hooff, 1962; Weigel, 1979), owing to an elaboration of the mimetic facial musculature compared to other mammals (Burrows, 2008; Burrows, Waller, Parr, & Bonar, 2006; Waller, Parr, Gothard, Burrows, & Fuglevand, 2008).

Experimental testing has shown that chimps can accurately interpret photographed expressions (Parr, 2003; Parr, Hopkins, & de Waal, 1998) and can, through experience, learn to categorize expressions of both monkeys and humans (Dittrich, 1990; Kanazawa, 1996).

As with humans, the eyes, including the closure of the lid and position of the brow, are important components of expression for many nonhuman primates (Andrew, 1963; Ghazanfar, Nielsen, & Logothetis, 2006), as are some aspects of mouth behavior. For example yawning can serve as a signal to conspecifics (Smith, 1999), with the exposure of canines serving as a low-grade threat among Old World monkeys (Hadidian, 1980). In both chimps and macaques, facial signals are coordinated with acoustic vocalizations. In extracting the social meaning of these signals, primates are therefore sensitive to the congruency of visual and acoustic facial signals (Ghazanfar & Logothetis, 2003; Parr, 2004) (Figure 2E). Accurate interpretation of facial and bodily expressions facilitates social learning in monkeys, as shown by macaques' acquisition of the fear of toy snakes and crocodiles after observing videos of their conspecifics reacting fearfully to them (Cook & Mineka, 1989).

Gaze

In addition to their role in emotional expression, eyes serve as important cues to gaze direction and objects of interest in the environment. Eyes, which are often high-contrast features, highlighted by coloration or patterning such as eye-rings to enhance visibility (Coss & Goldthwaite, 1995), attract primates' attention. For example, macaques focus their gaze on the eye region in pictures of monkeys (Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003; Keating & Keating, 1982; Kyes & Candland, 1987) and other animals (Demaria & Thierry, 1988). The importance of eyes and eye-like patterns is also evident in at least one prosimian species, as mouse lemurs were shown to have a selective aversion to looking at pairs of horizontally spaced dots (Coss, 1978c).

Accurate gaze monitoring is important in primate society, in which rules often govern who may look at whom. Prolonged gaze sometimes serves as an aggressive gesture to reinforce submissive gaze aversion in lower ranking group members (Coss, Marks, & Ramakrishnan, 2002; Deaner et al., 2005; Emery, 2000). Some primates can additionally infer the direction of another's gaze to an object or individual of interest (Emery, Lorincz, Perrett, Oram, & Baker, 1997; Tomasello, Call, & Hare, 1998). Rhesus monkeys rely primarily on head orientation for this, but follow eye-based direction of gaze under some conditions (Deaner & Platt, 2003; Ferrari, Kohler, Fogassi, & Gallese, 2000; Lorincz, Baker, Perrett, & Fagot, 1999). Chimps and bonobos are able to follow head orientation of a human experimenter to a target. Interestingly, they cease to do this when the object of attention is deemed to be out of the experimenter's line of sight (Okamoto-Barth, Call, & Tomasello, 2007). Humans are able to follow their mothers' gaze within the first year of life (Butterworth & Jarrett, 1991). In contrast to monkeys and apes, human infants rely primarily on the eyes rather than the head (Tomasello et al., 2007) (for a review, see Emery & Clayton, 2009).

Attraction

Like humans, rhesus macaques appear to find symmetry attractive, preferring to gaze at artificially symmetric photos of conspecific faces over asymmetric ones (Waitt & Little, 2006) (Figure 3B). Preference for symmetry may be related to phenotypic quality, as suggested by a study of fluctuating asymmetry (random deviations from perfect bilateral symmetry) of canine teeth in a wide range of primates (Manning & Chamberlain, 1993). It is not known whether non-human primates or other animals find averageness attractive, although it has been suggested that they might (Koeslag, 1990). It would be particularly interesting to know whether apes and monkeys share the human preference for averaged composite faces.

A particularly important facial cue for nonhuman primate mate selection is skin color. Primate faces are often decorated with patterns and colors that appear to play a role in mate

selection (Figure 3A, for a review, see Bradley & Mundy, 2008). Trichromatic primates are usually bare-faced, underscoring the potential role of color vision in primate face perception (Changizi, Zhang, & Shimojo, 2006). Facial skin coloration in chimps is variable within a social group (Bradley & Mundy, 2008), but its relationship to dominance and sexual selection is unknown. In monkeys, several studies have explored the connection between coloration and various social factors. Following computer graphic manipulation of redness in the coloration of faces, female rhesus macaques spent more time looking at artificially reddened male faces than the original versions of the same face, with increased looking times taken as a possible indicator of sexual attraction (Waitt et al., 2003) (Figure 3C). This preference may be because redness can signal male dominance rank and fitness (Setchell & Wickings, 2005). Their male counterparts showed no such preference for artificially reddened faces, but did prefer artificially reddened hindquarters (Waitt, Gerald, Little, & Kraisselburd, 2006). Both males and females attended to female facial coloration signaling pregnancy (Gerald, Waitt, & Little, 2009).

It is important to note that attractiveness in monkeys is often inferred by observing their gaze behavior when they are presented with multiple visual stimuli. This paradigm, which is similar to that used to assess novelty and recognition, must be interpreted with caution, as diverse social and non-social factors also contribute to gaze behavior. For example, male rhesus monkeys will spend more time looking at images containing sexual content than nonsexual images, and similarly spend more time looking at dominant than submissive male faces (Deaner et al., 2005; Sackett, 1965). Whether these stimuli should be considered attractive in the same sense as symmetrical and reddened faces, and how these factors contribute to paradigms using preferred looking to assess attraction, novelty, or recognition, remains an open question.

Development

The development of primate face processing is complex, involving an innate predisposition to look at the mother's face, along with a strong learning component. Chimpanzees can recognize their mother's face within a month of birth, with an increase in mutual gaze in the following month (Myowa-Yamakoshi, Yamaguchi, Tomonaga, Tanaka, & Matsuzawa, 2005; Tomonaga et al., 2004). Subsequent exposure is also important for their developing face recognition skills, as evidenced by the fact that chimps brought up primarily among humans become experts with human faces (Martin-Malivel & Okada, 2007).

Like humans, infant monkeys prefer schematic faces to other stimuli, with spatial configuration being the important factor for the first month, and feature details becoming important later (Kuwahata, Adachi, Fujita, Tomonaga, & Matsuzawa, 2004). Macaques deprived of any exposure to faces over the first 6-24 months of life showed immediate interest in subsequently shown faces, and gained expertise with *either* human or macaque faces thereafter, depending on subsequent experience (Sugita, 2008). Thus macaques exhibit both an innate preference for faces, along with a window of plasticity (abnormally extended in that case) in which their perceptual skills for a given category of faces are sharpened. A comparable developmental sharpening has also been observed in humans, whose capacity to discriminate monkey faces declines during development, presumably in part due to extensive selective exposure to human faces (Pascalis et al., 2002).

Neural Specialization

Most of our information about neural specialization for faces in nonhuman primates comes from electrophysiological single-unit experiments in macaques (see Gross, 2008 for a review). These studies reveal a core of face processing circuitry in the lower bank and fundus of the superior temporal sulcus and the adjacent surfaces of the inferior temporal

cortex, in cortical area TE (Desimone, Albright, Gross, & Bruce, 1984; Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982; Tanaka, Saito, Fukada, & Moriya, 1991). Face-selective responses have also been observed elsewhere in the cortex, including the superior temporal polysensory (Bruce, Desimone, & Gross, 1981), orbitofrontal (Rolls, Critchley, Browning, & Inoue, 2006) and ventrolateral prefrontal (Wilson, Scaldie, & Goldman-Rakic, 1993) cortical areas. More recent fMRI studies have supported and extended these initial findings (Logothetis, Guggenberger, Peled, & Pauls, 1999; Pinsk, DeSimone, Moore, Gross, & Kastner, 2005; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003), with combined fMRI/microstimulation demonstrating that patches of face responsive areas are functionally linked (Moeller, Freiwald, & Tsao, 2008). Other work suggests that the analysis of bodies takes place in regions of temporal cortex directly adjacent to face patches (Bell, Hadj-Bouziane, Frihauf, Tootell, & Ungerleider, 2009; Hasselmo, Rolls, & Baylis, 1989; Jellema & Perrett, 2003). And, as in humans, face processing shows hemispheric asymmetry, with strongest activation in the right hemisphere of both macaques (Pinsk et al., 2005) and vervets (Zangenehpour & Chaudhuri, 2005).

Some subcortical structures also show selective neural responses to faces. The macaque amygdala, for example, is sensitive to facial expressions (Gothard, Battaglia, Erickson, Spitzler, & Amaral, 2007; Hoffman, Gothard, Schmid, & Logothetis, 2007), with the eyes playing a particularly important role in its responses (Gothard et al., 2007; Hoffman et al., 2007; Leonard, Rolls, Wilson, & Baylis, 1985). Amygdala responses probably primarily reflect input from high-level visual cortex. Direct subcortical input to the amygdala might also contribute to face-selective responses passing through the superior colliculus and pulvinar (Adolphs, 2002; Johnson, 2005; Morris, Ohman, & Dolan, 1999; Palermo & Rhodes, 2007), though the existence of a viable functional pathway has not yet been firmly established in either humans or macaques (for a discussion, see Pessoa & Ungerleider, 2004 and Andino, Menendez, Khateb, Landis, & Pegna, 2009). Face-selective single-unit responses have also been reported in the macaque medial dorsal thalamus (Tanibuchi & Goldman-Rakic, 2003), striatum (Logothetis et al., 1999), superior colliculus (Arendes, 1994), and hippocampus (Hampson, Pons, Stanford, & Deadwyler, 2004).

Summary and Discussion

Primates extract a rich amount of social information from faces of their conspecifics. For the three species studied in the greatest detail, humans, chimps, and macaques, the many shared features of face processing, along with the apparently similar face-selective responses in the brain, suggests that our most recent common ancestor, living more than 20 million years ago, may have enjoyed a similar fluency with faces. The functional and anatomical similarities raise the possibility of evolutionary homology (similarity due to shared ancestry), between the primary face selective cortical areas in the macaque and human, albeit with a ventral shift in their anatomical location in humans (Pinsk et al., 2009; Tsao, Moeller, & Freiwald, 2008). However, to distinguish between homology and convergent (independent) evolution would require a detailed phylogenetic analysis of the species involved (Brooks & McLennan, 1991). While neural specialization for faces has not been investigated in New World monkeys, the few behavioral studies suggest that they also possess sophisticated face perception (Dufour et al., 2006; Phelps & Roberts, 1994), potentially pushing the origins of complex face processing back as far as stem anthropoid primates, who lived more than 40 million years ago (Janecka et al., 2007).

Did the exquisite face perception abilities we share with chimps and macaques evolve to fit the social needs of interactive primates, or did primate sociality exploit an existing fluency with faces? While evolutionary cause/effect relationships are notoriously difficult to establish, it is interesting to consider that *high spatial acuity* may have been the primary driver for the evolution of primate social vision. Nearly all anthropoid primates, including

apes, New World and Old World monkeys, have excellent acuity that stems from their large, forward-facing eyes and foveas. One theory holds that these features may, in part, reflect adaptations acquired during a nocturnal phase of their evolutionary history (Ross, 2000). A different theory attributes advances in the primate visual system to selection pressure arising from predation, in particular from snakes (Isbell, 2009). Whatever its basis, a pre-adaptation resulting in a high-resolution fovea that could be quickly directed to objects of interest would have greatly enhanced visual social communication (Allman, Sprague, & Epstein, 1977). It is interesting to note that extant primate species with larger eyes, and hence better acuity, have a particularly wide range of facial expressions (Dobson, 2009; Kiltie, 2000), consistent with this conjecture. In short, primate face perception and consequent aspects of sociality depend upon making quick and accurate visual discriminations at a distance. The emergence of our complex, vision-based sociality may ultimately be traced to a prior adaptation for visual acuity that emerged for reasons unrelated to social interaction.

Mammals

Compared to primates, other mammals rely less on vision and more on olfaction and audition for social communication. Nonetheless, many mammals have good visual acuity, though the use of vision in face perception has only been evaluated in a few species. Curiously, the most studied non-primate species, *sheep*, shows a pronounced visual specialization for faces at both behavioral and neural levels. In the mid 1980s, Keith Kendrick and colleagues began a series of landmark studies aimed at understanding social communication in sheep (for a review see (Tate, Fischer, Leigh, & Kendrick, 2006), and found that their face processing closely resembles that of humans and monkeys.

Identity

Sheep have excellent visual acuity (Kendrick, 2008), advanced social perception, and the ability to visually recognize faces of their conspecifics in photographs (Kendrick, da Costa, Leigh, Hinton, & Peirce, 2001)(Figure 1C, Figure 4A). They can recognize individual sheep on a computer screen even when identity information is reduced using morphing techniques, or when photographs are presented at a small scale (Tate et al., 2006). They can also recognize the faces of individual human caretakers and sheep dogs. Like primates, they prefer to look at pictures of their conspecifics over heterospecifics (Da Costa, Leigh, Man, & Kendrick, 2004).

Key features of sheep face perception are similar to those of primates. For example, the eyes seem to be a particularly important cue for discriminating individuals (Kendrick et al., 1995). Also, like humans, sheep exhibit a right hemisphere (left visual field) advantage for identifying other sheep based on photographs of their faces (Peirce, Leigh, & Kendrick, 2000), with lateralized activity in the right temporal cortex (Broad, Mimmack, & Kendrick, 2000; Peirce & Kendrick, 2002). Their individual recognition is dependent upon the correct configuration of facial features (Peirce et al., 2000) and their expertise appears greatest for their own species (Peirce, Leigh, daCosta, & Kendrick, 2001).

Recent work shows that sheep are not the only mammals capable of face recognition. Cattle are also able to recognize one another from photographs of their faces (Coulon, Deputte, Heyman, & Baudoin, 2009; Coulon et al., 2007). Domestic dogs can also recognize photographs of their owners' faces (Adachi & Fujita, 2007). These results suggest that the capacity for face recognition may, in fact, be common among mammals.

Several mammals have been tested for self-recognition in a mirror. The bottlenose dolphin exhibits some capacity for self-recognition (Marino et al., 2007; Marten & Psarakos, 1995; Reiss, 2001) (Figure 4B), though the interpretations of such experiments are not always

straightforward (Gallup, 1995). Killer whales also show signs of self inspection in a mirror, whereas sea lions do not (Delfour & Marten, 2001). Likewise, elephants have been reported to inspect marks on their face in front of a large mirror (Plotnik, de Waal, & Reiss, 2006) (but see (Nissani & Hoefler-Nissani, 2007)) (Figure 4C).

Emotional Expression

Some non-primate mammals convey their emotions using dynamic postures of the face and body, as documented by Darwin (Darwin, 1872). Muscles in the mammalian face permit a range of facial expressions involving the mouth, eyes, and ears, which are usually complemented by posturing of the body. Sheep readily communicate their facial expression of fear to one another, and can recognize emotion in photographs of their conspecifics (Da Costa et al., 2004; Tate et al., 2006) (Figure 4D). When given a choice between a distressed facial expression and a calm one, they choose the latter in exchange for food reward, even if it is displayed by a less familiar individual (overriding their preference for viewing familiar conspecifics). Again, the eyes appear to be the most important stimulus feature (Tate et al., 2006). In cattle, the percentage of eye white has been shown to be an indicator of stress, and may serve as an emotional signal for conspecifics (Sandem, Janczak, Salte, & Braastad, 2006).

In general, mammals display a wide range of facial behavior. Canids' expressive faces can signal both fear and aggression (Fox, 1969, 1970; Lorenz, 1966). Dogs, bears and related animals frequently engage in play, which involves gesturing with both the face and body (Bekoff, 1977; Henry & Herrero, 1974). Elephants use movements of the ears, head, and jaw to signal aggression or submission (Langbauer, 2000). Brow lowering, ear flattening, whisker movements, and the flehmen response (the stereotyped curling of the upper lip) are present in many mammalian species, and serve as salient cues for conspecifics (Andrew, 1963). However, little systematic work has been done to examine the mechanisms by which such visual expressions are processed and interpreted.

Gaze

The direction of gaze is likely to be important for many mammals, particularly those living in social hierarchies, though different species may use gaze differently. In canids, the use of direct gaze resembles that in primates: passive submission is associated with aversion of the eyes accompanied by flattening of the ears and a slight grimace, whereas aggression is associated with a direct stare, erect ears, and a slight pucker (Fox, 1970). In contrast, staring in domestic cats is associated with both offensive and defensive behaviors (van den Bos & de Vries, 1996).

Several mammalian species have been tested on their ability use gaze to infer a human's or conspecific's focus of attention. Testing often begins with asking whether an animal is able to find a hidden reward based on cues provided by the experimenter (for a review, see Emery & Clayton, 2009). Under such conditions, domestic dogs can follow their owner's head orientation and eye position to find a reward (Hare & Tomasello, 2005). This ability may be related to domestication, as the results in human-raised wolves are mixed (Hare, 2002; Virányi et al., 2008). However, the use of gaze cues is not strictly limited to domestication, since cetaceans, which are not the product of human domestication, can also follow human gaze (Pack & Herman, 2006, 2007; Tschudin, Call, Dunbar, Harris, & van der, 2001). Domestic goats, while unable to use either eye or head orientation to follow the gaze of humans, are able to use head orientation to follow the gaze of their conspecifics (Kaminski, Riedel, Call, & Tomasello, 2005). In summary, some non-primate mammal species that have been studied seem able to extract cues from the orientation of the eyes and

head to determine the direction of attention. Testing of additional species is needed to determine how widely this capacity is present.

A related issue is whether animals alter their gaze-following based on whether they believe an object is visible to the gazer. As mentioned above, chimps have this capability, though there is no evidence that monkeys do. While most species have not been tested in this regard, recent work demonstrated that domestic dogs are sensitive to the experimenter's field of visual attention (Miklosi, 2007). It is possible that this sensitivity is linked to dogs' general attentiveness to the human face and eyes (Gacsi, Varga, TopaL, & Csanyi, 2004).

Attraction

Mammals typically use multiple sensory modalities for mate selection, kin recognition, and the assessment of dominance. Vision is often of minor importance, playing a secondary role to acoustic, and particularly chemical, signaling (Brennan & Kendrick, 2006; Wyatt, 2003). For species that do rely on vision, the key features influencing mate selection are often aspects of the body, such as size, ornamentation, and posture. Nevertheless, some looking preferences for facial feature have been observed. For example, sheep prefer to look at faces of familiar over unfamiliar conspecifics, and conspecifics over heterospecifics (Da Costa et al., 2004). These preferences could be related to perceptions of attractiveness and mate choice, although they might simply be driven by a general preference for familiarity.

Development

It is unknown whether other non-primate mammals display innate preferences to face-like patterns, or whether their face processing improves with experience. There is a small amount of evidence for visual imprinting in mammals. Newborn guinea pigs, who, like some birds, are mobile and self-sufficient shortly after birth, will imprint upon and follow individual humans, though it is unknown which visual cues are used (Hess, 1959). It is clear, however, that at least in some non-primate mammals early experience with faces can significantly shape later behavior. In an ingenious cross-fostering experiment, baby goats were raised by sheep mothers, and vice-versa. As adults, when cross-fostered males from each species were shown photographs of sheep and goat faces, they preferred to look at females of the foster *mother's* species (rather than their own). Moreover, when placed in the pen with females of both species, they preferentially attempted to mate with the foster mother's species (Kendrick, Hinton, Atkins, Haupt, & Skinner, 1998), demonstrating that early facial experience determines sexual preference.

Neural Specialization

Aside from primates, neural specialization for faces has only been studied in sheep, whose brains display a striking similarity to those of monkeys in this regard. Single-cell recordings showed that neurons display a range of selectivity for faces, ranging from those selective for individuals, to those selective for stimulus categories (Kendrick, 1991, 2008; Kendrick & Baldwin, 1987). The demonstration of such *face cells* in the sheep's temporal cortex (Kendrick & Baldwin, 1987) is the sole piece of evidence that the brain's specialization for face processing extends outside the sphere of primates. Photographs of familiar faces elicited stronger neural responses than those of unfamiliar faces (Kendrick et al., 2001). Moreover, familiarity-based neural responses were not restricted to sheep faces, but extended to humans and sheepdogs. Interestingly, the tuning for "horn length" in one class of neurons (Kendrick, 1994) in the sheep temporal cortex bears more than a superficial resemblance to tuning for face distinctiveness by neurons in the monkey (Leopold, Bondar, & Giese, 2006) and human (Loffler, Yourganov, Wilkinson, & Wilson, 2005) temporal cortex (Figure 5). Finally, like neurons in the monkey temporal cortex, neurons in the sheep

temporal cortex respond to faces in a view-dependent manner (Perrett et al., 1985; Tate et al., 2006).

Discussion: Mammals

Many mammals readily produce and interpret facial gestures. Is this behavior the result of a shared and evolutionarily conserved cortical face processing circuitry? It is possible that at least *some* aspects of face perception were inherited from a common ancestor rather than that all aspects of face expertise emerged independently in all mammalian superorders. However, it is by no means obvious how shared modules for face processing could have been preserved: Much of mammalian evolution occurred during the age of the dinosaurs, where most mammals occupied nocturnal niches, thus diminishing the usefulness of visual cues for social signaling. Nonetheless, it is possible that some conspicuous facial markings such as eye-ring patterns that are commonly found in extant mammals (Caro, 2005; Ortolani, 1999) first evolved to make faces more conspicuous in moonlight, when some extant nocturnal prosimians are most active (Nash, 2007). During this nocturnal era, critical adaptations for facial signaling, such as moveable ears and elaborated mimetic musculature, became permanent fixtures of the mammalian face, though perhaps at first having little to do with visual signaling. Following the extinction of the dinosaurs, as some mammals became diurnal, these facial patterns and natural movements may have increasingly served as the basis for individual recognition and social signaling.

Clearly, there are many open questions regarding mammalian face processing and its evolutionary relationship to face processing in primates. Since neither brains nor cognitive processes leave behind a fossil record, the evolutionary history of face perception must be inferred from the similarity of behaviors, anatomy, and neural responses across different species. Distinguishing between homology and convergent evolution is particularly difficult (Wenzel, 1992). Homology would require functionally and anatomically similar face-responsive regions to be present in the common ancestor of mammals and primates, a mammal living with dinosaurs during the Cretaceous period (Springer, Murphy, Eizirik, & O'Brien, 2003). For some critical aspects of face processing, this intriguing possibility cannot be ruled out. Alternatively, given that both sheep and macaques are diurnal and social, their face-selective cortical machinery might have evolved independently, as parallel adaptations of a general visual processing system, driven by similar sources of natural and sexual selection. In either case, the functional and neural similarities of mammalian and primate face perception highlight the probable ancient evolutionary origins of face perception.

In the future, neurophysiology and imaging experiments in a wider range of mammalian species may shed light on the origins of primate face perception. For example, the presence of face selective cortical responses in a large proportion of mammals with widely varying different ecologies, perhaps diurnal and nocturnal carnivores, rodents, and marsupials, would be consistent with specialization for face processing as early as the Cretaceous period. If, on the other hand, the cortical specialization for faces is present in only a few species of mammals with very similar ecologies (e.g., highly social and diurnal) then it would seem more likely that face perception in primates and non-primate mammals are examples of convergent evolution arising in response to similar sources of natural selection. Given the multiple, interacting aspects of face processing in the primate brain, it may only be through comparative and behavioral studies that scientists are able to disentangle the recently evolved neural circuits specialized for primate sociality from older, more general mammalian circuits involved in the more basic visual analysis of faces.

Vertebrates

Reptiles, birds, and fish lack the elaborated facial musculature of mammals, and therefore have a limited repertoire of facial behavior. Nonetheless, many species depend on their vision for social interaction, with some paying particular attention to the face and head.

Identity

Visual conspecific recognition has been demonstrated in birds (Bird & Emery, 2008; D'Eath & Stone, 1999; Ryan & Lea, 1994; Thorpe, 1968), reptiles (Olsson, 1994; Van Dyk & Evans, 2007) and fish (Bshary, Wickler, & Fricke, 2002; Grosenick, Clement, & Fernald, 2007) (see Figure 1D,E). Some fish are able not only to visually recognize their conspecifics, but can even infer and remember their relative dominance rank based on appearance (Grosenick et al., 2007). Heterospecific individual recognition has also been demonstrated in some species of birds. For example, mockingbirds can recognize individual humans after repeated exposures (Levey et al., 2009). In crows, individual recognition of humans seems to be based on the face, since a familiar human wearing a mask is treated as a stranger (Cornell, Marzluff, & Peccorro, 2009).

Unfortunately, little is known about the specific cues underlying visual conspecific recognition in vertebrates, though a few studies suggest the face is sometimes important. For example, pigeons can discriminate pictures of conspecific faces (Nakamura, Croft, & Westbrook, 2003; Watanabe & Ito, 1991). In birds, plumage on the face supports individual recognition of conspecifics in white-throated sparrows (Whitfield, 1987), male ruffs (Dale, Lank, & Reeve, 2001), and budgerigars (Brown & Dooling, 1992). Experiments using parametrically manipulated stimuli have shown that budgerigars, like humans, rely on second order configural cues in their recognition (Brown & Dooling, 1993) (Figure 6A). Magpies, like chimps, and a few other mammalian species mentioned above, have also been reported to recognize their reflection, removing a mark on their face in front of a mirror (Prior, Schwarz, & Gunturkun, 2008).

Emotional Expression

For non-mammals, most communicative gestures involve displays of the body, which have been analyzed and quantified in birds (Davies, 1978; van Rhijn, 1981) and reptiles (Carpenter, 1977). Video playback testing has shown that such conspecific displays elicit appropriate behavioral responses (Ord & Evans, 2002). Though birds, lizards, and fish lack the capacity to make complex facial expressions, some basic facial musculature, such as the that involved in moving the eyes and jaw, is shared (Noden & Francis-West, 2006). This leaves open the possibility, albeit only weakly supported, that mouth and eye movements play a role in social signaling in non-mammalian vertebrates. There are some obvious facial gestures, such as stereotypical begging signals in nestling birds (Figure 6B) (Hunt, Kilner, Langmore, & Bennett, 2003; Kilner & Davies, 1998). In addition, communicative gestures of the head, mouth, and throat have been reported in some species of frogs (Hodl, Amezcuita, & Ryan, 2001), lizards (Jennsen, 1977), birds (Andrew, 1961), and fish (Baerends & Baerends-Van Roon, 1950).

Gaze

Eyes are an important stimulus for a wide range of non-mammalian vertebrates (reviewed in Emery, 2000). Previous work has shown that representatives of all major vertebrate taxa are capable of reacting to a pair of dark eyes. In some cases eye sensitivity is important for conspecific interactions, such as gaze aversion. In young jewelfish, for example, a pair of horizontally spaced black disks elicits an evasive response, while other spatial

configurations do not (Coss, 1979). This eye-specific reaction is thought to be innate and important for establishing social dominance (Coss, 1978a).

In other cases eye sensitivity appears to be more strongly geared for interspecific interactions, such as predator-avoidance. Eyes, as visual stimuli, serve as a basis for recognizing predators. For example, pied flycatchers respond to “dummy” birds shaped like natural predators (a shrike or owl) with anti-predator behavior in the form of mobbing, vocalization, freezing, and tail-flicks (Curio, 1975). However, when the eye stripe or eyes themselves were altered in the dummy, the incidence of these behaviors decreased significantly. Lizards and snakes also react with avoidance or defensive behavior to the presence of eyes, either the direct gaze of an experimenter or detached glass eyes (Bern & Herzog, 1994; Burger, 1998; Hennig, 1977). White Leghorn chicks avoided eye-like patterns compared to control patterns (Scaife, 1976b), and were more likely to approach a model of a stuffed hawk when its eyes were obscured with feathers (Scaife, 1976a). In addition, some birds and snakes are able to detect when they are the object of an experimenter's (or predator's) gaze, and adjust their behavior accordingly (Burghardt & Greene, 1988; Carter, Lyons, Cole, & Goldsmith, 2008; Hampton, 1994). This widespread sensitivity to eyes may stem from a simple principle of natural selection: those able to notice and avoid a pair of eyes fixed upon them are more likely to survive. At the same time, certain predators use their heterospecific eye perception as a target for attack, such as the spitting cobras, who consistently aim for the eyes in both natural and laboratory conditions (Westhoff, Tzschatzch, & Bleckmann, 2005).

In following visual gaze, birds show a striking, and somewhat surprising, convergence with primates. Like primates, ravens can follow shifts in combined head- and eye-gaze direction in humans. When a barrier is present, they move into a position in which they can determine the object of the experimenter's gaze (Bugnyar, Stowe, & Heinrich, 2004), with this latter skill requiring several months to develop (Schloegl, Kotrschal, & Bugnyar, 2008a). Interestingly, despite having the requisite perceptual skills to compute and follow gaze direction, ravens do not naturally seem to exploit such information to locate a food reward in an object choice task (Schloegl, Kotrschal, & Bugnyar, 2008b). In one experiment, however, jackdaws could do this, although only when the experimenter's gaze alternated back and forth between the bird and the reward providing a strong cuing signal (von Bayern & Emery, 2009).

Attraction

Social attraction and dominance of many non-mammalian vertebrates is often based on visual appearance. This is apparent in the beautiful displays of many birds, which are commonly used to illustrate principles of sexual selection (Pruett-Jones & Pruett-Jones, 1990; Trainor & Basolo, 2000). Some such displays involve markings on the face and head, such as the status marks on white crowned sparrows and great tits (Whitfield, 1987), as well as the markings on the cheeks and chest of the zebra finch (Brazas & Shimizu, 2002). Symmetry is also an important feature for sexual selection, although little is known about preferences for facial symmetry in vertebrates (Swaddle & Cuthill, 1994; Thornhill & Moller, 1998; Waas & Wordsworth, 1999).

Development

Like humans, some non-mammalian vertebrates are born with innate predispositions to react to certain visual patterns. These predispositions can serve as a basis for attraction, or as a signal of danger that causes them to flee. An example of the latter is in jewel fish, who, as early as 13-days post-spawning, instinctively avoid pairs of black dots resembling eyes, even in the absence of previous experience with real eyes (Coss, 1978a). Juvenile and adult

fish become highly sensitive to this cue and use it to guide their aggressive or avoidance behavior in the dominance hierarchy.

One aspect of avian visual development that resembles the development of face perception in primates is the innate preference to orient to a particular configural stimulus shortly after birth. In some birds, filial imprinting undergoes a similar temporal sequence to that seen in humans. For example, chicks are initially attracted to any stimulus with eyes and/or head and neck shape (Bolhuis & Honey, 1998). Then, following a relatively short period of experience, the preference becomes more narrowly focused on a single object or individual, a critical step in filial imprinting (Bolhuis & Honey, 1998). These two stages are thought to represent a transition from processing in the mesencephalon (e.g. optic tectum) to processing in the telencephalon (e.g. the mesopallium, formerly called hyperstriatum ventrale). Damage to the latter structure abolishes filial imprinting (Bolhuis & Honey, 1998; Johnson & Horn, 1987). Note that these two sequential mechanisms of orientation to conspecifics resembles those observed in human newborns and infants, and may represent a homologous ontogenic transition (Johnson, 2005).

Neural Specialization

To our knowledge, there are no reports of selective neural responses in the non-mammalian vertebrate brain to faces or other complex forms. It is presently difficult to assess whether this absence is because form-selective neurons do not exist, or simply because complex stimuli have not been systematically tested. Lesion studies in birds suggest that high-level specialization related to social aspects of vision may exist in the avian brain. In pigeons, damage to the entopallium (formerly called the *ectostriatum*) causes a deficit in complex form vision (Bessette & Hodos, 1989), including conspecific recognition, while damage to the Wulst does not. This dissociation is interesting, since the Wulst receives retinofugal input, and is thought to be homologous to mammalian primary visual cortex (Medina & Reiner, 2000; Pettigrew & Konishi, 1976), whereas the entopallium in birds and lizards receives tectofugal input, and may be homologous to mammalian extrastriate visual cortex (or possibly only to its input layers) (Krutzfeldt & Wild, 2005). Recent studies in the zebra finch further support the interpretation that the entopallium supports high-level vision (Watanabe, Maier, & Bischof, 2008).

Discussion: Vertebrates

Vision is abundantly used for social interplay among nonmammalian vertebrates, and particularly birds, although the role of the face is unclear and probably minor compared to mammals. The eyes appear to be important stimuli for all major vertebrate taxa, and the capacity of corvids to read human gaze is remarkable. Given that birds are so distantly related to primates and have such different brain structures, it seems likely that their gaze perception mechanisms evolved independently of those in primates. Nevertheless, it remains possible that while their common ancestors, who lived roughly 320 million years ago (Butler & Hodos, 2005), may not have had complex gaze following abilities, they had some sensitivity to eyes. Ancient circuits in the midbrain, diencephalon, and pallium mediating this sensitivity may have then evolved into more specialized face-processing circuitry in both primates and birds, and possibly many other vertebrates.

Invertebrates

For completeness, we also consider complex visual processing in invertebrates, asking whether there could be any connection to human face perception. Some invertebrates can learn and remember complex forms (Heisenberg, 1995) and vision is an important social sense for some invertebrate species, including butterflies (Vane-Wright & Boppre, 1993),

spiders (Clark & Uetz, 1990) (see Figure 1F), and horseshoe crabs (Barlow, Ireland, & Kass, 1982). In spiders, eyes seem to be a salient feature for visually mediated social interaction (Harland & Jackson, 2002). While there is good evidence that octopi can recognize objects, conspecific recognition in cephalopods has not yet been tested rigorously (Boal, 2006). In cuttlefish, five experiments failed to show vision-based individual recognition (Boal, 1996), despite rich intraspecific interaction, visual displays, and mate-guarding.

Some invertebrates can recognize each other visually using “facial” cues (Detto, Backwell, Hemmi, & Zeil, 2006; Tibbetts, 2002; Van Der Velden, Zheng, Patullo, Macmillan, & Brembs, 2008). In one study wasps treated familiar conspecifics as strangers when artificial markings were added to their faces or abdomens, effectively changing their visual identity (Tibbetts, 2002). In another, crayfish remembered the appearance of their opponents' faces following a direct conflict (Van Der Velden et al., 2008). Bees can discriminate and remember human faces, even interpolating between studied views to recognize novel views of these faces (Dyer, 2005; Dyer & Vuong, 2008). These observations demonstrate that comparatively simple visual systems are able to perform complex discriminations to support individual recognition (but see Pascalis, 2006).

Finally, in an ironic evolutionary twist, the sensitivity of vertebrates to faces has been unknowingly exploited by some invertebrates (Figure 7). For example, some Lepidoptera possess eye-like patterning on their wings, which is thought to protect them against predator attacks (Stevens, 2005) (although they may also be used in intraspecific visual mate selection (Robertson & Monteiro, 2005)). A remarkable example of eye patterning is found in cuttlefish, who dynamically create high contrast eyespots on their body before fleeing from visually oriented teleost fish, but not from crabs and dogfish, which are chemosensory predators (Langridge, Broom, & Osorio, 2007). Thus while invertebrates themselves may be somewhat indifferent to the visual appearance of faces, they exploit the fact that their predators are not!

Conclusions

This review has focused on the behavioral importance of faces in a wide range of animals. We first asked to what extent faces represent a special category of stimuli. We conclude that faces are important for a wide range of animals, as representative species from all vertebrate classes exhibit behavioral responses to faces that differ from those to non-face stimuli. In primates and sheep, for which face perception is highly developed and serves as the foundation of their social exchange, the brain contains neurons in multiple areas that are dedicated to the analysis of faces. Thus for these species, which are the only ones to have been systematically tested, the behavioral importance of faces appears to have fundamentally shaped processing in the visual pathway.

We next asked what types of visual information different animals extract from a face. At the most basic level, horizontally paired dark eyes elicit specific behavioral responses from a wide range of species, including primates, other mammals, birds, reptiles and fish. For visually oriented animals, the importance of eye detection may be understood in an evolutionary context, as it might indicate the approach of a competitor, predator, or potential mate, all of which have important implications for survival. In addition, some species of primates, sheep and birds were shown to extract more complex information from faces, such as species or individual identity, the direction of gaze, or the level of aggression, with primates showing the most sophisticated face-reading behavior. An intriguing possibility is that the shared perceptual basis reviewed here may be particularly suited to facilitate some forms of *heterospecific* interaction. This can include recognition of threatening species, which important for survival (Coss, Ramakrishnan, & Schank, 2005), as well as the playful

or nurturing behavior sometimes observed between members of different species living together under unnatural conditions.

Finally, we asked how different aspects of face processing might have evolved. We can speculate that paired dark eyes served as the earliest “face” cue, providing visible markers of sighted conspecifics to all sighted creatures. This important cue may have led to the evolution of eye-selective neural responses in animals living hundreds of millions of years ago, before the first dinosaur, and perhaps even before the first vertebrate. Other important aspects of face perception, such as the detection of an open mouth or a fixed gaze involved in predator detection, may also have very ancient origins and may have further shaped the evolution of visual processing in the brain. We can speculate that recognition based on faces came later, and probably first pertained to the identification of the species rather than the individual. It is possible that visual species recognition in mammals emerged while they were predominantly nocturnal, aided by highly visible and stereotyped patterns on the face and head. After the extinction of the dinosaurs, diurnal mammals may have then capitalized on this pre-existing recognition system and adapted it to identify and remember individuals based on more subtle cues. For many primates, including humans, face perception takes center stage in social signaling, and the origin of such signaling may lie in the enhanced sensitivity to detail afforded by high visual acuity. In addition, the learning of subtle facial gestures and the capacity to discriminate highly similar faces require a wide network of brain areas whose division of labor is presently under intense investigation along with an extended period of experience-dependent development. The preeminence face recognition in primates over that of other animals, which is exemplified by the use configural cues to recognize unfamiliar faces, appears to hinge on neural encoding that is both systematic and adaptable. Through experiential learning, primates including humans optimize their own personal face interpreting machinery, as both psychophysical and physiological experiments have demonstrated that, over time, the brain automatically tunes itself the natural statistical variation of the faces it has experienced (for a review, see Rhodes & Leopold, 2010).

In choosing animal models for biological research, there is a trade-off between depth and breadth of study. Systems and behavioral neuroscience has opted for depth, and has invested monumental effort into a small number of animal models. While this approach has uncovered a wealth of information about face processing in the (typically rhesus macaque) monkey and human brain, it has not led to the proper biological or evolutionary contextualization of this information. Dobzhansky's admonition that nothing makes sense except in the light of evolution can be applied just as well to face perception as it can to any other biological feature (Dobzhansky, 1973). If not for Kendrick's investigation in sheep, there would be no evidence that non-primate brains were specialized for perceiving complex visual stimuli, let alone faces. In the future, exploration of face processing in other animals, such as prosimians, carnivores, diurnal rodents, and marsupials, would be of great value for interpreting the currently available neurophysiological data from the temporal cortex of primates and sheep. Similarly, discovering whether vertebrates such as birds and lizards have specialized neural machinery responding to eyes and other natural stimuli would be highly informative, and might lead primate neurophysiologists to discover other circuits, perhaps subcortical ones that are homologous to circuits in the human brain, that would otherwise remain hidden. Discovery is, by definition, a process that is impossible to predict. When the experiments are too narrowly focused on a single species, however, some forms of discovery are ruled out from the start.

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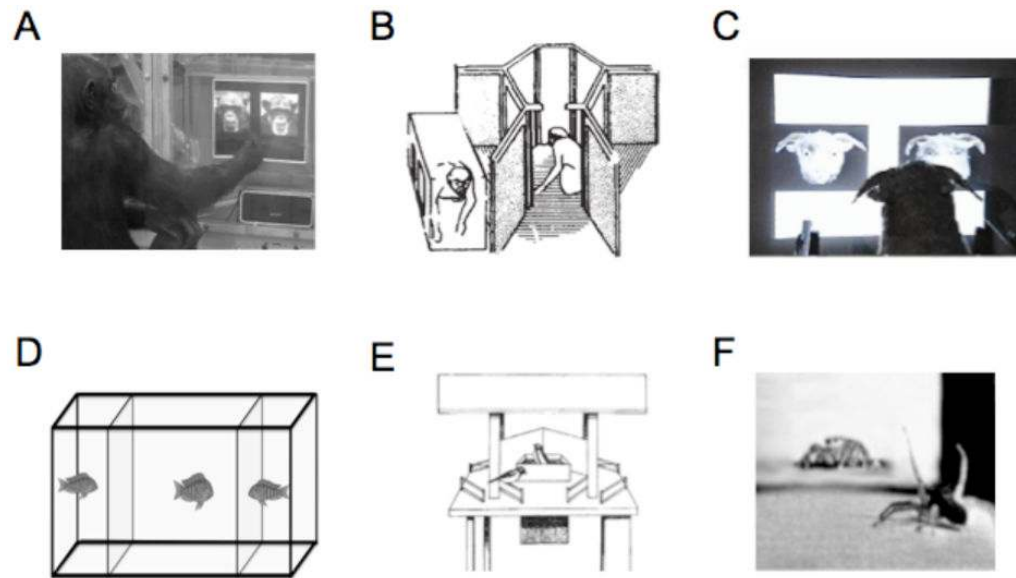


Figure 1.

Methods for testing animals on visual conspecific perception. A. A chimp indicates its recognition of a face by pressing on a touch-screen [1]. B. Macaque monkeys tested for capacity to visually recognize kin with whom they had no prior experience [2]. C. A sheep discriminates between two faces by pressing one of two panels in exchange for a food reward [3]. D. A fish inspects two neighbors in order to test whether it can subsequently recognize them [4]. E. Reactions of individual great tits to a radio-controlled maneuverable dummy was used to investigate the contribution of breast-stripe width to establishing social dominance [5]. F. A male jumping spider courts the video image of a female [6].

Figure 1 Citations

- [1] adapted from Martinez and Matsuzawa (2009). *Animal Cognition*, Suppl 1:S71-75.
 [2] adapted from Wu, H. M., Holmes, et al. (1980). *Nature*, 285(5762), 225-227.
 [3] adapted from Kendrick, K.M. (2008), in *The Welfare of Sheep*, (C. Dwyer, Ed.), Springer, Netherlands.
 [4] adapted from Balshine-Earn and Lotem (1997) *Behaviour* 135:369-386.
 [5] adapted from Jarvi and Bakken (1984) *Animal Behaviour* 32: 590-596.
 [6] adapted from Clark and Uetz (1990) *Animal Behaviour*. 40:884-890.

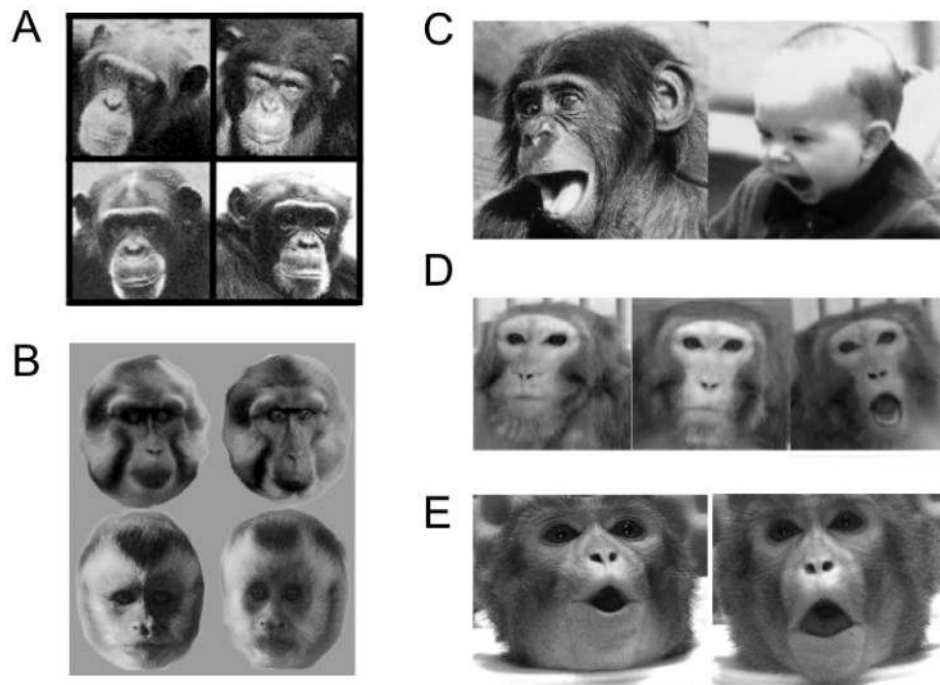


Figure 2.

The recognition and interpretation of conspecific primate faces. A. Chimps can recognize familial face similarity between mothers (left column) and their sons (right column) ^[1]. B. Tonkean macaques and brown-faced capuchins are better able to discriminate between members of their own species (top and bottom rows, respectively) than between members of other species ^[2]. C. Homologous play face in bonobo and human ^[3]. D. Lip-smacking, neutral, and threat expressions from a rhesus macaque, used as stimuli for neurophysiological experiments ^[4]. E. Images taken from video stimuli shown to macaques with either matching or nonmatching acoustic vocalizations ^[5].

Figure 2 Citations

[1] adapted from Parr and de Waal (1999) *Nature*, 399: 647-8.

[2] adapted from DuFour et al (2006) *Behavioral Processes*, 73: 107-13.

[3] adapted from Schmidt and Cohn (2001) *Yearbook of Physical Anthropology*, 44:8-24.

[4] adapted from Gothard et al (2007) *J Neurophysiology*, 97:1671-1683.

[5] adapted from Ghazanfar and Logothetis (2003) *Nature*, 423:937-8.

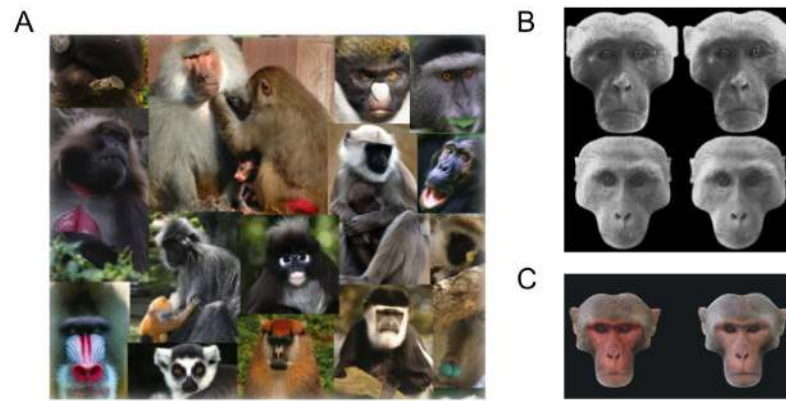


Figure 3.

Face attributes associated with sexual selection in primates. A. Primate faces are often high contrast or colored, often with highlights around the eyes ^[1]. B. Both male and females rhesus monkeys prefer symmetrical (left column) over asymmetrical (right column) faces ^[2]. C. Male facial coloration in rhesus macaques affects viewing preference of females, with artificially reddened faces attracting longer periods of inspection ^[3].

Figure 3 Citations

[1] adapted from Bradley B and Mundy N (2008). *Evolutionary Anthropology*, 17(2), 97-111.

[2] adapted from Waitt C and Little AC (2006) *International Journal of Primatology*, 27(1), 133-45.

[3] adapted from Waitt C et al (2003) *Proceedings of the Royal Society B: Biological Sciences*, 270, S144-6.

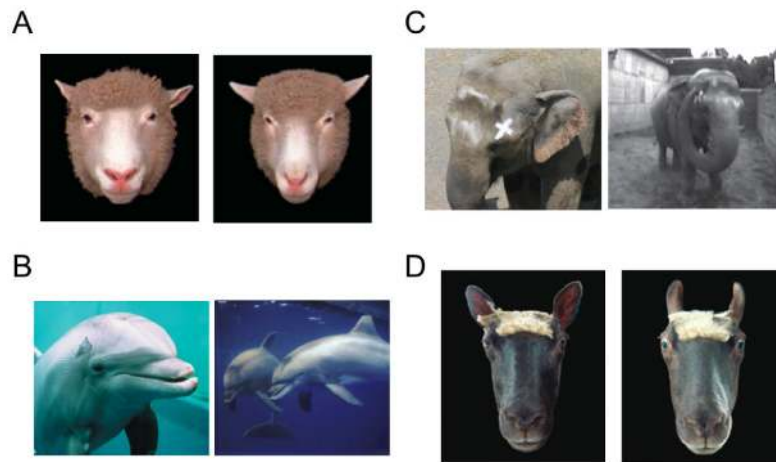


Figure 4.

The recognition of identity, expression, and self in mammals other than primates. A. Sheep (superorder Laurasiatheria) use the variation in the structure of the face to recognize one another ^[1]. B. Bottlenose dolphins (superorder Laurasiatheria) pass tests of self-recognition. When marked on the skin (left), they position themselves in front of the mirror in order to see the mark on their body (right) ^[2]. C. Similarly, elephants (superorder Afrotheria) pass tests of self-recognition. After receiving a mark on their face (left), they use their trunk in front of a mirror in an attempt to remove it (right) ^[3]. D. Sheep communicate emotion with their face, in this case indicating fear by drawing back the ears and opening the eyes ^[1].

Figure 4 Citations

[1] adapted from Tate AJ et al (2006) *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361: 2155-2172.

[2] adapted from Marino et al (2007) *PLOS Biology* 5(5):966-972 and Reiss and Marino (2001) *Proceedings of the National Academy of Sciences of the United States of America*, 98:5937-42.

[3] adapted from Plotnick et al (2006) *Proceedings of the National Academy of Sciences of the United States of America*, 103(45):17053-57.

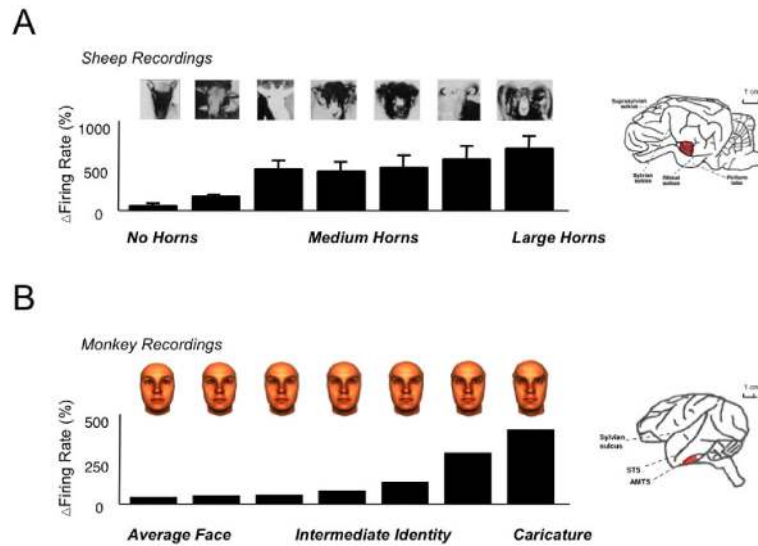


Figure 5.

Face processing in sheep and monkeys. (a) A subset of neurons in the sheep temporal cortex respond as a function of the visible length of the horns, a distinguishing feature for recognition of individual and species, as well as for social dominance [1]. (b) Neurons in the monkey temporal cortex respond to images of human faces, in this case responding monotonically to increasing amounts of “identity” level, or individuating feature information [2].

Figure 5 Citations.

[1] adapted from Kendrick, KM (1994) *Behavioral Processes* 33:89-112.

[2] Leopold DA et al (2006) *Nature* 442:572-575.

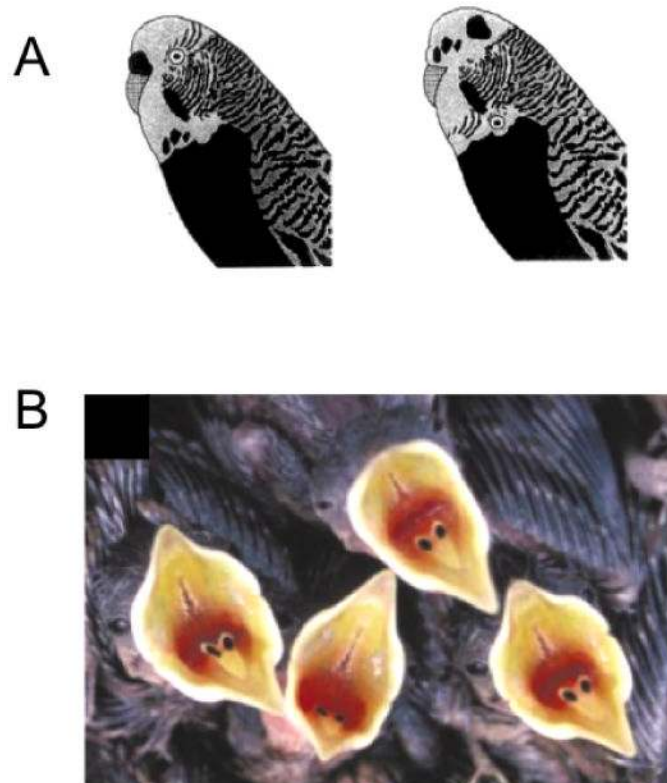


Figure 6.

Visual analysis of conspecific faces in birds. (a) Budgerigars can discriminate pairs of real and synthetic conspecific faces. They are quicker at discriminating pairs of individuals when faces are configurally intact (left) than when they are scrambled (right) ^[1]. (b) The appearance of a nestling's open mouth determines the parental feeding response. Visual features include the size of the gape, internal patterning, and coloration ^[2].

Figure 6 Citations

[1] adapted from Brown SD and Dooling RJ (1993) *Journal of Comparative Psychology*. 107(1):48-60.

[2] adapted from Kilner RM et al (1999) *Nature*, 397:667-72.

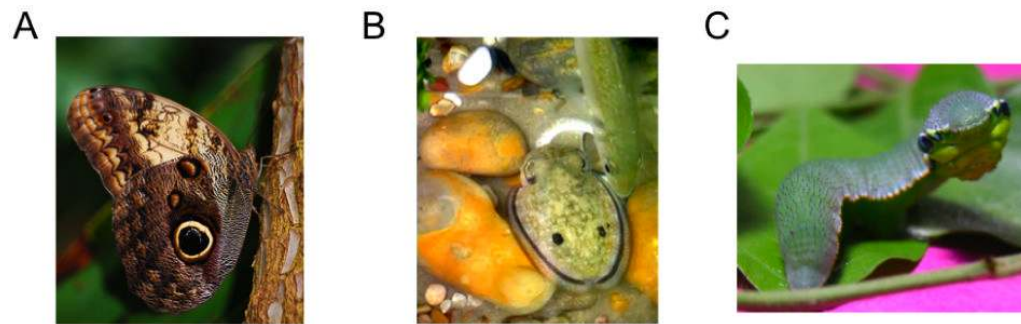


Figure 7.

Examples of invertebrate species with eyespot markings. (a) Owl butterfly with a conspicuous eyespot on its wing ^[1]. (b) Eyespot displays on the dorsum of a cuttlefish appear according to what type of predator is approaching ^[2]. (c) Caterpillar of the Great Orange Tip butterfly has false eyespots and the facial appearance of a green vine snake ^[3].

[1] adapted from http://en.wikipedia.org/wiki/Caligo_memnon.

[2] adapted from Langridge KV et al (2007) *Current Biology* 17:R1044-R1045

[3] http://en.wikipedia.org/wiki/Hebomoia_glaucippe