Chapter 4
It Takes One to Know One: Do Human and Nonhuman Primates Share Similar Face Processing?

Olivier Pascalis, Fabrice Damon, Kun Guo, and David Méary

Abstract The abilities to identify individuals within the group, and to interpret their expressions and intentions are essential for many social animals. Face recognition in human and nonhuman primates stems from a conjunction of evolutionary inheritance and experience via exposure to faces present in the environment. Individuation is clearly a vital mechanism for any social species. By uncovering similarities across primate face systems, comparative studies allow us to better understand the evolution of face processing capabilities in humans. Some researchers have argued that primates, including humans, may possess an innate face processing system that is predisposed to respond to conspecifics. The argument is supported by a study showing that monkeys raised without experience of own-species faces still prefer to look at faces of conspecifics (Fujita, Int J Primatol 11:553–573, 1990). However, this proposal does not fit well with findings from the human infant literature (Pascalis et al., Science 296:1321–1323, 2002) or with data on monkeys raised without seeing faces (Sugita, Proc Natl Acad Sci, 105, 394–398, 2008) which suggest that face processing is highly shaped by experience at an early age. We argue that human and nonhuman primates possess an evolved system for processing faces that becomes specialized as a consequence of predominant exposure to faces from a single species. According to this interpretation, a limitation of the face processing expertise to own species should be observed.

Keywords Face · Nonhuman primates · Humans · Development

O. Pascalis (✉) · D. Méary
Laboratoire de Psychologie et Neurocognition, Université Grenoble Alpes, Grenoble, France
e-mail: Olivier.Pascalis@univ-grenoble-alpes.fr; David.Meary@univ-grenoble-alpes.fr

F. Damon
Centre des Sciences du Gout et de l'Alimentation, Université Bourgogne Franche-Comté, Dijon, France

K. Guo
School of Psychology, University of Lincoln, Lincoln, UK
e-mail: kguo@lincoln.ac.uk

Introduction

The ability to identify individuals within the group, and to interpret their expressions and intentions is essential for many social animals. In humans, it is well established that face processing abilities underpin such functions, and comparative studies suggest a common evolutionary route for this important skill (Leopold and Rhodes 2010). Nonhuman primates have often been used as a model of human face processing. Fujita (1987) has been interested in nonhuman primate models for many years, and has continued to publish influential work on this topic. In this chapter, we will document some similarities in face recognition but also differences that make this cognitive system well adapted for each species.

Faces are omnipresent in our environment, and are crucial for our everyday social life. It has been suggested that face recognition might somehow be «special» (Farah 1996) compared to recognition of other objects. Indeed, faces provide an early channel of communication, operating prior to the onset of language between infant and caretaker. It has been shown that infants preferentially orient to faces during the first week of life (Goren et al. 1975; Johnson et al. 1991; Valenza et al. 1996). By the time they reach adulthood they can be considered as face experts. Diamond and Carey (1986) suggested that we learn to process faces differently than other visual stimuli. Information on a face can be construed as hierarchically organized with facedness information at the top (e.g., faces vs. objects), followed by species information (e.g., human vs. monkey), then by subordinate information such as gender and race, and at the lowest level, individual identity information. Individuating information can in turn be further divided into featural information (e.g., the shape or size of the eyes), configural information (e.g., the distance between the eyes), and holistic information (the face gestalt that binds featural and configural information into an unbreakable whole) (Leder and Bruce 2000). Despite the role of early visual experience in the development of configural and holistic processing, some researchers speculate that both are adult-like at a later age relative to featural face processing. This speculation was first proposed in the late 1970s with the introduction of the controversial encoding switch hypothesis (Carey and Diamond 1977; Diamond and Carey 1977). The encoding switch hypothesis proposes that young children encode faces in a piecemeal fashion (i.e., individual facial features), whereas older children—beginning at around the age of 10—encode the spatial relations between individual facial features. This hypothesis was based on findings regarding the effects of paraphernalia and inverting faces on children's recognition. This configural processing is responsible for the striking *inversion effect* (Yin 1969): inverted faces are less rapidly and accurately processed than upright faces (for reviews, see Rakover 2013; Rossion 2008). Carey and Diamond (1977) used inversion as a measure of children's use of spatial relations among features (i.e., involved in both configural and holistic processing). They found that the recognition of faces in 10-year-olds was disproportionately more impaired by inversion than the recognition of houses, whereas 6- and 8-year-olds showed similar impairment for both categories. Recent data suggest, however, that from a young age infants are

sensitive to configuration (Anzures et al. 2019). Diamond and Carey (1986) showed that this processing mode is a consequence of experience, and can be extended to other categories in which subjects are expert.

How Do Other Species Process Faces?

A variety of nonhuman social species possesses remarkable face discrimination abilities. Tibbetts (2002) reported that wasps, primarily reliant on chemical signatures for communication and identification of conspecifics, are also capable of hierarchical categorization (e.g., "worker") based on facial visual patterns only. Dyer et al. (2005) found that honeybees can learn the picture of a human face and recognize it when it is paired with a novel face (for similar findings with wasps, see also Avarguès-Weber et al. 2017). This result is consistent with what we already know about the visual ability of bees. However, Pascalis et al. (2006) pointed out that in the study by Dyer et al. (2005), recognition could have been performed on the basis of very simple pattern processing, and might not be related to face processing at all. Thus, for now there is no compelling evidence of human-like face processing in insects. Recently, sheep (*Ovis aries*) have been found to present advanced face recognition skills, including the ability to recognize and discriminate individual human faces (Knolle et al. 2017). However, the claim that sheep also possess human-like face processing seems too strong (for a discussion, see Kendrick 2019; Peirce 2019; Towler et al. 2019). Sheep and human performances were, for instance, not compared on equivalent tasks, as face recognition tasks typically require that humans learn new face identities in few seconds and in one trial, whereas sheep are trained over several consecutive days and throughout many trials (Towler et al. 2019). In addition, the strong advantage in processing familiar over unfamiliar faces, thought of as a key feature of human face processing (Young and Burton 2018), has not been found in sheep, suggesting qualitatively different mechanisms between two species (Towler et al. 2019). It is worth noting, however, that sheep are clearly better at processing sheep faces than human faces—as humans are at processing own- vs. other-species faces—hence, for a true comparison, both human and sheep faces should be used in future comparative studies (Kendrick 2019) to determine to what extent the face recognition mechanisms overlap between the species.

The situation is quite different for nonhuman primates, and comparative studies on face recognition in various primate species have burgeoned during the last 20 years. The adult face processing system of nonhuman primates shares several similarities with that of humans: eye scanning, region of interest, individual recognition of face pictures, sensitivity to face inversion (see Pascalis et al. 1999 for a review). Humphrey (1974) used a habituation task to show that rhesus monkeys can distinguish different individuals from their own species—but this performance did not extend to individuals from other, nonprimate species. Using a classic habituation paradigm, Dahl et al. (2007) found that individual recognition by macaques was better for conspecific faces than for other-species faces, and that, like humans,

macaques show holistic processing. Gothard et al. (2009) found the same result, and their detailed analysis of the eye scanning of the faces showed that whereas monkeys use both configural and feature-based processing to recognize the faces of conspecifics, they use primarily feature-based strategies to recognize human faces. These studies suggest the use of different strategies while processing other-species faces. Another study by Dahl et al. (2009) compared scanning strategies by humans and macaques when looking at conspecific or heterospecific faces. Both species displayed the same pattern of scanning for their own- versus other-species faces: more attention was directed to the eye region for their own species than for other species. Findings of better performance in face recognition tasks with own- versus other-species faces extend to other primates species (e.g., brown capuchin monkeys and Tonkean macaques, Dufour et al. 2006; chimpanzees, Martin-Malivel and Okada 2007; cotton-top tamarins, Neiworth et al. 2007; Japanese monkeys, Sugita 2008).

Although both humans and macaques can learn to individuate conspecifics by faces, the former outperform the latter in individual recognition of own-species faces (Rossion and Taubert 2019), and macaques need extensive operant conditioning to achieve even modest recognition performance. As noted by Parr (2011), studies using macaques have reported mixed evidence regarding the extent of human-like face processing (e.g., inversion effect, configural processing, etc.), with results varying depending on the methods used, perhaps suggesting that humans and monkeys have evolved different face processing strategies. By contrast, compared to macaques, chimpanzees have been found to present face processing mechanisms more homologous with those of humans (Parr 2011; Taubert et al. 2017; Wilson and Tomonaga 2018, but see Griffin 2020). Although the macaque–chimpanzee difference may be related to the latter's greater phylogenetic proximity to humans, it may also be related to species-specific social structures: chimpanzees and humans share a "fission–fusion" social organization (Parr 2011), whereas macaque monkeys live in more stable social groups with more or less strict, often linear dominance hierarchies. In fission–fusion society, group composition is dynamic and subject to frequent fracture and growth over time; hence, robust face processing mechanisms are highly advantageous, and there is a strong social pressure to recognize the faces of conspecifics. Strikingly, it has been reported that spider monkeys (*Ateles geoffroyi*), New World species with a fission–fusion social structure, also present more human-like face processing abilities than macaque monkeys (i.e., holistic processing for high-experienced face categories, Taubert 2010; Taubert and Parr 2009), further suggesting that socioecological pressures might contribute to the emergence of a specialized face processing system.

Beyond these differences, visual biases for own-species seem to be especially common across primates species (Scott and Fava 2013), including humans (Heron-Delaney et al. 2011). Fujita (1987), using an operant lever-pressing task, explored the extent to which different species showed conspecific preference, by comparing portrait preference in five macaques species (*Macaca fuscata, M. mulatta, M. radiata, M. nemestrina*, and *M. arctoides*). Each monkey was trained to press a lever to show a picture on a screen. The picture remained on-screen for as long as the

subject held the lever down. Using this simple method it was possible to assess the time spent looking at a picture of a conspecific compared to one showing a different species. In this task, it is assumed that habituation will occur more quickly (i.e., reduced looking time) with a picture of a heterospecific, which is less attractive for the subject. Fujita found that monkeys showed conspecific preference, with the exception of the stumptailed macaque *M. arctoides* (but see Demaria and Thierry 1988). Most of the subjects discriminated conspecifics in pictures, and preferred to look at their own species than macaques of a different species. Overall, Fujita's studies demonstrated that preference for pictures of own species is common across multiple macaque species (Fujita 1987, 1990, 1993a, Fujita and Watanabe 1995). Preferences were diluted when either the head, or head and tail, were removed from the picture (Fujita 1993b), suggesting that the head is a crucial cue driving the preference. Similarly, the face was found to be important in conspecific discrimination by longtailed macaques (Dittrich 1994), although it should be noted that this last study used line drawings, not halftone images of real faces.

Although own-species preference seems to be widespread in primates, its origin may differ between species. For instance, own-species preference can be spontaneously present at birth, or emerge from social experience with conspecifics during infancy. Cross-fostering studies can be especially informative to disambiguate this issue. Fujita showed that Japanese monkeys raised by rhesus macaque mother presented a preference for rhesus macaque faces (Fujita 1990, 1993a), while Japanese monkeys raised by their mother presented own-species preferences. By contrast, rhesus macaques showed own-species preferences regardless of their early social experience. Fujita concluded that rhesus have a hard-wired preference for their own species, whereas Japanese macaques have a more flexible preference that is influenced by experience. Related findings were reported in great apes, as adult chimpanzees that had been reared by humans preferred pictures of human faces over chimpanzee faces (Tanaka 2003, 2007). These biases may, in turn, influence face discrimination processes, as human-reared chimpanzees were found to be better at processing human faces than chimpanzee faces, compared to a group of chimpanzees who grew up in their own-species group (Martin-Malivel and Okada 2007).

From a theoretical point of view, preferences for own-species faces may have emerged from some ancient general perceptual bias shared among primates (Damon et al. 2017a; Rhodes 2006). This development might be linked to the ease of processing (i.e., perceptual fluency, Whittlesea and Leboe 2003), thus facilitating the development of familiarity preferences. Such frameworks extend beyond mere face processing mechanisms, and have been proposed as relevant for a general theory of object representation and recognition (Wallis 2013; Wallis et al. 2008). Interestingly, Fujita provided indirect evidence for such shared perceptual mechanisms between human and nonhuman primates, in reporting preferences for regular and symmetrical patterns in capuchin and squirrel monkeys (Anderson et al. 2005). These findings indicated that monkeys prefer visual stimuli that humans find aesthetically pleasing, as visual symmetry is perceived as attractive in a variety of domains (Little 2014). Furthermore, when it comes to faces, ratings of rhesus

macaque face attractiveness by human judges can predict implicit visual preferences in rhesus macaques (Damon et al. 2019).

However, mate selection mechanisms probably operate in addition to general perceptual biases for symmetry, as the effect of face attractiveness turned out to be species-specific. When two faces from the same species but differing in attractiveness were presented side-by-side, humans showed a visual preference for human faces (but not macaque faces) rated as attractive, and macaques displayed a visual preference for macaque faces (but not human faces) rated as attractive. Findings of similar preferences in human and nonhuman primates have also been reported for curved contours (humans and chimpanzees: Munar et al. 2015), and for prototypicality (human and macaque infants: Damon et al. 2017b), further highlighting shared underlying face/object processing mechanisms. Interestingly, face familiarity further shows differential impact on face preference in humans and rhesus macaques (Méary et al. 2014). When two faces of different species/races were presented side-by-side, Caucasian humans demonstrated clear visual preference for Caucasian faces over Asian faces (own-race bias), and human faces (regardless of races) over nonhuman primate (e.g., chimpanzee, Barbary, and rhesus macaque) faces (own-species bias). Rhesus macaques also showed visual preference for nonhuman primate faces over human faces regardless of race, but by contrast displayed preference for chimpanzee or Barbary macaque faces over own-species faces. This pattern suggests that face preference in macaques, unlike humans, is modulated by factors beyond familiarity, such as species.

How Does Face Processing Change Early in Life?

A developmental approach may help in determining what the common processes in different species are before experience influences the face processing system, if the developmental trend is similar across primates, and how flexible the system is for handling other-species faces. Faces represent a highly attractive stimulus for infant primates, including humans (Goren et al. 1975), pigtailed macaques (*Macaca nemestrina*, Lutz et al. 1998), gibbons (*Hylobates agilis*, Myowa-Yamakoshi and Tomonaga 2001), rhesus monkeys (*Macaca mulatta*, Kuwahata et al. 2004), and chimpanzees (*Pan troglodytes*, Tomonaga et al. 2004). Some researchers have argued that primates may possess an innate face processing system that is predisposed to respond to conspecifics (e.g., Sackett 1966). Two-month-old pigtailed macaques already demonstrate a strong preference for their own species (Kim et al. 1999). The argument is also supported by several studies demonstrating that rhesus macaques raised without any experience of monkeys still prefer to look at faces of conspecifics than other species (Fujita 1987, 1993a). This is not true for Japanese macaques; however, as mentioned above, rhesus monkeys may have a hard-wired preference for their own species, while Japanese macaques have a more malleable preference, influenced by experience.

An influential study by Sugita (2008) illustrated the critical role of experience in the development of face processing in macaques. Infant Japanese macaques separated from their parents at birth and reared by humans in a faceless environment for a minimal period of 6–24 months showed a preference for both monkey and human faces over objects, but no preference for either category of faces when tested in a visual preference task. Furthermore, they were able to recognize both monkey and human faces. Following the face deprivation period, half of the monkeys were introduced to macaques, and the other half to humans. When tested following a minimum of 1 month of exposure to faces, monkeys exposed to human faces displayed a preference for human faces over objects, and also for human over monkey faces. They displayed no preference between monkey faces and objects. Consistent with this pattern of results, monkeys exposed to monkey faces preferred monkey faces over objects and over human faces, but showed no preference when human faces and objects were presented simultaneously. Furthermore, when tested for recognition, monkeys were only able to recognize faces from the category to which they were exposed. These results highlight the crucial role visual experience can play in the specialization of the face system toward own-species faces. Japanese macaques are not displaying hard-wired preference for their own species, but an experience-dependent preference.

As mentioned above, Japanese macaque monkeys looked more at faces than objects regardless of species, even though they were deprived of face exposure. This suggests that a broad face detection mechanism was still functional despite the lack of exposure to faces, as if initial perceptual sensitivities for faces were preserved, and waiting for refinement through individualized experiences (i.e., experience-expectant processes, Nelson 2003). Are rhesus different from Japanese macaques as suggested by Fujita? Recent studies with nursery-reared infant rhesus macaques (with no exposure to adult macaque faces and limited face exposure in general) showed a "coarse to fine" pattern of face detection (Simpson et al. 2017). Three-week-old rhesus infants with very limited face exposure showed a bias for both own- and other-species faces over objects. Three-, and 6-month-olds, after peer exposure, also showed a similar bias for faces over objects, but also looked faster toward conspecific faces compared to heterospecific faces. Taken together, these results slightly qualify Fujita's earlier findings suggesting hard-wired preference for own-species faces in rhesus macaques, and indicate that the face processing system of rhesus monkeys undergoes a transition from experience-expectant to experience-dependent mechanisms. This developmental trajectory is not limited to nonhuman primates, but seems to extend to humans as well.

Nelson (2001) hypothesized that in humans the representation of faces at birth is broad and that it develops according to the type of facial input received, tuning toward the predominant faces in the environment. To test whether experience tunes face processing, Pascalis et al. (2002) investigated the ability of 6- and 9-month-old human infants to recognize faces from their own species and another species (rhesus macaques) using a standard recognition paradigm. Infants at both ages showed individual recognition with human faces, looking longer at a new face compared to a previously seen face. However, when tested with the monkey faces, only the

6-month-old group showed evidence of individual recognition. By contrast, 9-month-olds were unable to recognize which monkey face they had seen before. These findings suggest that the face system becomes "tuned" to human faces between 6- and 9-months of age (Pascalis et al. 2002). In a follow-up study, Pascalis et al. (2005) investigated the impact of experience with other-species faces on the development of face processing in relation to this species. They provided 6-month-olds' parents with a book containing a selection of monkey faces, which they were instructed to show to their infant following a fixed schedule. Tests showed that this exposure was sufficient to preserve recognition capabilities for monkey faces when the infants returned for testing at 9 months of age. Training experienced near the end of the tuning period appears to be effective for maintaining the ability to discriminate between individuals of other species. Thus, it is possible to alter the development of a cognitive system (for face processing) by providing training and learning via pictorial stimuli. However, it is still unclear how much training is necessary to produce other-species face processing skills at 9 months and for how long long-term training might affect the face system (for a review, see Maurer and Werker 2014).

Conclusion

Overall, the studies reviewed here illustrate that the similarity of the face processing systems of human and nonhuman primates is best found in their plasticity. The experience-expectant/dependent mechanisms progressively adjust the infant primate to its environment, refining the face processing system as the infant accrues experience with the facial characteristics of the individuals from its social group (Pascalis et al. 2014). Despite the indisputable importance of faces in many primate species, however, it is probably too far-fetched to conclude that cognitive and neural face processing mechanisms are continuous across all primates (Rossion and Taubert 2019). Some face processing mechanisms appeared to be shared among primate species whereas others have turned out to be species-specific, possibly reflecting solutions to evolutionary challenges imposed by particular ecological niches. However, these mechanisms always share a similar purpose: to subserve social cognition.

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