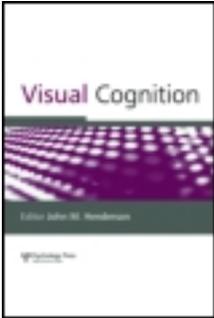


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The own-species face bias: A review of developmental and comparative data

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The own-species face bias: A review of developmental and comparative data

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Face recognition is characterized in part by biases resulting in enhanced perception and memory for individuals within frequently encountered groups and impaired recognition for individuals within uncommonly encountered groups. These biases are found across multiple categories and levels, including species, race, age, and gender (Scherf & Scott, 2012). At the highest level of categorization, human adults and nonhuman primates exhibit improved recognition (Dufour, Pascalis, & Petit, 2006; Pascalis & Bachevalier, 1998) and discrimination abilities (Pascalis, de Haan, & Nelson, 2002) for individuals within their own species, reflecting what has been called an “own-species” or “species-specific” bias in face processing. The own-species bias is a model system for delineating the role of experience and the developmental trajectory of face-processing biases, for further understanding the malleability of face biases in adults, and for examining and comparing face-processing abilities across species. Here, we will review findings from studies investigating the perception of other-species faces during development, into adulthood and across species.

Keywords: Face perception; Own-species effect; Development.

The visual world is comprised of complex and dynamic stimuli. Among the most salient of these stimuli is the face. Humans use faces to identify individuals and make inferences about intentions and emotions. We readily glean information about race, gender, and age with a single fixation. Although

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humans tend to be extremely proficient at recognizing and identifying faces, this proficiency decreases for faces within unfamiliar or infrequently encountered groups of people. For example, human adults are better able to discriminate and recognize faces within their own race relative to within another race; this bias is called the “own-race” effect (ORE; also called the cross-race effect, the other-race effect, the own-race bias, and the other-race bias, e.g., Hugenberg, Young, Bernstein, & Sacco, 2010; Levin, 1996, 2000; Meissner, Brigham, & Butz, 2005; Rhodes, Brake, Taylor, & Tan, 1989; Rodin, 1987; Sporer, 2001; Tanaka, Kiefer, & Bukach, 2004; Valentine, 1991). The ORE is a within-species effect that further biases recognition, discrimination judgements, and emotion perception.

Studies have shown that adult humans, as well as adult nonhuman primates, exhibit superior recognition abilities for faces within their own species (Dufour, Pascalis, & Petit, 2006; Pascalis & Bachevalier, 1998). This effect, often called the “other” or “own” species effect (OSE), has been extensively investigated despite being less relevant to everyday human face perception. This review will highlight the research that has focused on understanding the OSE beginning in infancy, through childhood, into adulthood, and across species. Within each of these developmental time periods, we have centred our discussion on a multifaceted theoretical question related to the importance of experience in shaping face-processing abilities. More specifically, although evidence supports the development of highly skilled and expert face recognition abilities in human adults, there is much debate over the origins and mechanisms driving the acquisition of this expertise. Here, we argue that the use of other-species faces has proven extremely helpful for elucidating the importance of face experience across human development and across species. There are several reasons why investigators choose to use other-species faces to investigate face-processing abilities. First, unlike human other-race faces, it can typically be assumed that participants have very little experience with other-species faces. This inexperience allows investigators to parcel out the influence of environmental exposure and, in some cases, to use laboratory experience to examine training effects. Second, comparisons of human and nonhuman participants and stimuli are of particular importance to investigators who are interested in further understanding the evolutionary origins of face perception. Finally, nonhuman primate faces contain some of the same low-level properties that characterize human faces, such as two eyes in the front of the head, which lie above a nose and a mouth. This similarity between human and nonhuman primate face structure allows researchers to compare and contrast recognition and discrimination strategies (e.g., holistic processing) across species and across stimuli.

OWN- AND OTHER-SPECIES FACE PROCESSING IN INFANCY

Other-species face processing has been examined in populations as young as newborns (Di Giorgio, Leo, Pascalis & Simion, 2012; Heron-Delaney, Wirth, & Pascalis, 2011). Investigations of general face-processing abilities in newborns suggest that they orient preferentially towards faces and face like-stimuli relative to objects (Fantz, 1961; Goren, Sarty, & Wu, 1975; Johnson & Morton, 1991; Macchi-Cassia, Turati, & Simion, 2004; Valenza, Simion, Macchi Cassia, & Umiltà, 1996). This early preference for faces has led some researchers to hypothesize that face-specific perception is, to some extent, hard-wired (e.g., Farah, Rabinowitz, Quinn, & Liu, 2000; Slater & Quinn, 2001). However, others have found rapid learning at birth and suggest that newborns have face preferences because of strong associations formed between the mother's face and voice in the first few moments of life (Sai, 2005). This debate has led to a discussion about whether early face perception may be explained by a domain-specific evolutionary mechanism for faces or a domain-general evolutionary mechanism for rapid associative learning that is driven by pre- and postnatal experience and constrained by the development of the visual system. Here, we discuss ways in which experience shapes the development of face processing in infancy and whether or not the current literature allows us to determine whether own-species face advantages arise from an innate representation of conspecifics, from the greater lifetime experience with conspecifics, or from a combination of both.

Three investigations have specifically tested newborns' preferences and discrimination of nonhuman primate faces. The first study suggests that, although newborns prefer to look at human faces over nonhuman primate faces when presented side by side, they have no preference when a whole human body is paired with a nonhuman primate body (Heron-Delaney et al., 2011). Unlike newborns, 3.5- and 6-month-old infants both prefer to look at humans relative to nonhuman primates, regardless of whether the face or the full body is presented. The authors concluded that exposure to human faces during the first days of life is sufficient to allow development of a representation specific to human faces.

However, recently, Di Giorgio et al. (2012) argue that the findings reported by Heron-Delaney and colleagues (2011) may be the result of low-level contrast differences between the nonhuman primate and human stimuli, resulting in visibility differences across the pairs. To address this issue, Di Giorgio and colleagues conducted three experiments and found that, when low-level differences were equated, newborns did not show a spontaneous preference between the paired human and nonhuman primate faces, and equally discriminated between two exemplars of human faces and between two exemplars of nonhuman primate faces. In addition, newborns preferred to look at upright human and monkey faces relative to inverted

human and monkey faces (Di Giorgio et al., 2012). These results are in contrast to those of Heron-Delaney et al., and suggest that the system underlying face processing is broad at birth, allowing newborns to similarly process and attend to both human and nonhuman primate faces.

Taken together, these findings suggest that the human newborn face-processing system begins oblivious to species distinctions but is sensitive to the orientation of the face. In addition, the results reported by Di Giorgio et al. (2012) are also consistent with an investigation that found that, although 3.5-month-olds prefer to look at own-race relative to other-race faces, newborns showed no such preference (Kelly et al., 2005). Finally, newborns also prefer to look at a video of a vocalizing monkey with its corresponding audible call or an audiovisual tone match relative to a silent video (Lewkowicz, Leo, & Simion, 2010). Lewkowicz and colleagues (2010) suggest that newborn multisensory face processing is not tuned to specific real audible monkey calls but is instead dependent on the detection of audiovisual synchrony more generally. These results suggest that, similar to static face tasks, newborns also show a nonspecific preference in audiovisual face tasks.

Combined, these three studies (Di Giorgio et al., 2012; Heron-Delaney et al., 2011; Lewkowicz et al., 2010) do not address the question of whether or not the newborn face-processing system is specific to primate faces (human and nonhuman primates), all face types (including nonprimate faces), or whether newborns prefer and preferentially discriminate any visual stimulus that is face-like and contains a greater number of elements in the upper half (as proposed by, Simion, Valenza, Macchi Cassia, Turati, & Umiltà, 2002). Future studies should examine the limitations of this broad newborn face-processing system in order to determine whether there is a primate specific or more general low-level stimulus driven evolutionary basis for face processing. However, previous work (e.g., Sai, 2005) has found rapid, single-trial, associative face/voice learning at birth and so any future investigations should also incorporate and/or control for this factor in their design.

Face perception and discrimination abilities become increasingly tuned to groups of people present in the early learning environment, in addition to a coincident decrease in sensitivity to racial/ethnic groups not present in the environment (Nelson, 2001; Scott, Pascalis, & Nelson, 2007). This developmental process, called “perceptual narrowing” or “perceptual tuning” has robust empirical support (Kelly et al., 2007, 2009; Pascalis et al., 2002, 2005; Scott & Monesson, 2009; Vogel, Monesson, & Scott, 2012). It appears to result in increased difficulty telling apart individuals within unfamiliar groups *relative* to individuals within familiar groups. Investigators report visual perceptual narrowing between approximately 6 and 9 months of age using other-race faces (Kelly et al., 2007, 2009; Vogel et al., 2012; for a review, see Anzures, Quinn, Pascalis, Slater, & Lee, this issue 2013),

nonhuman primate other-species faces (Pascalis et al., 2002, 2005; Scott & Monesson, 2009), and nonprimate faces (Simpson, Varga, Frick, & Frigaszy, 2011).

Pascalis et al. (2002) were the first to show perceptual narrowing using nonhuman primate faces. To investigate visual perceptual narrowing in infants, researchers typically rely on looking time methods, including the Visual Paired Comparison (VPC) and Habituation techniques. These procedures rely on infants' relative interest in novelty, and index the ability or tendency to discriminate a recently familiarized stimulus from a new stimulus. These authors found that, although 6-month-olds readily discriminated between familiar and novel monkey and human faces, 9-month-olds and adults only discriminated between familiar and novel human faces (Pascalis et al., 2002).

To further understand how experience (i.e., training) with other-species faces can change face processing, Scott and Monesson (2009) examined discrimination of monkey faces because of their similarity to human faces and because of infants' lack of previous experience with monkey faces. When infants were trained to associate individual labels (e.g., "Fiona", "Boris") with individual monkey faces, from 6 to 9 months, they maintained the ability to discriminate monkey faces immediately after training. In contrast, training with a generic, category-level label (e.g., all faces labelled "Monkey") or exposure to faces without labels, led to perceptual narrowing (Scott & Monesson, 2009). These results suggest that, whereas learning a category-level label teaches infants to look for similarities between stimuli, learning an individual-level label teaches infants to look for *differences* between stimuli. Category- versus individual-level learning also lead infants to form distinct perceptual representations and to represent these stimuli differentially at the neural level (Scott & Monesson, 2010).

In a recent investigation, event-related potentials (ERPs) were recorded while infants viewed upright and inverted monkey faces before and after 3 months of monkey face book training (Scott & Monesson, 2010). In adults, investigators consistently report a negatively peaked component occurring around 170 ms after stimulus onset (the "N170") that differentiates faces and objects (e.g., Carmel & Bentin, 2002) and is delayed (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996) and enhanced (e.g., Rossion et al., 1999) to inverted relative to upright faces. In infants, face processing is indexed by two ERP components, the N290 and P400 (de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003; Scott & Monesson, 2010; Scott & Nelson, 2006; Scott, Shannon, & Nelson, 2006; Vogel et al., 2012). Although holistic processing is multifaceted, one of the most robust markers of holistic face processing in adults is the face-inversion effect, or impaired recognition, delayed responses, and differential neural activity, when faces are presented upside-down relative to upright (e.g., Rossion et al., 1999; Yin,

1969). Scott and Monesson (2010) investigated whether or not infants trained at the individual level with monkey faces exhibit an inversion effect for novel monkey faces. Results revealed inversion effects, beginning at the N290 and continuing to the P400 component only after individual-level training, suggesting that individual, but not category or exposure training, led to more specialized, holistic, and face-like (as opposed to object-like) neural responses. Furthermore, these results suggest that specialized neural representations for faces develop over the first year of life and are the result of experience learning to individuate faces. However, these investigations do not tell us if or how infants alter their visual strategies to process own- and other-species faces after training or experience. Future eye-tracking investigations could help us better understand how infants generally visually analyse faces as well as how training might influence the visual strategies used to process trained and untrained faces.

Cross-sectional ERP investigations have also examined the underlying neural correlates of other-species face perception across the first year of life (de Haan et al., 2002; Halit et al., 2003; Scott et al., 2006). These investigations all report increased neural specificity to human faces relative to nonhuman primate faces with age. For example, in one study, ERPs were recorded while 6-month-old infants and adults viewed upright and inverted human or monkey faces (de Haan et al., 2002). Adults exhibited the expected N170 inversion effect for human faces but not for monkey faces. The 6-month-olds also showed differential responses for human and monkey faces and for upright and inverted faces, but these effects were distributed across the N290 and P400. Moreover, whereas infants viewing monkey faces were reported to only exhibit an inversion effect in the left hemisphere, infants viewing human faces showed bilateral inversion effects. These results suggest that the infant ERP response to monkey and human faces is immature relative to the adult N170 response and that infants already show differences in processing human and monkey faces at 6 months of age. A follow-up investigation of this effect found that the adult-like pattern of inversion effects for human relative to monkey faces was present by 12 months of age (Halit et al., 2003). Finally, in another investigation, 9-month-old infants viewed a recently familiarized (habituated) and unfamiliar monkey or human face in either a frontal or profile upright orientation (Scott et al., 2006). The earlier occurring N290 component was found to be greater for familiar compared to unfamiliar faces, regardless of species or orientation. However, for the P400 component, unfamiliar monkey faces elicited a greater amplitude response than familiar monkey faces, regardless of orientation. In contrast, the P400 to human faces differentiated the orientation of both familiar and unfamiliar faces. These results suggest that the neural responses of 9-month-olds differentiate familiar and unfamiliar frontal and profile faces for human faces but not monkey faces, as reflected in the P400 component. This finding

provides further support for increased neural sensitivity to faces from familiar groups relative to unfamiliar groups beginning in the first year of life (for similar neural differentiation of other-race perception in 9-month-olds, see Balas, Westerlund, Hung, & Nelson, 2011; Vogel et al., 2012).

Combined with the behavioural results presented earlier (Pascalis et al., 2002, 2005; Scott & Monesson, 2009), investigations of neural development suggest increased sensitivity to faces within groups of people whom infants learn to individuate. However, infants decline in their sensitivity to discriminate faces within unfamiliar groups (Pascalis et al., 2002, 2005; Scott & Monesson, 2009; Scott et al., 2007). Recently, this decline was investigated in more detail in 12-month-old infants (Fair, Flom, Jones, & Martin, 2012). Fair and colleagues (2012) familiarized 12-month-old infants to monkey faces, using a short (20 s of familiarization and 10 s of test) and a long (40 s of familiarization and 20 s of test) VPC task. Consistent with previous reports (Pascalis et al., 2002, 2005; Scott & Monesson, 2009), discrimination of monkey faces was not observed for the short duration VPC task. However, 12-month-old infants did discriminate monkey faces in the longer duration VPC task. These results imply that previously reported data showing a decline in discrimination for monkey faces between 6 and 9 months of age should not be thought of as a permanent change in perceptual processing. However, it is important to note that these authors did not include a human face control condition. It is likely that discrimination for monkey faces is still impaired relative to human faces at 12 months of age. This relative impairment is not present in 6-month-old infants (Pascalis et al., 2002, 2005; Scott & Monesson, 2009) and so the decline in sensitivity to faces within unfamiliar groups, and the concept of perceptual narrowing, after 6 months of age likely holds.

The preceding review has focused on studies using static images of human and nonhuman primate faces and suggests a decline in sensitivity to faces within unfamiliar groups, including nonhuman primate faces, during the first year of life. This decline is accompanied by increased sensitivity to familiar groups of faces, as indexed by neural responses to these face types. However, a more ecologically valid approach to understanding face perception and memory is to use dynamic and multisensory faces. In one such study, 4-, 6-, 8-, and 10-month-old infants viewed pairs of monkey faces producing two different vocalizations while they heard one of the two vocalizations (Lewkowicz & Ghazanfar, 2006). Four and 6-month-old infants looked longer to the matching face, whereas 8- and 10-month-old infants looked equally long at both the match and the mismatch. These results are consistent with behavioural findings using static images (Pascalis et al., 2002, 2005) and suggest that perceptual narrowing also occurs with multisensory stimuli. In addition, intersensory deficits for matching monkey faces with corresponding calls continued to 12- and 18-months of age, suggesting these impairments are

long lasting in the absence of experience with monkey faces (Lewkowicz, Sowinski, & Place, 2008). Electrophysiological evidence for multisensory perceptual narrowing was also recently reported (Grossmann, Missana, Friederici, & Ghazanfar, 2012). In this study, ERPs were recorded in response to audiovisual presentations of congruent and incongruent monkey and human vocalizations. The ERP results indicate that 4-month-old ERP components distinguished between congruent and incongruent faces and voices regardless of species, whereas 8-month-old ERP responses only discriminated congruent and incongruent human faces and voices. Combined, these results suggest that perceptual narrowing for multisensory stimuli follows the same developmental trajectory as static faces during the first year of life.

Face-processing abilities likely begin with preferences for looking at faces and face-like stimuli as newborns. Infants continue to orient preferentially towards faces for a variety of reasons including both the perceptual and social properties inherent in face stimuli. Face-processing abilities continue to develop during the first year of life as infants learn from their surrounding environment. This learning leads infants to focus their attention towards familiar faces and results in biased perception of individuals within unfamiliar groups. Monkey face stimuli have proven useful for understanding initial newborn face preferences, the trajectory of the development of face biases, the role of experience, and the underlying neural mechanisms.

OWN- AND OTHER-SPECIES FACE PROCESSING IN CHILDHOOD

As we have seen, face processing develops dramatically during infancy; however, one large difference between infant and child populations is that the infant visual system is developing rapidly, whereas children have comparatively mature visual perception.¹ General cognitive capacities such as attention and memory do continue to develop into childhood and face perception and recognition should be examined in a way that allows for the dissociation of general cognitive abilities and face-processing biases. Finally, cortical responses to faces change throughout childhood and adolescence and likely underlie experience-dependent changes in face processing (e.g., Aylward et al., 2005; Scherf, Behrmann, Humphreys, & Luna, 2007).

In general, areas that have been associated with face processing in adults include functionally defined areas such as the fusiform face area (FFA), the

¹ Although beyond the scope of this review, some aspects of visual development are still maturing into childhood (e.g., contrast sensitivity) and may have consequences for the development of face perception (see Maurer, Mondloch, & Lewis, 2007).

occipital face area (OFA), and anatomically defined regions such as the fusiform gyrus, and the superior temporal sulcus (STS) (Haxby et al., 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Tarr & Gauthier, 2000). When 5- to 8-year-olds viewed videos of faces, however, they activated more dorsal and medial portions of the right lateralized fusiform gyrus, compared to the adult-defined face areas in the FFA, OFA, and STS (Scherf et al., 2007). This right lateralized pattern of mid-fusiform activation for faces was also present during static picture presentations for 4- to 5-year-olds, whereas adults utilized left-lateralized FFA activity (Cantlon, Pinel, Dehaene, & Pelphrey, 2011). In addition to lateralization changes, 5- to 8-year-olds showed a shift from more posterior visual association areas in bilateral occipital gyri to more anterior regions with age (when viewing pictures of faces compared with objects). It is possible that this change reflects a developmental shift in strategy from featural-based processing towards adult-like configural processing (Gathers, Bhatt, Corbly, & Joseph, 2004). Thus, the neural substrates of face-processing abilities appear to continue to develop into childhood. In this section, we examine how experience shapes children's responses to human, nonhuman primate, and animal faces in both typically and atypically developing populations.

Adult-like expertise for faces is multifaceted and likely takes several years to fully develop (for a review, see Scott, Tanaka, & Curran, 2009). One aspect of face processing that has been investigated in childhood is the relative use or disruption of configural or holistic processing across development (de Heering, Rossion, & Maurer, 2012; e.g., Diamond & Carey, 1977; Mondloch, Le Grand, & Maurer, 2002; but see Schwarzer, 2000). Holistic face processing is not a unitary construct; instead, several components of holistic processing have been identified (for a review, see Maurer, Le Grand, & Mondloch, 2002). Inversion of faces is thought to tap an aspect of holistic processing called first-order configural processing, and the manipulation of the spatial layout of facial elements is thought to tap second-order configural processing (for a review, see Maurer et al., 2002). Although results are mixed, much of the literature suggests that holistic face-processing skills continue to develop well into childhood. What is still not completely understood is how much of this development is specific to face processing and how much is due to improvements of general cognitive skills (e.g., attention, memory), use of different strategies relative to adults, or the use of similar processing strategies used to different extents (for a review, see de Heering et al., 2012). If the development of general cognitive mechanisms such as memory and attention do account for changes in face processing, we would expect those changes to influence all aspects of face processing and all types of faces and not be limited to certain groups of familiar or unfamiliar faces.

The extant literature comparing own- and other-species face processing in children is currently rather limited. However, it has served to help us to better understand how aspects of face processing, such as reliance on holistic facial cues, and experience continue to develop during childhood. These studies give us insight into processing advantages for own-species faces and allow for specific hypotheses to be made about mechanistic changes related to experience. For example, Pascalis, Demont, de Haan, and Campbell (2001) showed 5-, 6-, 7-, and 8-year-olds upright and inverted pictures of human, monkey and sheep faces in a two-alternative forced choice task. Accuracy overall increased with age, and children recognized human faces better than monkey faces, and monkey faces better than sheep faces, suggesting that recognition is better for faces that closely resemble human faces. In addition, upright faces were better recognized compared with inverted faces overall, implicating reliance on holistic cues. However, only human and nonhuman primate faces produced a behavioural inversion effect, and there was no difference in accuracy for inversion of sheep faces. These results suggest that between 5 and 8 years of age, children consistently process the faces of own and other species in a manner similarly to that of adults. In addition, face processing in humans may be tuned to the characteristics of primate (human and monkey) faces by 5 years of age. However, this study left open the question of why both monkey and human faces produced inversion effects given that children's previous experience with faces was limited to human faces. In addition, as will be described later, several human adult investigations find differential effects for human compared to nonhuman primate faces (de Haan et al., 2002; Itier, Van Roon, & Alain, 2011; Scott, Shannon, & Nelson, 2005).

Mondloch, Maurer, and Ahola's (2006) study built on Pascalis' work by investigating the role of second-order configural cues (i.e., the relation of the features to one another), by varying the distance between facial features of upright human and monkey face stimuli. When looking at human faces and monkey faces, adults were more accurate than 8-year-olds in their same/different judgments for both stimulus types. Both adults and children better discriminated human compared with monkey faces, and the size of this species effect was identical for the two age groups. Taken together, these results suggest that in addition to children using first-order configural or holistic processing, as indexed by the inversion effect, children are able take into account second-order relations in order to process faces. Children were more accurate at detecting second-order changes for human compared to monkey faces, suggesting that experience with human faces facilitated second-order configural processing.

Additional support for the importance of early experience in shaping face processing abilities comes from patients who experienced early visual deprivation caused by bilateral congenital cataracts (Robbins, Nishimura,

Mondloch, Lewis, & Maurer, 2010). The ability to detect both featural and configural human, monkey, and object changes were tested in adolescent and adult patients and age-matched controls. Relative to the control group, the cataract patients showed no impairment for discriminating configural differences in monkey faces or in houses but were impaired at discriminating configural changes for human faces. Based on these findings, the authors argue that early visual experience is necessary to build a foundation for processing conspecific faces, but not monkey faces or objects. It would be interesting to investigate whether training these patients to recognize monkey faces at the individual-level (similar to human faces) would lead to increased second-order configural processing or whether configural processing would be spared in newly formed domains of expertise (i.e., car or bird expertise).

Another way to examine other-species face processing is to consider the development of visual processing strategies used by adults to look at faces. The left-side looking bias is a robust strategy, where adults preferentially scan and rely on the left side of the face (Butler et al., 2005; Mertens, Siegmund, & Grüsser, 1993) when performing a variety of face-related judgements (e.g., identity, emotion, gender) (Burt & Perrett, 1997; Gilbert & Bakan, 1973; Wolff, 1933). Balas and Moulson (2011) attempted to characterize how this strategy developed during childhood, and how different categories of faces were processed according to side bias. To do so, the authors presented one original face and two symmetrical faces created by splitting the original face into vertical halves and doubling the left half (left-side symmetrical face), and the right half (right-side symmetrical face). Stimuli were arranged in a triangular pattern such that the original image was situated at the top, with two symmetrical faces below the original image. Children were asked to pick which symmetrical face best matched the original. Stimuli included adult human male faces, and adult monkey faces. Results indicated that the human left-side bias (LSB) developed at a faster rate compared with the monkey LSB. The children's LSB for human faces tended to increase with age, whereas the monkey face LSB did not. Overall, these results show that the LSB for human faces is present as early as 5 years of age, and continues to develop through middle childhood. Furthermore, these results show qualitative changes in face processing that develop during middle childhood, as demonstrated by the increased adoption of an adult face-processing strategy. This change in strategy does not seem to apply to other species faces, suggesting that experience plays an important role in how the LSB strategy is used in childhood and that different strategies may narrow at different rates during development. An interesting follow-up of this investigation would be to determine whether infants also show an LSB and how this differs across species. If the development of the LSB follows perceptual narrowing, one could hypothesize that it would not be different

for human and nonhuman primate faces before 6 months of age, but would emerge for human faces by 9 months of age.

Taken together, the behavioral literature has shown that, in most circumstances, children treat the faces of other species differently than own species faces. Furthermore, the cortical areas underlying face-processing abilities continue to develop into childhood, suggesting that experience with own-species faces likely continues to influence face processing well into childhood. Relative to investigations in infancy, very few investigators have compared the perception and recognition of human relative to nonhuman primate faces in childhood. This comparison has proven useful for furthering our understanding of the role of experience and should be included in future investigations. For example, Scherf and Scott (2012) argue that developmental changes in face-processing abilities are influenced by transitions in age appropriate developmental tasks or goals (e.g., development of motor abilities in infancy or the new interest in peers and potential romantic partners in adolescence). Scherf and Scott emphasize the possibly embodied nature of face processing, and suggest that development might follow a nonlinear developmental trajectory, in line with dynamic systems theory (Smith & Thelen, 2003). Based on this hypothesis, it is possible that differences in face processing of own- and other-species faces changes throughout development and depending on context and task.

OWN- AND OTHER-SPECIES FACE PROCESSING IN ADULTS

Now that we have discussed how a developing system acquires biases in face processing, we will move on to investigating how a mature face system processes own- and other-species faces. Adult face processing operates within a mature visual system and years of experience with faces in a variety of contexts. Of course, the advantage of the examining human adults is that a variety of tasks and methods can be used, as adults are capable of completing more trial exposures as well as following more complex instructions than children or infants. Unfortunately, this flexibility in task use has also led to varying results that are somewhat difficult to reconcile. Investigations of other-species face processing in adults have examined behavioural measures of discrimination and memory (Dufour, Coleman, Campbell, Petit, & Pascalis, 2004; Dufour & Petit, 2009; Pascalis & Bachevalier, 1998) adaptation effects (Little, DeBruine, Jones, & Waitt, 2008), the detection of category boundaries using morphing (Campbell, Pascalis, Coleman, Wallace, & Benson, 1997), eye-tracking differences (Conway, Jones, DeBruine, Little, & Sahraie, 2008), and neural differences as indexed by ERPs (de Haan et al., 2002; Itier et al., 2011; Scott et al., 2005).

Pascalis and Bachevalier (1998) examined face discrimination abilities using a VPC task in both humans and monkeys and found that humans were more skilled at discriminating human faces, whereas monkeys were more skilled at discriminating monkey faces. More recently, this finding was replicated using a more demanding recognition memory task, and human adults demonstrated significant impairment when recognizing monkey faces, regardless of orientation, compared to upright human recognition (Dufour et al., 2004). As expected, recognition for inverted human faces was also impaired relative to upright human faces. In a follow-up experiment that examined the effects of expertise and experience, own- and other-species face-processing differences were examined in expert primatologists, using a memory task for upright and inverted faces as well as a VPC task (Dufour & Petit, 2009). Results revealed that experts were more accurate than nonexperts at explicitly identifying previously viewed monkey faces. In addition, experts were more affected by inversion of monkey faces than nonexperts, suggesting that expert processing of monkey faces is similar to human face processing. This expertise finding replicates a classic finding in dog experts (Diamond & Carey, 1986). However, Dufour and Petit (2009) report better VPC discrimination for human relative to monkey faces in primate experts. Combined, these results suggest that although expertise for monkey faces increases memory and holistic processing of these faces relative to novices, human face processing is still superior to monkey face processing.

In contrast, somewhat conflicting findings were reported when adults perceptually discriminated faces that were morphed on a gradient from human to macaque or human to bovine (Campbell et al., 1997). They showed the human–cow and monkey–cow morphs elicited enhanced perceptual discrimination for images that straddled the morph boundary, but the human–monkey morphs did not elicit the same increased pattern of discrimination for images that crossed the human and monkey boundary. The authors suggested that adults formed a single category or prototype for primate (human and monkey) faces, whereas two separate categories were formed for nonprimates and primates. The authors posit that years of experience with human faces generalize to macaque faces within this categorical discrimination task. This finding is consistent with developmental results reported by Pascalis et al. (2001), and suggests that, although there are differences between human and monkey face processing, these differences are smaller than those between human and nonprimate animal face processing.

Adaptation, or the finding that exposure to faces influences subsequent novel face perception, has been a powerful tool for understanding the characteristics of face perception and memory (Leopold, O'Toole, Vetter, & Blanz, 2001). For example, adaptation to faces with contracted features leads

adults to perceive novel faces with contracted features as more normal than before adaptation (Rhodes, Brake, & Atkinson, 2003; Rhodes et al., 2004). Adaptation aftereffects have also been used to determine whether visual aftereffects cross category boundaries (Little et al., 2008). In this study, Little and colleagues (2008) exposed adults to human male faces with narrow or wide set eyes and determined whether that exposure influenced subsequent perception of faces of different races, age, or species. Unlike results reported by Campbell et al. (1997), these authors found category contingent effects, indicating that race, age, and species are represented as separate categories. The authors of this study suggest that these effects are indicative of discrete neural representations of human and monkey faces in humans. Adaptation effects have yet to be thoroughly investigated in infant and child populations or after expertise training in adults. It would be interesting to determine whether these category boundaries develop in line with perceptual narrowing and whether or not expertise can shift these boundaries.

As already mentioned, human adults exhibit impaired recognition for inverted relative to upright faces (Yin, 1969). Although the mechanisms that underlie this inversion effect are controversial, this robust effect has been found across a variety of domains using various methods and is used as a benchmark to gauge the extent to which objects or unfamiliar face types are processed like familiar human faces (Farah, Tanaka, & Drain, 1995; Freire, Lee, & Symons, 2000; Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Sadeh & Yovel, 2010). Adults have been found to exhibit increased detection of feature spacing differences for human relative to monkey faces and this performance is impaired when human faces (but not monkey faces) are inverted (Mondloch et al., 2006). These data suggest that adults are preferentially applying holistic/configural-based strategies to human faces, and that previous face experience is an important factor driving holistic processing of faces. Consistent with this finding, in another investigation using eye-tracking, adults showed greater transient pupil constrictions to upright human faces compared with scrambled and inverted human faces, but not for macaque faces (Conway et al., 2008). These findings imply that pupil constrictions to faces are sensitive to both face orientation and species. Conway and colleagues (2008) suggest that, since inversion is thought to disrupt configural processing of faces (Maurer et al., 2002) and configural processing is more pronounced for human faces than monkey faces (Mondloch et al., 2006), it is possible that the reported pupil responses may index configural and/or expert processing of faces. Pupillary responses have yet to be used to study face processing in developmental populations, but could prove useful for further characterizing the developmental trajectory.

Studies using ERPs have also reported differential responses when humans recognize and differentiate human and nonhuman primate faces. In adults,

the N170 ERP component in response to monkey faces is longer in latency (Carmel & Bentin, 2002) and less susceptible to inversion effects (de Haan et al., 2002) compared to human faces (see Ito & Senholzi, this issue 2013, for a review of ERP components and race perception). More recently, Itier and colleagues (2011) examined whether any discrepancy existed when differentiating between human and animal faces (ape, cat, dog) for the N170 component and whether individual facial features influenced this differentiation. Participants viewed upright and inverted full faces, eyes, and eyeless humans and animals, and the N170 was found to peak faster and be smaller in amplitude in response to human relative to animal faces and greater in amplitude in response to human compared to animal eyes. Only human faces elicited the typical inversion effect. These results suggest differential neural processing of human and animal faces and as well as isolated eyes. Finally, Scott et al. (2005) report that human adults more readily learn and subsequently recognize human compared to monkey faces. More specifically, adult humans showed increased recognition accuracy and were better able to generalize learning from the frontal orientation to a profile image for human relative to monkey faces. Furthermore, the amplitude of the vertex positive potential (VPP) component, which is thought to arise from the same neural source(s) as the N170 component (Joyce & Rossion, 2005; Rossion, Joyce, Cottrell, & Tarr, 2003), increased as accuracy increased for the human but not the monkey faces. Importantly, this positive correlation was found despite the fact that accuracy was well above chance for both human and monkey faces. These data support the hypothesis that previous experience with certain types of faces influences subsequent behavioral and neural processing and that this experience does not generalize to the recognition of nonhuman primate faces.

Overall, studies in adults overwhelmingly suggest increased expertise and differential neural processing for human relative to nonhuman primate faces. However, some studies report greater similarity between human and nonhuman primate faces relative to other animal faces. At this time it is unclear whether this increased similarity is due to stimulus similarity or due to an evolutionary mechanism. We now turn to a review of own- and other-species face processing in nonhuman primates in order to better characterize face-processing abilities across evolutionary time.

OWN- AND OTHER-SPECIES FACE PROCESSING IN NONHUMAN PRIMATES

Relative to human work, there is less of a consensus about the ability of nonhuman primates to process and use faces within their social environment (for a review, see Parr, 2011). The inconsistencies within the nonhuman primate literature appear to be due to task and species differences across

investigations. Although an exhaustive review of the nonhuman primate literature is beyond the scope of this paper, it is important to highlight some of the similarities and differences between developmental investigations in humans and nonhuman primates, as well as studies that examine face strategy and processing differences in nonhuman primates.

Understanding the evolutionary origins of face processing requires investigations that take a comparative approach (for review, see McKone & Crookes, 2007). As described earlier, there is robust evidence that face-processing abilities are influenced and shaped by experience in humans, beginning early in infancy. However, there is also evidence that newborns have a specialized system that facilitates directing their attention towards faces and/or face-like stimuli from birth. A comparative approach to studying face perception and recognition may allow researchers to show whether or not there is evolutionary pressure to discriminate/recognize conspecific faces over faces from other species, resulting in advantages for conspecific or closely related other-species faces from birth.

Very few investigations have examined own- and other-species face-processing abilities in newborn or infant nonhuman primate populations. However, there are a few notable exceptions. In one study, Japanese monkeys (*Macaca fuscata*) and rhesus monkeys (*Macaca mulatta*) were separated from their mothers a few days after birth and reared by own- or other-species monkeys (Fujita, 1990). Fujita (1990) compared the duration of lever-press responses monkeys made in order to view own- and other-species monkey faces. The author reports that Japanese infant monkeys reared by a rhesus foster mother viewed rhesus monkeys longer than Japanese monkeys. However, rhesus monkeys raised by Japanese monkey mothers did not show a clear preference. This study showed that rhesus, but not Japanese macaques, exhibit signs of a genetically determined species preference. This preference is cited as supporting Yoshikubo's (1985) "psychological isolation hypothesis" because Japanese monkeys live in an area that has no overlap with other species, whereas rhesus monkeys live with other species of monkeys in more heterogeneous environment. Although difficult to compare to humans, it is interesting to consider whether or not the level of human face-related genetic influence could differ depending on the region and population being investigated.

In a more recent investigation, Sugita (2008) reared infant monkeys (Japanese macaques, *Macaca fuscata*) in a visually stimulating environment that did not contain any monkey or human faces from birth until 6 to 24 months of age. Similar to human newborns, these monkeys showed a preference for looking at faces relative to nonface objects. Importantly, this preference was maintained regardless of deprivation duration (up to 2 years). In addition, the deprived monkeys looked as long at human faces as at

monkey faces. However, monkeys in the control group (colony reared) looked longer towards the monkey faces.

Sugita's (2008) results are consistent with the investigation described earlier which shows that human newborns do not exhibit a spontaneous preference between paired human and nonhuman primate faces when the low-level stimulus differences are equated (Di Giorgio et al., 2012). Sugita also reports that, despite the lack of experience with faces, the monkeys could discriminate between novel and familiar human and monkey faces in a VPC task. Nondeprived monkeys only discriminated novel and familiar monkey faces, not human faces. These results are also consistent with human newborn (Di Giorgio et al., 2012) and 6-month-old (Pascalis et al., 2002) VPC results, which find equivalent discrimination for human and monkey faces. Following the face deprivation period, monkeys in Sugita's investigation were exposed to either monkey or human faces for 1 month. After this exposure period, monkeys exposed to human faces showed a strong preference for, and better discrimination of, human faces, and monkeys exposed to monkey faces showed the same strong preference for, and better discrimination of, monkey faces. These findings are in line with the human infant perceptual narrowing results described earlier (Pascalis et al., 2005; Scott & Monesson, 2009) and point to experience as an important factor driving the specificity of the face-processing system in both humans and nonhuman primates. However, based on Fujita's (1990) findings, it is possible that experience may play a differential role depending on the species (and evolutionary history) of the monkeys tested. In addition, Sugita reports that the duration of the deprivation period (between 6 and 24 months) did not influence the results, suggesting that factors involved in the maturation of the visual system, including synaptogenesis and pruning, may not be linked to perceptual narrowing. The visual systems of these monkeys developed typically during the deprivation period and biased face processing was found after deprivation regardless of the duration or age. Although these results point to strong similarities between early face-processing abilities of human and nonhuman primates, it is possible that the evolutionary mechanism driving these similarities is not specific to faces but specific to more general preferences of the visual system followed by similar learning mechanisms.

In another developmental investigation, infant vervet monkeys (*Cercopithecus aethiops*), ranging in age from 23 to 65 weeks, completed a face- and voice-matching task for rhesus monkey (*Macaca mulatta*) stimuli (Zangenehpour, Ghazanfar, Lewkowicz, & Zatorre, 2009). Despite the fact that the vervet monkeys had no prior exposure to rhesus monkey faces/voices, results show that infant vervet monkeys detect nonnative mismatching faces and voices and continue to do so throughout development. These authors found no evidence of perceptual narrowing in vervet monkeys and suggest that

either intersensory perceptual narrowing does not occur in Old World monkeys, or that it occurs later in development. These findings are in contrast to perceptual narrowing in Japanese monkeys (Sugita, 2009) and human infants (Pascalis et al., 2002, 2005; Scott & Monesson, 2009) and highlight another important nonhuman primate species difference that should be examined further.

The role of experience in shaping other-species face biases has been recently investigated in adult chimpanzees (Dahl, Rasch, Tomonaga, & Adachi, 2013; Martin-Malivel & Okada, 2007). In one study, chimpanzees from a primate center with more exposure to human faces than to chimpanzee faces were better at discriminating unfamiliar human faces than they were at discriminating unfamiliar chimpanzee faces (Martin-Malivel & Okada, 2007). Chimpanzees from a different primate center with relatively limited exposure to human faces did not show an advantage for one species over the other. In addition to investigating discrimination abilities of these chimpanzees, the authors also tested their categorical perception (CP) of human and monkey faces using human–monkey morphs. For the CP task, chimpanzees with a long history of human face experience showed categorical perception for human faces but not chimpanzee faces. Alternately, chimpanzees with relatively little human face experience did not show CP for chimpanzees or human faces. These results are not consistent with Campbell et al.'s (1997) report suggesting that human adults formed a single category or prototype for primate (human and monkey) faces, whereas two separate categories were formed for nonprimates and primates. Instead, Martin-Malivel and Okada (2007) interpret this set of findings as in line with human expertise studies. Similar to Martin-Malivel and Okada's results, Little and colleagues (2008) found category contingent effects in humans, indicating that race, age, and species are represented as separate categories. Several possible study differences may account for the discrepant findings both across and within species, including amount, duration and quality of experiences, age of testing, and species tested.

In another investigation examining the role of experience, Dahl and colleagues (2013) evaluated the face discrimination abilities of three older adult chimpanzees (approximately 30 years old) and three younger chimpanzees (approximately 10 years old) who were socially housed in a facility where they were exposed to both chimpanzees and humans. Chimpanzees in this study were unique in that they were only exposed to a low number of conspecific faces and hundreds of nonconspecific human faces over the course of a lifetime. Chimpanzees completed a Delayed Match to Sample (DMS) task with familiar and unfamiliar chimpanzee and human face stimuli. They report that older chimpanzees exhibited better performance for human faces relative to chimpanzee faces and the younger chimpanzees showed the opposite pattern. The authors hypothesize both an

early and late developmental component to account for these findings and tested this hypothesis using Hebbian learning in an artificial computational model. The learning model consisted of two components and simulated greater exposure to one face type during early learning (chimpanzee faces) followed by a gradual shift to greater exposure to a second face type during late learning (human faces) (see O'Toole & Natu, this issue, 2013, for a review of computational investigations of the role of experience in human face perception). Similar to previous findings in Japanese monkeys (Sugita, 2008) and in human infants (Pascalis et al., 2002, 2005; Scott & Monesson, 2009), chimpanzees may exhibit an early developmental component akin to perceptual narrowing that tunes perception towards faces that are frequently encountered. However, Dahl and colleagues proposed an additional late component that adapts and responds flexibly to changes in the environment. This late component may be governed by the same mechanisms that allow a human adult to acquire perceptual expertise in a nonface domain. The existence of two learning based-components based on these data is intriguing and is largely consistent with a human study finding that adult Koreans adopted into Caucasian environments as children show a "reverse" other-race effect and are better at differentiating Caucasian than Asian faces (Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005).

Several recent investigations have also begun to examine whether or not nonhuman primates employ similar or different face-processing strategies (holistic/configural processing) to discriminate and recognize own- and other-species faces (Dahl, Logothetis, Bülthoff, & Wallraven, 2010, 2011; Dahl, Logothetis, & Hoffman, 2007; Dahl, Wallraven, Bülthoff, & Logothetis, 2009; and see Parr, 2011, for a review). For example, in one investigation with chimpanzees, novel upright and inverted images of chimpanzees (*Pan troglodytes*), brown capuchins (*Cebus apella*), and humans were presented to chimpanzees in a match to sample task (Parr, Dove, & Hopkins, 1998). After a training period, chimpanzees were required to sequentially match upright stimuli to both upright and inverted matches. Results indicated that upright stimuli were better matched relative to inverted stimuli and that accuracy was greater for upright chimpanzee and human face matches, relative to inverted matches. This inversion effect was not found for capuchin faces. The chimpanzees in this experiment were primarily exposed to other chimpanzees and human faces; thus, the authors hypothesize an expertise effect for both species of faces. However, they also discuss the possibility that the lack of an inversion effect for capuchin faces could be due to stimulus differences (chimpanzee and human faces are more similar to each other than capuchin faces) or because chimpanzees and humans are closer evolutionary relatives. In addition, the use of a paradigm that allows participants to use view-based object recognition strategies has been criticized (Dahl et al., 2011) because it is difficult to isolate the face-specific inversion effect from simple

picture-based matching strategies. In tasks where picture-based matching is possible, participants may be using a simple strategy that does not require recruitment of face-specific configural/holistic processing.

Holistic/configural processing of own- and other-species faces has also been investigated using a variety of tasks and eye-tracking methodology (Dahl et al., 2007, 2009, 2010, 2011, 2013). In these previous studies, clear other-species biases have been observed across a variety of tasks and species. For example, adult rhesus macaques exhibited an increased rebound from adaptation using a face composite task for macaque faces but not for pictures of marmosets or other animals (e.g., dogs), which suggests a species-specific holistic process in these adult monkeys not unlike what is found in humans (Dahl et al., 2007). In another study, eye movements and fixations were recorded while human adults and rhesus macaques viewed upright, inverted, and blurred human and macaque faces (Dahl et al., 2009). Results demonstrate a species-specific pattern of eye movements such that there were increased fixation durations towards the eyes for upright but not inverted own-species faces. In addition, manipulations that reduced holistic or featural face information altered scan patterns in similar ways across species. These findings suggest similar face-processing strategies are employed across species and that expertise acquired through experience is driving face-processing strategy use. The significance of the eye region in face processing has also been found in chimpanzees (Hirata, Fuwa, Sugama, Jusunoki, & Fujita, 2010), pointing to the importance of the eye region in own-species but not other-species face processing in rhesus macaques, chimpanzees, and humans. Additionally, disruptions in second-order relational face information (manipulating distance between face features) are detected in upright own-species, but not other-species or inverted faces, for both humans and rhesus macaques (Dahl et al., 2011). Finally, using a habituation task, the Thatcher Illusion has also only been found in humans and rhesus macaques for upright own-species faces (not for inverted or other-species faces) (Dahl et al., 2010). Combined, these findings show clear other-species biases, similar to humans, across several measures of configural/holistic face processing, further pointing to expertise effects across species of nonhuman primates.

Although many nonhuman primate investigations have shown analogous face-processing abilities in humans and monkeys, differences are also reported. For example, in a review of face processing in primates, Parr (2011) suggests that although many studies find similar face processing for monkeys and humans there are methodological issues that should be addressed prior to making strong conclusions. Moreover, Parr argues that studies have included a variety of species and, as reviewed above, there are notable species differences in monkeys individuation of faces, their use of configural/holistic processing, as well as the importance of experience.

Although, some discrepancies exist, face-processing abilities in nonhuman primates appear to also be shaped by experience with frequently encountered groups of nonhuman or human primates. The majority of studies with chimpanzees appear to support similar face-processing abilities as humans, but investigations of other species are less consistent. In addition, perceptual narrowing is present in Japanese macaques but not rhesus macaques or vervet monkeys, suggesting important species differences in the development of face-processing abilities that should be examined in the future.

CONCLUSIONS

The purpose of this review was to further examine how studies comparing own- and other-species face processing informs our understanding of face-processing abilities more generally, to further understand why comparing own- and other-species face processing is important for elucidating the developmental trajectory and neural underpinnings of face processing, and to compare studies using human and nonhuman participants in order to better characterize the evolutionary origins of face perception. We highlighted research that has focused on understanding other-species face processing beginning in newborns into infancy, through childhood, and into adulthood.

In general, the literature on other-species face processing supports the existence of an early tuning processing, called perceptual narrowing. Although infants up to age 6 months appear to process human and nonhuman primate faces equivalently, by 9 months of age they have tuned their perceptual abilities to better discriminate faces from groups they experience most frequently (Lewkowicz & Ghazanfar, 2006; Pascalis et al., 2002, 2005; Scott & Monesson, 2009). This perceptual narrowing effect is also found in Japanese macaques (Sugita, 2008) but not vervet monkeys (Zangenehpour et al., 2009). Studies with children and adults suggest that, although perceptual narrowing seems to set a foundation for face processing, learning continues throughout the lifespan and other-species (and other-race) biases are likely to be flexible and adaptive to changing environments. Dahl and colleagues (2013) hypothesize that chimpanzees exhibit an early developmental component akin to perceptual narrowing, which tunes perception towards faces that are frequently encountered. This early component is followed by an additional late component that responds flexibly to changes in the environment and may be related to perceptual expertise in adults. This model suggests that developmental changes in face-processing abilities continue to be malleable and are influenced by an accumulation of quantitative and qualitative experiences. Human adults show considerable processing advantages, as well as neural processing

differences, for human compared to nonhuman primate faces. However, adults also show advantages for nonhuman primate faces relative to other animal face types (Campbell et al., 1997). Combined with differences between nonhuman primate species, this finding suggests that, although humans and nonhuman primates are best at perceiving and recognizing faces from groups with which they have the most experience (typically conspecific faces for humans), it is possible that they still show an advantage for monkey faces relative to other animals (or even chimpanzees relative to other old world monkeys). Therefore, studies investigating face-processing abilities based on evolutionary relatedness might significantly improve our understanding of the contributions of evolution. However, it is important to control for rapid learning abilities, as well as stimulus and task differences (faces may look more or less similar, tasks may allow for variable strategy use). Currently, it is not clear whether general learning mechanisms present in both human and nonhuman primates combined with the unique perceptual and social properties of faces lead to expert-like face-processing abilities or whether face-specific evolutionary mechanisms account for expertise with faces.

Although not reviewed here (see Anzures et al., this issue 2013, and Balas, this issue 2013), studies examining other-race effects appear to be consistent in terms of patterns of effects and timing of perceptual narrowing. These similarities suggest comparable underlying mechanisms driving these face biases. However, when investigating the other-race effect, it is unlikely that there is an influential evolutionary mechanism, and explicit and implicit stereotypes and prejudices are also not likely to influence the other-species effect. Thus, thoughtful study designs that take into account several influential factors and longitudinal investigations are important for further understanding the acquisition of face-processing biases such as the other-species and other-race effects.

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