INFANT AND ADULT FACE DISCRIMINATION BEYOND PRIMATES: PERCEPTUAL NARROWING OF FACIAL IDENTITY

by

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(Under the Direction of Dorothy M. Fragaszy)

ABSTRACT

Human adults recognize faces extremely well; however, the way in which this expertise develops remains unknown. One developmental model of face recognition is perceptual narrowing, which contends that at birth perception is broadly tuned, but narrows as a function of experience. According to this model, infants transition from being face generalists—broadly discriminating facial identity for numerous species—to being face specialists, who are experts in discriminating human faces. To test this model, facial identity discrimination was measured in 4- to 6-month-olds, 9- to 12-month-olds, and adults in two experiments: one using natural faces, and one using systematically varied faces. The first study revealed that 4- to 6-month-olds (n = 26) and adults (n = 27) discriminate sheep (*Ovis aries*) faces (ps < .05), while 9- to 11-month-olds (n = 26) showed no evidence of discrimination (p > .05). The fact that young infants discriminate sheep faces is consistent with the perceptual narrowing model, which posits that perception is broad early in the first year of life and narrows with age. However, the ability to discriminate some types of animal faces does not disappear, as we found adults could also discriminate sheep faces. In the second study, we examined the properties of faces viewers can use for discrimination by systematically varying faces of humans, capuchin monkeys (*Cebus* *apella*), and sheep (*Ovis aries*) in their outer features (contour, hair), inner features (eyes and mouths), or spacing among inner features (distance between eyes, vertical position of eyes and mouth). Results indicated that 4- to 6-month-olds ($n = 61$) showed no evidence of discriminating systematically varied faces. In contrast, 9- to 12-month-olds ($n = 41$) discriminated human and monkey faces that varied in either outer features or inner features (ps $< .05$). Adults ($n = 71$) discriminated all three species using inner and outer features, and additionally discriminated human and monkey faces that varied in their spacing (ps $< .05$). This finding suggests that adults may use configural processing for primate, but not nonprimate faces. Taken together, findings from both experiments differ from predictions derived from a perceptual narrowing model of development. An alternative model—learned attention—is discussed.

INDEX WORDS: Face recognition, Facial identity, Infant, Discrimination, Configural processing, Learned attention, Perceptual narrowing

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Faces are one of the most important stimuli for humans and other vertebrate species (Ellis, 1990; Leopold & Rhodes, 2010). Humans can extract a large amount of information from faces (e.g., recognizing identity, interpreting facial expressions); in fact, face perception may be the most highly developed visual skills in humans (Haxby, Hoffman, & Gobbini, 2000). Humans, and many other species, can identify and interpret the rich amounts of information faces convey, including relatively invariant information about identity, age, sex, ancestry, mate value (i.e., health, symmetry; e.g., Sacco, Hugenberg, & Sefcek, 2009), personality (e.g., Naumann, Vazire, Rentfrow, & Gosling, 2009), and physical formidability (e.g., fighting ability or resource-holding potential; Sell et al., 2009). Faces also convey variant information, including emotional and attentional states, language, and other communicative gestures (for reviews see Bruce & Young, 1998; Kanwisher & Yovel, 2006; Peterson & Rhodes, 2003; Tsao & Livingstone, 2008).

Face perception is a complex process, shaped by evolutionary pressures (Leopold & Rhodes, 2010), genetics (McKone & Palermo, 2010; Wilmer et al., 2010; Zhu et al., 2010), personality (e.g., temperamental shyness; Brunet, Mondloch, & Schmidt, 2010), and individual experiences (e.g., Martin-Malivel & Okada, 2007; Park, Newman, Polk, 2009; Rennels & Davis, 2008; Vervloed, Hendriks, & van den Eijnde, 2011). Numerous top-down processes may influence face perception, including a viewer's goals, such as to recognize identity or emotional expressions, identify or evaluate a mate, or affiliate after social rejection (e.g., Bernstein, Young, Brown, Sacco, & Claypool, 2008). Face perception is influenced by viewers' emotional states (Leppänen & Hietanen, 2003), hormonal states (e.g., pregnancy; Anderson & Rutherford, 2010), and facial and body postures (e.g., Davis, Senghas, Brandt, Ochsner, 2010; Harmon-Jones & Peterson, 2009), as well as the language used to name faces (e.g., labeling faces at either the individual level or species level; Scott & Monesson, 2009).

Given the wealth of information faces provide, and the numerous processes that influence face perception, faces are a popular topic for study. Much research has focused on understanding facial identity recognition, and a great number of theories of face recognition in adults attest to this interest (e.g., Catz, Kampf, Nachson, & Babkoff, 2009; Diamond & Carey, 1986; O'Toole, Vetter, & Blanz, 1999; Valentine, 1991). There is disagreement, however, regarding the development of facial identity recognition. This disagreement is due, at least in part, to the varying methods used for measuring face recognition. Below, I review the literature on the developmental emergence of facial identity recognition, specifically focusing on older infants (i.e., 4- to 12-month-olds) and adults. I then identify outstanding questions and introduce two studies which sought to answer these questions.

Methods for Measuring Face Recognition

Facial identity recognition measures exist for numerous populations, including healthy infants, children, and adults, as well as measures specifically for atypically developing populations and individuals with brain lesions (Crookes & McKone, 2009; Young, De Haan, & Bauer, 2008). Techniques range from paper-and-pencil tests, to physiological and brain imaging measures, to passive viewing paradigms. In the present review, I focus primarily on measures that have been used with nonverbal individuals (e.g., infants and nonhuman primates), and only briefly review work with older individuals that is relevant for comparing infant and adult face recognition.

To determine the ways in which faces are recognized across development, the properties of faces that vary across individuals must first be uncovered. Most faces have the same basic configuration—two eyes above a nose and mouth—known as *first-order* configuration (Bhatt, Bertin, Hayden, & Reed, 2005). Thus, *first-order* configurations alone are not helpful for distinguishing individuals. Instead, viewers must possess sensitivity to interindividual differences in face properties, including faces' outer features (e.g., hairline, jaw line, ears), inner facial features (e.g., size and shape of the eyes, eyebrows, nose, and mouth), and inner feature configuration (i.e., spacing among inner facial features; sometimes referred to as *second-order* relational information; Diamond & Carey, 1986). Faces can also be processed *holistically*—as opposed to processing them in a piecemeal fashion—whereby each feature is processed in conjunction with every other feature (e.g., Maurer, Grand, & Mondoch, 2002). Human adults recognize faces using some combination of the above properties. That is, adults use both feature-based and configural processing for recognizing faces (e.g., Kimchi & Amishav, 2010). Face researchers generally accept that holistic processing (e.g., integrating face properties in parallel) appears more important for face recognition compared to the recognition of other objects (Farah, Wilson, Drain, & Tanaka, 1998; McKone, Kanwisher, & Duchaine, 2007).

The relative contributions of feature-based and configural processing to face recognition throughout development are of great interest (Carey, 1992). Though feature-based processing can be distinguished from configural and holistic processing, to my knowledge, researchers have yet to develop ways of distinguishing holistic and configural processing (although see Maurer, Le Grand, & Mondloch, 2002). Thus, in the literature, as well as in the current series of studies, the labels configural and holistic are used interchangeably to refer to recognition based not on individual inner features or outer features, but some combination.

Much work has focused on determining the extent to which humans use one or more of these characteristics—inner features, spacing among inner features, or outer features—to distinguish individuals. Face recognition can be measured in adults and older children using explicit tasks, such as by asking an individual to identify two faces, or two face parts, as either the same individual or different individuals (e.g., Mondloch, Le Grand, & Maurer, 2002; 2003). Match-to-sample tasks are also commonly used (e.g., Habak, Wilkinson, & Wilson, 2008). In these tasks, two or more individual faces must be matched, based on identity, to a sample face that typically differs in some way (e.g., orientation, facial expression, eye gaze).

Several methods have been developed for testing facial identity recognition in nonverbal individuals, such as in passive viewing tasks where looking is measured. For example, the visual paired comparison task takes advantage of spontaneous novelty preferences (Fantz, 1964). In this task, an individual is first familiarized with a face for a specified duration, then subsequently is presented with pairs of faces, one of which is the same individual and one of which is novel, and looking durations to both faces are measured. Both novelty and familiarity preferences have been interpreted as indicating discrimination (e.g., Houston-Price & Nakai, 2004). However, novelty and familiarity preferences may reflect different underlying processes (e.g., Hunter & Ames, 1988; Pascalis & de Haan, 2003). In addition, a lack of looking preference does not necessarily indicate a lack of discrimination (e.g., Richmond, Colombo, & Hayne, 2007). A lack of looking preference may simply indicate that the novel and familiar stimuli are equally interesting to the participant (Pascalis & de Haan, 2003). Infants may find a familiar stimulus initially rewarding, and therefore may show a familiarity preference early on (Hunt, 1963).

However, with repeated exposure the infant may habituate to the familiar stimulus and then look more to a novel stimulus. This difference in preference may be due to differences in encoding, with a well-encoded stimulus no longer attracting as much attention (Hunter & Ames, 1988; Pascalis & de Haan, 2003). Many things influence encoding, including the duration of a familiarization (longer familiarization results in better encoding), stimulus complexity (more complex stimuli take longer to encode), and the age of the participant, as information processing speed increases with age (Nelson, 1995; Sophian, 1980). In addition, the viewer's emotional state may influence whether there is a preference for the novel or the familiar: infants in a positive emotional state show a preference for the familiar, while infants in a neutral emotional state show a preference for novelty (Nachman, Stern, & Best, 1986), which may be because emotional state influences learning speed, with faster learning in a neutral compared to a positive emotional state (Rose, Futterweit, & Jankowski, 1999).

Eye-tracking can also reveal differences in the ways faces are examined, which can inform our understanding of looking preferences (e.g., Liu et al., 2011). For example, eye tracking reveals a decrease with age in the amount of time looking at the inner contents of the face relative to the outer contents of the face for unfamiliar types of faces (e.g., other-race; Liu et al., 2011). Other measures with either real or schematic faces include the extent of tracking (e.g., Goren et al., 1975), total fixation time (e.g., Aslin, 2007; Dannemiller & Stephens, 1988), duration of first look (e.g., Valenza, Simion, Macchi Cassia, & Umiltá, 1996), and the proportion of time looking at a novel face (e.g., Schwarzer, Zauner, & Jovanovic, 2007). Additional measures of visual object discrimination, that have not—to our knowledge—been used for face recognition, include the direction of first look (e.g., Snyder, Blank, & Marsolek, 2008), and the number of comparison gaze shifts (e.g., Colombo, Mitchell, & Horowitz, 1988). Additionally, physiological measures of face discrimination include the timing and amount of brain activity (e.g., event-related potentials; Scott, Shannon, & Nelson, 2006), and skin-conductance (an index of physiological arousal; e.g., Tranel & Damasio, 1985).

One common method for assessing configural processing is to measure how face inversion affects recognition speed and accuracy. Humans and other animals are worse at recognizing an inverted image relative to an upright image—especially for faces—a phenomenon known as the *inversion effect* (this effect has been shown in multiple species, e.g., dogs, Racca et al., 2010; chimpanzees, Parr, Dove, & Hopkins, 1998; humans, Diamond & Carey, 1986; Kohler, 1940; Robbins & McKone, 2007; Scapinello & Yarmey, 1970; Yin, 1969). This disruption of face recognition may be because inverting faces disrupts configural processing more so than featural processing (Freire, Lee, & Symons, 2000; Leder & Bruce, 2000; Maurer, Grand, & Mondoch, 2002; Valentine & Bruce, 1988; Yin, 1969). On the other hand, there is also evidence that inversion makes the extraction of information from faces difficult, and may not exclusively disrupt configural processing (Nachson & Shechory, 2002; Rakover, 2002; Sekuler, Gaspar, Gold, & Bennett, 2004).

Another method for distinguishing featural and configural processing relies on the *composite effect*. The composite effect is elicited by taking faces and cutting them horizontally then laterally shifting the top and bottom halves so they no longer match up. Participants are asked—either explicitly or through passive viewing paradigms—whether the top or bottom portion of the face is novel or familiar. If the face halves are lined up, the face is processed holistically and identifying a novel part is difficult; but, if the faces are laterally shifted so they do not line up, recognizing a novel part is easier because the parts can be processed independently rather than in a configural fashion (e.g., Turati, Di Giorgio, Bardi, & Simion, 2010; Young, Hellawell, & Hay, 1987).

Faces can also be distorted either in whole or in part to determine whether removing certain information disrupts recognition. For example, spatial filtering—which removes either high spatial frequencies or low spatial frequencies—can selectively disrupt different aspects of face processing. Early in visual processing we encode the spatial frequencies of faces and other objects. Cells which are sensitive to high spatial frequencies encode abrupt spatial changes in an image, such as fine edges and details, while cells sensitive to low spatial frequencies encode coarse cues in an image, such as global information, including shape, orientation, and proportions (Goffaux, Hault, Michel, Vuong, & Rossion, 2005). Feature-based processing can be disrupted when high spatial frequencies are removed, and configural processing can be disrupted when low-spatial frequencies are removed (Goffaux, Hault, Vuong, & Rossion, 2005; Sergeant, 1986). The outer features of faces are often removed to ensure they are not relied upon for distinguishing individuals (e.g., Turati, Macchi Cassia, Simion, & Leo, 2006). One face property to which humans are sensitive is the relation (i.e., distance) between the inner features and outer features. The extent to which an individual detects changes to this face property can be measured by familiarizing individuals with two different faces, then taking the inner features of one familiar face and the outer features of the other familiar face and combining them in a new way to make a *switch face* (e.g., Cashon & Cohen, 2004; Cohen & Cashon, 2001; Schwarzer et al., 2007). Increased looking to this novel combination indicates discrimination of faces changing in their configuration.

Researchers have also measured the extent to which humans can detect changes in inner facial features (e.g., eyes, nose, mouth), to determine the importance of inner features in face recognition. When alterations are made to inner features' orientation, size, or shape, human adults detect these changes, especially when they are made within the context of upright faces whose configurations (i.e., spacing among features) have not been altered. Human adults are much worse at recognizing features outside the context of the face, compared to within a face, known as the *part-whole effect* (Tanaka & Farah, 1993). Individuals are better at detecting local changes in features when they are presented upright, compared to inverted, known as the *Thatcher Illusion* (e.g., Bertin & Bhatt, 2004). Adults are also worse at recognizing features when they are presented in a face whose configuration (i.e., spacing among features) has been changed, relative to when the spacing among features has been unchanged, known as the *part-in-spacing-changed-whole* variant (Tanaka & Sengco, 1997). Together, these studies suggest inner feature recognition is important, but also that contextual information (e.g., outer features and head contours) influences the perception of individual features.

Though there is a wealth of information about face recognition, comparing studies can be difficult given that procedural and stimulus differences are confounded across studies, both for studies of newborns, as well as for studies of older infants (i.e., 4- to 12-month-olds) and adults (e.g., Fagan, 1974; Mondloch et al., 1999). Across studies, face stimuli ranged from relatively simple (e.g., black and white schematic faces: Johnson, Dziurawiec, Ellis, & Morton, 1991) to complex (e.g., dynamic stimuli, Otsuka, Konishi, Kanazawa, Yamaguchi, Abdi, & O'Toole, 2009). Additional differences across studies include the number of stimuli presented at once (typically either one or two), and the length of presentation time, which can either be tailored to each individual participant (e.g., Pascalis, de Haan, & Nelson, 2002), or standardized across participants (for a review of familiarization procedures for visual stimuli see Bornstein, 1985). Even the age and gender of faces can differently influence recognition across age groups (e.g., Anastasia & Rhodes, 205). For example, most studies use adult faces, but when children's faces are used, children show more configural processing than adults (Susilo, Crookes, McKone, & Turner, 2009).

Much work has examined natural faces, which vary on more than one dimension, and therefore do not allow tests of the specific face properties viewers can use for discrimination. Though these studies are valuable contributions to our understanding of face recognition, they do not allow us to test which specific properties of faces are used for facial identity recognition. In contrast, the *Face Dimensions Test* determines which face properties can be used for recognition through the use of systematically varied faces that vary in only one dimension at a time, such as in the inner features, outer features, or spacing among inner features (Freire et al., 2000; Goffaux et al., 2009; Mondloch et al., 2002; Scott & Nelson, 2006; Sugita, 2009; Thompson et al., 2001; Quinn & Tanaka, 2009). However, a limitation of these studies is that they failed to manipulate faces in natural ways (Taschereau-Dumouchel, Rossion, Schyns, & Gosselin, 2010). For example, the spacing among the facial features exceeded the natural variability within the population, limiting the generalizability of the findings. Thus, the extent to which individuals distinguish identity based on a single face property remains unknown.

Theories of the Development of Facial Identity Discrimination

Beginning in the first few hours after birth, infants' attention is captured and held by faces and face-like patterns (e.g., Fantz, 1964; Goren, Sarty, & Wu, 1975; Johnson, Dziuarawiec, Ellis, & Morton, 1991; Valenza et al., 1996). This initial interest in faces facilitates face learning (Morton & Johnson, 1991), as well as increases interactions with social partners, facilitating attachment (e.g., Blehar, Lieberman, & Ainsworth, 1977). Models characterize face perception in early infancy (i.e., newborns; for a recent review see Pascalis & Kelly, 2009); however, the present review focuses on later infancy (i.e., 4- to 12-months-olds).

There is considerable disagreement as to whether face perception specialization is driven primarily by an innate module (e.g., Farah, Rabinowitz, Quinn, & Lie, 2000; de Schonen & Mathivet, 1989; Morton & Johnson, 1991), or whether specialization is primarily acquired through experience (Gautheir & Nelson, 2001; Le Grand, Mondloch, Maurer, & Brent, 2001, 2003). Converging data suggest dedicated and complex neural systems for face perception that are phylogenetically old, perhaps even dating back 220 million years to our mammalian common ancestor (Pascalis & Kelly, 2009). In addition, most face researchers would agree that the development of face perception involves both innate predispositions (i.e., present at birth) to attend to face-like patterns, as well as experiential contributions for face specialization (for a recent review, see Scott, in press). Infants' preferences for face-like patterns are instrumental in ensuring adequate exposure to faces, especially faces important for survival (e.g., mother's face, which conveys important information through expressions and gaze). Infants' innate attraction to faces, among other things, makes infants engaging social partners; consequently, this increases infants' exposure to faces, which aids in the specialization of their perceptual systems.

The face recognition system is challenging to study due to its complexity. Experiential contributions have been investigated to a greater extent than innate predispositions, likely due to the challenges of testing newborns. Though selectively depriving human infants of experience with faces in unethical (though, see face-deprivation studies with monkeys: Sugita, 2008; 2009), research has been carried out on individuals who, due to cataracts, experienced visual deprivation in the first part of their life. Adults with bilateral congenital cataracts removed between two and six months of age demonstrate impaired configural and holistic face processing, but not impaired feature-based face processing (Le Grand, Mondloch, Maurer, & Brent, 2001; Le Grand, Mondloch, Maurer, & Brent, 2004). Visual input to the right hemisphere appears especially important for later configural face processing (Le Grand, Mondloch, Maurer, & Brent, 2003).

In addition to examining individuals who lacked experience with faces during critical periods of development, researchers have also examined individuals who have additional experience with faces during critical periods of development (Pascalis et al., 2005; Scott & Monesson, 2010). For example, infants can be given additional exposure to faces that they would not otherwise get, such as through picture books with monkey faces (e.g., Pascalis et al., 2005; Scott & Monesson, 2010). When given additional experience with individually-named monkey faces, then subsequently tested on novel monkey faces, infants retain the ability to discriminate monkey faces beyond 9 months (Pascalis et al., 2005; Scott & Monesson, 2010). In addition, the role of experience can be examined by measuring the outcomes of natural differences in exposure to different face types, such as the ages, genders, and ethnicities of faces to which infants are exposed (e.g., Rennels & Davis, 2008; Vervloed et al., 2011). By the end of their first year of life, infants have specialized in processing the faces to which they are most regularly exposed, including face ethnicity (e.g., Kelly et al., 2007), gender (e.g., Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002), age (e.g., Cassia, Kuefner, Picozzi, & Vescovo, 2009), and species (Pascalis, de Haan, & Nelson, 2002; Pascalis et al., 2005). Together, this work suggests that there is an enormous amount of plasticity in face perception in the first year of life.

Numerous studies in the last decade provide evidence that a general-purpose perceptual system may be responsible for the development of face recognition in the first year, as a consequence of both experience (e.g., Gauthier & Nelson, 2001; Cassia, Kuefner, Picozzi, &

Vescovo, 2009) and infants' preference for face-like stimuli from birth (e.g., de Haan, Humphreys, & Johnson, 2002). According to this model, there is a domain-general change in perception, known as perceptual narrowing. This model's predictions are consistent with findings that we are better at recognizing faces of individuals when those individuals are from familiar species (e.g., adults are better at recognizing humans compared to monkeys and sheep, Dufour, Coleman, Campbell, Petit, & Pascalis, 2004; Pascalis, de Haan, & Nelson, 2002; Pascalis et al., 2005; infants are better at recognizing pets compared to non-pets, Hurley, Kovack-Lesh, & Oakes, 2010), ages (Cassia et al., 2009; Kuefner, Cassia, Picozzi, & Brocolo, 2008; Kuefner, Cassia, Vescovo, & Picozzi, 2010), genders (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002; Quinn et al., 2008; Ramsey, Langlois, & Marti, 2006), and races (Kelly et al., 2007). Thus, there appears to be a decrease in perceptual discrimination abilities for unfamiliar relative to familiar faces (Nelson, 2001).

Although perceptual narrowing is widely accepted as a model of the development of facial identity discrimination in the first year of life, alternative explanations should also be considered. One alternative, which may occur instead of, or concurrently with, perceptual narrowing, is learned attention (e.g., Heckler, Kaminski, & Sloutsky, 2006; Kruschke, 2001; Mackintosh, 1975). Learned attention refers to the fact that if a contrast on a given dimension is not predictive of any important outcome (e.g., /r/ and /l/ phonemes in the Japanese language), an organism will learn to ignore this contrast. In the first year of life, infants begin to learn which properties of faces can be used for distinguishing individuals (e.g., shape and color of the eyes) and which cannot be used (e.g., the arrangement of the inner features, with the eyes above the nose and mouth). Infants may be better at discriminating animal faces early in development, compared to later in development, because early in development they do not yet exhibit learned attention biases to certain face properties, which are useful for human face discrimination, but not animal face discrimination. In other words, older infants may not be as good at discriminating animal faces because they are selectively attending to the wrong face properties, due to their experience with primarily human faces. This, of course, assumes that the face properties useful for discriminating individual identity are different for humans and animals. In contrast, if the face properties useful for discriminating individuals are the same across humans and animals (e.g., human faces and monkey faces both vary in the color and shape of the eyes), then with age, individuals should show an improvement in both human and animal facial identity discrimination. In this case, experience with human faces can help animal face recognition.

Evidence in support of learned attention comes from Hill and Lewis' (2006) study in which adults were trained to attend to certain features of faces, and this training resulted in a reduction of the own-race bias through shifting attention to relevant features. Whether similar attentional training for face recognition can be successfully carried out with younger individuals (e.g., infants), or with other types of faces (e.g., animal faces), to my knowledge, remains unknown.

Evidence that Infants are Face Generalists

Though counter-intuitive, research suggests that young infants (e.g., younger than 6 months old) may be better than adults at recognizing the faces of nonhumans. Pascalis and colleagues (2002) found that in a visual paired comparison task, 6-month-olds, 9-month-olds, and adults could discriminate human faces, but only 6-month-olds could discriminate monkey faces. The authors conclude that this 'species-specific effect' might reflect perceptual narrowing (Pascalis et al., 2002). According to this view, rather than being born as human face specialists, infants are born as face generalists, and slowly become human face experts over time and with experience. This developmental process has been characterized as a fine-tuning of perception with age (e.g., Nelson, 2001). From birth, perception starts out broadly tuned to all stimuli, both relevant and irrelevant, but narrows during the first months of life (by about 9- to 12-months of age), becoming selective to process only relevant stimuli. Having a broadly-tuned perceptual system at birth would allow enormous flexibility during development, which helps infants adapt to their particular environment. For example, between 6 and 12 months of age, discrimination declines among speech sounds that are not in the infants' native languages (Werker & Tess, 2005). If this narrowing of perception does occur, experience is important; infants selectively retain discrimination among native phonemes, while experiencing a decline in the discrimination of non-native phonemes. Perceptual narrowing has been characterized as a widespread developmental phenomenon, which may also occur for face-voice matching and the detection of violations in musical structure (for a review see Scott, Pascalis, & Nelson, 2007). Considering perceptual narrowing as a model for development allows for testable predictions. Though there is much support for this model, no widely discussed alternative interpretations for these phenomena exist.

Perceptual narrowing is also thought to occur for facial identity recognition. Facial identity discrimination (i.e., recognizing whether a face is new or familiar) among faces of unfamiliar races declines from 6 to 9 months of age, while facial identity discrimination of familiar races remains intact (Hayden, Bhatt, Joseph, & Tanaka, 2007; Kelly et al., 2007). Likewise, face discrimination is influenced by the target face's gender (e.g., Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002; Ramsey et al., 2006) and age (Cassia et al., 2009a; Cassia, Picozzi, Kuefner, Bricolo, & Turati, 2009b; Cassia, Picozzi, Kuefner, & Casati, 2009c).

The perceptual narrowing of identity discrimination is also thought to extend to other species' faces as well. For example, 6-month-old humans, but not 9-month-old humans, can discriminate crab-eating macaque monkey faces (*Macaca fascicularis*; Pascalis et al., 2002) and barbary macaque monkey faces (*Macaca sylvanus*; Pascalis et al., 2005). However, the reported decline in infants' discrimination of monkey faces can be prevented with certain experience. For example, infants who were exposed to a picture book containing individual monkey names (e.g., Boris) and faces from 6 to 9 months retained discrimination among *unfamiliar* monkey faces at 9 months (Pascalis et al., 2005; Scott & Monesson, 2009). Interestingly, the experience with faces was not what allowed the infants to retain the monkey face recognition abilities at 9 months, but rather the individual naming of the monkey faces (Scott & Monesson, 2009). Infants who viewed the same faces, but learned them categorically (i.e., all labeled "monkey") did not retain the ability to discriminate the faces. Monkeys (*Macaca fuscata*) also selectively discriminate facial identities of the species to which they have been exposed (Dufour, Pascalis, & Petit, 2006; Pascalis & Bachevalier, 1998; Sugita, 2008), though the time course of monkeys' proposed perceptual narrowing may be different from humans' (Sugita, 2009). This finding suggests if perceptual narrowing occurs with respect to face discrimination, it is unlikely to have emerged recently in our evolutionary history.

Whether human infants show the same developmental pattern of facial identity discrimination for both unfamiliar and more distantly related species remains unknown, as only phylogenetically closely related species (Old World monkeys and humans) and pets (dogs and cats) have been examined. One exception is a study by Quinn and Eimas (1996), which found that 3- to 4-month-old infants discriminated facial identity for both cat and dog faces. However, this discrimination may not reflect perceptual narrowing, as Quinn and Eimas did not examine whether this ability is lost in later infancy (e.g., after 9 months). Therefore, changes in human infants' facial identity discrimination abilities for more distantly related species (e.g., New World monkeys and sheep) remain unknown. In addition, some infants in Quinn & Eimas's study population likely had experience with cats and dogs, given that they are common pets in western countries. Early experiences with these animals may have influenced the 3- to 4-month-olds' discrimination abilities in Quinn and Eimas's study.

Similarities in Adults' Recognition of Human and Other Animal Faces

The argument that young infants are face generalists, and that by their first year they have begun to specialize in processing human faces, is weakened by the many similarities in the ways human adults perceive and recognize human and nonhuman faces, particularly primate faces. Adult humans can accurately recognize both human faces (e.g., Standing, Conezio, & Haber, 1970), and nonhuman primate faces (e.g., rhesus monkeys; Dufour et al., 2004) in active recognition tasks (though passive viewing tasks have not found looking preferences). Moreover, the brain areas involved in human and nonhuman face recognition appear to be similar. For example, the fusiform face area (FFA)—a brain area involved in face recognition—is especially active when viewing human and nonhuman faces, compared to non-face objects (e.g., houses, other body parts; Kanwisher et al., 1999; Maguire, Frith, & Cipolotti, 2001). Humans' recognition of human and nonhuman faces is impaired when faces are vertically inverted (e.g., human faces, Valentine, 1991; nonhuman primate faces, Wright & Roberts, 1996; dog faces, Diamond & Carey, 1986). Impaired recognition with inversion, however, does not occur for other non-face objects, indicating that faces are recognized differently from non-face objects.

Additional evidence for similarities in the processes underlying the recognition of human and nonhuman faces comes from studies of individuals with prosopagnosia, a disorder characterized by an inability to recognize faces with relatively intact abilities to recognize other objects. This inability to recognize faces can extend to nonhuman faces for which a person previously had expertise (Bornstein, Sroka, & Munitz, 1969). For example, one individual who grew up on a farm—and previously had outstanding nonhuman face recognition—lost the ability to recognize nonhuman faces, along with the recognition of faces of familiar humans, while the recognition of non-face objects remained intact (Bornstein et al., 1969).

Categorical perception for face images of different species can be examined by morphing images of one species into that of another (Campbell, Pascalis, Coleman, Wallace, & Benson, 1997). Interestingly, though non-primate and primate faces (e.g., cow and rhesus monkeys) have clear category boundaries, no clear category boundaries exist between primate species (e.g., rhesus monkeys and humans). Campbell and colleagues (1997) suggest that this lack of a category boundary could be because a single prototype primate face subserves face recognition for all primate faces. Thus, monkey faces are judged by the same criteria as human faces. Congruent with this idea are recent findings by Taubert (2009) that adult humans engage the human-face recognition system when recognizing primate, but not nonprimate (e.g., sheep, hen, lizard) faces. Together, these studies suggest similarities in the way adult humans recognize human and nonhuman primate faces, though there may be differences in the processing of nonprimate faces.

Differences in Adults' Recognition of Human and Other Animal Faces

Despite these similarities in the processing of human and nonhuman faces, there is also evidence that human adults are better at recognizing human faces relative to the faces of other animals. For example, prosopagnosia is sometimes very specific to human faces, and results from a few studies suggest that there may be distinct cortical systems for recognizing human (and possibly other primate) faces, which are separate from systems involved in recognizing non-primate animal faces. For example, a patient with severe prosopagnosia who later became a sheep farmer could easily recognize and name his sheep by their faces, but could not do the same with human faces (McNeil & Warrington, 2006). Another prosopagnosic farmer with impaired human face recognition showed the same spared recognition of cow and dog faces (Bruyer et al., 1983). This double dissociation suggests that human and nonhuman face recognition—or primate and non-primate face recognition—may be subserved by separate brain areas.

Human adult face recognition for human, macaque monkey, and sheep faces was examined in a forced-choice matching task in which face recognition to inverted and upright faces was examined (Dufour, Coleman, Campbell, Petit, & Pascalis, 2004). Difficulties recognizing inverted faces reflect the fact that faces are processed in a holistic, rather than feature-based manner; therefore, inverting faces interferes with this process. Using familiarization periods of 750 ms, an inversion effect was present for human and monkey faces, but not sheep faces. The authors interpreted this finding as indicating that experience with a particular species (e.g., monkeys) is not necessary for holistic processing. However, with a shorter 50 ms familiarization, there was an inversion effect only for human faces. Therefore, the processing of human faces may be more efficient than that for monkey faces.

Hershler and Hochstein (2005) found that photographs of human faces “pop out” when surrounded by photos of non-face objects, as indicated by significantly shorter search times; nonhuman mammal faces, however, do not. This finding suggests that adults’ attention is captured by human faces in a way that is qualitatively different from attention to other animals’ faces. One limitation of this work is that it only used a variety of nonprimate faces. If primate faces were used exclusively this pop-out effect for faces may extend to the faces of other primates, too.

Differences in Face Processing between Infants and Adults

In addition to developmental changes in the discrimination of individual identities across species, the properties of faces viewers can use for discrimination also change with age. In fact, differences in sensitivities to different face properties may underlie the apparent changes in face recognition across species (see Chapter 3). For example, infants can be tested using a *switch face*, which is a face that has the inner features (eyes, eyebrows, nose, and mouth) of one face and the outer features (hair, outer contours) of another face, both of which have been seen previously but are novel in their combination (i.e., the distance between the inner facial features and the outer facial features). An infant is first familiarized with two natural faces, then infants' relative interest in measured for three faces: a novel face, a familiar face (i.e., one viewed previously), and a switch face (containing the inner features of one familiar face and the outer features of another familiar face). Results suggested that 3-month-olds and 4-month-olds recognize faces using inner features (e.g., eyes and mouths), 7 and 10-month-olds additionally detect changes to the relation between the inner features and the outer features (i.e., holistic representation), but only in upright faces, and 6-month-olds are in a transition stage between the two, in which some features are processed holistically (e.g., the mouth), and others (e.g., the eyes) independently (Cohen & Cashon, 2001; Cashon & Cohen, 2004; Schwarzer, Zauner, & Jovanovic, 2007). Others have found that 3- to 4-month-olds and 6- to 7-month-olds rely on the eyes for recognition, but not the mouth (Quinn & Tanaka, 2009). The switch design has also been used with schematic faces, which revealed 4-month-olds were not engaging in holistic processing and instead used the facial features, while 6- and 8-month-olds processed the mouths holistically, but the eyes featurally (Schwarzer & Zauner, 2003; Zauner & Schwarzer, 2003). Thus there seems to be much evidence that infants are capable of at least using the eyes for facial identity recognition.

Others have measured whether infants detect changes to the spacing among inner facial features. Seven-month-olds prefer faces that conform to average distance measurements (Bertin & Bhatt, 2004; Thompson, Madrid, Westbrook, & Johnson, 2001). This result was interpreted as suggesting 7-month-olds discriminate second-order relational information in faces. Others have found 3- to 7-month-olds attend more to faces when there are alterations to the spacing among features (Bhatt, Bertin, Hayden, & Reed, 2005; Hayden, Bhatt, Reed, Corbly, & Joseph, 2007; Quinn & Tanaka, 2009). However, when feature spacing only varies to a normal degree (as in natural faces), as opposed to an exaggerated degree, this preference disappears (Taschereau-Dumouchel, Rossion, Schyns, & Gosselin, 2010). Additional tests have shown infants also experience the inversion effect, interpreted as reflecting configural processing (e.g., Hayden et al., 2007; Leo & Simion, 2009); however, the inversion effect also disrupts feature-based processing (Nachson & Shechory, 2002; Rakover, 2002; Sekuler et al., 2004), so disrupted face recognition with inversion tells us little of what properties of the face infants are using. The composite face paradigm has also been used with infants (Turati, Giorgio, Bardi, & Simion, 2010). In this paradigm, participants are familiarized with the top half of a face, and then tested with two aligned or misaligned (i.e., laterally shifted) faces, one which has the familiar top part. If the faces are processed holistically, participants should have difficulty recognizing the top half as familiar in the aligned faces, but should recognize the face as familiar in the misaligned faces. They found that 3-month-olds showed a familiarity preference only for the misaligned face, adults showed a novelty preference only for the misaligned face, and newborns showed no preference. These results were interpreted as evidence that 3-month-olds have some degree of holistic face processing.

Together, this work suggests rudimentary holistic processing may be present in infancy; however, just because infants process faces holistically, does not mean that they rely primarily on holistic processing for face recognition. In fact, holistic processing remains relatively poor throughout childhood and early adolescence. A large body of research documents a transition in childhood (the exact age is debated, but may fall between 3 and 10 years), in which there is a change from recognizing faces primarily in a piece-meal, feature-based way, to recognizing them holistically, using configural information, by processing the relationships among the features (Carey & Diamond, 1977; Cassia et al., 2009b; Sinha, Balas, Ostrovsky, & Russel, 2006; for a review of configural processing see Maurer, Le Grand, & Mondloch, 2002). In adulthood, faces are recognized using a different type of computation than objects, with face recognition more reliant on inner feature shape (e.g., shape of the eyes), spatial relational information (e.g., the distances between facial features), and holistic processing (McKone et al., 2006).

Some argue that children do not show adult-like holistic processing until about 10 years of age (Sinha et al., 2006). For example, children less than about 10 years of age are equally good at remembering inverted and upright faces (Carey & Diamond, 1977; though inversion effects are present in infancy, Rose, Jankowski, & Feldman, 2008), whereas adults perform poorly when recognizing inverted faces (Phillips & Rawles, 1979; Yin, 1969). In addition, children under age 10 make facial identity recognition mistakes when faces have superficial disguises, such as hats (Carey & Diamond, 1977; Diamond & Carey, 1977).

From 5 to 10 years there is an the increase in holistic processing for human faces relative to animal faces comes from studies using the composite effect (defined earlier). When children are presented with human and monkey faces, they make facial identity recognition mistakes more often for human faces, as they get older (from 5 to 10 years). Older children are worse at recognizing the human face composites because they are using configural processing (Moulson & Balas, 2009). Other adult-like face processing characteristics are also developing during this time (between 5 and 10 years), including the emergence of a left-side bias (i.e., the tendency for humans to rely more on the left side of the face for identity recognition) for human faces, but not monkey faces (Moulson & Balas, 2009). Given that much face processing development emerges after 11 months of age, examining infants' looking relative to adults' is important.

General Research Goals and Specific Objectives

As outlined here, numerous methods exist for measuring facial identity recognition across the lifespan, each with particular strengths and weaknesses. These methods can allow us to test different models of face recognition development, namely perceptual narrowing and learned attention. Work thus far has revealed both similarities and differences in the ways we recognize human and animal faces, as well as similarities and differences in the ways faces are recognized across the lifespan. In the present studies, we examined these factors—age of viewer and species of face viewed—concurrently, to test the predictions of both perceptual narrowing and learned attention. Thus, the overarching goal of this research was to examine the development of face recognition and the extent to which face recognition is species-specific. Though much work shows faces are processed differently from other visual stimuli, less work has directly compared the processing of human and nonhuman animal faces, or human and nonhuman primate faces. Such studies are important because they can clarify at what point in development, and through which mechanisms humans specialize in processing human (or primate) faces.

In our first study (Chapter 2), we examined the breadth of face discrimination in 4- to 6-month-olds, 9- to 11-month-olds, and adults, using a phylogenetically distantly related (i.e., nonprimate) animal: sheep (Simpson, Varga, Frick, & Fragaszy, 2010a, 2010b). Thus far, studies of perceptual narrowing have focused only on infants' face discrimination abilities for primates and companion animals (e.g., dogs); therefore, we examined facial discrimination of an unfamiliar nonhuman species. Sheep facial discrimination was assessed through a passive viewing visual paired comparison task using the continuous familiarization technique (Rose, Feldman, & Jankowski, 2002). This study assessed whether young infants (4- to 6-month-olds) have face recognition abilities that are broad enough to encompass even nonprimate animals, and whether this ability declines with age, as predicted by the perceptual narrowing model.

In a second study (Chapter 3), we measured discrimination of systematically manipulated faces of humans, monkeys, and sheep, also in a visual paired comparison task with 4- to 6-month-olds, 9- to 12-month-olds, and adults (Simpson, Varga, Frick, & Fragaszy, 2011, in preparation). We ensured that species differences were not due to lower level differences in the variability among species (with some species being more variable and therefore easier to discriminate than others). This study also explored whether infants and adults equally discriminate faces which have feature identity changes (e.g., eyes, mouths), configural changes (e.g., spacing between the eyes, distance between the mouth and chin), and head contour changes, in human, nonhuman primate, and nonprimate animal faces. We predicted that older infants and adults, despite having similar discrimination abilities (e.g., Pascalis et al., 2002), are sensitive to different properties of faces (e.g., featural or configural; Carey & Diamond, 1977). The type of face processing being utilized is difficult to determine from previous studies in infants because prior work only reported the outcomes of measures of looking (i.e., whether or not there was discrimination; Pascalis et al., 2002); the present study additionally reports the properties of faces to which infants and adults can discriminate. We systematically varied three properties of faces—outer and inner features and the spacing among features—and tested discrimination in faces of human and animal faces concurrently, to examine developmental changes from infancy. We were interested in whether different face properties would be used consistently across species, or whether they vary as a function of species. Specifically, we tested whether human faces are processed differently from nonhuman faces, or whether primate faces are processed differently from nonprimate faces.

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CHAPTER 2

INFANTS EXPERIENCE PERCEPTUAL NARROWING FOR NONPRIMATE FACES[1]

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Abstract

Perceptual narrowing—a phenomenon in which perception is broad from birth, but narrows as a function of experience—has previously been tested with primate faces. In the first 6 months of life, infants can discriminate among individual human and monkey faces. Though the ability to discriminate monkey faces is lost after about 9 months, infants retain human face discrimination, presumably because of their experience with human faces. The current study demonstrates that 4- to 6-month-old infants are able to discriminate nonprimate faces as well. In a visual paired comparison test, 4- to 6-month-old infants (n = 26) looked significantly longer at novel sheep (*Ovis aries*) faces, compared to a familiar sheep face (p = .017), while 9- to 11-month-olds (n = 26) showed no visual preference, and adults (n = 27) had a familiarity preference (p < .001). Infants' face recognition systems are broadly tuned at birth—not just for primate faces, but for nonprimate faces as well—allowing infants to become specialists in recognizing the types of faces encountered in their first year of life.

INDEX WORDS: Facial identity, Perceptual narrowing, Cross-species, Discrimination, Sheep

Introduction

Much debate has surrounded the special nature of face processing. Interestingly, our sensitivity to faces is not limited to human faces, but extends to the faces of other animals. Research suggests that young infants (e.g., younger than 6 months old) may be better than adults at discriminating faces of nonhuman animals. Pascalis, de Haan, and Nelson (2002) found 6-month-olds, 9-month-olds, and adults could discriminate human faces, but only 6-month-olds could discriminate monkey faces (Pascalis et al., 2002). The authors concluded that this species-specific effect might reflect perceptual narrowing, a phenomenon that occurs for faces, much like that for speech sounds. For example, between 6- and 12-months of age, discrimination of speech sounds not in one's native language declines (Werker & Tees, 2005). Perceptual narrowing is dependent on experience; infants selectively discriminate among native phonemes, whereas discrimination of phonemes to which they are not exposed declines. Perceptual narrowing has been characterized as a fine-tuning of perception with age (Nelson, 2001). From birth, perception starts out broadly tuned to all stimuli, both relevant and irrelevant, but narrows during the first year of life (by about 9- to 12-months of age), processing relevant stimuli in greater depth. Perceptual narrowing is a widespread developmental phenomenon, that occurs for vocalizations (Vouloumanos, Hauser, Werker, & Martin, 2010), face-voice matching (Lewkowicz & Ghazanfar, 2006; Lewkowicz, Leo, & Simion, 2010; Pons, Lewkowicz, Sebastián-Gallés, & Soto-Faraco, 2009; see also Zangenehpour, Ghazanfar, Lewkowicz, & Zatorre, 2009), musical structure (Hannon & Trehub, 2005; Trehub & Hannon, 2006), and visual language processing (Weikum et al., 2007).

As suggested by Pascalis et al. (2002), perceptual narrowing also occurs for facial identity discrimination (i.e., recognizing whether a face is new or familiar). According to this view, rather than being born human face specialists, infants are born face generalists, and become human face experts with experience. Perceptual narrowing of facial identity occurs for face ethnicity (e.g., Kelly et al., 2007), gender (e.g., Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002), and age (e.g., Cassia, Kuefner, Picozzi, & Vescovo, 2009).

It is unknown whether human infants' perceptual narrowing for facial identity occurs for nonprimates, as researchers have only examined phylogenetically closely related species (Old World monkeys and humans: Pascalis et al., 2002, 2005; Scott & Monesson, 2009). Quinn and Eimas (1996) found that 3- to 4-month-old infants are able to discriminate facial identity for both cat and dog faces; however, these data cannot be used to determine whether perceptual narrowing occurs for nonprimate faces as Quinn and Eimas did not examine whether this ability declines in later infancy (e.g., after 9 months). In addition, some infants have experience with cats and dogs as pets, so this experience may have influenced the 3- to 4-month-olds' discrimination abilities in the Quinn and Eimas study. More recently, 6- to 24-month-old infants matched emotional dog facial expressions and vocalizations (Flom, Whipple, & Hyde, 2009); however, perceptual narrowing may not have occurred because many infants have experiences with dogs. In addition, faces and voices were matched on the basis of emotional information, not facial identity. Therefore, it remains unknown whether human infants can discriminate facial identity alone for more distantly related species.

The current study examined whether human infants' perceptual narrowing of facial identity occurs for an unfamiliar and phylogenetically more distantly related species: sheep (Ovis aries). It could be that human infants are born with the ability to discriminate all or some primate faces, but not nonprimate animal faces. To this end, we tested face recognition in 4- to 6-month-olds, 9- to 11-month-olds, and adults, who viewed sheep faces in a passive viewing visual paired comparison task (Fagan, 1970). Sheep were chosen because of their phylogenetic distance from humans, being more distantly related than species studied previously. In addition, most infants and adults have very little exposure to sheep faces, relative to human faces or common pets, such as dogs. Moreover, adult sheep vary in their facial characteristics, and sheep can recognize one another using such characteristics (Kendrick, da Costa, Leigh, Hinton, & Peirce, 2001). The present study allowed for a test of whether humans can also recognize sheep based on these facial characteristics.

Purpose and Predictions

The purpose of the present experiment was to examine differences in how 4- to 6-month-olds, 9- to 11-month-olds, and adults discriminate sheep facial identity in a passive-viewing visual paired comparison task. Testing all three age groups in the same manner allowed for direct comparisons among groups. We predicted that 4- to 6-month-olds—who have not yet undergone perceptual narrowing for facial identity—would be able to discriminate sheep faces, as reflected by a novelty preference. In contrast, we predicted that 9- to 11-month-olds and adults would not be able to discriminate sheep faces, as reflected by no visual preferences.

Method

Participants

Twenty-six 4- to 6-month-olds (age range = 129–188 days; 17 females), and twenty-six 9- to 11-month-olds (age range = 274–458 days; 14 females), were included in the final data set. All infants were healthy and full-term. Names were found using newspaper birth notices, and families were contacted by telephone. Twenty-seven adults (age range = 19–33 years; 13 females) were recruited through the research participant pool of a large southern university. These sample sizes do not include five 4- to 6-month-olds, who were excluded because of fussiness (*n* = 2) or equipment malfunction (*n* = 3), and one 9- to 11-month-old, who was excluded because of fussiness.

Apparatus

Testing took place within a darkened and quiet room. A 2.3 × 1.3 m black curtain enclosed the area on three sides to prevent distraction. Infants sat in an infant seat or on their parent's lap. All participants were seated 60 cm from the presentation screen (43 × 58 cm). The stimuli were presented using rear projection on an InFocus projector (model LT755; Portland, OR). Each session was recorded using two Panasonic VHS cameras (model AG-188-Proline; Secaucus, NJ). One camera recorded the participant and the other recorded the stimulus presented on the screen. These images were combined using a Videonics Digital Video Mixer (model MX-1; Campbell, CA). Behaviors were coded offline using the Noldus Observer 5.0; Asheville, NC. The stimuli were presented using Inquisit software by Millisecond (http://www.millisecond.com), version 2.0.61004.7.

Stimuli

Thirty sheep photos were provided by Keith Kendrick et al., 2001 of Cambridge University and were confirmed by Reefmann, Kaszàs, Wechsler, & Gygax (2009) to be neutral expressions. All photos were of different individuals. AdobePhotoshop™ software (San Jose, CA) was used to center, crop, and adjust the size of all photos to 400 × 400 pixels (10° × 16° on the presentation screen), as well as to adjust the contrast and brightness. Necks, shoulders, and ear tags were removed. All photos were given uniform white backgrounds (see Figure 2.1).

Prior to each trial, all participants viewed a dynamic centering stimulus (e.g., flashing bull's-eye or cartoon character) that was 12° × 12° on the presentation screen, and lasted 1,500 msec.

Procedure

Each participant was randomly assigned to one of two conditions, each with a different familiar face. First, participants were familiarized with a face through the Continuous Familiarization Technique (Rose, Feldman, & Jankowski, 2002) in which two identical faces were shown, side by side, until the participant accumulated 20 sec of looking to one or both faces (Figure 2.1). Next, participants viewed 29 paired comparisons, consisting of pairs of faces: One face was the same as that shown in the familiarization phase (i.e., familiar face) and one face was novel. In keeping with other researchers (e.g., Rose et al., 2002), we chose to use 29 test trials so we could examine both the emergence, and the durability, of looking preferences that have been shown to change over the course of numerous test trials in adults (Park, Schimoho, & Shimojo, 2010) and infants (Rose et al., 2002). The 29 novel faces were presented in a random order, and appeared on the right and left with equal probability. Faces remained on the screen until a cumulative looking time of 4 sec was established; between each trial there was a 1,500 msec intertrial interval that included the centering stimulus. Measures of participants' looking—durations of looks toward and away from the novel and familiar faces—were coded off-line for analysis. Testing continued until all 29 trials were completed, or until the participant (or parent) wished to end the experiment.

Coding training and reliability

All participants' eye movements were coded off-line frame-by-frame (resolution of measurement is 33 msec) from video using the Noldus Observer 5.0. Observers recorded the location (i.e., left face, right face, away) and duration (i.e., start and stop times) of participants' looks during the familiarization phase and paired comparison test trials. Observers were blind to the location of the familiar and novel faces. Interobserver reliability was assessed for the frequency of the look location for each observer. The average level of agreement among observers was 92% (range 81–97%).

Results

A preliminary analysis revealed no gender differences, no effect of the side of the novel face, and no differences across the two familiar faces, so data were collapsed across gender, side of novel face, and familiarization stimulus in subsequent analyses. A one-way analysis of variance (ANOVA) revealed no differences in the total looking time during the familiarization among the three age groups: 4- to 6-month-olds (M = 22.8 sec, SD = 9.0), 9- to 11-month-olds (M = 21.0 sec, SD = 4.6), and adults (M = 20.7 sec, SD =1.5), $F(2, 73) = .90$, $p = .41$.

To examine whether participants discriminated the novel and familiar sheep faces, we examined the total amount of time looking to each face type, across the first four test trials. Four test trials were chosen because all of the infants in the sample completed at least this many test trials. In addition, novelty preferences have been found in previous work with as few as two test trials (Pascalis et al., 2002). We conducted a 3 × 2 mixed design ANOVA that examined the within-subjects factor of face type (novel, familiar) and the between-subjects factor of age group (4- to 6-month-olds, 9- to 11-month-olds, adults). We found an interaction between age and face type, $F(2, 76) = 15.32$, $p < .001$, $\eta^2 = .29$. Paired samples t tests were then conducted for each age group to determine the general patterns of looking during these first four test trials. As depicted in Figure 2.2, 4- to 6-month-olds show a novelty preference, $t(25) = 2.57$, $p = .017$, $d = .50$, preferring to look at novel faces (M = 2.75, SD = 1.14) over familiar faces (M = 2.13, SD = .64). In contrast, 9- to 11-month-olds demonstrated no looking preferences, $t(25) = .16$, $p = .87$, looking equally long to the novel faces (M = 2.40, SD = .78) and familiar faces (M = 2.36, SD = .61). Adults showed a familiarity preference, whereby they looked longer at the familiar (*M* = 2.65, *SD* = .54) compared to the novel (*M* = 1.67, *SD* = .54) faces, $t(26) = 5.68$, $p < .001$.

Finally, we examined whether there were overall looking preferences for all trials each participant completed (at least four, but up to 29 trials). A one-way ANOVA revealed that age influenced the proportion of time looking to the novel faces for the entire set of 29 test trials, $F(2, 77) = 10.58$, $p < .001$, $\eta^2 = .01$; however, follow-up paired comparison *t* tests examining the mean look durations to novel and familiar faces indicated that only adults showed a preference that lasted throughout the entire 29 trials, consistently preferring the familiar face, $t(26) = 4.42$, $p < .001$, $d = .85$. Neither infant group revealed any overall differences in the proportion of time looking to the novel faces (*p*s > .50) when all trials were included, suggesting that infants' discrimination skills on the first four trials may have faded as more time elapsed since familiarization.

Discussion

The aim of the current study was to investigate whether infants and adults could discriminate individual faces of a nonprimate species. The results reported here provide evidence that young infants are able to discriminate unfamiliar nonprimate faces, but that this ability declines in the first year, then appears as a familiarity preference in adulthood. Below, we will interpret these data within a perceptual narrowing framework.

First, we found that 4- to 6-month-olds demonstrate a novelty preference for sheep faces, which is in line with our predictions, and indicates that young infants have not yet undergone perceptual narrowing. In addition, this finding provides evidence that face discrimination abilities in early infancy (before about 6 months) are even broader than previously thought. That is, not only can young infants discriminate primate faces, and the faces of familiar animals (dogs and cats), but they also have the ability to discriminate the faces of unfamiliar phylogenetically more distantly related (nonprimate) species.

Also consistent with our predictions is the finding that 9- to 11-month-olds did not discriminate sheep faces. This is consistent with the developmental pattern of perceptual narrowing, and indicates that older infants have already undergone perceptual narrowing. It is important to keep in mind, however, that older infants' failure to discriminate in the present investigation may be a consequence of their need for a longer familiarization time in order to discriminate. For example, 12-month-olds are able to discriminate monkey faces in a visual paired comparison task when familiarized for 40 sec, then tested in trials lasting 10 sec (Flom, 2010). Thus, 9- to 11-month-olds' failure to discriminate may not reflect an inability to discriminate, but rather the fact that discrimination is more challenging at this age. Nonetheless, the fact that discrimination of nonprimate faces is either lacking or especially difficult at this age is still consistent with perceptual narrowing.

Though we predicted adults would show no evidence of discriminating the sheep faces—consistent with Pascalis et al.'s (2002) findings that adults cannot discriminate monkey faces in the visual paired comparison task—adults showed a familiarity preference. Such a result is consistent with the idea that adults—who have undergone perceptual narrowing—have more difficulty recognizing animal faces. These results fit with the model presented by Hunter and Ames (1988) regarding exploratory looking, which he proposed follows a consistent pattern throughout development. Specifically, Hunter and Ames argued that participants show familiarity preferences for stimuli that are more difficult to discriminate, for which they need longer familiarization times to develop a novelty preference. That is, if the stimulus is not well encoded, participants will exhibit a familiarity preference. As familiarization time increases, preferences shift from the familiar to the novel (for a review see Pascalis & de Haan, 2003). In contrast, participants show a novelty preference for more easily discriminated stimuli, for which they need a shorter familiarization time. Hunter and Ames's model would lead to the interpretation that adults in the present study were not familiarized for long enough. Though both novelty preferences and familiarity preferences allow us to infer discrimination, these theoretical models argue that the underlying processes behind the two types of discrimination are not the same. Event-related potential work suggests novelty and familiarity preferences have different neural correlates (for a review see Pascalis & de Haan, 2003). Moreover, while novelty preferences are generally accepted as indicative of declarative or explicit memory, familiarity preferences may indicate residual nondeclarative or implicit memory (Richmond, Colombo, & Hayne, 2007).

Finally, we examined all completed test trials (up to 29) to determine whether looking patterns persisted over time. When all trials were averaged, no preferences for the novel sheep face were observed in either infant group. Thus, the novelty preference demonstrated by the younger infants appears to be somewhat transient; however, this may be because of inattention and disinterest in the photographs over the course of numerous trials or a fading of the memory of the familiarization stimulus as more time elapsed since familiarization. Adults, in contrast, demonstrated a lasting familiarity preference, that persisted over the course of all 29 test trials. Infants' perceptual narrowing responses seem to be apparent most strongly in the initial response to these stimuli; adults, in contrast, maintained focused attention for a greater number of trials.

Two possible explanations exist for the differential discrimination of different species that has been found in the present investigation, as well as in previous work. One possibility is that differences exist in the way that human and animal faces are recognized; this is the most common interpretation of the data (e.g., Pascalis et al., 2002; Scott & Monesson, 2009; Scott, Pascalis, & Nelson, 2007; Sugita, 2008). A single prototype primate face may subserve face recognition for all primate faces, but this system is not employed for nonprimate faces (Campbell, Pascalis, Coleman, Wallace, & Benson, 1997).

Another possibility is that differential discrimination across species is because of different amounts of interindividual variability within each species. Variability in facial features is not equivalent across species (Simpson, Varga, Frick, & Fragaszy, in preparation); therefore, better discrimination for any given species may simply be because of the fact that those faces are more heterogeneous. In other words, apparent differences in face discrimination across species may be because of uncontrolled interstimulus perceptual (physical) variance. Consequently, comparisons among conditions that differ concurrently in species and in interstimulus perceptual variance are difficult to interpret (Knebel, Toepel, Judry, le Coutre, & Murray, 2008).

Additional work must test which of these possibilities best accounts for previous findings. By systematically varying aspects of human and animal faces—such as the spacing among facial features, or head contours—we can determine if equivalent variations in faces across species are distinguished at equal rates across development. Such a test would also allow an examination of what strategies individuals of different ages use to discriminate faces, and whether these strategies vary as a function of the species viewed.

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Figures

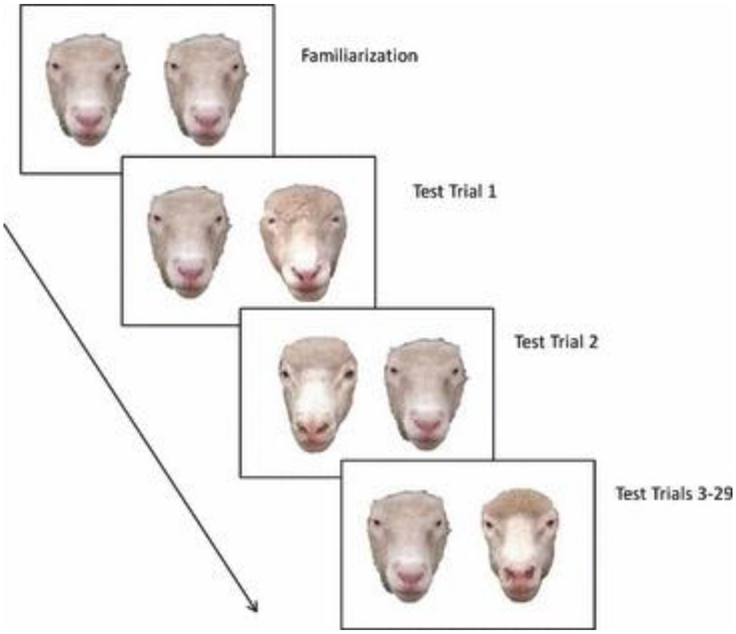

Figure 2.1. Sample presentation sequence. Participants were first familiarized with a face (*familiarization*), then viewed a novel and familiar face on 29 subsequent test trials (*paired comparison*).

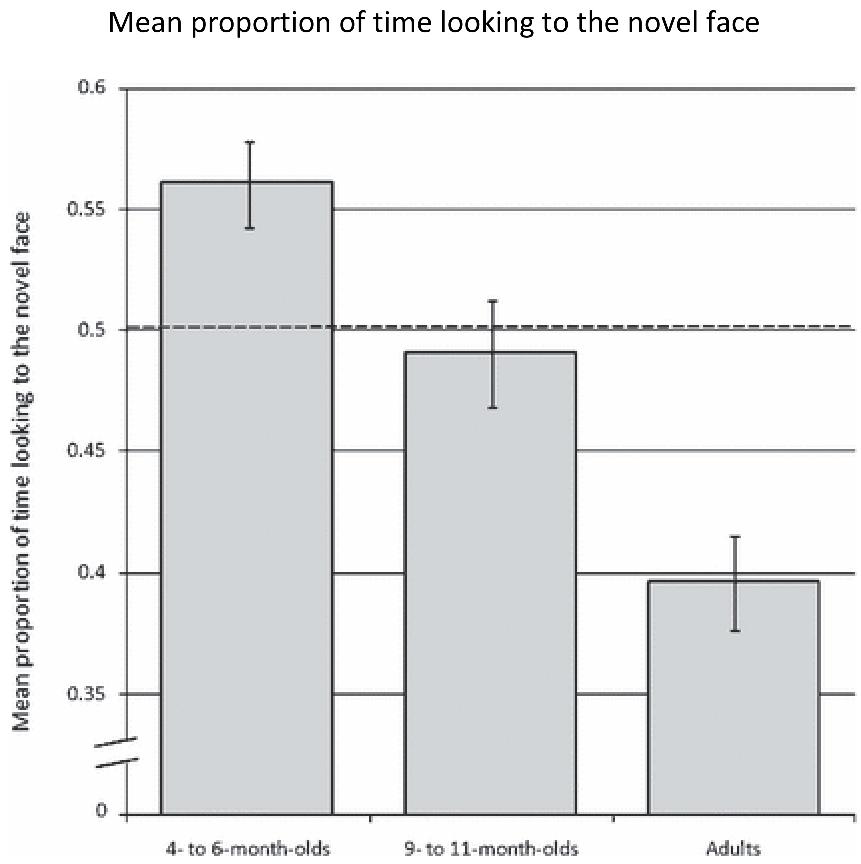

Figure 2.2. Mean proportion of time looking to the novel face, out of the total amount of time looking to the faces, for the first four trials. Error bars represent standard error of the mean. Dashed line indicates chance performance (50%).

Erratum[1]

In Elizabeth Simpson, Krisztina Varga, Janet Frick, and Dorothy Fragaszy's article ''Infants Experience Perceptual Narrowing for Nonprimate Faces,'' [Infancy (2010) Advanced online publication. doi: 10.1111/j.1532-7078.2010.00052.x] the face types ''novel'' and ''familiar'' were reversed throughout the paper; however, this does not change the overall conclusion of the study. In the abstract, results, and discussion sections, all references to ''novel'' should be ''familiar,'' and all references to ''familiar'' should be ''novel.'' This includes Figure 2.2, which should have the y-axis labeled ''Mean proportion of time looking to the familiar face.'' We found that 4- to 6-month-olds had a familiarity preference, 9- to 11-month-olds showed no preference, and adults had a novelty preference. This suggests that while young infants (4- to 6-month-olds) and adults can discriminate sheep faces, older infants (9- to 11-month-olds) may not. Infants may need a longer familiarization time to develop a novelty preference for sheep faces, given that familiarity preferences appear when stimuli are more difficult to discriminate (Hunter & Ames, 1988). Thus, the overall conclusions of the paper remain unchanged: young infants can discriminate sheep faces, but this ability declines in the first year of life, consistent with perceptual narrowing. We regret the error.

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[1] Simpson, E., Varga, K., Frick, J., Fragaszy, D. (2010b). Erratum for Infants experience perceptual narrowing for nonprimate faces. *Infancy*. Advance online publication. doi: 10.1111/j.1532-7078.2011.00071.x

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CHAPTER 3

THE PROPERTIES OF FACES TO WHICH VIEWERS ARE SENSITIVE DIFFER ACROSS DEVELOPMENT FOR HUMAN AND ANIMAL FACES[1]

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[1] Simpson, E., Varga, K., Frick, J., & Fragaszy, D. To be submitted.

Abstract

There is debate as to whether the development of facial identity recognition is due to changes in perception or changes in attention. To explore this change, we measured facial identity discrimination of systematically varied human, monkey, and sheep faces in a visual paired comparison task in infants (4- to 6-month-olds and 9- to 12-month-olds) and adults. Faces varied in their outer features (contour, hair), inner features (eyes and mouth), or configuration (spacing among inner features). Importantly, we controlled for interindividual variability across species, which has not been taken into account in previous work. We found that with age, there was an increase in the number of species discriminated, raising doubts about the usefulness of a perceptual narrowing model of facial identity discrimination. Interestingly, primates were apparently discriminated using different face properties—namely, the spacing among the inner facial features—compared to nonprimates, who were discriminated using the inner features.

INDEX WORDS: Facial identity, Facial feature, Configural processing, Discrimination, Learned attention

Introduction

Humans possess remarkable face recognition abilities. Even newborn infants can discriminate facial identity (e.g., Turati, Macchi Cassia, Simion, & Leo, 2006). Much work supports the view that face processing is qualitatively different from the processing of other complex visual stimuli (Park, Newman, & Polk, 2009). For example, individuals with brain damage can have impaired face recognition but relatively intact object recognition, known as prosopagnosia (e.g., Nunn, Postma, & Pearson, 2001), or the reverse: impaired object recognition and relatively intact face recognition (Germine, Cashdollar, Duzel, & Düchaine, 2010). All major vertebrate taxa are sensitive to conspecifics' faces, suggesting an early evolutionary emergence (Leopold & Rhodes, 2010), not human-specific (Pascalis & Kelly, 2009). The special nature of faces for humans is not limited to human faces, but extends—at least to some extent—to the faces of other animals (e.g., Dufour & Petit, 2010; Itier, Latinus, & Taylor, 2006; Kanwisher, Stanley, & Harris, 1999). How our face expertise emerges in development, however, remains largely unknown (Pascalis & Kelly, 2009).

Though at first counter-intuitive, research on human infant face perception suggests that young infants (4- to 6-months-olds) outperform older infants (9- to 12-month-olds) in the discrimination of nonhuman animal faces, including monkeys (Pascalis, de Haan, & Nelson, 2002; Pascalis et al., 2005; Scott & Monesson, 2009) and sheep (Simpson, Varga, Frick, & Fragaszy, 2010). This decline in face discrimination has been attributed to a domain-general developmental process known as perceptual narrowing (Scott, Pascalis, & Nelson, 2007), whereby face perception is fine-tuned with age, as a function of experience, allowing for better recognition of commonly experienced face groups (Nelson, 2001). A window of plasticity for facial identity discrimination begins closing at approximately six to nine months of age, resulting in a decrease in discrimination for unfamiliar faces. Consequently, humans become experts at discriminating human faces, as these are the faces we most commonly view early in life.

Controlling for Interindividual Differences in Face Stimuli

One limitation of this interpretation, however, is that previous work measured discrimination of photographs of natural faces. Natural faces of different species may not vary equivalently; that is, some species may be more variable and therefore more easily discriminated relative to others. Thus, two potential explanations exist for the differential discrimination of species found by others (e.g., Pascalis et al., 2002; Pascalis et al., 2005; Scott & Monesson, 2009; Simpson et al., 2010). One possibility is that human and nonhuman (or primate and nonprimate) faces are discriminated differently. For example, with age, humans may specialize in the discrimination of human faces, and begin to process human faces holistically (i.e., recognizing the configuration or spacing among features), while processing nonhuman faces using features (e.g., eyes). This interpretation is supported by work with adults (Itier et al., 2006; Pascalis, Coleman, & Campbell, 1998; Pascalis & Bachevalier, 1998), and children (Pascalis, Demont, de Haan, & Campbell, 2001), but has not been examined in infants. The most common interpretation of the data is that differential discrimination is due to category differences (i.e., species-level) in human and animal faces (e.g., Pascalis et al., 2002; Scott & Monesson, 2009; Scott et al., 2007; Sugita, 2008). That is, human faces are discriminated differently from nonhuman faces because they are different species.

Alternatively, differential discrimination among species may be due to different amounts of interindividual variability within each species at the population level (Martin-Malivel & Okada, 2007). Differences in discrimination across species may be due to uncontrolled interstimulus perceptual (physical) variance; therefore, comparisons between conditions that differ both in species and in interstimulus perceptual variance are difficult to interpret (Knebel, Toepel, Judry, le Coutre, & Murray, 2008; McKone & Crookes, 2007). In the present investigation, we tested whether humans' differential discrimination across species may be due to differences in interindividual variability. Face sets were created such that variability was equivalent across species.

Properties of Faces that Influence Face Recognition in Adults

An additional goal of the present study was to determine the properties of faces which infants and adults use for identity discrimination. Human adults can distinguish effortlessly among hundreds of human faces (Bahrick, Bahrick, & Wittlinger, 1975). In fact, one study found accuracy rates greater than 90% for matching names with yearbook photos of schoolmates, and distinguishing photos of schoolmates form non-schoolmates, independent of class size (90-900) and time since graduation, which spanned up to 35 years (Bahrick et al., 1975). Though few would argue with the position that humans have remarkable face recognition abilities, there is debate as to which properties of faces are used for discrimination and recognition (Catz, Kampf, Nachson, & Babkoff, 2009; Diamond & Carey, 1986; Farah, Wilson, Drain, & Tanaka, 1998; Sinha, Balas, Ostrovsky, & Russell, 2006; Valentine, 1991). While some face properties contribute to cohesive, holistic (configural) processing (i.e., perceiving relations among the features) for recognition, others contribute to feature-based recognition (i.e., recognizing faces as a collection of disparate features).

There is a debate as to whether adults rely more on one process than another (Carey, De Schonen, & Ellis, 1992; Diamond & Carey, 1986; Haig, 1984; Maurer, Le Grand, & Mondloch, 2002), or whether the properties to which viewers are sensitive vary depending on the species viewed (McKone & Crookes, 2007). Most studies have only examined human adults' perception of human faces. Thus, we know little of humans' perception of other species' faces, and also know little of how these abilities develop. Nonetheless, studies with human adults have begun to uncover the human face properties used for recognition. For example, many consider configural processing the hallmark of face processing, compared to the processing of other objects (Carey & Diamond, 1984; Farah et al., 1995; Rhodes, 1988; Rhodes, Brake, & Atkinson, 1993; Sergent, 1984; McKone, Martini, & Nakayama, 2001; Murray, Rhodes, & Schuchinsky, 2003). The importance of configural processing for faces, relative to other objects, has been discovered through selective manipulations to face stimuli which selectively impair different types of processing.

To impair configural processing, faces can be scrambled, inverted, or the top and bottom halves of a face can be cut and shifted laterally (for a review, see Maurer et al., 2002). Though inverted faces are recognized more slowly and with less accuracy, compared to upright faces (due to configural processing being disrupted), inverted faces are still recognized at levels above chance performance (Freire, Lee, & Symons, 2000; Murray, Yong, & Rhodes, 2000). These results suggest that for adults, configural processing is helpful, but not necessary, for face recognition (Yin, 1969; although see Sekuler, Gaspar, Gold & Bennnet, 2004).

To impair feature-based processing, faces can be blurred, such that individual features cannot be recognized, while the second-order properties of the face (i.e., distances among features) remain unaffected (Freire et al., 2000; Murray, et al., 2000). Again, recognition performance is slower and less accurate, but remains above chance, suggesting that feature-based processing is helpful but not necessary for face recognition. Also, participants are better at recognizing the identity of individual features when they are presented in the context of the rest of the face (e.g., Tanaka, & Sengco, 1997), which indicates there may be an interaction between the face properties to which a viewer is sensitive, such that recognition performance is best when configural and feature information is present. These results highlight the need to explore face properties used for recognition, individually and in combination.

Feature-based manipulations (i.e., altering local features, such as blurring pupils, blackening teeth) have been pitted against configural manipulations (i.e., altering distances among features) in inverted human faces (Leder & Bruce, 1998). Alterations to local features appear more grotesque compared to configural alternations (i.e., in the spacing among inner facial features), which are less noticeable (Leder & Bruce, 1998), consistent with the proposal that inversion impairs configural processing. These manipulations have been criticized: some argue that the amount of variability in the spacing of facial features is not reflective of the natural variations in feature distances in real faces (Taschereau-Dumouchel, Rossion, Schyns, & Gosselin, 2010). Taschereau-Dumouchel and colleagues created sets of systematically manipulated faces which varied in the spacing of facial features to the same degree as real faces (i.e., not exceeding the variability of natural faces). They discovered that adults had poor recognition of upright faces (mean accuracy of 65% in a match-to-sample task; Taschereau-Dumouchel et al., 2010). On the other hand, adults recognized faces nearly perfectly on the basis of feature shapes and skin reflectance properties (Caharel, Jiang, Blanz, & Rossion, 2009; Hill, Bruce, & Akamatsu, 1995; O'Toole, Vetter, & Blanz, 1999; Taschereau-Dumouchel et al., 2010). In fact, the eyes and the eyebrows may be the most important features for face recognition (Davies, Ellis, & Shepherd, 1977; Haig 1985, 1986; Sheperd, Davis, & Ellis, 1981; Walker-Smith, Gale, & Findlay, 1977; Dupuis-Roy, Fortin, Fiset, & Gosselin, 2009; Sadr, Jarudi & Sinha, 2003; Sekuler et al., 2004), and an inversion effect is present for the eye/brow region when presented alone (Leder, Candrian, Huber, & Bruce, 2001).

In summary, human adults attend to a number of face properties during human face recognition. Configural processing may be especially prominent when recognizing human faces; but, when configural information is unavailable (e.g., inversion), adults employ feature-based recognition.

Properties of Faces that Influence Face Recognition in Infancy

Though extensive work has examined the properties of faces adults use for face recognition, much less is known about the development of recognition based on these face properties. Four-day-old neonates look longer at their mother's face, relative to a stranger's face (Bushnell, Sai, & Mullin, 1989; Field, Cohen, Garcia, & Greenberg, 1984), even when outer features (e.g., hair) are removed (Turati et al., 2006). By two months of age infants focus primarily on the interior, rather than the exterior, of the face (Salapatek, 1975).

Disagreement exists as to whether newborns (immediately after birth) discriminate faces using the relative spatial relations among features (e.g., understanding that the eyes are above the nose, which is above the mouth). Developmental researchers generally agreed that newborns prefer faces with normal first-order spatial relations, which are the arrangement of parts of the face without reference to any prototypical arrangement (Diamond & Carey, 1986; Fantz, 1961; Mondloch et al. 1999; Simion, Cassia, Turati, & Valenza, 2003), though there is also evidence that infants do not prefer the typical face arrangement until 2- to 4-months of age (Acerra, Burnod, de Schonen, 2002; Haaf, 1974; Maurer & Barrera, 1981). Nonetheless, by four months of age, infants discriminate the identity and the rough location of facial features. Three- to seven-month-old infants can detect large configural changes (e.g., distance between the eyes, height of mouth) and feature changes (e.g., size of the eyes, mouth) in human faces, and more easily discriminate faces with changes in the eyes than the mouth (Quinn & Tanaka, 2009).

However, the face manipulations (e.g., spacing among features, size of features) were not within the range of natural variability, and thus findings of recognition may be biased (Taschereau-Dumouchel et al., 2010). Nonetheless, by 9 months of age, infants may, like adults, discriminate eye and mouth identity changes in faces, with eye changes eliciting the most attention (Key, Stone, & Williams, 2009).

Four-month-olds familiarized separately with inner features and outer features show novelty preferences when these inner and outer parts are presented in new combinations, suggesting four-month-olds detect changes to the spatial relations between inner and outer face parts (Cashon & Cohen, 2003). However, human infants' holistic processing of internal facial features has been examined only to a limited extent. Less is known about the development of using second-order relational information, or the fine spatial information among facial features.

Though adults experience inversion effects, inversion effects in infancy are not as clear. Some studies suggest three- to eight-month old infants experience inversion and therefore are processing faces holistically (e.g., Bertin & Bhatt, 2004; Bhatt, Bertin, & Hayden, 2004; Bhatt, Bertin, Hayden, & Reed, 2005; Cohen & Cashon, 2001; Rose, Jankowski, & Feldman, 2002; Scott & Nelson, 2006; Thompson, Madrid, Westbrook, & Johnson, 2001; Turati, Giorgio, Bardi, & Simion, 2010; Turati, Sangrigoli, Ruel, & de Schonen, 2004). Others failed to find that infants experience inversion (e.g., Carey & Diamond, 1994; Chung & Thompson, 1995; Mondloch, le Grand, & Maurer, 2002). Physiological evidence also indicates infants and adults attend to different properties of faces. For example, adults display a N170—a face-sensitive brain electrical potential—for upright human faces, which is faster and larger relative to upright monkey faces and inverted human and monkey faces. In contrast, 6-month-olds' N170 is not influenced by inversion of either human or monkey faces (de Haan, Pascalis, & Johnson, 2002;

also see Rousselet, Mace, & Fabre-Thorpe, 2004). This finding suggests 6-month-olds may be relying primarily on feature-based recognition, which is not as disrupted by inversion as configural recognition. Together, these studies reflect the fact that the development of face recognition in infancy remains a topic of considerable disagreement. Though there is evidence that infants can use first-order, second-order, and facial features for recognition, each of these findings has more than one interpretation.

Disparate findings are a consequence of the many methods used to measure configural processing (e.g., inversion, lateral shifting), and the difficulty in isolating the properties of faces used for recognition. Even when face properties are systematically manipulated, they are not manipulated in a way that reflects natural amounts of variability in the population, but are manipulated to a greater degree (Taschereau-Dumouchel et al., 2010). Additionally, there may be more than one shift from feature-based to configural-based processing in the first year of life (Cashon & Cohen, 2004; Cohen & Cashon, 2001; Le Grand, Mondloch, Maurer, & Brent, 2001; Younger & Cohen, 1986). Nonetheless, changes in face recognition have been documented into childhood (Mondloch et al., 2002), and changes in the sensitivity to configural information increases through childhood until at least age 10 (e.g., Carey & Diamond, 1977; Carey, Diamond, & Woods, 1980).

Are There Differences in Humans' Discrimination of Different Species?

Though multiple primate species use holistic and feature-based processing when recognizing own-species faces (Dufour, Pascalis, & Petit, 2006; Gothard, Brooks, & Peterson, 2009; Mondloch et al., 2004; Parr, Heintz, Akamagwuna, 2006; Rotshtein, Geng, Driver, & Dolan, 2007; Sugita, 2009), whether these processes can also be used for discriminating other (non-conspecific) species' faces remains unknown. In one study, human adults completed an active discrimination task with natural human and chimpanzee faces (Itier et al., 2006). There were decreases in response time and accuracy when human faces were inverted, but not when chimpanzee faces were inverted, suggesting adult humans used configural processing only with human faces. Similarly, 5- to 8-year-old children (Pascalis et al., 2001) and adults (Pascalis et al., 1998a, 1998b; Pascalis et al., 2001; Pascalis et al., 2002) experienced inversion effects for human and monkey faces, but not for sheep faces, suggesting the use of a primate-template for face recognition (Dufour, Coleman, Campbell, Petit, & Pascalis, 2004). Interestingly, monkey experts show no inversion effect for monkey faces, suggesting, though counter-intuitive, they may rely on different recognition processes for monkey and human faces (Pascalis et al., 1998a; 1998b).

Another study found rhesus monkeys and naïve humans (who have no extensive experience with monkeys) had inversion effects for human faces, but not monkey faces of various species (Wright & Roberts, 1996). The monkeys were exposed to both humans and other monkeys; thus, the monkeys' lack of an inversion effect for conspecifics' faces was surprising. Wright and Roberts concluded that humans and monkeys may processes faces in similar ways, in spite of different experiences; however caution is in order when interpreting the null result of no difference between upright and inverted monkey faces for the monkey participants, as the sample size was relatively small (*n* = 3). Given the small sample size, these results cannot be generalized.

One limitation of previous studies of cross-species face recognition in humans is that they rely heavily on the inversion effect. Though the inversion effect is generally accepted to disrupt configural processing—including second-order processing—some configural processing may occur even in inverted faces (Richler, Mack, Palmeri, & Gauthier, 2010; Yin, 1969) and feature-based recognition may also be disrupted when faces are inverted (Rhodes et al., 1993); therefore, a stronger test of sensitivity to second-order information is needed. A stronger test of configural processing, which could provide converging evidence of face discrimination based on second-order information, is the systematic manipulation of the spacing among facial features (e.g., distance between the eyes, height of the mouth). Monkeys reared with no exposure to faces for the first six to 24 months of their lives discriminated faces of humans and monkeys, which varied in either the feature identity or spacing, suggesting configural and feature-based face recognition may be present prior to exposure to faces (Sugita, 2009). Once the monkeys were selectively exposed to the faces of one species—either humans or monkeys—they retained the ability to discriminate the feature identity manipulated set and the spacing manipulated set for the species to which they were exposed, while they lost the ability to discriminate the faces of the species to which they were not exposed (Sugita, 2009; also see Martin-Malivel & Okada, 2007). Given that exposure to faces of a given species is crucial for discrimination in monkeys (Sugita, 2009), we may find similar results in humans. We predicted that by adulthood humans can use configural or feature-based recognition for human faces, but cannot use configural recognition for distinguishing unfamiliar faces, such as those of nonhuman animals. Similar findings in monkeys using eye tracking methods suggest that monkeys rely on both configural and feature-based recognition for conspecifics' faces, but rely primarily on feature-based recognition for distinguishing human faces (Gothard, Brooks, & Peterson, 2009).

The Role of Experience

Some changes in face recognition appear to be driven by experience. In adults, experience influences the type of processing—feature-based or configural—that is used in face recognition, and different types of processing may be differently influenced by experience

(McKone & Crookes, 2007). Specifically, configural processing occurs more often for items of expertise. For example, human adults who have experience with faces of nonhuman species (e.g., macaque monkeys, dogs) demonstrate more configural processing of that species' face, relative to human adults who do not have experience with those species (Diamond & Carey, 1986; Dufour & Petit, 2010). Monkey experts experience a greater inversion effect of monkey faces, compared to non-experts (Dufour & Petit, 2009). Additionally, participants trained as greeble experts (greebles are a type of object which are similar to faces), compared to nonexperts, demonstrate impaired processing when the configural information in the greebles is disrupted (Gauthier & Tarr, 1997). The same is true of car experts (Gauthier, Curran, Curby, & Collins, 2003). Moreover, developmental evidence comes from nine-year-old participants with bilateral congenital cataracts removed between two and six months of age, who demonstrate impaired configural face processing, but not impaired feature-based face processing (Le Grand et al., 2001). Experience with faces in the first six months of life appears important for the development of face expertise (although see McKone, Kanwisher, & Duchaine, 2006).

But what mechanisms can account for the influence of experience? Two possibilities are perceptual narrowing and learned attention. According to perceptual narrowing, face perception is fine-tuned with age, as a function of experience, characterized by a decrease in perceptual discrimination abilities for unfamiliar relative to familiar faces (Nelson, 2001), perhaps due to an increase in the focus on faces learned at the individual level (Scott & Monesson, 2010), driven by synaptic pruning in the infant brain (Gelskov & Kouider, 2010; Scott & Monesson, 2010). An alternative explanation for early developmental patterns of face recognition is learned attention (e.g., Heckler, Kaminski, & Sloutsky, 2006). Learned attention is a phenomenon which refers to the fact that individuals can learn to not attend to certain properties of a stimulus, usually through shifting attention to other more salient properties. If a contrast on a given dimension is not predictive of any important outcome (e.g., /r/ and /l/ phonemes in the Japanese language), an organism will learn to ignore this contrast (i.e., learned inattention). For example, infants must learn what properties of faces aid in discrimination (e.g., eyes, eyebrows) and which do not (e.g., hat, glasses). Early in development infants may be better at discriminating animal faces, such as monkeys and sheep, because they are attending to all properties of the faces (they do not yet exhibit learned attention biases). But with age, they learn which properties to ignore because they are not useful for discrimination of human faces. However, they may be useful for the discrimination of animal faces. Thus, older infants would appear to show a decline in the ability to discriminate animal faces in later infancy because they are selectively attending to the wrong features, due to their experience with primarily human faces. The present study will help to uncover which interpretation best can account for previous findings through the use of systematically varied faces.

Purpose and Predictions

In the present investigation we examined the development of facial identity discrimination through comparing face discrimination abilities of 4- to 6-month-old infants, 9- to 12-month-old infants, and adults in a visual paired comparison task, a commonly used method for measuring visual recognition memory in preverbal and nonverbal individuals (Fagan, 1970). We created three systematically varied sets of faces, one for each species: humans, capuchin monkeys, and sheep (see examples in Figure 3.1). Each face set contained three types of faces: one which varied in the identity of the facial features (i.e., eyes and mouths; Figure 3.1a), a second set which varied in the location of the facial features (i.e., location of the eyes and mouths; Figure 3.1b), and a third which varied in the outer features (i.e., external contours, such as the chin and hair; Figure 3.1c). The systematic creation of the face sets ensured equal variability within each species.

We designed the study with the following goals in mind: (1) test three face recognition processes in isolation through the use of systematically varied faces that are reflective of natural amounts of difference in the population (as opposed to other studies which have manipulated faces to unnatural degrees); (2) uncover developmental changes in the properties of faces which viewers can use to discriminate individual faces; (3) examine whether face recognition processes vary across species, even when the individual differences in those species are carefully controlled, by comparing human, primate, and nonprimate species; and (4) utilize a measure that is can detect varying levels of discrimination through continuously familiarizing participants for up to 30 test trials (as opposed to others who have used as few as one or two test trials).

Given that developmental changes in human face recognition processes have been documented in the first year of life (e.g., Cashon & Cohen, 2003), infants and adults may show differences in the properties of faces to which they are sensitive, with the latter group exhibiting more mature (i.e., configural) processing than the former. Given Cashon and Cohen's work, there are likely age differences in the properties of faces which viewers can use for discrimination (e.g., features, spacing among features, and peripheral features). Moreover, we predicted faster development of discrimination for human faces, compared to monkey and sheep faces. If this prediction is accurate, experience with a particular species may be especially important for the development of facial identity discrimination.

We also expected to see patterns consistent with a perceptual narrowing model of face recognition, which predicts different developmental patterns for each species. Specifically, perceptual narrowing models predict that early in development (4- to 6-months), humans are sensitive to the same face properties across all species, and discriminate all species equally well. By later infancy (9- to 12-months), infants' perceptual systems begin to specialize for processing human faces and therefore recognition of human and animal faces should differ at this age, as well as in adults. Infants beyond age 9 months should be better at discriminating human faces relative to nonhuman faces. We also predicted that configural processing—which is used more often for face processing relative to the processing of other objects—would be used more over time with human faces relative to monkey and sheep faces. This finding would be consistent with other reports that configural information is relied upon more with human faces relative to other objects (e.g., Farah et al., 1995; McKone, et al., 2001; Murray et al., 2003; Rhodes, 1988; Rhodes et al., 1993).

Outer features (e.g., outer contours, hair) are relied upon when configural processing is not yet developed (birth to about 5 weeks; Bushnell et al., 1989; Field et al., 1984); however, the reliance on outer features in newborns does not mean that outer features are not also utilized later in development, or in adulthood, when internal feature information is unavailable (e.g., wearing a mask, sunglasses). The ability to use the outer features of faces for recognition has been explored little beyond early infancy, so this portion of the investigation was exploratory. Given that outer features can be discriminated even in newborns (Bushnell et al., 1989; Field et al., 1984), we predicted that all ages should discriminate all species using just the outer features.

Finally, adults and infants may only discriminate manipulations of human faces. Previous work has demonstrated that adults discriminate all three systematic manipulations of human faces (Freire et al., 2000; Goffaux, Rossion, Sorger, Schiltz, & Boebel, 2009; Mondloch et al., 2002; Scott & Nelson, 2006; Sugita, 2009; Thompson et al., 2001). The present investigation extended this method, systematically manipulating nonhuman faces for the purpose of measuring discrimination abilities in human participants. Therefore, humans (of any age) may not discriminate nonhuman face manipulations for some or any of the manipulation types (i.e., feature-based, configural, head contour). If this is the case, then this will be a powerful demonstration that human faces are special relative to the faces of other species.

Methods

Participants

The participants included 61 healthy, 4- to 6-month-olds (age range: 121-192 days; 31 females; 70% Caucasian), 41 healthy, 9- to 12-month-olds (age range: 280-364 days; 23 females; 85% Caucasian), and 71 healthy adults (age range: 17-60 years; 58 females; 72% Caucasian). Names were found using newspaper birth notices, and we contacted families by telephone. We recruited adults through the research participant pool of a large southern university. These sample sizes do not include 4- to 6-month-olds (*n* = 4), 9- to 12-month-olds (*n* = 3), and adults (*n* = 3), excluded due to equipment malfunction or experimenter error, 4- to 6-month-olds (*n* = 5), and 9- to 12-month-olds (*n* = 2) excluded due to fussiness or inattention, 4- to 6-month-olds (*n* = 2) excluded due to side bias (looked to one side > 80%), and adults (*n* = 4) excluded for not following directions.

Apparatus

Testing took place within a darkened and quiet room. A 2.3 × 1.3 m black curtain enclosed the area on three sides to prevent distraction. Infants sat in an infant seat or their parent’s lap. All participants sat 60 cm from the presentation screen (43 by 58 cm). The stimuli were presented using rear projection on an InFocus projector (model LT755; Portland, OR). Each session was recorded using two Panasonic VHS cameras (model AG-188-Proline; Secaucus, NJ). One camera recorded the participant and the other recorded the stimulus being presented on the screen. A Videonics Digital Video Mixer (model MX-1; Campbell, CA) combined these videos. Scoring of look locations was done offline using the Noldus Observer XT; Asheville, NC. We presented visual stimuli using Inquisit software by Millisecond (www.millisecond.com), version 2.0.61004.7.

Stimuli

Natural face stimuli of different species do not vary equally. Our goal was to create systematically varied faces which varied equally in their properties. To this end, we first gathered 90 natural face photos: 30 male human faces, 30 male capuchin monkey (*Cebus apella*) faces, and 30 female sheep (*Ovis aries*) faces. The 90 photos consisted of 16 human faces from the NimStim Face Stimulus Set (Tottenham et al., 2009), and 14 human faces from the Japanese and Caucasian Neutral Faces Set (Matsumoto & Ekman, 1988). Given that differences have been found in identity discrimination among familiar and unfamiliar races (Hayden, Bhatt, Joseph, & Tanaka, 2007; Kelly, Quinn, Slater, Lee, Ge, & Pascalis, 2007), ages (Cassia, Kuefner, Picozzi, & Vescovo, 2009a; Cassia, Picozzi, Kuefner, & Casati, 2009b; Kuefner, Cassia, Picozzi, & Brocolo, 2008; Kuefner, Cassia, Vescovo, & Picozzi, in press), and between male and female faces (Ramsey, Langlois, & Marti, 2006), we kept these factors uniform, and we used all Caucasian male faces.[1] We used 20 monkey photos from the Living Links, Yerkes National Primate Research Center and Emory University, three from Yo Morimoto, Kyoto University, and seven from the University of Georgia (Simpson, 2008). Keith Kendrick of Cambridge University (Kendrick, da Costa, Leigh, Hinton & Peirce, 2001) allowed us to use 30 sheep photos, all of which had neutral expressions (Reefmann, Kaszàs, Wechsler, & Gygax, 2009). The human face photos all had neutral expressions (i.e., lacking emotion), as rated by adult observers (Matsumoto & Ekman, 1988; Tottenham et al., 2009). Naïve humans, as well as humans who work with capuchin monkeys, rated the monkey photos as neutral (Simpson, 2008). Sheep photos were confirmed by Reefmann, Kaszàs, Wechsler, & Gygax (2009) to be neutral expressions. We removed necks, shoulders, and ear tags (on sheep), and gave all photos uniform white backgrounds.

We selected 18 properties of faces that are known to influence recognition (e.g., Sadr et al., 2003; Schwarzer, Zauner, & Jovanovic, 2007), and measured them in our 90 natural faces (Table 3.1). We found the properties of our faces (e.g., distance between the eyes) did not vary equally across species. To determine whether one species was overall more variable than another, we conducted a one-way ANOVA on the 18 coefficients of variation—indices of how much each face property varies within each species—which revealed none of the species overall varied more than the others, $F(2,48) = 1.48$, $p = .24$. An examination of the frequency at which each species was the most variable revealed more variability in the monkeys, compared to the humans and sheep, for a larger number of the face properties, compared to the number of times that the human or sheep varied more than the monkeys.

Creation of equivalent groups of faces across species. Given that our natural face stimuli varied to different degrees, we sought to create artificial face sets that could be matched on their variability across species. One face was selected from each species based on pilot study data which indicated the individual was average in attractiveness and distinctiveness. That photo was used to create sets of systematically varied faces using the 90 face photos selected (samples in Figure 3.1). We used Adobe Photoshop and prepared photos in a manner similar to previous systematically varied faces studies (Freire et al., 2000; Goffaux et al., 2009; Mondloch et al., 2002; Scott & Nelson, 2006; Sugita, 2009; Thompson et al., 2001; Quinn & Tanaka, 2009). Following the recommendations of Taschereau-Dumouchel and colleaugues (2010), manipulations of interattribute distances fell within the natural variability of the population (Figure 3.1b). To this end, we considered our sampling of interattribute distances from our real-world distributions (Table 3.1), and distance manipulations did not exceed one standard deviation from the mean for the height of the eyes and mouth and two standard deviations from the mean for the distance between the eyes (Mondloch et al., 2002; Taschereau-Dumouchel, 2010). In cases in which there were statistically significant species differences in the variability of interattribute distances (e.g., distance between the eyes), the coefficient of variation value was used from the species that had the smallest amount of variability (Table 3.1). This method ensured that the variability in interattribute distances was equivalent across species, while not outside of the range of normal variability for any of the three species.

Additionally, the attributes that varied the most in a species may be most critical for recognition. To examine whether similar properties varied in each species, each of the 16 face properties were ranked, within each species, from being the least variable (1) to the most variable (16), within that species. These ranks were then correlated. Although human and monkey faces varied on similar properties ($r(58) = .83$, $p < .001$), the sheep faces did not (ps > .60), suggesting that the properties of the sheep faces that varied were different from the properties that varied in the humans and monkeys. For example, we found sheep varied the most in the distance between the mouth and the chin (ranked 16) compared to other properties; humans (ranked 13) and monkeys (ranked 15.5) also had large amounts of variability in this distance, but other features varied more (e.g., in humans, the width of the ear was equally variable, and in the monkeys three features were more variable: width of ear, distance between mouth and chin, and height of mouth). The sheep varied more in the height of the eyes (distance between the eyes to the top of the head; ranked 9), compared to the humans (ranked 3.33) and monkeys (ranked 6.5). The humans and monkeys had more variability in the distance between the eyes (both ranked 10.5), compared to the sheep (ranked 5.5).

If the features that vary more are those that are more often used for recognition, we might expect participants to discriminate sheep more when they vary greatly in the height of the eyes on the face, while the monkeys and humans may be more easily discriminated when they vary more on the location of the mouth on the face. Given that the properties of the sheep faces that varied were different from the properties that varied in the humans and monkeys, these rank orders were used to make sure the attributes selected were together equally varying across the three species. For the configuration manipulation, the height of the eyes and distance between the eyes were manipulated, as was the height of the mouth (Figure 3.1b). For the feature identity manipulation, the identity of the eyes, eyebrows, and mouth were manipulated (Figure 3.1a). We kept the size of the facial features (eyes and mouth) constant to ensure that the distances among the features were equivalent; therefore, in some cases we had to adjust the size of the features. For the head contour manipulations the face features (i.e., eyes, eyebrows, nose, and mouth) were consistent, but the head contours (hair, jaw line) were from different individuals (Figure 3.1c).

All photos were 400 × 400 pixels (10° × 16° on the presentation screen). Prior to each trial, all participants viewed dynamic centering stimuli (e.g., flashing bull's-eye or cartoon characters) that were 12° × 12° on the presentation screen, and lasted 1,500 msec.

Procedure

First, all procedures were explained to the participants (i.e., adult participants or the infants' parents), and informed consent was obtained. Each participant was randomly assigned to one of three conditions—human, monkey, or sheep—each containing a different set of 30 faces: 10 faces with the spacing systematically manipulated, 10 faces with features (i.e., eyes and mouths) systematically manipulated, and 10 faces with head contour systematically manipulated. A visual paired comparison task was used (Fagan, 1970). Adults were instructed to keep their eyes on the screen and view the pictures that appear, like they were watching television. Participants were familiarized with a face through the continuous familiarization technique (Rose, Feldman, & Jankowski, 2002; Rose et al., 1999), in which a set of identical faces were shown until the participant accumulated 20 seconds of looking to one or both faces (Figure 3.2). Next, participants viewed up to 30 *paired comparison* test trials, consisting of pairs of faces: one face was the same as that shown in the familiarization (i.e., familiar face) and one face was novel (see Figure 3.2).

Looking time to the faces was measured live using a stopwatch, to ensure that stimuli were presented for the correct amount of time (i.e., to ensure that each participant had a 20 second total cumulative looking time to the faces for the *familiarization*, and 4 seconds of cumulative looking time to the faces in the 30 *paired comparison* trials). The 30 novel faces were presented in a random order, and appeared on the right and left with equal probability. All stimuli were presented on white boxes surrounded by a black background. Faces remained on the screen until a cumulative looking time of 4 seconds was established, and between each trial there was a 500 ms inter-trial interval. The frequencies and durations of looks towards and away from the novel and familiar faces were later coded off-line for analysis. Testing continued until all 30 trials were completed, or until the participant (or parent) wished to end the experiment. In total, the experiment took less than 15 minutes.

Coding Training and Reliability

All participants' eye movements were coded off-line frame-by-frame (resolution of measurement is 33 ms) from video using the Noldus Observer XT. Coders recorded the location (i.e., left face, right face, away) and duration (i.e., start and stop times) of participants' looks during the familiarization phase, and paired comparison test trials. Two observers coded eye movements from randomly selected samples from each of the three age groups. In these samples, interobserver reliability was assessed between an anchor observer, and each additional observer. Cohen's Kappa was used to assess inter-rater reliability. Cohen's Kappa for the frequency of each look location (e.g., left picture, right picture, or away) was $\kappa = .88$.

Data Analysis

We completed four analyses. First, we examined the proportion of time looking to the novel face out of the total time looking to both faces to see if viewing patterns differed significantly from chance (50%) for each age group in each condition. To this end, we separated our data into nine independent groups by age (4- to 6-month-olds, 9- to 12-month-olds, and adults) and species (human, monkey, sheep), which were between subjects factors. Within each group, we conducted three one-sample *t* tests, one for each level of our within subjects factor of face manipulation type (feature, spacing, contour). Each of these comparisons was tested at the .017 level (.05 divided by the number of tests conducted for each group). After determining which groups exhibit looking preferences we examined those groups further in our second analysis, to determine what was guiding those preferencing, using a mixed design ANOVA to see whether proportion of time looking to the novel faces varied across ages as a function of species and face manipulation type. In our third analysis, we carried out an additional mixed design ANOVA, this time including all age groups, again examining the proportion of time looking to the novel face across age, species, and face manipulation type. In our final analyses we examined comparison gaze shifts (i.e., alternating fixations in gaze between the two faces) in a mixed design ANOVA to determine whether the number of shifts in gaze varied as a function of age, species, and face manipulation type.

Results

Preliminary Analyses

The 4- to 6-month-olds completed an average of 18 test trials (*SD* = 10), 9- to 12-month-olds completed an average of 22 test trials (*SD* = 9), and all adults completed 30 test trials. A preliminary analysis revealed no gender or ethnicity differences, no differences between full-term and premature infants (4- to 6-month-olds: *n* = 5; 9- to 12-month-olds: *n* = 6), and no effect of the side of the novel face, so these factors were not included. Levene's test revealed unequal variance across groups; therefore, we report values with the Huynh-Feldt correction.

A one-way analysis of variance (ANOVA) confirmed there were no differences in the total looking time during the familiarization among the three age groups (*M* = 21.48 sec, *SD* = 4.74), *F*(2, 175) = 26.37, *p* = .31. The three age groups did vary in the amount of time looking away during the familiarization, *F*(2, 175) = 32.38, *p* < .001, with the 4- to 6-month-olds looking away the most (*M* = 47.67 sec, *SD* = 49.49), followed by the 9- to 12-month-olds (*M* = 28.58 sec, *SD* = 35.01), and adults (*M* = .42 sec, *SD* = .43), independent samples *t* tests, *p*s < .001.

Did the Proportion of Time Looking to Novel Faces Vary From Chance?

We carried out one-sample *t* tests for each age, species, and face manipulation type to see if the proportion of time looking to the novel face, out of the total amount of time looking to both faces, differed from chance (50%), Figure 3.3. There were nine groups, since individuals in each age group (4- to 6-month-olds, 9- to 12-month-olds, adults) were randomly assigned to view one of three species (human, monkey, sheep). We carried out three one-sample *t* tests for each group; each of these comparisons was tested at the .017 level (.05 divided by the number of tests conducted for each group). Four- to six-month-olds had no looking preferences, *p*s > .01. This result indicates that 4- to 6-month-olds were rather poor at discriminating systematically varied faces. Nine- to twelve-month-olds, in contrast, had novelty preferences for human feature manipulations (*M* = 54.98%, *SD* = 7.44, *p* = .017) and the monkey head contour manipulation (*M* = 58.62%, *SD* = 8.39, *p* = .002), but no other novelty preferences (*p*s > .01). Thus, 9- to 12-month-olds discriminated primate faces using two different face properties—inner features and outer features—but showed no novelty preferences for the sheep faces or to any species in the spacing manipulation. Adults spent a longer proportion of time looking at the novel faces for all species, for the head manipulation (human: *M* = 68.61%, *SD* = 10.49; monkey: *M* = 69.70%, *SD* = 12.69; sheep: *M* = 57.78%, *SD* = 11.23; *p*s < .001) and feature manipulation (human: *M* = 67.78%, *SD* = 11.36; monkey: *M* = 66.62%, *SD* = 10.14; sheep: *M* = 57.02%, *SD* = 6.01; *p*s < .001). But for the spacing manipulation, adults only had a novelty preference for the humans (*M* = 61.36%, *SD* = 10.43, *p* < .001) and monkeys (*M* = 53.68%, *SD* = 5.39, *p* = .002). This result indicates that adults can discriminate faces that vary in any one of the three face properties (i.e., outer features, inner features, or spacing among features) for primate faces, but sheep faces were discriminated only using inner features and outer features.

For Groups Who Discriminated, Did Looking Vary with Species and Manipulation?

We next looked at only the age groups that demonstrated face discrimination (older infants and adults), to see whether they differed from one another when viewing different species and different face manipulation types. We conducted a 2 × 3 × 3 mixed-design ANOVA examining whether the proportion of time looking to the novel face, out of the total time looking to the faces, varied as a function of the between subjects factors age (9- to 12-month-olds, adults) and species (human, monkey, sheep), and the within subjects factor of face manipulation type (features, outer head contour, spacing). Results are reported in Table 3.2. We found a main effect of age, *F*(1, 106) = 41.21, *p* < .001, whereby adults overall exhibited a stronger novelty preference (*M*=61.4%, *SD*=9.1%) compared to 9- to 12-month-olds (*M*=52.2%, *SD*=6.7%). There was also a main effect of species, *F*(2, 106) = 14.59, *p* < .001. Participants spent a greater proportion of time looking to the novel faces of humans (*M*=60.1%, *SD*=10.2%) and monkeys (*M*=59.1%, *SD*=7.9%), compared to sheep (*M*=51.2%, *SD*=7.7%), *p* < .001, Fisher's LSD. There was also a main effect of face manipulation, *F*(2, 212) = 27.30, *p* < .001. The proportion of time looking to the novel face was greater for the feature manipulated faces (*M*=59.0%, *SD*=11.1%) and the outer contour manipulated faces (*M*=59.4%, *SD*=13.9%), compared to the spacing manipulated faces (*M*=52.0%, *SD*=9.5%), *p* < .001, Fisher's LSD. There were also interactions between face manipulation type and age, *F*(2, 212) = 27.30, *p* = .043, and between face manipulation type and species, *F*(4, 212) = 3.06, *p* = .018.

The face manipulation type by age interaction was first examined, and was found to be an ordinal interaction (in which the order of the differences across our age groups were the same order, but of differing magnitudes), Figure 3.4. One-way ANOVAs confirmed there was a main effect of face manipulation for each age group: 9- to 12-month-olds, *F*(2, 80) = 3.76, *p* = .028, and adults, *F*(2, 140) = 46.96, *p* < .001. Specifically, the 9- to 12-month-olds had a longer proportion of time looking to the novel face for the feature manipulation (*M*=54.2%, *SD*=9.6%) and the head manipulation (*M*=53.6%, *SD*=12.8%), compared to the spacing manipulation (*M*=48.9%, *SD*=10.2%), *p*s < .05, Fisher's LSD. We found that adults showed the same pattern, but to an even greater extent: they had a longer proportion of time looking to the novel face for the feature manipulation (*M*=64.0%, *SD*=10.1%) and head manipulation (*M*=65.7%, *SD*=12.6%), compared to the spacing manipulation (*M*=55.2%, *SD*=8.4%), *p*s < .05, Fisher's LSD. Examining these findings in light of our first analysis (Figure 3.3), we can see that while older infants exhibited a small novelty preference for the feature and outer contour manipulated faces, they had no preference for the spacing manipulated faces. Adults, in contrast, had a large novelty preference for feature and outer contour manipulated faces, but only a slight novelty preference for the spacing manipulated faces. Therefore we concluded that adults gained more information for discrimination from the outer and inner feature manipulated faces relative to the spacing manipulated faces, compared to the older infants (Figure 3.4).

We next followed up the interaction between face manipulation type and species by conducting one-way ANOVAs for each face manipulation type to see if there was a main effect of species, Figure 3.5. For the facial feature manipulation, there was a main effect of species, *F*(2, 112) = 7.38, *p* = .001. The proportion of time looking to the novel face was greater for the feature manipulated faces of humans (*M*=62.5%, *SD*=11.7%) and monkeys (*M*=62.9%, *SD*=11.3%), compared to sheep (*M*=54.6%, *SD*=8.0%), *p*s = .001, Fisher's LSD. There was a main effect of species for the outer head contour manipulated faces, *F*(2, 111) = 10.35, *p* < .001. The proportion of time looking to the novel face was greater for the faces of humans (*M*=63.6%, *SD*=13.3%) and monkeys (*M*=65.8%, *SD*=12.5%), compared to sheep (*M*=53.1%, *SD*=12.8%), *p*s ≤ .001, Fisher's LSD. These findings suggest that when faces varied in their features or outer head contours older infants and adults more easily discriminated them if they were primate faces, compared to sheep faces. There was a main effect of species for the spacing manipulated faces, *F*(2, 110)=8.96, *p* < .001. The proportion of time looking to the novel face was greater for the faces of the humans (*M*=57.4%, *SD*=11.6%), compared to both the monkeys (*M*=52.3%, *SD*=6.6%) and sheep (*M*=48.7%, *SD*=7.7%), *p*s < .05, Fisher's LSD. This suggests that when faces varied in the spacing among the facial features, older infants and adults had a stronger novelty preference—indicative of stronger discrimination—for the human faces, relative to the faces of the monkeys and sheep. In other words, when faces varied only in their configuration, human faces were distinguished more easily than faces of nonhuman animals. However, this effect was primarily driven by the adults, as the older infants showed no evidence of discriminating faces that varied in their configurations (Figure 3.4).

Did the Proportion of Time Looking to Novel Faces Vary Across Age, Species, and Manipulation?

We next carried out a 3 × 3 × 3 mixed-design ANOVA examining whether the proportion of time looking to the novel face, out of the total time looking to the faces, varied as a function of the between subjects factors age (4- to 6-month-olds, 9- to 12-month-olds, adults) and species (human, monkey, sheep), and the within subjects factor of face manipulation type (outer features, inner features, spacing among inner features). Results are reported in Table 3.2. We found a main effect of age, *F*(2, 159) = 33.60, *p* < .001, whereby adults overall exhibited a stronger novelty preference (*M*=61.5%, *SD*=7.6 %) compared to either infant group (*M*=51.9%, *SD*=7.5%, and *M*=52.2%, *SD*=7.7%, for 4- to 6-month-olds and 9- to 12-month-olds, respectively), *p* < .001, Fisher's LSD. There was also a main effect of species, *F*(2, 159) = 9.49, *p* < .001. Participants spent a greater proportion of time looking to the novel faces of humans (*M*=57.0%, *SD*=7.7%) and monkeys (*M*=57.1%, *SD*=7.5%), compared to sheep (*M*=51.5%, *SD*=7.2%), *p* < .001, Fisher's LSD. There was also a main effect of face manipulation, *F*(2, 318) = 16.17, *p* < .001. The proportion of time looking to the novel face was greater for the feature manipulated faces (*M*=56.3%, *SD*=16.1%) and the outer feature manipulated faces (*M*=57.7%, *SD*=17.9%), compared to the spacing manipulated faces (*M*=51.6%, *SD*=14.3%), *p* < .001, Fisher's LSD. There were also interactions between face manipulation type and age, *F*(4, 318) = 3.47, *p* = .009, between face manipulation type and species, *F*(4, 318) = 3.76, *p* = .005, and between age and species, *F*(4, 159) = 3.35, *p* = .012.

The face manipulation type by age interaction was first examined, by carrying out one-way ANOVAs on each age group to see if there were differences across face manipulation type. There was no main effect of face manipulation type for the 4- to 6-month-olds, *F*(2, 110) = .98, *p* = .38. There was a main effect of face manipulation type for the 9- to 12-month-olds, *F*(2, 80) = 3.76, *p* = .028, whereby the proportion of time looking to the novel face was greater for the inner feature manipulated faces (*M*=54.3%, *SD*=9.3%) and the outer feature manipulated faces (*M*=53.9%, *SD*=12.8%), compared to the spacing manipulated faces (*M*=48.8%, *SD*=10.0%), *p*s < .05, Fisher's LSD. There was also a main effect of face manipulation type for the adults, *F*(2, 140) = 46.96, *p* < .001, whereby, like with the 9- to 12-month-olds, the proportion of time looking to the novel face was greater for the inner feature manipulated faces (*M*=64.1%, *SD*=10.5%) and the outer feature manipulated faces (*M*=65.7%, *SD*=12.6%), compared to the spacing manipulated faces (*M*=55.3%, *SD*=8.7%), *p*s < .001, Fisher's LSD. This is the same pattern found in our previous ANOVA which included only the older age groups (see Figure 3.4).

We next followed up the interaction between face manipulation type and species by conducting one-way ANOVAs for each face manipulation type to see if there was a main effect of species. Within the inner feature manipulation, there was a main effect of species, *F*(2, 171) = 5.64, *p* = .004, in which participants spent a greater proportion of time looking to the novel faces of humans (*M*=58.5%, *SD*=14.5%) and monkeys (*M*=60.2%, *SD*=12.3%), compared to sheep

(*M*=52.6%, *SD*=10.6%), *p*s < .05, Fisher's LSD. For the outer feature manipulation there was also a main effect of species, *F*(2, 171) = 11.25, *p* < .001, in which participants spent a greater proportion of time looking to the novel faces of humans (*M*=59.1%, *SD*=14.2%) and monkeys (*M*=63.9%, *SD*=14.3%), compared to sheep (*M*=51.7%, *SD*=12.9%), *p*s < .01, Fisher's LSD. But there was no difference between the human and monkey, *p* = .063, Fisher's LSD. For the spacing manipulation, there was not a main effect of species, *F*(2, 171) = 2.49, *p* = .086. Thus, the patterns were the same as in the first ANOVA (see Figure 3.4), with the exception of the spacing manipulation. In our first ANOVA, which only included the 9- to 12-month-olds and adults, we found stronger novelty preferences for human faces that varied in their spacing, compared to animal faces; however this effect was lost when including the 4- to 6-month-olds in the ANOVA.

Finally, we followed up the interaction between age and species by carrying out one-way ANOVAs on each age group to see if there was a main effect of species (Figure 3.6). There was no main effect of species for the 4- to 6-month-olds, *F*(2, 60) = 1.68, *p* = .195. There was a main effect of species for the 9- to 12-month-olds, *F*(2, 41) = 5.68, *p* = .007, whereby they spent longer looking to the novel faces of humans (*M*=53.1%, *SD*=5.5%) and monkeys (*M*=54.8%, *SD*=3.9%), compared to sheep (*M*=47.4%, *SD*=8.2%), *p*s < .05, Fisher's LSD. There was also a main effect of species for the adults, *F*(2, 68) = 11.38, *p* < .001, whereby they spent a greater proportion of time looking to the novel faces of humans (*M*=66.0%, *SD*=9.8%), and monkeys (*M*=63.3%, *SD*=7.9%), compared to sheep (*M*=55.1%, *SD*=5.8%), *p* < .001, Fisher's LSD. Together, these results reflect face specialization with age, whereby face discrimination is becoming more sensitive to primate faces, by later infancy, and lasting into adulthood.

Did the Comparison Gaze Shifts Vary with Age, Species, and Manipulation?

Comparison gaze shifts between faces are believed to reflect how similar the viewer finds the faces (e.g., Colombo, Mitchell, & Horowitz, 1988). A 3 × 3 × 3 mixed design ANOVA tested whether comparison gaze shifts varied as a function of the between subjects factors of age (4- to 6-month-olds, 9- to 12-month-olds, adults) and species (human, monkey, sheep), and the within subjects factor of face manipulation type (outer features, inner features, spacing among inner features), as shown in Table 3.3 and Figure 3.7. There was a main effect of age ($F(2, 161) = 72.95$, $p < .001$). Adults made the most comparison gaze shifts ($M = 3.77$, $SD = 1.08$), followed by 9- to 12-month-olds ($M = 2.75$, $SD = 1.04$), and 4- to 6-month-olds ($M = 1.62$, $SD = .84$), *p*s < .001, Fisher's LSD. There was also a main effect of face manipulation type ($F(2, 332) = 9.47$, $p < .001$). Participants made more comparison gaze shifts for the spacing manipulation ($M = 2.98$, $SD = 1.58$) compared to the feature manipulation ($M = 2.79$, $SD = 1.45$), and the outer feature manipulation ($M = 2.57$, $SD = 1.40$), as well as more gaze shifts to the feature manipulated faces, compared to the outer feature manipulated faces, *p*s < .05, Fisher's LSD.

There was also an interaction between the face manipulation type and age for the number of comparison gaze shifts ($F(4, 332) = 3.89$, $p = .004$), Figure 3.7 and Table 3.3. Follow-up one-way ANOVAs examined each age group to see whether the frequency of comparison gaze shifts varied across face manipulation types. There was a main effect of face manipulation for 4- to 6-month-olds, $F(2, 114) = 5.34$, $p = .006$. Four- to six-month-olds made fewer comparison gaze shifts for the outer feature condition ($M = 1.40$, $SD = .89$), compared to the other two conditions (feature: $M = 1.76$, $SD = 1.10$; spacing: $M = 1.76$, $SD = 1.03$, *p*s < .01, Fisher's LSD), suggesting even though they did not discriminate the faces, they compared the faces that differed in outer features the least, which suggest they may have noticed differences between the faces. In contrast, 9- to 12-month-olds had no main effect of face manipulation type, making an equal number of comparison gaze shifts across all three manipulations (*M* = 2.73, *SD* = 1.24), $p > .05$. This result indicates 9- to 12-month-olds' perception of similarity among faces may not be affected by the type of manipulation. Adults, in contrast, had a main effect of face manipulation type, $F(2, 140) = 17.75$, $p < .001$. Adults made the largest number of comparison gaze shifts for the spacing condition (*M* = 4.16, *SD* = 1.31), relative to the other two manipulation conditions (feature: *M* = 3.69, *SD* = 1.20; contour: *M* = 3.46, *SD* = 1.15, *p*s < .001, Fisher's LSD). This result suggests adults perceived the spacing manipulated faces as the most similar. Adults also made slightly more comparison gaze shifts for the feature identity manipulated faces, compared to the contour manipulated faces ($p < .05$, Fisher's LSD). Therefore we concluded that adults may have perceived the outer feature manipulated faces as the easiest to distinguish. There were no other main effects or interactions, *p*s > .05.

Discussion

In the present study, we sought to uncover whether the differences in humans' perception of natural human and animal faces are due to categorical differences (in species), or are due to differences in interindividual variability within each species. To this end, we created systematically varied faces of humans, monkeys, and sheep that were manipulated in one of three ways (outer features, inner features, spacing among inner features), and measured discrimination with a visual paired comparison test in 4- to 6-month-old infants, 9- to 12-month-old infants, and adults. Though others have examined systematically varied human faces in studies of human infants (Bhatt et al., 2005; Scott & Nelson, 2006; Schwarzer et al., 2007) and adults (Freire et al., 2000; Le Grand, Mondloch, Maurer, & Brent, 2001), and systematically varied nonhuman primate faces in studies of nonhuman primates (Martin-Malivel & Okada, 2007; Sugita, 2009), we combined these design elements into one study with human participants. Additionally, we ensured faces were manipulated equally across species, and within a natural range of variability; previous work using systematically varied faces often manipulated faces to a greater degree than what occurs in the natural population (Taschereau-Dumouchel et al., 2010). This design allowed us to more carefully test the hypothesis that infants show perceptual narrowing of facial identity discrimination across species.

We discuss three key findings: (1) the number of face properties individuals can discriminate increases with age, (2) the number of species discriminated increases with age, and (3) primate faces are discriminated using different face properties compared to nonprimate faces. We interpret these findings to indicate that a perceptual narrowing model may not accurately predict the development of facial identity recognition across species.

The Number of Face Properties Viewers Can Use for Discrimination Increases with Age

The proportion of time looking to the novel face during the test trials varied across age, species, and face manipulation types (Figure 3.3). Four- to six-month-olds failed to discriminate any of the systematically varied faces. Nine- to twelve-month-olds only discriminated faces that varied in either their inner features or outer features. Only adults discriminated alternations to the spacing among facial features. These findings are congruent with human face perception work, which suggests configural processing—measured by determining discrimination of faces with alterations in the spacing among facial features—is relatively poor in children (e.g., Mondloch et al., 2004), but is established in adults. In addition, though adults discriminated all three manipulation types, novelty preferences were greatest for the head contour and facial feature manipulations, suggesting that even for adults, discriminating faces based on facial configuration alone is relatively difficult (Figure 3.4).

Comparison gaze shifts (i.e., shifts in gaze between two faces), are believed to reflect how similar the viewer finds the faces (e.g., Colombo et al., 1988). This measure provided the same findings as look durations for the adult participants: the contour manipulated faces were the easiest discriminate, as there were fewer gaze shifts. In adults, an intermediate number of gaze shifts occurred for the feature manipulated faces, suggesting they were not as easy to distinguish as the contour manipulated faces. In adults, the spacing manipulated faces elicited the largest number of comparison gaze shifts, and therefore we concluded that they were the most difficult to distinguish. We are not sure why the 9- to 12-month-olds made an equal number of comparison gaze shifts across all manipulation types. This result suggests they perceived all face manipulation types as equally similar; however, this interpretation seems unlikely, given that they discriminated some face manipulation types (i.e., outer and inner features), but not others (i.e., spacing).

Number of Species Discriminated Increases with Age

Numerous studies on the development of facial identity discrimination have been interpreted as reflecting perceptual narrowing, a process in which perception is broad in early infancy, but narrows as a function of experience by about nine months. The present findings, however, are incongruent with perceptual narrowing. Perceptual narrowing predicts that 4-to six-month-olds should discriminate human, monkey, and sheep faces equally well, while 9- to 12-month-olds and adults should be relatively better at discriminating human faces, compared to nonhuman animal faces. Perceptual narrowing of nonhuman animal faces has received some support in previous work with natural faces (e.g., Pascalis et al., 2002; Simpson et al., 2010).

In the present study, 4- to 6-month-olds showed no evidence of discriminating human, monkey, or sheep faces. This failure to find evidence of discrimination may be because younger infants rely on multiple face properties for discrimination. In this study, the faces varied in only one property at a time. In adults, face recognition is better when more than one face property varies concurrently (e.g., Tanaka, & Sengco, 1997); the same appears to be true for young infants.

In contrast to 4- to 6-month-olds, 9- to 12-month-olds discriminated human and monkey faces, but showed no evidence of discriminating sheep faces. While previous studies found no evidence that 9- to 12-month-olds can behaviorally discriminate unfamiliar monkey faces, our results suggest infants of this age can behaviorally discriminate unfamiliar monkey faces. Our findings are consistent with findings that 9-month-old infants have brain activity differences for novel and familiar monkey faces—measured using event-related potentials (ERPs)—suggesting discrimination at the neural level (Scott, Shannon, & Nelson, 2006). Our findings are also consistent with work showing 12-month-olds discriminate monkey faces when familiarized for an extended time period (i.e., continuous familiarization technique with a 40 second long familiarization followed by four 10-second long test trials; Flair, 2009). In addition, we found older infants discriminated monkey faces even when they varied in only one face property at a time, which is more challenging than discriminating natural faces (which vary in numerous properties). For example, 9- to 12-month-olds' proportion of time looking to the novel faces was greater than chance for monkey faces that varied in their outer features (Figure 3.4). The finding that 9- to 12-month-olds discriminated monkey faces as well as human faces is counter to the predictions of the perceptual narrowing model.

Given that our results are inconsistent with the perceptual narrowing model of development—which predicts a decrease in discrimination ability for unfamiliar (animal) species with age—what other model may account for our findings? One possibility is that with age individuals learn to attend to the face properties that are useful for distinguishing individual humans. They selectively attend to those predictive features, while ignoring other face properties. This type of learning has been described as learned inattention (i.e., learning to ignore irrelevant stimuli), and was first demonstrated in animals (Mackintosh, 1975). If human and animal faces vary in the features that best distinguish individuals (i.e., the features that help us distinguish human faces are different from the features that help us distinguish other animals' faces)—as our results (Table 3.1) suggest—humans may become worse at distinguishing animal faces with age because they are attending to the properties of faces predictive of individual differences in humans, but not animals.

Additional parallels exist within human face discrimination: humans are better at recognizing faces with the morphology to which they are most commonly exposed, including ethnicity (Hayden et al., 2007; Kelly et al., 2007), gender (e.g., Ramsey et al., 2006; Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002; Ramsey et al., 2006), and age (Cassia et al., 2009a; Cassia, Picozzi, Kuefner, Bricolo, & Turati, 2009b; Cassia, Picozzi, Kuefner, & Casati, 2009c; Kuefner et al., in press). With age, humans experience a decline in the ability to distinguish individuals with less familiar face morphologies. Though others have interpreted these findings as reflecting perceptual narrowing, an alternative explanation is that humans learn to attend selectively to the features that vary the most in the faces they most commonly encounter. Consistent with this alternative explanation are findings—via eye tracking methods—that viewing patterns of human faces differ across geographical groups, such as Western Caucasians and East Asians (Blais, Jack, Scheepers, Fiset, & Caldara, 2008). Differences in viewing patterns across these groups may reflect learned attention to the facial features that best distinguish individuals in a particular culture. For example, Westerners fixate more on the eyes and use feature-by-feature processing, while Easterners fixate more on the nose and use integrative global processing (Caldara, Zhou, & Miellet, 2010). However, there is evidence that both Westerners and Easterners are extracting the same types of information from faces, just using different fixations to do so (Caldara et al., 2010).

Previous findings of species differences may have been due to differences in interindividual variability (Knebel et al., 2008; McKone & Crookes, 2007). Thus, when variability within each species is carefully matched—as in the present study—a different pattern of development emerges: an increase in the number of species discriminated with age. In addition, we utilized a more sensitive task for detecting discrimination by continuously familiarizing participants on each test trial, and by using a large number of test trials (up to 30 test trials). Previous work has used as few as one or two test trials (e.g., Pascalis et al., 2002), which may not reveal discrimination abilities that require additional familiarization time or which have smaller effect sizes.

Primate Faces are Processed Differently than Nonprimate Faces

We predicted that human faces would be processed differently from nonhuman animal faces, particularly for older infants and adults, who have more experience with human faces and are (or are well underway in becoming) human face specialists. In adults and older infants, human faces were discriminated differently from nonhuman animal faces. Specifically, when the spacing among features was manipulated, 9- to 12-month-olds and adults had stronger novelty preferences for human faces, compared to monkey and sheep faces (Figure 3.5). This result suggests that with age, humans more easily use configural processing for distinguishing human faces. Additionally, 9- to 12-month-olds and adults had stronger novelty preferences for faces that varied in their outer or inner features, for primate faces, compared to sheep faces (Figure

3.5). This result suggests that for older infants and adults, recognition based on outer features and inner features is especially useful for primate faces, relative to nonprimate faces.

Nine- to twelve-month-old infants only discriminated human and monkey faces, and showed no evidence of discriminating sheep faces. This result is consistent with findings that 9- to 11-month-old infants show no evidence of discriminating natural sheep faces (Simpson, Varga, Frick, & Fragaszy, 2010a, 2010b). This failure to find sheep face discrimination in older infants may be because primate faces are easier to distinguish because they vary in the same facial properties as human faces (Table 3.1). Older infants have had sufficient exposure to human faces by this age to learn what properties of faces are useful for distinguishing individuals. The same facial properties useful for distinguishing other primate faces may not be useful for distinguishing nonprimate faces, such as sheep.

Though adults discriminated all three species when they differed in outer and inner features, adults failed to discriminate sheep faces that varied in the spacing among inner features. Others have found similar results in adults using another method: the inversion effect, a phenomenon in which we are worse at recognizing an inverted image, relative to an upright image. This inversion effect is especially large for faces relative to other objects (e.g., Diamond & Carey, 1986; Kohler, 1940; Robbins & McKone, 2007; Scapinello & Yarmey, 1970; Yin, 1969). Inverting faces may disrupt configural processing more so than featural processing (Freire, Lee, & Symons, 2000; Leder & Bruce, 2000; Maurer, Grand, & Mondoch, 2002; Valentine & Bruce, 1988; Yin, 1969). While adults experience an inversion effect for primate faces, they do not experience an inversion effect for nonprimate animal faces (e.g., Dufour et al., 2004; Pascalis et al., 1998a; 1998b; Pascalis et al., 2001). Thus, primate faces may be processed in a holistic manner, while nonprimate faces may be processed in a more piecemeal feature-based fashion. In the present study, adults may have used feature-based processing, since they were unable to discriminate sheep faces that only varied in the spacing among their features.

What Developmental Model Can Account for Face Recognition?

Given that our findings are inconsistent with the predictions of a perceptual narrowing model, but are consistent with an alternative model, learned attention, previous findings supportive of perceptual narrowing should be reexamined to determine whether they are also congruent with the learned attention model. Previous work can be reinterpreted as consistent with a learned attention model. For example, the finding that 4- to 6-month-olds and adults can discriminate sheep faces, but 9- to 11-month-olds showed no evidence of discrimination (Simpson et al., 2010) could be interpreted as a gradual improvement in face recognition with age, that is not species-specific. Nine- to eleven-month-olds may be transitioning between stages, shifting from familiarity preferences to novelty preferences, and thus did not consistently prefer either the familiar or novel faces. These older infants may, however, be capable of discrimination. In fact, studies with EEG suggest older infants are capable of discriminating monkey faces (Scott et al., 2006), even though they do not show discrimination in looking time measures. Therefore, results that are congruent with perceptual narrowing are not sufficient to demonstrate perceptual narrowing. Tests are needed to distinguish among these competing models.

General Conclusions

Previous work has found differences in the ways humans discriminate human and nonhuman faces (Dufour et al., 2004; Pascalis et al., 1998a, 1998b; Pascalis et al., 2001; Simpson et al., 2010a, 2010b). Human, monkey, and sheep faces are not equivalent in the variability of their facial features (see Table 1). Through the use of systematically varied faces we controlled the amount of variability in our face sets, equating variability across three species: humans, monkeys, and sheep. We found when variability is equated, young infants (4- to 6-month-olds) no longer excel in face discrimination, but instead perform poorly, suggesting they are unable to rely on only one facial property for discrimination. This finding is in contrast to previous work using natural faces, which found young infants outperformed older infants, and even adults, by discriminating natural human, monkey, and sheep faces (e.g., Pascalis et al., 2002; Simpson et al., 2010).

The present study also showed that 9- to 12-month-olds discriminated systematically varied human and monkey faces, but not sheep faces, even though the variability across individuals' faces was systematically controlled. These findings are somewhat congruent with previous findings that these older infants cannot discriminate natural sheep faces (Simpson et al., 2010a, 2010b). However, the finding that these infants can behaviorally discriminate monkey faces is in contrast to previous findings (e.g., Pascalis et al., 2002, 2005). Perhaps the larger number of test trials (i.e., up to 30 test trials here, compared to as few as one or two previously) or increased familiarization time, through the continuous familiarization technique (Rose et al., 2002), allowed for a more sensitive test of older infants' discrimination. Adults discriminated all species, with the exception of the sheep in the spacing condition. This result is consistent with others who have found adults can discriminate natural animal faces (Simpson et al., 2010), and suggests that others who have failed to find discrimination by adults (Pascalis et al., 1998a, 1998b; Pascalis et al., 2001; Pascalis et al., 2002) may not have employed sufficiently sensitive tests (e.g., using only a small number of test trials).

This work contributes to our knowledge of the development of human face perception through three primary contributions. First, this work demonstrates similarities in the discriminability of human and monkey faces across the lifespan, suggesting faces of different species of primates are discriminated using similar processing (e.g., configural). Additionally, we found an increase with age in the number of face properties which individuals are capable of using, starting with at least two properties in later infancy (outer features and inner features), and expanding to at least three strategies in adulthood (with the addition of discriminating based on the spacing among inner features). Finally, we demonstrate limitations in humans' discrimination abilities of sheep, across all ages. Sheep faces were discriminated with more difficulty when only feature or contour varied, but were not discriminated when spacing varied. Thus sheep faces were processed differently than primate faces.

A limitation of this work is that we only used the faces of three species. Testing infants' and adults' discrimination other primate and nonprimate animal faces would allow for an examination of the consistency of these patterns across species. For example, recently we examined discrimination of wasp faces (*Polistes fuscatus*) using the same methods as the present study, and found neither 4- to 6-month-olds nor 9- to 12-month-olds showed evidence of discrimination (Simpson, unpublished data; wasp faces from Sheehan & Tibbetts, 2008). Though wasps can recognize one another's faces (Sheehan & Tibbetts, 2008), human infants may be unable to discriminate wasp faces. This result suggests human face discrimination may not be so broad that it encompasses insect faces.

An additional limitation of this study is our small sample size, particularly with the 4- to 6-month-olds (n = 61) and 9- to 12-month-olds (n = 41). To detect a moderate effect size (f=.25), with a low Type I error rate (α=.05), and a large amount of power ($1 - \beta$=.80), 66 participants were needed from each age group (Cohen, 1988). Thus, the results here should be interpreted with caution, as we have an increased likelihood of making a Type II Error. In other words, there may be differences present in the infants that we were unable to detect due to our small sample size. To remedy this problem, we will continue collecting data from infants until the necessary sample sizes are obtained.

This work examined the development of recognition processes (e.g., configural and feature-based), by humans, for nonhuman species' faces. Such findings complement existing studies which have used human faces exclusively, and which have failed to control for individual differences in face variability. Future work is needed to explore the driving force for developmental changes in facial identity discrimination, especially to uncover the role of learning to attend selectively to certain facial properties and not others. Counter-training may be used in infants and adults, to shift attention to certain face properties that would improve discrimination of different species' faces. For example, older infants may be trained to attend to properties of sheep faces that are useful for discrimination. Additionally, systematically varied faces have been used to study recognition processes in special populations (e.g., individuals with cataracts, Le Grand et al., 2001), but could also uncover recognition processes used in other atypical populations, such as individuals with autism spectrum disorders.

The current findings also have implications for our understanding of perception more broadly, and highlight the need for tests to clarify whether a perceptual narrowing framework is the best model for perceptual development in other areas. For example, in the development of auditory perception, it is widely accepted that infants retain the ability to discriminate phonemes in their native language, but experience a decline in their ability to discriminate phonemes not in their native language by the end of the first year (e.g., Werker & Tees, 2005). However, neural measures (i.e., event-related potentials) reveal that 12-month-olds discriminate at least some non-native phonemes (e.g., Cheour et al., 1998; although see Conboy & Kuhl, 2011). Thus, by the end of the first year, in both the visual and auditory modalities, there is not a loss of perception of unfamiliar phonemes or faces. Also, this developmental change may be due to learned attention, rather than a decline or loss of perception with age. Thus, studies in this area contribute broadly to our understanding of experience-expectant components of perception and attention, as well as the role of experience during critical periods in infancy and beyond.

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Footnote

[1] The majority of the population in the county and the state is Caucasian (69% and 66%, respectively; Georgia County Guide, 2009); therefore, we assumed that participants would be familiar with Caucasian faces. We also confirmed there were no differences between Caucasian and non-Caucasian participants by including ethnicity as a variable in the initial analyses. The use of female—as opposed to male—sheep faces was for reasons of convenience, and is not expected to bias the study, as human adults could not tell the sex of the sheep.

Table 3.1

Measurements of variability of face stimuli among species

	Human			Monkey			Sheep			Levene's Test		
Property	*M*	*SD*	*CV*	*M*	*SD*	*CV*	*M*	*SD*	*CV*	*F*	*p*	*CV*
Shape and size of features												
Width of right eye	43	3.5	0.08	50	6	0.12	18	4	0.21	2.8	0.067	n.s.
Height of right eye	14	2	0.16	28	3	0.11	13	4	0.28	0.99	0.38	n.s.
Width of nose	55	5	0.09	68	6	0.09	77	8	0.1	3.49	0.035	S > H
Length of nose	66	8	0.12	65	10	0.15	137	14	0.1	8.35	<.001	H > S; M > S
Width of mouth	75	8	0.1	97	18	0.19	93	17	0.18	7.31	0.001	M > H; S > H
Height of mouth	28	7	0.26	19	5	0.29	0	0	0	25.62	<.001	H > S; M > S
Width of left ear	26	7	0.26	20	18	0.89	0	0	0	81	<.001	M > H > S
Shape and size of head												
Height of face	371	7	0.02	367	13	0.04	307	15	0.05	4.08	0.02	S > M
Width of face at eyes	205	11	0.05	224	15	0.06	209	13	0.06	0.7	0.5	n.s.
Width of face at mouth	181	14	0.08	234	24	0.1	93	17	0.18	3.23	0.04	M > H
Configuration of features												
Distance between eyes	56	6	0.11	48	7	0.15	151	8	0.06	3.82	0.026	H > S
Tip of nose to chin	113	12	0.11	109	18	0.17	51	13	0.26	1.48	0.23	n.s.
Mouth to chin	60	9	0.15	57	20	0.35	17	7	0.44	6.96	0.002	S > M > H
Between eyes top head	190	12	0.06	180	19	0.11	92	9	0.1	6.03	0.004	M > H; M > S
Angle of pupil, nose	51	5	0.09	55	8	0.14	61	4	0.07	4.53	0.013	M > H; M > S
Luminosity	192	12	0.06	164	12	0.07	227	5	0.02	8.2	0.001	H > S; M > S
Attractiveness	3.2	1.3	0.41	3	1.6	0.53	3.1	1.7	0.55	0.35	0.7	n.s.
Distinctiveness	4.3	0.8	0.186	3.9	0.4	0.103	3.6	0.4	0.111	4.9	0.007	H > M > S

Note. Means (*M*), standard deviations (*SD*), and coefficients of variation (*CV*) for group differences are presented for 18 different properties of 90 natural human (H), monkey (M), and sheep (S) faces. We used these 90 faces to determine natural amounts of variability within each species. These faces were then used to create our 90 systematically varied faces. Length measurements are in pixels, and angle measurements are in degrees. Attractiveness and distinctiveness ratings were made by human adults ($n = 27$) on a 7 point scale from 1 (very unattractive or not very distinctive) to 7 (very attractive or distinctive). n.s. = $p > .05$.

Table 3.2

Mixed design analysis of variance results for look duration to novel faces for 9- to 12-month-olds and adults

Source	*df*	*SS*	*MS*	*F*	*p*	η^2 or η_p^2
			Between Subjects			
Age	1	.67	.67	41.21	<.001	.28
Species	2	.48	.24	14.59	<.001	.22
Age × Species	2	.02	.01	.65	< .01	.01
Error 1	106	1.73	.02			
			Within Subjects			
Manipulation	2	.36	.18	27.30	<.001	.20
Age × Manipulation	2	.04	.02	3.20	.043	.03
Species x Manipulation	4	.05	.02	3.06	.018	.05
Age × Species × Manipulation	4	.02	.01	.82	.510	.01
Error 2	212	1.38	.01			

Note. *Age* refers to the age group (9- to 12-month-olds or adults), *Species* refers to the species in the face photographs presented (human, monkey, or sheep), and *Manipulation* refers to the type of face manipulation stimulus (outer features, inner features, spacing among inner features).

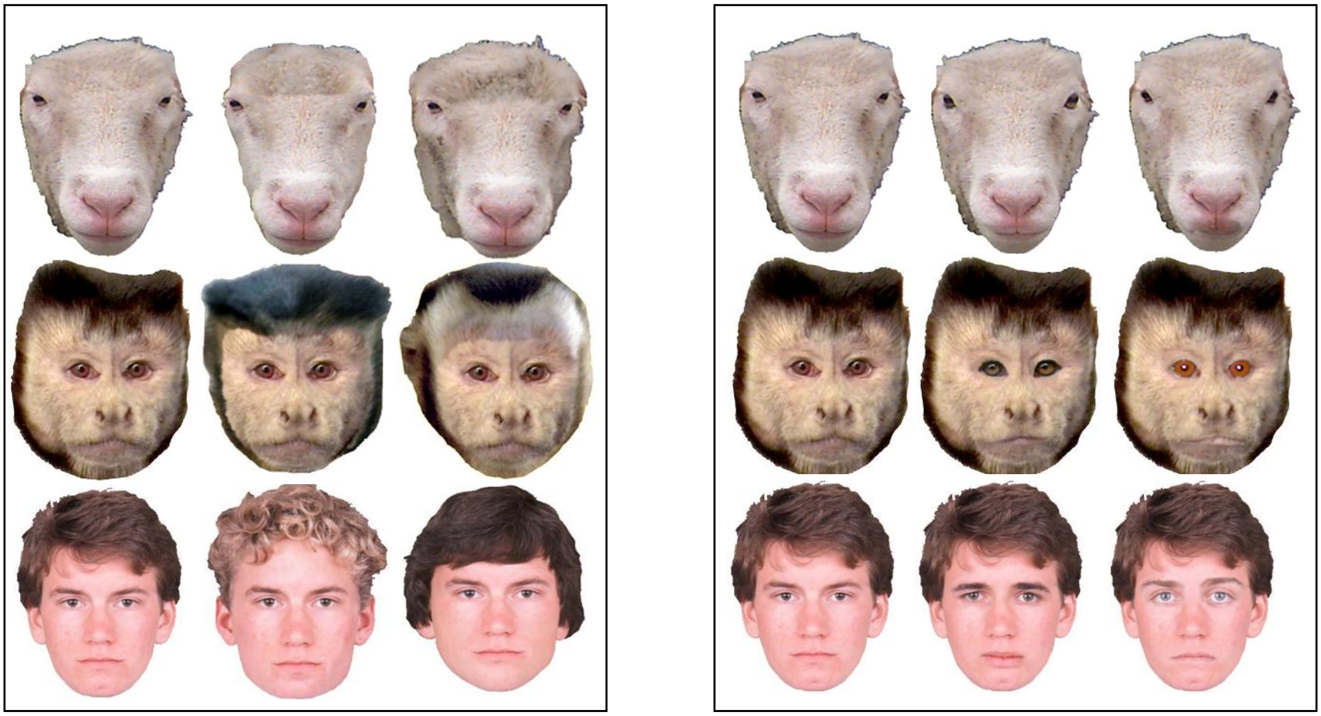
Table 3.3

Mixed design analysis of variance results for the frequency of comparison gaze shifts

Source	*df*	*SS*	*MS*	*F*	*p*	η^2 or η_p^2
			Between Subjects			
Age	2	441.89	220.95	0.27	0.76	0.48
Species	2	1.64	0.82	72.95	<.001	0.90
Age × Species	4	13.01	3.25	1.07	0.37	
Error 1	161	487.66	3.03			
			Within Subjects			
Manipulation	2	9.31	4.66	9.47	<.001	0.05
Age × Manipulation	4	7.66	1.92	3.89	<.01	0.04
Species × Manipulation	4	3.52	0.88	1.79	0.13	
Age × Species × Manipulation	8	3.03	0.38	0.77	0.63	
Error 2	332	163.29	0.49			

Note. *Age* refers to the age group (4- to 6-month-olds, 9- to 12-month-olds, or adults), *Species* refers to the species in the face photographs presented (human, monkey, or sheep), and *Manipulation* refers to the type of face manipulation stimulus (outer features, inner features, spacing among inner features).

Figures



(a) Outer features manipulated:

(b) Inner features manipulated:

(c) Spacing of inner features manipulated:

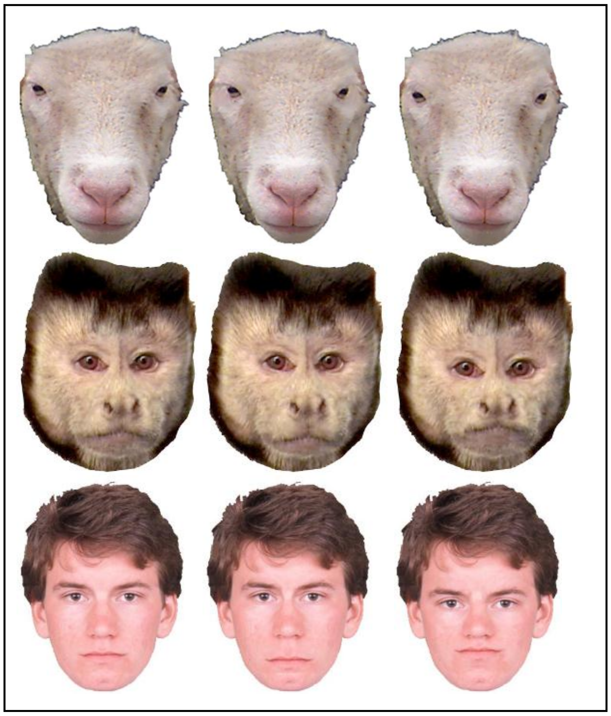


Figure 3.1. Sample face stimuli. A natural face (far left in each box) served as the familiar face, and was used to create three new face sets, which varied in: (a) the outer facial features (contour, hair), (b) inner facial features (eyes, mouth), and (c) the spacing among the inner features.

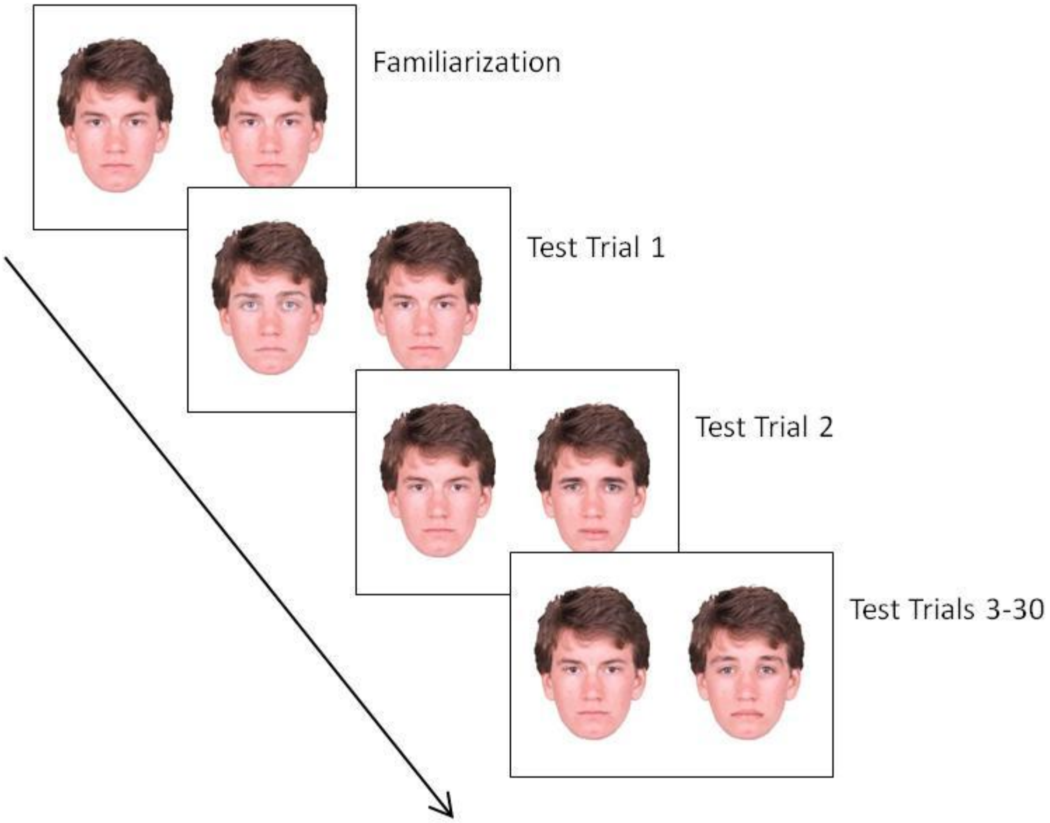


Figure 3.2. Sample presentation sequence. Participants were first familiarized with a face (familiarization), for 20 seconds, then viewed a novel and familiar face on up to 30 subsequent test trials (paired comparison), each lasting 4 seconds. In the example shown here, the inner facial features (eyes and mouth) changed for one face in each test trial.

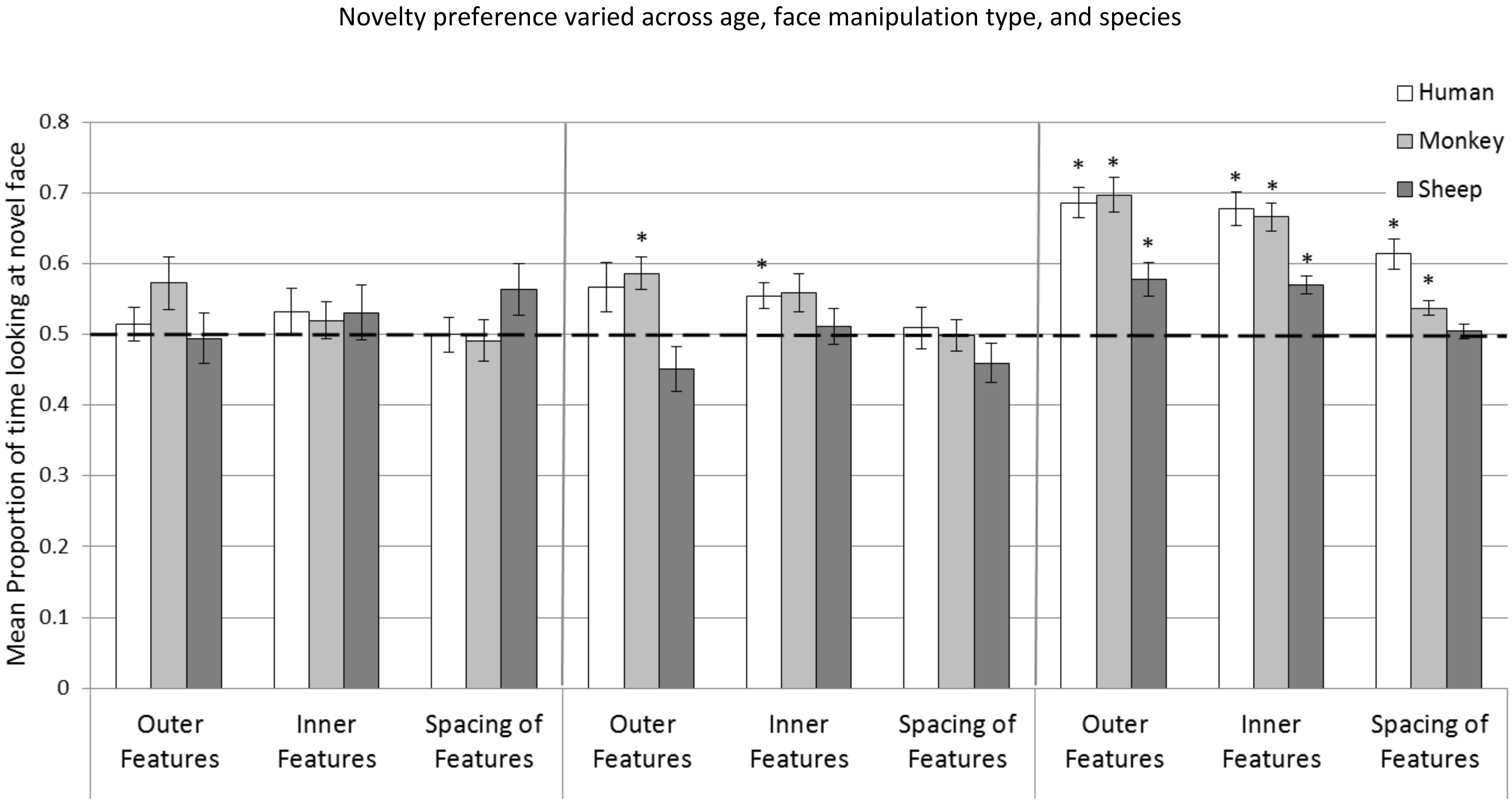


Figure 3.3. Mean proportion of time looking to the novel face, out of the total time looking to the faces, for the three face manipulation types (outer features, inner features, and spacing of features). Error bars represent one-sample *t* tests, to determine which conditions differed from chance (.50), at $^*p < .017$ (.05 divided by 3 tests for each group). Chance looking indicated by dashed line.

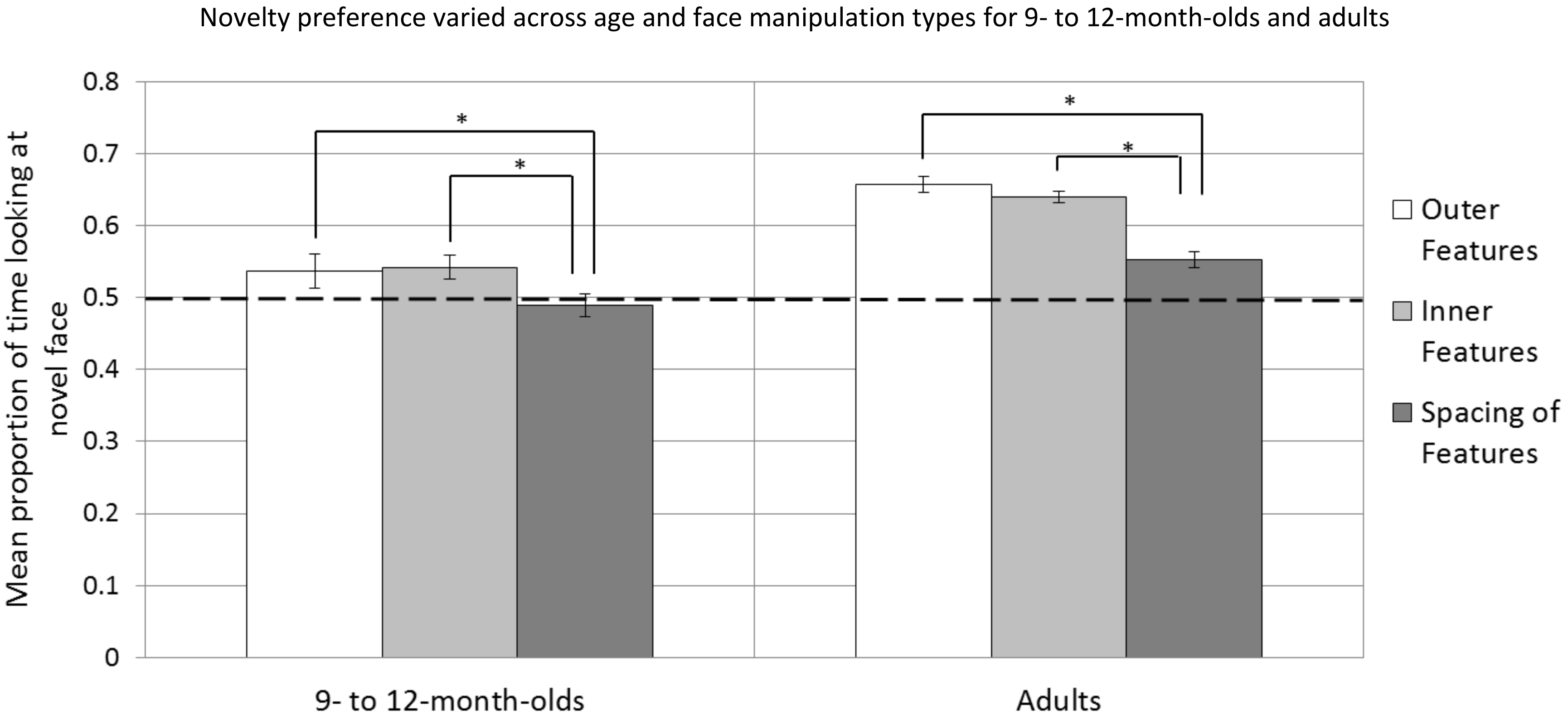


Figure 3.4. Mean proportion of time looking to the novel face, out of the total time looking to the faces, for 9- to 12-month-olds and adults, across the three face manipulation types (outer features, inner features, and spacing of features). Paired samples *t* tests within each age group,*$p < .05$, Fisher's LSD. Error bars reflect within subject standard error of the mean, corrected for between subjects variability (Morey, 2008). Chance looking indicated by dashed line.

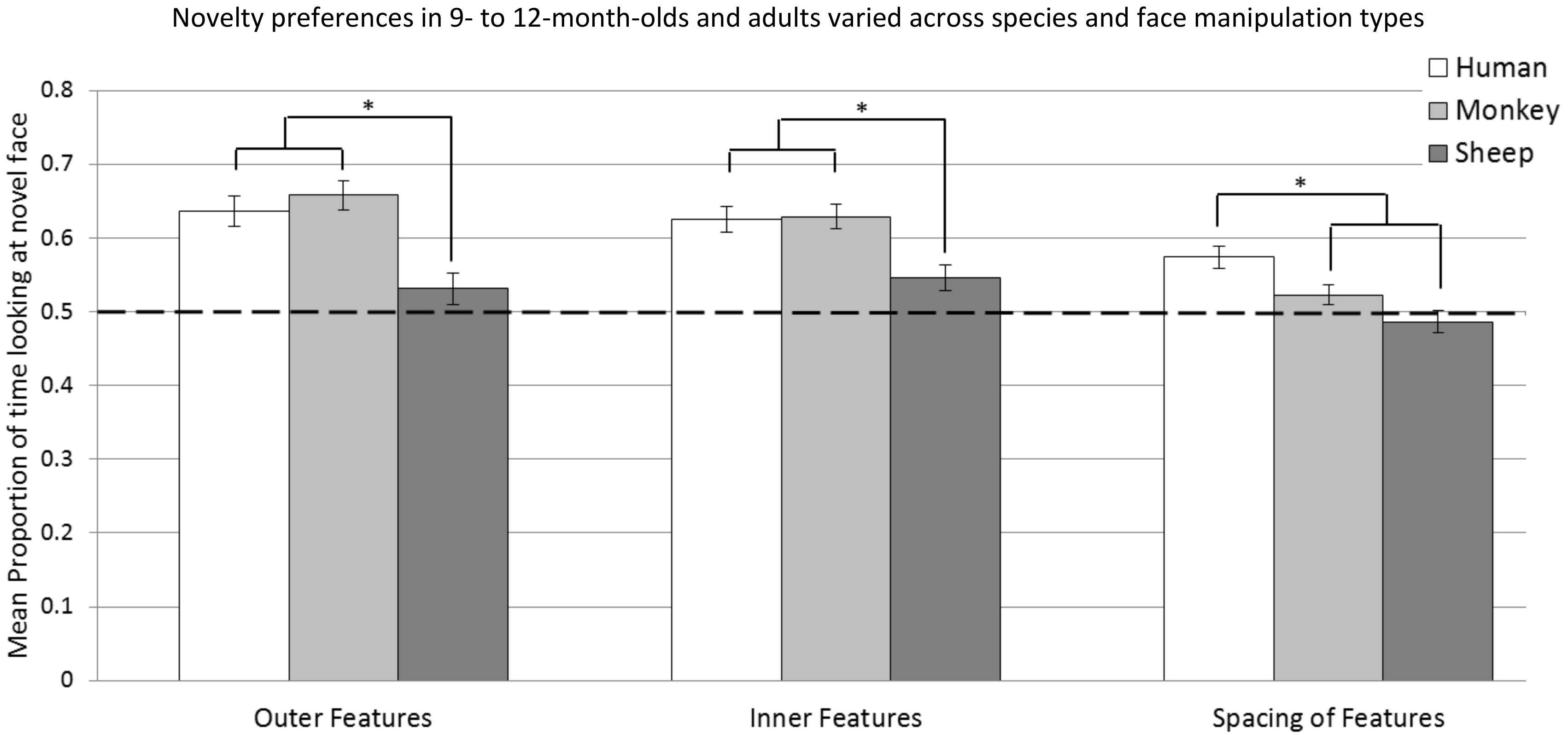


Figure 3.5. Mean proportion of time looking to the novel face, out of the total time looking to the faces, in 9- to 12-month-olds and adults, across the three face manipulation types (outer features, inner features, and spacing of features). Independent samples *t* tests,**p* < .05, Fisher's LSD. Error bars reflect between subjects standard error of the mean. Chance looking indicated by dashed line.

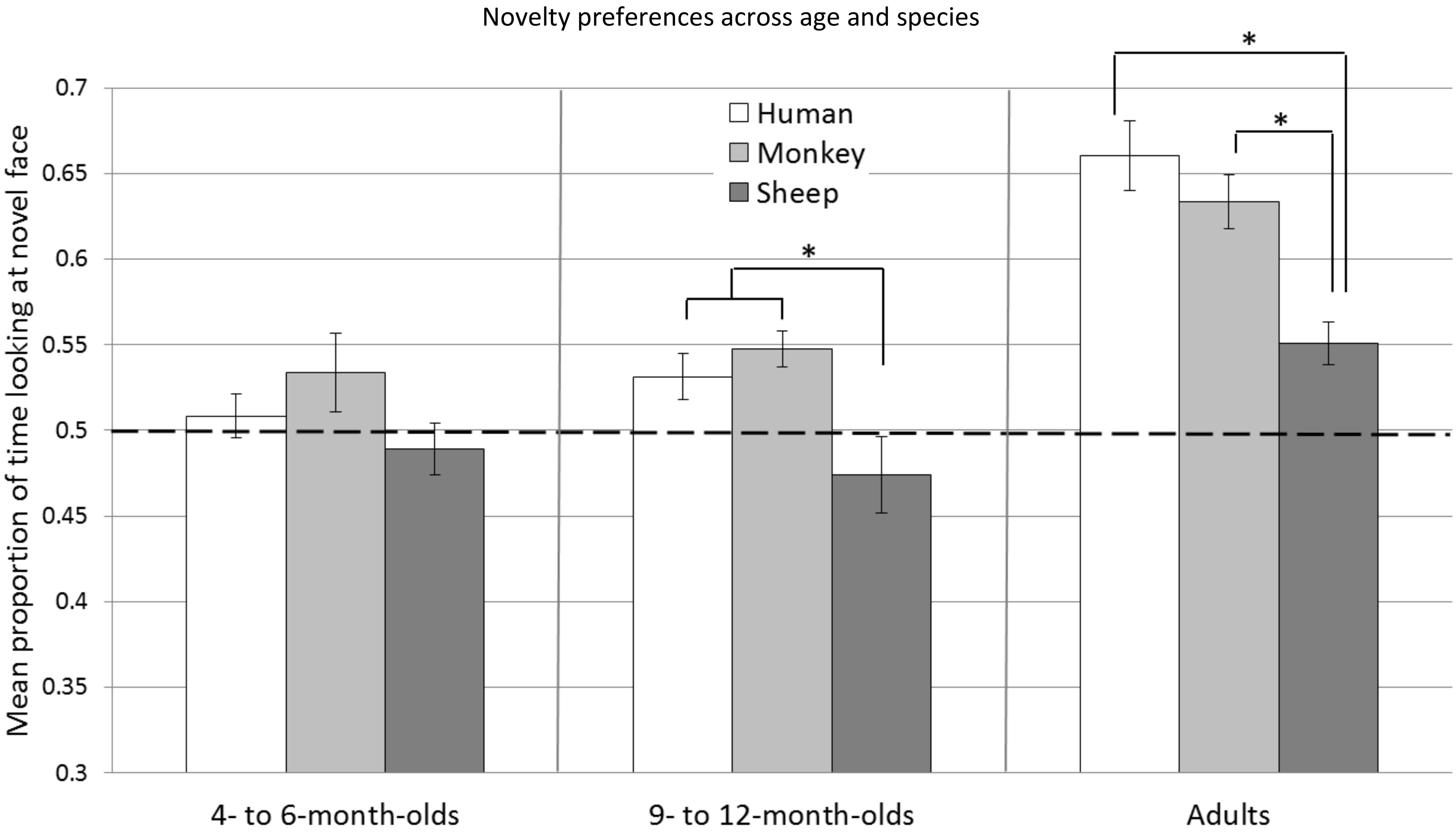


Figure 3.6. Independent samples *t* tests,*$p < .05$, Fisher's LSD. Error bars reflect between subjects standard error of the mean. Chance looking indicated by dashed line.

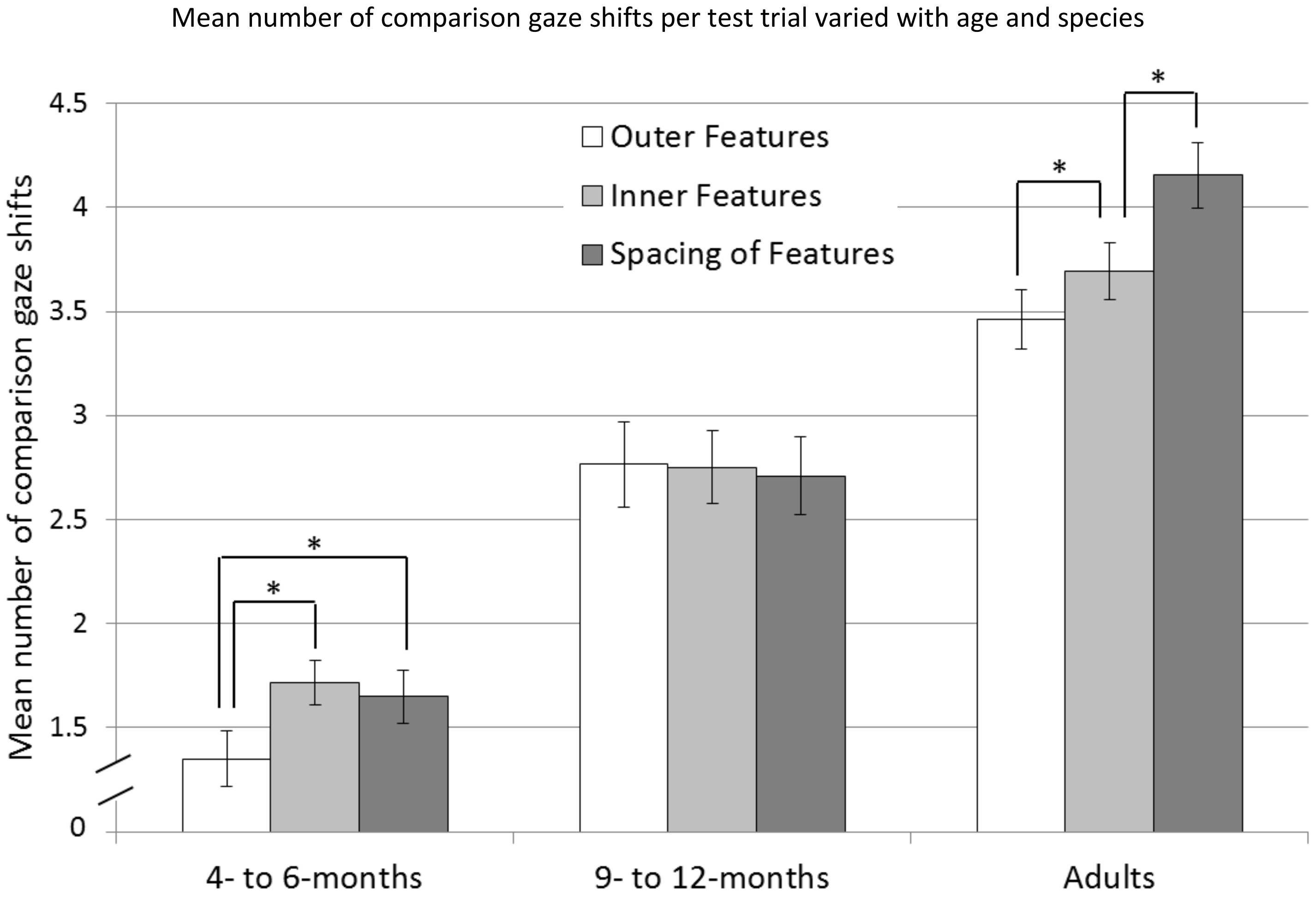


Figure 3.7. Error bars represent standard error of the mean for between subjects comparisons. * $p < .05$, Fisher's LSD.

CHAPTER 4

GENERAL CONCLUSIONS

For many species, perceiving and interpreting information conveyed by the face is necessary for living in complex social groups. In humans, the existence of a neural architecture specialized for faces (e.g., Farah, 1996; Pascalis & Kelly, 2009) is a testament to the evolutionary importance of faces. Faces convey rich amounts of information, including identity, age, sex, ethnicity, health, personality, and physical formidability, as well as emotional and attentional states (e.g., Naumann, Vazire, Rentfrow, & Gosling, 2009; Sacco, Hugenberg, & Sefcek, 2009; Sell et al., 2009). Humans possess a collection of skills to identify and interpret these diverse types of facial information. Face recognition has an extended period of development, not reaching adult levels—behaviorally and neurally—until adolescence or beyond (e.g., Germine, Duchaine, & Nakayama, 2011; Peelen, Glaser, Vuilleumier, & Eliez, 2009). Studies of the developmental emergence of specialized human face processing can inform our understanding of how facial information is processed, and what qualities of individuals and their environments influence face recognition. In the present studies, we examined the development of facial identity recognition, which is of great importance throughout development. As adults, distinguishing individuals is important for telling friends from foes, distinguishing competitors, and identifying mates; likewise, as infants, distinguishing individuals is important for recognizing family members, especially primary caregivers, who provide nourishment and protection, as well as for identifying strangers, who may pose a threat.

Face recognition has been the focus of study in newborns (e.g., Pascalis & Kelly, 2009), and young children (e.g., Crookes & McKone, 2009); however, less is known about older infants' face recognition (e.g., 3- to 12-month-olds). Additionally, though a number of studies have examined the perception of human faces, less work has examined humans' perception of animal faces. Such investigations can help determine the extent to which face recognition is species-specific. The species specificity of face recognition is a topic of great theoretical interest, given that the primary model of face discrimination for later infancy—perceptual narrowing—makes specific testable predictions about cross-species face recognition. One clear prediction is that infants early in life (i.e., before 6 months of age) have broad perceptual abilities, which allow them to distinguish individuals within a variety of species, and that perception narrows in the first year of life (by about 9 months of age) resulting in an improvement or specialization in the discrimination of human faces, along with a decline in the discrimination of animal faces (e.g., Pascalis, de Haan, & Nelson, 2002). According to this view, rather than being born human face specialists, infants are born face generalists, and become human face experts with experience (Nelson, 2001; for a recent review, see Slater et al., 2010).

Thus far, little work has examined face recognition in infancy, and that which has been done has only used primate faces (Pascalis et al., 2002; Pascalis et al., 2005; Scott & Monesson, 2009), or companion animal faces (Quinn & Eimas, 1996). These findings are limited in their generalizability to other species as recognition could be due to the fact that the species are either closely related (i.e., primates) or familiar (i.e., dogs and cats). Additionally, previous studies used natural faces, and therefore neglected to control for interindividual variability across species. Thus, findings of species differences could be due to differences in the variability within each species, with more variable species being easier to distinguish. Consequently, many questions remain regarding face recognition in the first year of life.

Though much work shows faces are processed differently from other visual stimuli (e.g., Young, De Haan, & Bauer, 2008), less work has directly compared the processing of human and nonhuman animal faces, or human and nonhuman primate faces. Such studies are important because they can clarify at what point in development, and through what processes, humans specialize in processing human (or primate) faces. As discussed previously, at least two models can account for face recognition in later infancy: perceptual narrowing, whereby infants are born with general face processing systems that are modified as a direct consequence of facial input (Nelson, 2001), and learned attention, whereby infants learn which face properties are useful for distinguishing individuals and selectively attend to those properties in particular (Heckler, Kaminski, & Sloutsky, 2006; Kruschke, 2001; Mackintosh, 1975). In the present studies, our goal was to examine the development of face recognition and the extent to which face recognition is species-specific. We tested predictions derived from both models of facial identity development (Chapters 2 and 3), and measured what face properties (outer features, inner features, spacing among inner features) are used across development (4- to 6-month-olds, 9- to 12-month-olds, adults) and across species (Chapter 3).

Summary of Findings from Present Studies

Breadth of Face Recognition Extends to Nonprimate Animal Faces

In our first study (Chapter 2), we examined the breadth of face discrimination in 4- to 6-month-olds, 9- to 11-month-olds, and adults, using a phylogenetically distantly related (i.e., nonprimate) animal: sheep (Simpson, Varga, Frick, & Fragaszy, 2010a, 2010b). Thus far, studies of perceptual narrowing have focused only on infants' face discrimination abilities for primates and companion animals (e.g., dogs); therefore, we examined facial discrimination of an unfamiliar nonhuman species. Infants' and adults' discrimination of sheep faces was assessed through a passive viewing visual paired comparison task using the continuous familiarization technique. This study assessed whether young infants have face recognition abilities that are broad enough to encompass even nonprimate animals, and whether this ability declines with age, as predicted by the perceptual narrowing model. We found 4- to 6-month-olds and adults discriminate sheep faces, but older infants (9- to 11-month-olds) showed no evidence of discrimination. Our findings suggest that early face discrimination is not exclusive to primate faces, but is broad enough to encompass nonprimate faces as well. These findings are consistent with a perceptual narrowing model of face recognition.

However, these findings are also consistent with an alternative model: learned attention (e.g., Heckler, Kaminski, & Sloutsky, 2006; Kruschke, 2001; Mackintosh, 1975). According to a learned attention model, infants do not lose the ability to discriminate unfamiliar faces, but instead attend to faces differently. Thus, there is not a loss of perception, but a change in attentional focus. Specifically, infants may learn certain face properties (e.g., eyebrows) are useful for distinguishing the faces to which they are most commonly exposed (e.g., human faces). They then attend more to these features at the expense of attending less to other features (i.e., learned inattention). Thus, if the properties of faces that vary in humans are different from the properties of faces that vary in other species' faces (as suggested by our measurements in Table 3.1), infants may appear to become worse at distinguishing animal faces. We tested this possibility by examining specific recognition processes in a second study (Chapter 3; Simpson, Varga, Frick, & Fragaszy, 2011, in preparation).

Properties of Faces Viewers Can Use for Discrimination Vary across Age and Species

Though nonprimate faces are discriminated in infancy and adulthood, whether nonprimate faces are recognized in the same way as primate faces remained untested. The perceptual narrowing model makes no predictions about specific face recognition processes, but simply predicts a decline in animal face recognition, with a concurrent improvement in human face recognition, in the first year of life. The learned attention model, in contrast, predicts an increase in attention to face properties that can be used to distinguish individual human faces. To the extent that those same processes are also useful for distinguishing nonhuman faces, there should likewise be an increase in discrimination abilities for animal faces as well.

To this end, in our second study (Chapter 3) we sought to test face recognition more systematically, through using carefully controlled faces matched on their face properties that varied (Simpson et al., 2011, in preparation). We measured 4- to 6-month-olds', 9- to 12-month-olds', and adults' discrimination of systematically manipulated faces of humans, monkeys, and sheep, also in a visual paired comparison task. We ensured that species differences were not due to differences in the variability among species (with some species being more variable and therefore easier to discriminate than others). This method allows us to conclude that differences found across species are not due to differences in each species' individual variability, and therefore provided stronger evidence that not all species' faces are discriminated equally well across development. This study also explored whether infants and adults discriminate faces that vary only in their features (e.g., eyes, mouths), the spacing among the features, and the head contour, in human, nonhuman primate, and nonprimate animal faces.

We found 4- to 6-month-olds did not discriminate systematically varied faces. This result is inconsistent with previous findings that young infants can discriminate natural human, monkey, and sheep faces. Our findings suggest that young infants typically rely on more than one feature for face discrimination; therefore, when we varied only one feature at a time, recognition was difficult. We also found that older infants discriminated human and monkey faces, and adults discriminated all three species. These findings are inconsistent with predictions based on the developmental process of perceptual narrowing. Perceptual narrowing predicts a decline in the breadth of face recognition with age; instead, we found an increase in the number of species discriminated with age. Thus, a perceptual narrowing model of the development of facial identity discrimination did not make accurate predictions.

Our second study revealed another interesting pattern: the number of face properties that can be discriminated increases with age, and are used to unequal degrees across primate and nonprimate faces. Specifically, primate faces (humans and monkeys) can be discriminated using configural processing (i.e., spacing among inner facial features), while nonprimate (sheep) faces can only be distinguished using feature-based processing, relying on the eyes, mouth, or outer features of the face. Differences in processing primate and nonprimate faces were not present in the younger infants, but were present in the older infants and adults, suggesting we may begin to specialize in processing primate faces as we get older. Also, adults may employ human face recognition processes with other primates' faces, but not with nonprimate faces. Finally, we found human faces were special for adults in that adults had greater novelty preferences—indicating easier discrimination—for faces varying in their spacing for human faces moreso than either monkey or sheep faces. Thus, configural or holistic processing may be more automatic for human faces.

Practical Implications

Understanding human face recognition will aid in the development of automatic face recognition systems, a goal of computer vision researchers (Sinha, Balas, Ostrovsky, & Russell, 2006). Additionally, this research has implications for clinical psychology, as a number of populations suffer from face recognition deficits, including individuals with prosopagnosia

(Duchaine & Nakayama, 2006; Farah, 1996), autism (Klin et al., 2004), Turner's Syndrome (Elgar & Campbell, 2001), William's Syndrome (Elgar & Campbell, 2001), the elderly (Ferris, Crook, Clark, McCarthy, & Rae, 1980), and even family members of individuals with autism (e.g., parents and siblings; Dawson, 2008).

Our investigation contributes to the understanding of such disorders by elucidating developmental processes subserving facial identity recognition. Deficits in face recognition in autism have been specifically linked to impairments in configural processing (Behrmann et al., 2006), which highlights the need for understanding the development of different face recognition processes. In addition, individuals with cataracts for the first months of life are not exposed to faces during the critical period in development and consequently experience impairments in configural processing (Le Grand, Mondloch, Maurer, & Brent, 2003). An understanding of healthy face perception will inform studies of social pathology in psychiatric disorders (Elgar & Campbell, 2001). This understanding may lead to early tests to identify deficits in face recognition, which—if identified prior to critical periods in development—will allow for more effective treatments (e.g., Dawson, 2008) or training procedures (Powell, Letson, Davidoff, Valentine, & Greenwood, 2008) to improve face recognition in individuals with impairments.

Future Directions

Given that a perceptual narrowing model of facial identity development does not provide accurate predictions with regard to animal face discrimination (Chapter 3), alternative models should be tested. One alternative, as described earlier, is learned attention (e.g., Heckler et al., 2006; Kruschke, 2001; Mackintosh, 1975). With experience, humans learn what to attend to and what to ignore. The properties of faces that vary (e.g., distance between the eyes, length of the mouth) are not the same for humans, monkeys, and sheep (Simpson et al., 2011, in preparation).

Consequently, in the first year of life, infants learn what face properties to attend to for distinguishing individuals (e.g., eyes) and which are not useful (e.g., general configuration of the faces, accessories). Early in development young infants (i.e., 4- to 6-month-olds) may be better at discriminating animal faces, compared to older infants (i.e., beyond 9 months of age), because they do not yet exhibit learned attention biases to only some face properties. Thus, older infants are not as good at discriminating animal faces because they are selectively attending to the wrong features, due to their experience with primarily human faces. Thus, difficulties in discriminating natural animal faces in later infancy and beyond is not a reflection of limited of perception—as proposed by perceptual narrowing—but instead, is a limitation of attention. Some species' faces (e.g., sheep) are more difficult for older individuals to identify because older individuals are looking at the wrong features. Evidence in support of learned attention comes from a study in which adults were trained to attend to certain features of faces, and this training resulted in a reduction of the own-race bias, through shifting attention to relevant features (Hills & Lewis, 2006). Similarly, counter-training may be used in infants and to shift attention to certain face properties that would improve discrimination of different species' faces. For example, an older infant may be trained to attend to properties of sheep faces that are useful for discrimination.

Learned attention of facial identity recognition could also be tested through examining gaze patterns across development, to see if the facial features that are the most varied within a given species are the ones that receive the most attention. A learned attention model predicts that early in infancy infants would not yet have learned what features to attend to, so all animal faces would be processed in similar ways. However, by older infancy, and into adulthood, the features that vary the most in humans may be the ones that receive the most attention across all species. If this prediction is true, older infants and adults may be attending to the face properties that aid in human face recognition for all species. Sensitivity could be measured by determining whether facial feature variation predicts gaze fixation. In addition, the amount of time looking to the inner contents of the faces of out-group, but not in-group members, decreases with age (Liu et al., 2011). There may be a similar developmental change in viewing patterns for viewing nonhuman animal faces. Eye tracking methods could also be employed to measure the parts of the face (e.g., outer features, eyes) used for recognizing human and animal faces.

I am also interested in exploring similarities and differences in the ways that human and animal faces capture and hold attention, to see if these patterns are consistent with the predictions of perceptual narrowing. In the our second study (Chapter 3) we found infants and adults looked more often to the novel face at the beginning of each test trial, suggesting their attention was captured by the novel face. To explore attention capture of human and animal faces I am now using the pop-out effect paradigm, in which adult participants are instructed to find a target (e.g., monkey face) among distracters (e.g., non-primate animal faces). If parallel processing is used, the target appears to pop-out, and is found relatively quickly. If serial processing is used—and the viewer must search through all the distracters to find the target—then the target does not appear to pop-out, and if found relatively slowly. Though human faces pop out when surrounded by animal faces, the reverse is not true (Hershler & Hochstein, 2005). I am currently examining whether this effect extends to primate faces. In other words, do primate faces pop out, when surrounded by nonprimate animal faces? The extent to which faces of different species pop-out across development has yet to be explored. This is a theoretically interesting question, as the perceptual narrowing model makes predictions that early in infancy—before narrowing occurs—all animal faces should pop out equally, among non-face distracters. By late infancy—after about nine months—only human faces should pop out. Alternatively, there may be something special about primate faces, which are processed differently from nonprimate faces, and therefore capture attention differently. In the future we plan to examine the developmental emergence of the pop-out effect through eye tracking with infants in the first year of life.

Conclusions

The studies reported here further our understanding of the emergence of humans' face recognition through revealing its breadth early in life and uncovering the different face properties that are used for facial identity discrimination. Importantly, our findings are inconsistent with a perceptual narrowing model. Instead, the development of face recognition is better modeled by taking into account the roles of learning and attention, as they mediate perception. This work contributes broadly to our understanding of visual attention, social perception, learning, and skill development.

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