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The Development of Facial Identity Discrimination Through Learned Attention

ABSTRACT: *Learned attention models of perceptual discrimination predict that with age, sensitivity will increase for dimensions of stimuli useful for discrimination. We tested this prediction by examining the face dimensions 4- to 6-month-olds (n = 77), 9- to 12-month-olds (n = 66), and adults (n = 73) use for discriminating human, monkey, and sheep faces systematically varying in outer features (contour), inner features (eyes, mouth), or configuration (feature spacing). We controlled interindividual variability across species by varying faces within natural ranges and measured stimulus variability using computational image similarity. We found the most improvement with age in human face discrimination, and older participants discriminated more species and used more facial properties for discrimination, consistent with learned attention models. Older infants and adults discriminated human, monkey, and sheep faces; however, they used different facial properties for primates and sheep. Learned attention models may provide insight into the mechanisms underlying perceptual narrowing.* © *2014 Wiley Periodicals, Inc.* Dev Psychobiol

Keywords: *facial identity; visual attention; facial feature; configural processing; discrimination; learned attention; perceptual narrowing; human infant; computation simulation method; systematically varied faces; monkey faces; sheep faces*

INTRODUCTION

Humans possess remarkable face discrimination abilities, even as newborns (e.g., Turati, Macchi Cassia, Simion, & Leo, 2006). 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. For example, studies with infants have found that young infants discriminate a variety of species' faces, but with age there is a decline in animal face discrimination (e.g., McKone, Crookes, & Kanwisher, 2009; Pascalis, de Haan, & Nelson, 2002; Pascalis et al., 2005; Scott & Monesson, 2009; Simpson, Varga, Frick, & Fragaszy, 2011). In the present investigation, we sought to better understand potential mechanisms of this differential discrimination across species by examining the extent to which different facial properties are used for face discrimination across development for different species' faces. Specifically, our first goal was to test whether infants and adults can use feature-based and configural processing for human and animal face recognition. Second, we tested learned attention models of facial identity development and considered whether our results are consistent with perceptual narrowing. Previous studies that have attempted to examine differences in the development of facial identity discrimination of human and animal faces have encountered some challenges, described further below, which may limit the conclusions of previous work. Thus, our third goal was to overcome these challenges through the use of systematically varied faces that varied to a natural

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degree, and to determine whether there are differences in the development of discriminating human and animal faces when controlling for this variability.

FEATURE-BASED AND CONFIGURAL PROCESSING

Two types of face processing are commonly examined. Feature-based processing is discrimination based on individual facial features (e.g., eyes, eyebrows, nose), such as size, shape, texture, or color. Configural processing is based on sensitivity to three things (Maurer, Le Grand, & Mondloch, 2002): (1) *First-order relations* refer to the relative position of the features that allow one to identify a stimulus as a face (e.g., the eyes are above the nose, which is above the mouth). (2) *Second-order relations* refer to the spacing among the features (i.e., the distances between the features themselves, such as the space between the eyes or how far the nose is above the mouth), within the context of a normally configured faces (eyes above the nose, and nose above the mouth). (3) *Holistic processing* refers to perceiving the face as an unbroken whole with the parts integrated into a whole, rather than as a collection of features, or "glueing [*sic*] together the features into a gestalt" (Maurer et al., 2002, p. 255), representing a fusion of both featural and configural information. Researchers disagree on the relative importance of different types of processing used for facial identity discrimination, as well as their developmental emergence (for recent reviews see Kadosh, 2011; McKone, Crookes, Jeffery, & Dilks, 2012; Meinhardt-Injac et al., 2011).

Previous studies have attempted to isolate feature-based and configural processing of faces to determine the relative extent to which they are used in facial identity discrimination throughout development, but the findings thus far have been unclear. Most of these studies used methods based on the inversion effect, which is a phenomenon in which viewers are worse at recognizing an inverted image, relative to an upright image; this effect is especially large for faces relative to other objects (e.g., Kohler, 1940; Yin, 1969). Though the inversion effect is generally accepted to reflect a disruption of configural processing (Richler, Mack, Palmeri, & Gauthier, 2011; Yin, 1969), feature-based discrimination may also be disrupted (Rhodes, Brake, & Atkinson, 1993). This is problematic because many studies assume that the inversion effect is indicative of configural face processing; therefore, the face inversion paradigm may not be well suited to identify an individual's face discrimination strategies (Dahl, Logothetis, & Hoffman, 2007). Thus, in our current study we isolated feature-based and configural processing using systematically varied faces. However, before describing this method, it is useful to consider how researchers conceptualize the development of face discrimination.

PERCEPTUAL NARROWING

The manner in which humans' face expertise emerges during infancy remains largely unknown (Pascalis & Kelly, 2009). Most work examining the developmental emergence of facial identity discrimination in infancy beyond the newborn period (i.e., from about 4 to 12 months of age) has been explained within a framework known as perceptual narrowing (for a review see Pascalis & Kelly, 2009). Perceptual narrowing is described as a domain-general process in which infants are born with broad perceptual abilities to discriminate stimuli; these perceptual abilities change as a function of age and experience, such that perceptual discrimination increases for familiar stimuli, while it decreases, or fails to increase, for unfamiliar (Scott, Pascalis, & Nelson, 2007; Werker & Tees, 2005). Nelson (2001) suggested that perceptual narrowing may occur for facial identity discrimination. Indeed, young infants (4- to 6-month-olds) outperform older infants (9- to 12-month-olds) on the discrimination of nonhuman animal faces, including monkeys (e.g., Pascalis et al., 2002) and sheep (Simpson et al., 2011). Work with both infant monkeys (e.g., Sugita, 2008) and humans (e.g., Scott & Monesson, 2009) demonstrates that perceptual narrowing of particular species' faces can be altered as a function of early exposure. It appears that the nature of this early exposure is also of utmost importance: 6-month-old human infants trained for 3 months with individually named monkey faces (e.g., Boris) continued to discriminate individuals of this species at 9 months, but infants who received training at the categorical level (i.e., referring to all individuals as "monkey"), like infants who received no training at all, failed to demonstrate discrimination at 9 months (Scott & Monesson, 2009). This suggests that, with typical human experiences, while discrimination of own-species faces may improve with age, discrimination of nonhuman animal faces appears to decline.

Relatively little is known, however, about *how* changes in face discrimination occur or what facial properties can be used for discrimination (Balas, 2012). In fact, recent work measuring event-related potentials (ERPs) demonstrates that apparent declines in face discrimination for less familiar face types (e.g., other-age faces) may in fact reflect changes in later-stage processing, namely, memory retrieval, rather than changes in early-stage perceptual processing or perceptual expertise (Wiese, Wolff, Steffens, & Schweinberger, 2013). If this is the case, then the description of this pattern as *perceptual* may in fact be misleading. In support of this, others have found that 12-month-olds can discriminate monkey faces, if given sufficient familiarization time (Fair, Flom, Jones, & Martin, 2012), consistent with the notion that the apparent decline in unfamiliar face discrimination may actually be a consequence of memory rather than changes in perceptual expertise. In the present study, our goal was to examine whether there are developmental models that can bring additional insight to our understanding of facial identity discrimination.

LEARNED ATTENTION AND PERCEPTUAL LEARNING MODELS

One model of early developmental patterns of face discrimination, which addresses these questions, but has not yet received thorough consideration in the perceptual narrowing literature, is Mackintosh's (1975) classic model of attention. According to this model, learned attention is a phenomenon in which individuals can learn to attend to certain properties of a stimulus, usually through shifting attention away from less 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 individual will learn to ignore this contrast (i.e., learned inattention). This model is congruent with Gibson's perceptual learning model (1969): developing perceptual expertise in any domain involves "an increase in the ability to extract information from the environment, as a result of practice" (p. 3). According to this view, with age, perceptual abilities become increasingly differentiated and refined, allowing for the extraction of new information (Gibson & Gibson, 1955). Perceptual learning may be important for face discrimination (Goldstone, 1998). For example, repeated exposure to particular types of faces may result in the acquisition of a face schema; the more a given face varies from this schema, the less efficiently it may be processed (Chance, Goldstein, & McBride, 1975). This is consistent with the multidimensional face space model (Valentine, 1991), that there may be a face prototype that is broad from birth, but changes after exposure to certain face types, resulting in differential sensitivities to different face dimensions, with some carrying more weight than others (Balas, 2012; Pascalis & Kelly, 2009). Because human and animal faces may vary in the features that best distinguish individuals (see Tab. 1 for more details on this), humans may become worse at distinguishing animal faces with age because they are attending to the wrong face properties: those predictive of individual differences in humans, but not animals. Further evidence in support of the importance of attentional processes in perceptual narrowing come from findings that improving selective attention may attenuate the typical developmental decline in animal face recognition (Zhang, Guy, Reynolds, Jewett, & Whitfield, 2012); such questions deserve further study.

The present investigation allows us to begin to test *how* developmental changes in facial identity discrimination occur, and whether infants and adults can recognize equivalent changes in carefully controlled human and animal faces, as predicted by learned attention models. For example, infants must learn which properties of faces aid in discrimination (e.g., eyes, eyebrows) and which do not (e.g., first-order relations). Our measurements (see Tab. 1)—to be described in detail later—suggest that human and animal faces may vary in the features that best distinguish individuals (i.e., the features that help humans distinguish humans' faces are different from the features that help humans distinguish other animals' faces). As a consequence, humans may become worse at distinguishing animal faces with age because they are attending to the wrong properties of faces: those predictive of individual differences in humans, but not animals.

METHODOLOGICAL CHALLENGES

Researchers have encountered methodological challenges in attempts to determine which models of face discrimination best account for developmental changes (for a review, see Hole & Bourne, 2010). In particular, we have two concerns regarding previous work on face discrimination that may limit the interpretation and generalizability of existing findings.

Remaining Within the Natural Range of Variability of Faces

Researchers have attempted to isolate the properties of faces that can be used for discrimination through the use of systematically varied faces (Bhatt, Bertin, Hayden, & Reed, 2005; Dahl et al., 2007; Freire, Lee, & Symons, 2000; Le Grand, Mondloch, Maurer, & Brent, 2001; Martin-Malivel & Okada, 2007; Schwarzer, Zauner, & Jovanovic, 2007; Scott & Nelson, 2006; Sugita, 2008, 2009). However, Taschereau-Dumouchel, Rossion, Schyns, and Gosselin (2010) propose that many previous studies that use these faces have low ecological validity because the amount of variability in

Table 1. Measurements of Variability of Natural 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	.08	50	6	.12	18	4	.21	2.8	.067	n.s.
Height of right eye	14	2	.16	28	3	.11	13	4	.28	.99	.38	n.s.
Width of nose	55	5	.09	68	6	.09	77	8	.1	3.49	.035	S > H
Length of nose	66	8	.12	65	10	.15	137	14	.1	8.35	<.001	H > S; M > S
Width of mouth	75	8	.1	97	18	.19	93	17	.18	7.31	.001	M > H; S > H
Height of mouth	28	7	.26	19	5	.29	0	0	0	25.62	<.001	H > S; M > S
Width of left ear	26	7	.26	20	18	.89	0	0	0	81	<.001	M > H > S
Shape and size of head												
Height of face	371	7	.02	367	13	.04	307	15	.05	4.08	.02	S > M
Width of face at eyes	205	11	.05	224	15	.06	209	13	.06	.7	.5	n.s.
Width of face at mouth	181	14	.08	234	24	.1	93	17	.18	3.23	.04	M > H
Configuration of features												
Distance between eyes	56	6	.11	48	7	.15	151	8	.06	3.82	.026	H > S
Tip of nose to chin	113	12	.11	109	18	.17	51	13	.26	1.48	.23	n.s.
Mouth to chin	60	9	.15	57	20	.35	17	7	.44	6.96	.002	S > M > H
Between eyes top head	190	12	.06	180	19	.11	92	9	.1	6.03	.004	M > H; M > S
Angle of pupil, nose	51	5	.09	55	8	.14	61	4	.07	4.53	.013	M > H; M > S
Luminosity	192	12	.06	164	12	.07	227	5	.02	8.2	.001	H > S; M > S
Attractiveness	3.2	1.3	.41	3	1.6	.53	3.1	1.7	.55	.35	.7	n.s.
Distinctiveness	4.3	.8	.186	3.9	.4	.103	3.6	.4	.111	4.9	.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. Length measurements are in pixels, and angle measurements are in degrees. All measurements were taken using Adobe Photoshop. Human adults ($n = 27$) rated faces on attractiveness and distinctiveness using a seven-point scale from 1 (very unattractive or not very distinctive) to 7 (very attractive or distinctive). n.s. $= p > .05$.

the spacing of facial features in these stimuli is not reflective of the natural variations in feature distances in real faces. These researchers (Taschereau-Dumouchel et al., 2010) found adults had poor discrimination of human faces that varied in the spacing of their inner features to a natural degree, suggesting adults may not rely on configural processing to the extent previously suspected.

Comparing Face Discrimination of Different Species

Our second concern stems from the fact that much previous work (e.g., Dufour, Coleman, Campbell, Petit, & Pascalis, 2004; Pascalis et al., 2002; Simpson et al., 2011) measured discrimination of photographs of natural faces. Natural faces of different species may not vary equivalently; that is, some species may be more variable in certain perceptual properties, and therefore, more easily discriminated relative to others. Thus, two potential explanations exist for previous findings of differential discrimination of various species (i.e., decline in discrimination with age for animal faces, relative to human faces). One possibility is that human and nonhuman faces are discriminated differently due to high-level (i.e., categorical) qualitative differences in the ways humans process human and nonhuman faces. For example, with age, humans may specialize in the discrimination of human faces, and begin to process human faces holistically, while processing nonhuman faces using features (e.g., Itier, Latinus, & Taylor, 2006). Another possibility is that human and animal faces are recognized in similar ways, and apparent differences found previously are simply due to the fact that some species have greater interindividual variability than others (Martin-Malivel & Okada, 2007). Differences in discrimination across species may be due to unaccounted-for interstimulus perceptual (physical) variance; therefore, comparisons between conditions that differ both in species and in interstimulus perceptual variance are difficult to interpret. One way of addressing this problem is by selectively exposing infants to certain face types (e.g., certain species) to see if these early experiences shape discrimination abilities. Specifically, Sugita (2008) found that monkeys deprived of early experiences with faces, then selectively exposed to either human or monkey faces, demonstrate retained perceptual discrimination for the faces of the species to which they were selectively exposed, even if this species is not their own species. Interstimulus perceptual variance cannot account for these results. Of course, in studies with human infants it is impossible to deprive them of early face exposure for ethical reasons. Instead, this study took a different approach by controlling the interstimulus perceptual variance of facial stimuli of three different species.

PURPOSE AND PREDICTIONS

The current study was conducted in an attempt to overcome these previous limitations, by using systematically varied faces to test whether humans' differential discrimination across species may be due to differences in interindividual variability. The systematically varied sets of faces included three species: humans, capuchin monkeys, and sheep (see examples in Fig. 2). Each face set contained three types of faces: one which varied in the identity of the inner features (i.e., eyes and mouths; Fig. 2A), a second set which varied in the outer features (i.e., external contours, such as the chin and hair; Fig. 2B), and a third which varied in the location of the facial features (i.e., location of the eyes and mouths; Fig. 2C). Face sets were created such that variability was more equally matched across species than in previous studies; further, the variability in these features was designed to fall within the limits of natural variability observed in the population. This method additionally allowed for selective alterations of facial properties to examine whether viewers use feature-based or configural processing strategies for facial identity discrimination. This method of using systematically varied faces is in contrast to previous studies documenting perceptual narrowing for facial identity discrimination across species (e.g., Dufour et al., 2004; Pascalis et al., 2002; Simpson et al., 2011), which used natural human and animal faces. Our use of systematically varied faces made discrimination more challenging.

We examined the development of facial identity discrimination by 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 in which participants were first presented with a face (which became the "familiar" face), then were presented with up to 30 test trials in which they viewed the same familiar face alongside a novel face which changed on each trial. This method is commonly used for measuring visual recognition memory in infants (Fagan, 1970; Hole & Bourne, 2010), and is based upon assumptions of the exploratory looking model (Hunter & Ames, 1988). We chose these age groups in order to assess face discrimination before perceptual narrowing (4- to 6-month), immediately following perceptual narrowing (9- to 12-month-olds), and in adulthood. According to the exploratory looking model (Fig. 1), looking follows a consistent pattern throughout development in which viewers initially show familiarity preferences for stimuli to which they are first exposed, and for which they need longer familiarization times to fully encode and process. Once a stimulus is fully encoded, viewers look longer to a novel stimulus with which the familiar stimulus is paired. That is, if a stimulus is not well encoded, viewers will exhibit either a familiarity preference or no preference at all (Pascalis & de Haan, 2003). Relative looking to novel stimuli served as the dependent measure across all conditions.

Consistent with perceptual narrowing, learned attention models predict faster development of discrimination for human faces, compared to monkey and sheep faces, as a consequence of experience, which is

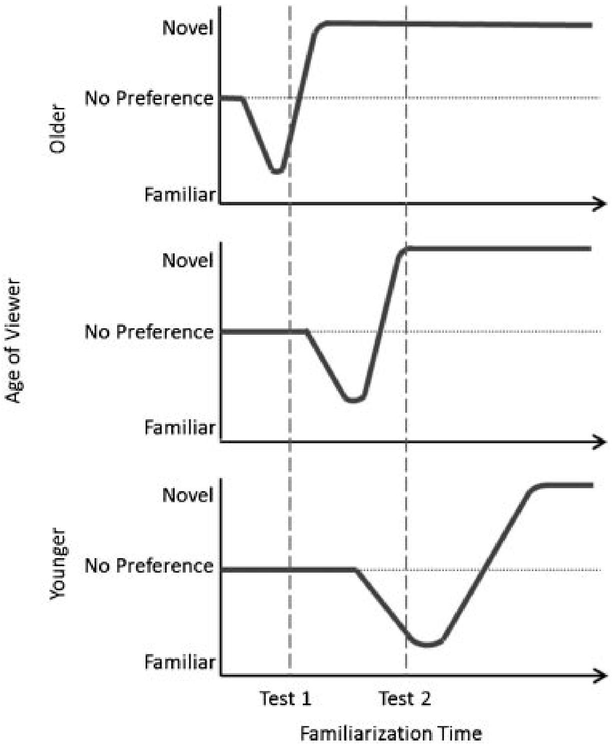

FIGURE 1 Exploratory looking model (adapted from Hunter & Ames, 1988). Looking follows a consistent pattern, whereby the longer an individual is familiarized with a visual stimulus, the more likely that individual is to show first a familiarity preference, followed by a novelty preference. With age, information is processed more quickly, thus individuals go through this pattern at a faster rate, with younger individuals (bottom graph) needing a longer familiarization time to show preferences, and older individuals (top graph) needing only a shorter familiarization time to show preferences. Thus, tests of looking preferences at different time points (e.g., *Tests 1 and 2*) can reveal different preferences across age groups. Reproduced with permission.

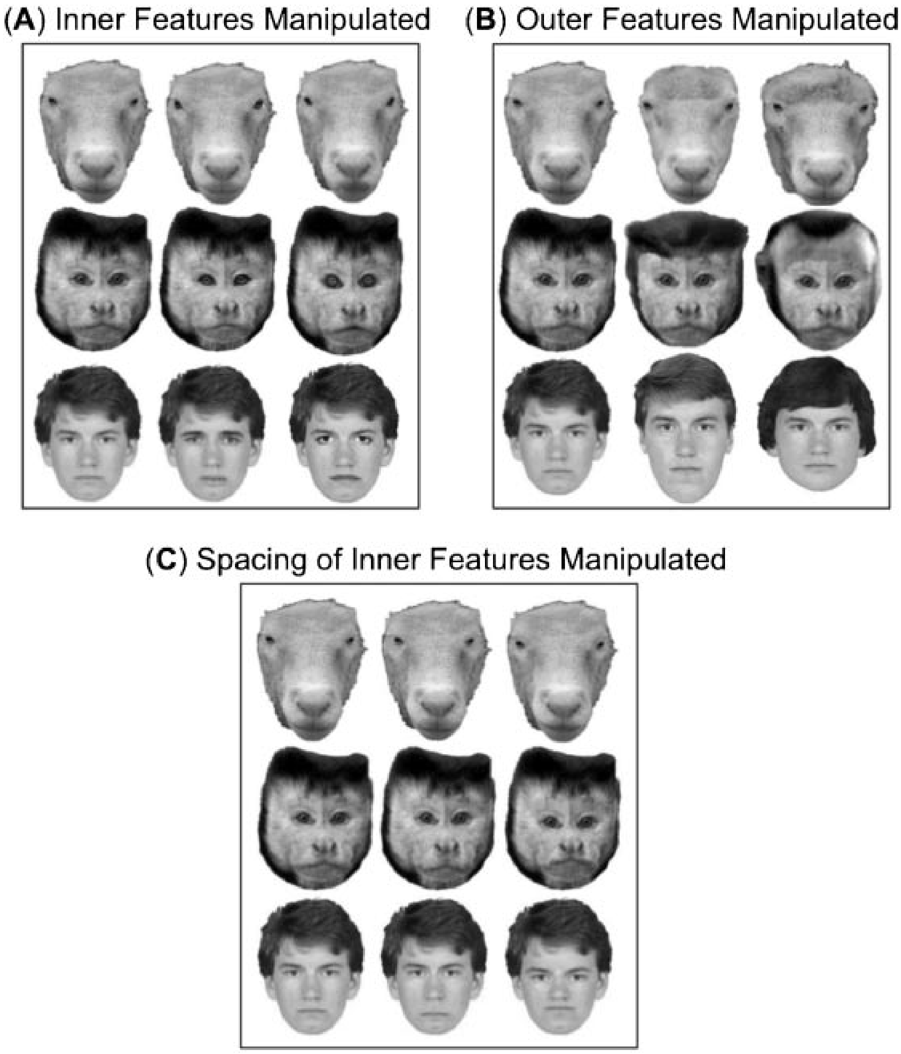

FIGURE 2 Sample face stimuli. A natural face (far left in each box) served as the familiar face, and was used to create three new face sets, which varied in: (A) inner facial features (eyes, mouth), (B) the outer facial features (contour, hair), and (C) the spacing among the inner features.

typically greater with one's own species relative to other species. The learned attention models additionally predict that improvements in discrimination occur through various mechanisms, including *attention weighting*—increased attention to important dimensions relative to unimportant dimensions—and *imprinting*—increased sensitivity or specialization for stimuli or parts of stimuli (Goldstone, 1998). That is, there should be an improvement in face discrimination for human faces, and species that share important features with human faces (e.g., other primates), from 4 to 6 months to 9 to 12 months, then additionally from 9 to 12 months into adulthood. These models also predict that, with age, there will be an increase in the number of facial properties that can be used for discrimination, a mechanism known as *unitization* (Goldstone, 1998). It is noteworthy that while the perceptual narrowing perspective predicts that with age there will be improvements in human face discrimination, but little or no improvements in animal face discrimination, the learned attention model predicts there will be improvements in both human and animal face discrimination, particularly for animals that share face properties with humans, such as other primates.

METHODS

Participants

The participants were 77 healthy 4- to 6-month-olds (age range: 121–192 days; 34 females; 70% Caucasian), 66 healthy 9- to 12-month-olds (age range: 280–364 days; 27 females;

85% Caucasian), and 73 healthy adults (age range: 17–60 years; 64 females; 72% Caucasian). Names were obtained from newspaper birth notices, followed by telephone recruitment. 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%; e.g., Fisher-Thompson & Peterson, 2004), and adults ($n = 4$) excluded for not following directions.

Apparatus

Testing took place within a darkened and quiet room. 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. The goal of this study was to create systematically varied faces that were closely matched in the variability of their properties. To this end, we first gathered 90 natural face photos: 30 male human faces, 30 male capuchin monkey (*Cebus apella* spp.) faces, and 30 female sheep (*Ovis aries*) faces. Of the 30 human faces, 16 were from the NimStim Face Stimulus Set (Tottenham et al., 2009), and 14 were 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 et al., 2007), ages (e.g., Kuefner, Cassia, Picozzi, & Brocolo, 2008), and between male and female faces (Ramsey, Langlois, & Marti, 2006), these factors were kept uniform by using all Caucasian male faces. Twenty monkey photos were used 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 provided 30 sheep photos (Kendrick, da Costa, Leigh, Hinton, & Peirce, 2001). The human face photos all had neutral expressions, as rated by adult observers (Matsumoto & Ekman, 1988; Tottenham et al., 2009). Expressions were rated as neutral for both monkeys (Simpson, 2008) and sheep (Reefmann, Kaszàs, Wechsler, & Gygax, 2009).

Next, we selected 18 properties of faces that are known to influence discrimination (e.g., Sadr, Jarudi, & Sinha, 2003; Schwarzer et al., 2007); these properties were measured in our 90 natural faces using Adobe Photoshop (further details about how variation of facial features was measured can be found in Tab. 1). We found that the properties of the faces (e.g., distance between the eyes) did not vary equally across species, consistent with evolutionary models of individual differences in appearance (for a review see Tibbetts & Dale, 2007). To determine whether the natural faces of one species were 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, $F(2, 48) = 1.48$, $p = .24$. However, this is not to say that the species did not differ in their variability of particular facial features, so we examined that next. 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 facial properties, compared to the number of times that the human or sheep varied more than the monkeys.

Creation of Systematically Varied Faces. Given that these natural faces varied to different degrees, the next step was to create artificial face sets from these natural faces that were more closely matched on their variability across species. One face was selected from each species based on pilot study data that indicated the individual was average in attractiveness and distinctiveness (see Tab. 1). That photo was used to create sets of systematically varied faces using the 90 face photos selected (samples in Fig. 2), and served as the familiar face for that species. We prepared photos using Adobe Photoshop in a manner similar to previous systematically varied faces studies. Following the recommendations of Taschereau-Dumouchel et al. (2010), manipulations of interattribute distances fell within the natural variability of the population (Fig. 2B). To this end, we considered the sampling of interattribute distances from real-world distributions (see Tab. 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, Le Grand, & Maurer, 2002; Taschereau-Dumouchel et al., 2010).

For the inner feature identity manipulation, the identity of the eyes, eyebrows, and mouth were manipulated (Fig. 2A). We kept the size of the facial features (eyes and mouth) constant to ensure that the distances among the features were as equal as possible. For the outer feature manipulations, the facial features (i.e., eyes, eyebrows, nose, and mouth) were consistent, but the outer features (hair, jaw line) were from different individuals (Fig. 2B). For the configuration manipulation, the height of the eyes and distance between the eyes were manipulated, as was the height of the mouth (Fig. 2C).

To measure the variability of our systematically varied face stimuli, we used a computation simulation method (Martin-Malivel & Okada, 2007; Okada et al., 1998), a neuroscientifically-plausible model of face perception by humans (Biederman & Kalocsai, 1997). This involved computing similarity coefficients for pairs of pictures within each species and face manipulation set, and then comparing the variability of those sets across each species-pair (human-monkey, human-sheep, monkey-sheep), as described in Table 2. Similarity coefficients were computed by placing a rectangular grid representing a regular lattice with 10 × 10 nodes on both photos; the model then computed local descriptors (Gabor jets) at each of the 100 corresponding nodes. One image was used as a reference, and the grid was translated on the second image, looking for the best match location. The average of local similarities computed for corresponding Gabor jets at the best match was used as a similarity coefficient between the images (see Okada et al., 1998 for details). We computed nine sets of similarity coefficients to compare each novel to the familiar face with which it was paired: 3 species × 3 face manipulations (Tab. 2). The average similarity coefficients indicate strong correlations (from +.9826 to +.9958) for all species among inner feature manipulations and feature spacing manipulations, but somewhat weaker correlations (from +.8257 to +.8849) among outer feature manipulations, reflecting higher amounts of variability in the outer feature manipulation stimulus set, as expected. Levene's Tests for Equality of Variance among the novel-familiar faces revealed equal variability among all species pairs for the inner feature manipulation set of faces, but in the outer feature manipulation set the monkey faces were more variable than the human faces ($p = .017$), and in the spacing manipulation set the sheep faces were less variable than either the human or monkey faces ($p\text{s} < .001$). No other species differences in variability were found ($p\text{s} > .10$). This indicates that the monkey faces with manipulated outer features may have been easier to discriminate compared to the human faces with manipulated outer features, though neither differed from the sheep faces. The sheep faces with the feature spacing manipulation were less variable than either the human or monkey faces due to the fact that the sheep faces have smaller facial features (eyes and mouths), so even though the features were moved the same distances, the move in the sheep produced less overall change to the faces. However, to keep the faces within the parameters of natural variability, the size of the sheep facial features was not increased. These details are discussed further in the Discussion Section.

All photos were presented on white backgrounds and had a height of 400 pixels and a width of 298–304 pixels (approximately 20° by 10° on the presentation screen). All participants viewed the faces at a distance of 60 cm. Prior to each trial, all participants viewed dynamic centering stimuli (e.g., cartoon characters) that were 12° by 12° on the presentation screen, and lasted 1,500 ms.

Procedure

First, all procedures were explained to the participants (i.e., adult participants or the infants' parents), and we obtained informed consent. 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 outer features systematically manipulated. We presented stimuli using a visual paired comparison task (Fagan, 1970). Adults were instructed to keep their eyes on the screen and view the pictures like they were watching television. Parents were instructed to focus on an "X" taped just above the screen, to ensure their gaze did not bias their infants; all parents complied with this request. Participants were familiarized with a face through the continuous familiarization technique (Fantz, 1964; Rose, Feldman, & Jankowski, 2002; Rose, Futterweit, & Jankowski, 1999), in which two identical faces were shown, side-by-side, until the participant accumulated 20 s of looking to one or both faces (Fig. 3). One natural face served as the familiar face, so all participants assigned to a given species were familiarized with the same face. This familiar face was the one used to create the systematically varied versions (the novel faces), so the novel and familiar faces differed in only one systematically varied property at a time. Next, participants viewed up to 30 *paired comparison*

Table 2. Computational Image Similarity Measure of Face Photos to Test for Equality of Variance

	Novel Versus Familiar Faces				
	Similarity Coefficient			Levene's Test	
	n	*M*	*SD*	p_{monkey}	p_{sheep}
Inner features					
Human	10	.9923	.0021	.221	.573
Monkey	10	.9859	.0032		.378
Sheep	10	.9958	.0022		
Outer features					
Human	10	.8672	.0185	.017	.376
Monkey	10	.8373	.0359		.110
Sheep	10	.8849	.0243		
Spacing					
Human	10	.9852	.0073	.123	<.001
Monkey	10	.9872	.0085		<.001
Sheep	10	.9926	.0039		

Note: Similarity coefficients were computed for each novel and familiar face pair, within each face manipulation type and species.

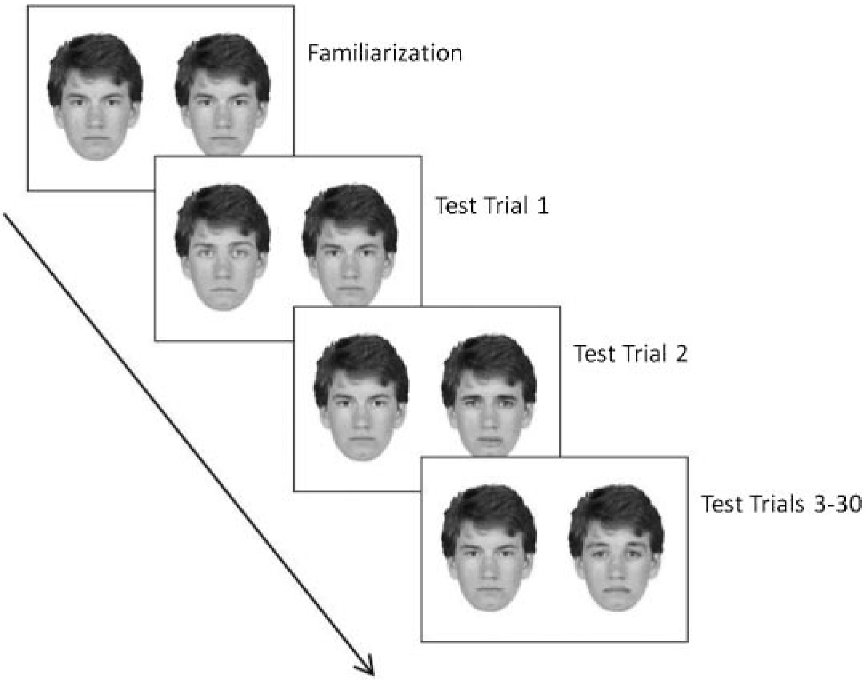

FIGURE 3 Sample presentation sequence. Participants were first familiarized with a face (familiarization), for 20 s, then viewed a novel and familiar face on up to 30 subsequent test trials (paired comparison), each lasting 4 s. In the example shown here, the inner facial features (eyes and mouth) changed for one face in each test trial.

test trials, consisting of pairs of faces: one was the same as that shown in the familiarization (i.e., familiar face) and one was novel. In keeping with other researchers (e.g., Rose et al., 2002), we used 30 test trials to examine the emergence and the durability of looking preferences. Additionally, looking preferences are known to change over the course of numerous test trials in adults (Park, Shimojo, & Shimojo, 2010) and infants (Hunter & Ames, 1988; Rose et al., 2002), so this method allowed for testing of these changes. The novel face appeared on the left and right with equal probability. Infants saw the same number of each type of systematically varied face due to random presentation of one of each type in the first three test trials, followed by one of each type in trials 4 through 6, and so on. Looking was measured in real-time to ensure each participant had a 20 s total cumulative looking to the faces for the *familiarization*, and 4 s of cumulative looking to the faces in the 30 *paired comparison* trials. Faces remained on the screen until a cumulative looking time of 4 s 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 min.

Coding Training and Reliability

Eye movements were coded off-line frame-by-frame (33 ms resolution) by a blind observer from video using the Observer XT. In 20% of sessions, randomly selected samples were chosen from each age group and interobserver reliability was assessed between an anchor observer and one additional observer. Cohen's Kappa for the frequency of each look location (e.g., left picture, right picture, or away) was $\kappa = .89$.

RESULTS

Preliminary Analyses

We conducted a $3 \times 3 \times 3$ mixed-design analysis of variance (ANOVA) on the number of trials completed, with the between subjects factors of age and species and the within subjects factor of face manipulation type. The number of trials completed varied with age, $F(2,\ 88) = 26.09$, $p < .001$. Not surprisingly, adults completed more trials than the infants: 4- to 6-month-olds completed an average of 17 test trials ($SD = 9.3$), 9- to 12-month-olds completed an average of 20 test trials ($SD = 8.8$), and all adults completed 30 test trials ($SD = 0$). The number of trials completed did not vary across species ($F(2,\ 88) = .391$, $p = .677$), or face manipulation type ($F(2,\ 176) = 1.41$, $p = .246$), nor were there any significant interactions ($p\text{s} > .10$), confirming that the number of trials was distributed roughly equally across species and face manipulation types for each age group. A preliminary analysis revealed no ethnicity differences,[1] no differences based on gestational age at birth, and no effect of the side of the novel face (e.g., no side preferences). A one-way ANOVA confirmed that (as expected) there were no differences in the total looking time during the familiarization among the three age groups ($M = 21.83$ s, $SD = 5.00$), $F(2, 213) = .28$, $p = .76$. In the results that follow, the proportion of time looking to the novel face is calculated by dividing the time looking to the novel face by the total time looking at both faces. Proportion of time was used as the dependent measure in order to examine the participant's relative interest in the novel face in relation to the interest in the familiar face. All a priori one-sample and paired-samples *t* tests are two-tailed and include least significant difference (LSD) adjustments for multiple comparisons. For all independent samples post hoc *t* tests, follow-up comparisons were conducted using Tukey HSD (honestly significantly different) corrections.

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

We averaged look durations across all test trials and analyzed each age, species, and face manipulation type with one-sample *t* tests to determine if the proportion of time looking to the novel face differed from chance (.50; Fig. 4 and Tab. 3). Four- to six-month-olds spent a greater proportion of time looking to the novel faces, compared to the familiar faces, for the faces of monkeys that varied in their outer features, $p = .021$, but had no other looking preferences, $ps > .05$, indicating 4- to 6-month-olds were rather poor at discriminating systematically varied faces, as only one face type elicited a significant novelty preference. To determine whether the 4- to 6-month-olds performed better in early trials within the test session, we additionally examined only the first three test trials and only the first six test trials (as each contained an equal number of each face manipulation), and carried out one-sample *t* tests on the proportion of time looking at the novel face. This revealed only one significant difference: in the first three test trials the 4- to 6-month-olds, much like the 9- to 12-month-olds, demonstrated a familiarity preference for sheep faces that varied in their feature spacing (proportion of time looking at the novel face: $M = .31$, $SD = .26$), $p = .011$, but there were no other differences from chance looking, $ps > .05$.

Nine- to twelve-month-olds, in contrast, had novelty preferences for human inner feature manipulations ($p = .045$), human outer feature manipulations ($p = .045$), monkey inner feature manipulations ($p = .038$), and monkey outer facial manipulations ($p < .001$). Nine- to twelve-month-olds also exhibited familiarity preferences for sheep faces that varied in the spacing among inner facial features ($p = .025$). Older infants had no other looking preferences that differed from chance ($ps > .05$). We also examined whether the 9- to 12-month-olds performed better in early trials within the test session, by examining only the first three test trials and only the first six test trials, and carried out one-sample *t* tests on the proportion of time looking at the novel face, but there were no additional significant differences beyond those already reported. Thus, 9- to 12-month-olds discriminated primate faces using inner and outer features, but discriminated sheep faces only using the spacing among features.

Adults spent a longer proportion of time looking at the novel faces for all species, for the outer features manipulation ($ps < .001$) and feature manipulation ($ps < .001$). For the spacing manipulation, adults had a novelty preference for the humans ($p < .001$) and monkeys ($p = .002$), but not sheep ($p = .75$). An examination of only the first three or first six test trials revealed no additional significant difference beyond those already reported. This result indicates that adults discriminate primate faces that vary in any one of the three facial properties (i.e., outer features, inner features, or spacing among features), but only inner and outer features were used to discriminate sheep faces.

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

Next, we conducted a $3 \times 3 \times 2 \times 3$ mixed-design ANOVA to examine whether the proportion of time looking to the novel face varied as a function of the between-subjects factors age (4- to 6-month-olds, 9- to 12-month-olds, adults), species (human, monkey, sheep), and sex of participant (male, female), and the within-subjects factor of face manipulation type (outer features, inner features, spacing among inner features). We found main effects of age, species, and face manipulation (Tab. 4). There were also two interactions: face manipulation type × species, $F(4, 364) = 2.43$, $p = .047$, $\eta^2 = .026$, and age × species, $F(4, 182) = 3.28$, $p = .013$, $\eta^2 = .07$. There were no other main effects or interactions, $ps > .05$.

We first examined the face manipulation type × species interaction by conducting one-way ANOVAs

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[1] The majority of the population in the county and the state is Caucasian (69% and 66%, respectively; Georgia County Guide, 2009); therefore, it was assumed that participants would be familiar with Caucasian faces. Results were the same whether we included all infants or only Caucasian infants, so we chose to include all infants.

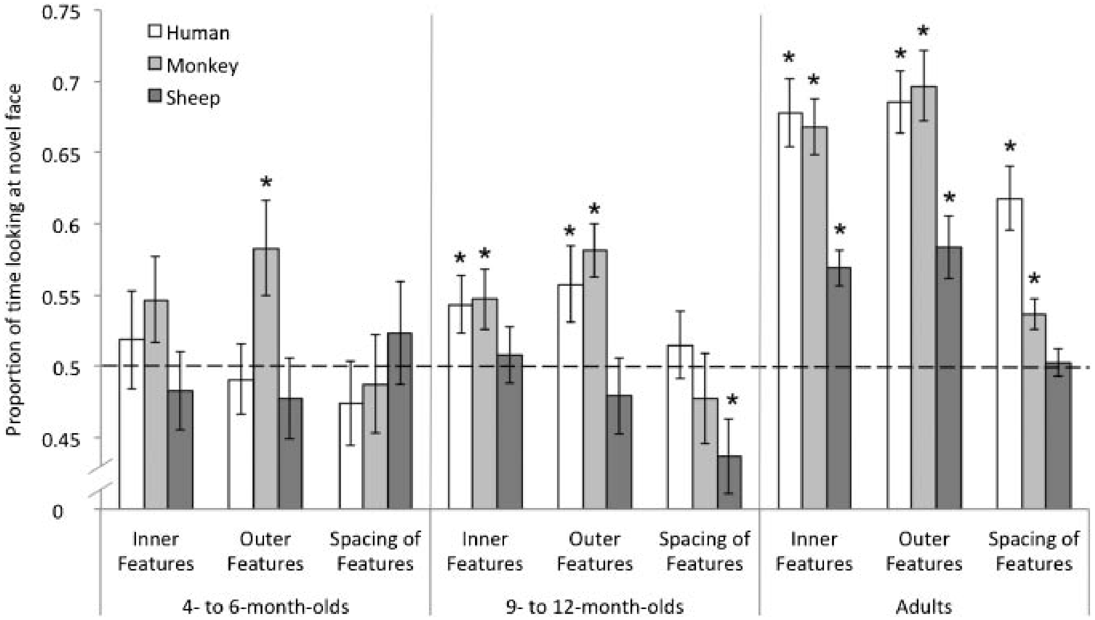

FIGURE 4 Novelty preference varied across age, face manipulation type, and species. Mean proportion of time looking to the novel face, out of the total time looking to the faces, for the three face manipulation types (inner features, outer features, and spacing of features). Error bars represent one-sample *t* tests, to determine which conditions differed from chance (.50), at $^{*}p < .05$ (for exact *p* values see Tab. 3). Chance looking indicated by dashed line.

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, $F(2, 209) = 6.10$, $p = .003$, $\eta^2 = .05$, and independent samples *t* tests revealed a greater proportion of time looking to the novel faces of humans ($M = .579$, $SD = .145$) and monkeys ($M = .591$, $SD = .123$), compared to sheep ($M = .520$, $SD = .106$), $p = .021$ and $p = .004$, respectively. For the outer feature manipulation there was also a main effect of species, $F(2, 209) = 11.37$, $p < .001$, $\eta^2 = .10$, in which participants spent a greater proportion of time looking to the novel faces of humans ($M = .577$, $SD = .142$) and monkeys ($M = .625$, $SD = .143$) compared to sheep ($M = .513$, $SD = .129$), $p = .020$ and $p < .001$, respectively. For the spacing manipulation, there was no main effect of species, $F(2, 208) = 2.11$, $p = .124$.

Table 3. Novelty Preferences Varied Across Age, Species, and Face Manipulation Types

	4- to 6-month-olds						9- to 12-month-olds						Adults					
	M	*SD*	*df*	*t*	*p*	*d*	*M*	*SD*	*df*	*t*	*p*	*d*	*M*	*SD*	*df*	*t*	*p*	*d*
Inner features																		
Human	51.9	16.8	23	.54	.591		54.3	9.8	22	2.13	.045	.44	67.8	11.4	22	7.51	<.001	1.57
Monkey	54.7	15.0	24	1.56	.133		54.7	14.1	19	2.23	.038	.50	66.8	10.0	25	8.60	<.001	1.69
Sheep	48.3	13.5	23	.62	.544		50.8	9.6	22	.41	.683		56.9	6.2	23	5.46	<.001	1.11
Outer features																		
Human	49.1	12.2	23	.37	.706		55.8	13.1	22	2.13	.045	.44	68.6	10.5	22	8.48	<.001	1.77
Monkey	58.3	16.4	23	2.47	.021	.50	58.1	8.4	19	4.34	<.001	.97	69.7	12.7	25	7.92	<.001	1.55
Sheep	47.8	14.4	25	.79	.435		47.9	12.4	21	.79	.441		58.4	10.9	23	3.76	.001	.77
Spacing																		
Human	47.4	14.6	23	.86	.399		51.5	10.7	20	.65	.525		61.8	10.8	22	5.25	<.001	1.09
Monkey	48.8	17.2	24	.36	.722		47.8	14.1	19	.71	.486		53.7	5.4	25	3.48	.002	.68
Sheep	52.4	18.3	25	.66	.518		43.7	12.3	21	2.41	.025	.51	50.3	4.8	23	.32	.751	

Note: Mean proportion of time looking to the novel face out of the total time looking to both faces (*M*), standard deviations (*SD*), one-sample *t* tests to determine whether looking differed from chance (50%), and effect sizes (Cohen's *d*) are reported for each age group and each stimulus type (human, monkey, and sheep faces, which varied in either inner features, outer features, or spacing among inner features).

Table 4. Mixed Design Analysis of Variance Results for Look Duration to Novel Faces

	Between Subjects					
Source	*df*	*SS*	*MS*	*F*	*p*	η^2 or η_p^2
Age	2	125.65	.30	17.76	<.001	.16
Sex	1	.05	.05	2.78	.097	.02
Species	2	.35	.18	10.26	<.001	.10
Age × sex	2	.01	<.01	.26	.769	<.01
Age × species	4	.22	.06	3.28	.013	.07
Sex × species	2	.03	.02	.91	.406	.01
Age × sex × species	3	.02	.01	.31	.8190	.01
Error 1	182	3.10	.02			

	Within Subjects					
Source	*df*	*SS*	*MS*	*F*	*p*	η^2 or η_p^2
Manipulation	2	.32	.16	12.21	<.001	.06
Age × manipulation	4	.08	.02	1.47	.212	.02
Age × sex						
Sex × manipulation	2	.04	.02	1.54	.215	.01
Species × manipulation	4	.13	.03	2.43	.047	.03
Species × sex						
Age × species × manipulation	8	.07	.01	.63	.751	.01
Age × sex × manipulation	4	.01	<.01	.21	.932	<.01
Sex × species × manipulation	4	.02	<.01	.28	.888	<.01
Age × sex × species × manipulation	6	.04	.01	.53	.789	.01
Error 2	364	4.70	.01			

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

We next examined the face manipulation type × species interaction by conducting one-way ANOVAs for each species to see if there was a main effect of face manipulation type. For human faces, there was a main effect of face manipulation type, $F(2, 134) = 2.89$, $p = .05$, $\eta_p^2 = .04$, in which participants spent a greater proportion of time looking to the novel faces with the manipulation of inner features ($M = .581$, $SD = .148$) and outer features ($M = .577$, $SD = .144$), compared to the feature spacing ($M = .536$, $SD = .135$), $ps < .05$. For monkey faces, there was a main effect of face manipulation type, $F(2, 138) = 19.35$, $p < .001$, $\eta_p^2 = .22$, in which participants spent the largest proportion of time looking to the novel faces when the manipulation was of the outer features ($M = .625$, $SD = .141$), followed by inner features ($M = .591$, $SD = .131$), and feature spacing ($M = .503$, $SD = .131$), $ps < .05$. For sheep faces, there was no main effect of face manipulation type, $F(2, 132) = 1.82$, $p = .166$, likely due to the fact that sheep faces were generally not discriminated.

Next, we further explored the age × species interaction by carrying out one-way ANOVAs on each age group to see if there was a main effect of species (Fig. 5). In the 4- to 6-month-olds there was a marginal main effect of species, $F(2, 77) = 3.04$, $p = .054$, $\eta^2 = .076$, whereby the proportion of time looking to the novel face was greater for the faces of monkeys ($M = .536$, $SD = .090$) compared to sheep ($M = .484$, $SD = .080$), $p = .045$, but neither the monkeys or sheep differed from the human faces ($M = .502$, $SD = .059$), $ps > .10$. There was a large main effect of species for the 9- to 12-month-olds, $F(2, 63) = 8.16$, $p = .001$, $\eta^2 = .206$, with the proportion of time looking to the novel face being greater for faces of humans ($M = .534$, $SD = .051$) and monkeys ($M = .539$, $SD = 3.09$), compared to sheep ($M = .476$, $SD = .064$), $p = .003$ and $p = .002$, respectively. Adults exhibited the same pattern as the 9- to 12-month-olds, with a large main effect of species, $F(2, 70) = 12.14$, $p = .001$, $\eta^2 = .258$, in which adults spent a greater proportion of time looking to the novel faces of humans ($M = .660$, $SD = .098$), and monkeys ($M = .633$, $SD = .079$), compared to sheep ($M = .551$, $SD = .058$), $ps \leq .001$.

Finally, we followed up the age × species interaction by carrying out one-way ANOVAs on each species to see if there was a main effect of age group. Indeed,

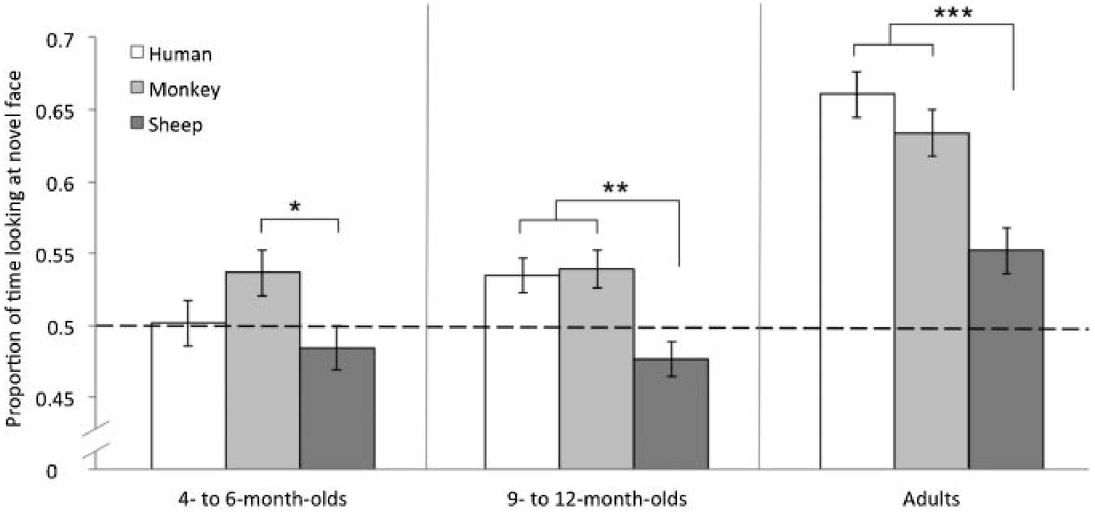

FIGURE 5 Novelty preferences across age and species. Independent samples *t* tests, $^{*}p = .045$; $^{**}ps = .002$ (Human vs. Sheep) and $^{**}p = .003$ (Monkey vs. Sheep); $^{***}ps \leq .001$, Tukey HSD corrections. Error bars reflect between-subjects standard error of the mean. Chance looking indicated by dashed line.

there were large main effects of age group for each of the three species. For human faces, there was a main effect of age group, $F(2, 67) = 31.62$, $p < .001$, $\eta_p^2 = .486$, whereby the proportion of time looking to the novel face was greater for the adults ($M = .660$, $SD = .098$), than for either the 4- to 6-month-olds ($M = .501$, $SD = .059$) or the 9- to 12-month-olds ($M = .534$, $SD = .051$), $ps < .001$, but the infant groups did not differ from one another, $p = .274$. A main effect of age group was also found for monkey faces, $F(2, 68) = 13.56$, $p < .001$, $\eta_p^2 = .285$, with adults looking to the novel face a greater proportion of time ($M = .634$, $SD = .079$), compared to the 4- to 6-month-olds ($M = .536$, $SD = .090$) and the 9- to 12-month-olds ($M = .539$, $SD = .038$), $ps < .001$, but the infant groups did not differ from one another, $p = .992$. Finally, there was also a main effect of age group for the sheep faces, $F(2, 72) = 8.16$, $p = .001$, $\eta_p^2 = .185$, again with was a stronger novelty preference in the adults ($M = .558$, $SD = .059$), compared to the 4- to 6-month-olds ($M = .484$, $SD = .080$), $p = .003$, and the 9- to 12-month olds ($M = .476$, $SD = .075$), $p = .002$, but the infant groups did not differ from one another, $p = .920$. To determine whether adults were better at detecting spacing changes in the human faces, compared to the monkey faces, we conducted an independent samples *t* test, which revealed this was in fact the case, $t(47) = 3.395$, $p = .001$, $d = 3.21$. Together, these results indicate that by late infancy, infants are becoming more sensitive to primate faces, and this primate-advantage seems to last into adulthood.

DISCUSSION

This study tested predictions of learned attention models, as they relate to the development of facial identity discrimination. In addition, this study aimed to uncover whether differences in humans' perception of natural human and animal faces are due to categorical differences (in species), or differences in interindividual variability within each species. We present three key findings of the present study: (1) with age, there is an increase in the number of facial properties discriminated; (2) an increase is observed with age in the number of species discriminated; and (3) primate faces are discriminated using different facial properties compared to nonprimate faces. Given that each age group viewed the same sets of stimuli, the first two findings of age differences are not due to differences in the variability of the face stimulus sets; however, the third finding—that primate faces were discriminated using different properties than sheep faces—needs to be interpreted with caution, given that there were differences in variability across species, which we discuss below. Nonetheless, these findings indicate that learned attention models additionally contribute to understanding the development of facial discrimination, providing not only a description of what species' faces are best discriminated, but also providing insight into how this differential discrimination emerges developmentally. Specifically, we found that with age an increasing number of facial features could be used for face discrimination, which we discuss next.

The Number of Facial 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 (Fig. 2). Four- to six-month-olds only discriminated the monkey faces that varied in their outer features and sheep faces that varied in feature spacing (the later found only when examining just the first three test trials). Nine- to twelve-month-olds only discriminated human and monkey faces that varied in either their inner features or outer features, and sheep faces that varied in the spacing among features. Adults discriminated all face manipulation types. These findings are consistent with learned attention models, which predict increased sensitivity or specialization for stimuli or parts of stimuli, with age (i.e., *imprinting*; Goldstone, 1998). Similarly, it has been found that 7-month-olds demonstrate face novelty preferences when there are small physical differences between faces, while 4-month-olds require larger differences between faces for discrimination (Humphreys & Johnson, 2007). These findings are also congruent with human face perception work, which suggests configural processing—defined as the discrimination of alterations in the spacing among facial features—is relatively poor in children (e.g., Mondloch, Dobson, Parsons, & Maurer, 2004), but is established in adults.

Number of Species Discriminated Increases With Age

The present finding that there are improvements in human face discrimination with age, which were relatively larger than improvements in monkey or sheep faces with age, is consistent with perceptual narrowing. However, we also found that 4- to 6-month-olds showed no evidence of discriminating human faces which varied in only one carefully controlled perceptual property at a time, and only showed evidence of discriminating monkey faces varying in outer features (which were more variable than the human faces, and therefore, may have made them easier to discriminate) and sheep faces varying in feature spacing. This failure to find evidence of discrimination may be because younger infants rely on multiple facial properties for discrimination. In adults, face discrimination is better when more than one face property varies concurrently (e.g., Tanaka & Sengco, 1997); the current results suggest the same may be true for infants, though this needs to be systematically tested (e.g., varying one or more face properties at a time). It is also possible that 4- to 6-month-olds may have had more difficulty discriminating the systematically varied faces due to other aspects of their visual system that improve from 6 to 9 months, such as their visual acuity (Dobson & Teller, 1978) or contrast sensitivity (Peterzell, Werner, & Kaplan, 1995). In addition, infants of this age, on average, have more experience with and prefer female faces (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2001; Ramsey-Rennels & Langlois, 2006) whereas only male faces were used in the present study. This may explain why this study did not replicate findings that young infants discriminate faces varying in outer contours (e.g., Cashon & Cohen, 2004; Turati et al., 2006). Another possibility is that 4- to 6-month-olds are capable of discriminating some (or all) of these systematically varied faces, but simply needed more familiarization time. Future work using a standard infant-controlled habituation procedure is necessary to test this possibility as well.

In contrast to 4- to 6-month-olds, 9- to 12-month-olds exhibited novelty preferences for human and monkey faces, and a familiarity preference for sheep faces, suggesting they discriminated all three species. While previous studies found no evidence that 9- to 12-month-olds can behaviorally discriminate unfamiliar monkey (Pascalis et al., 2002, 2005) or sheep faces (Simpson et al., 2011), unless they are given training (Scott & Monesson, 2010), the current results suggest infants of this age can discriminate monkey and sheep faces. These results are consistent with findings that 9-month-old infants show differential neural activity to novel and familiar monkey faces—measured using event-related potentials (ERPs)—suggesting discrimination at the neural level (Scott, Shannon, & Nelson, 2006). The present findings also corroborate previous work showing 12-month-olds discriminate monkey faces when familiarized for an extended period (Fair, 2009; Fair et al., 2012). In addition, older infants discriminated monkey and sheep faces even when they varied in only one face property, a more challenging task than discriminating natural faces (which vary in numerous properties). Methodological differences between this study and previous studies may explain some of the findings: the current method involved the continuous familiarization technique, presenting up to 30 test trials (while others typically use only 2 test trials), so in the present study, infants had more opportunities to be familiarized with the familiar face. In addition, we used a different species—capuchin monkeys—that may have been more variable in their faces relative to the monkey faces used previously (macaques). This again highlights the importance of considering inter-individual variability within species when carrying out animal facial identity discrimination tasks.

We also found that adults—who discriminated nearly all face types—showed stronger novelty preferences for human faces, compared to monkey faces, when faces varied in their inner feature spacing, consistent with previous work (Mondloch, Maurer, & Ahola, 2006). This may be due to adults' experiences with human faces (e.g., differentiating individual faces; Nelson, 2003), or due to more general improvements in cognitive capacities (e.g., memory; Mondloch et al., 2006). Nonetheless, it reflects own-species specialized processing, which was not evident in the data for either infant group.

Primate Faces Are Processed More Efficiently Than Sheep Faces

We predicted that human faces would be processed differently from animal faces, particularly by older infants and adults who have more experience with human faces and are, or are well underway to becoming, human face specialists. Indeed, the 4- to 6-month-olds showed no evidence of discriminating sheep faces, in contrast to previous findings that, using this same procedure, infants of this age exhibit familiarity preferences for natural sheep faces (Simpson et al., 2011). It is possible that the youngest infants may need more information (e.g., variation in more than one feature at a time) or more time for discrimination. As predicted by learned attention models, experience with human faces may have helped older infants and adults to discriminate other primate faces.

In contrast, adults and older infants discriminated all three species, but also showed some differences across species. Adults and older infants had stronger novelty preferences for primate faces compared to sheep faces (Fig. 3), which—according to the exploratory looking model—suggests that primate faces were more easily discriminated (Hunter & Ames, 1988). This might be because experience with human faces also aids in discrimination of monkey faces, which are structurally similar. In this way, both monkey and human faces better match a face prototype, relative to sheep faces (Valentine, 1991), or learned attention may have resulted in heightened sensitivities to the properties of primate faces that vary, which may be different from the properties that vary in sheep faces (Zhang et al., 2012). Though adults discriminated all three species when they differed in outer or inner features, adults failed to discriminate sheep faces that varied in the spacing among inner features, consistent with findings that adults experience an inversion effect for primate faces, but not for nonprimate animal faces (e.g., Dufour et al., 2004; Pascalis & Bachevalier, 1998; Pascalis, Coleman, Stirnemann, Petit, & Campbell, 1998; Pascalis, Demont, de Haan, & Campbell, 2001). Thus, primate faces may be processed in a more holistic manner, while sheep faces may be processed in a more feature-based manner. This is consistent with findings that human adults process chimpanzee faces in a holistic manner, but do not appear to process phylogenetically more distantly related species—including sheep, chickens, and lizards—holistically (Taubert, 2009).

One caveat is necessary to mention when comparing primate and sheep faces in the *feature spacing manipulation condition*: the computational image similarity analysis revealed that sheep faces were less variable than either the human or monkey faces; therefore, this may have made the sheep faces in this condition the most difficult to discriminate. It is possible that this is why human adults showed no evidence of discriminating these feature spacing manipulated sheep faces; however, it does not explain why 4- to 6-month-olds or 9- to 12-month-olds discriminated these faces. In older infants, primate faces were distinguished when they varied in either their inner or outer features; sheep faces, in contrast, were only distinguished when they varied in the feature spacing. Additionally, infants' discrimination of sheep faces took the form of a familiarity preference, suggesting the sheep faces may not have been fully encoded during the familiarization period (Hunter & Ames, 1988). Therefore, it appears that all age groups failed to demonstrate novelty preferences for the sheep faces with inner feature spacing manipulated, but it is unclear whether this may be due to the subtle nature of differences in this stimulus set (i.e., less variability), or whether it may reflect a more general limit of humans' ability to discriminate non-primate faces. Tests with a wider variety of animal faces, including other primates, will more thoroughly test this possibility.

GENERAL CONCLUSIONS

Previous work has found differences in the ways humans discriminate human and nonhuman faces (e.g., Dufour et al., 2004; Pascalis & Bachevalier, 1998; Pascalis et al., 1998, 2001). Human, monkey, and sheep faces are not equivalent in the variability of their facial features (see Tab. 1). The presented study used systematically varied faces to make three species—humans, monkeys, and sheep—more similar in their variability. Results indicated that when variability is more equally matched, 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., 2011). Thus, though others have documented declines in animal face discrimination with development (e.g., McKone et al., 2009; Scott & Monesson, 2010), the present results suggest this is not the case, and apparent declines in performance should be reconsidered, because they may be due to the way in which a task is perceived differently by different age groups (Cashon, Ha, Allen, & Barna, 2012; Vouloumanos, 2011). A functionalist approach, which considers an individual's changing goals across development, may be especially helpful (Scherf & Scott, 2012). For example, is it plausible that faces may mean something different to an older infant or to an adult than they do to a younger infant; perhaps older infants are attending more to regions of the face that convey emotion, as they have learned faces often convey important communicative meanings through their expressions. Thus, an older infant's discrimination may not be weakened, but rather, the child is simply approaching the task differently with age. For example, Cashon et al. (2012) report that face recognition is related to 5- and 7-month-olds' sitting abilities: non-sitters and expert-sitters processed faces holistically, but near-sitters and new-sitters did not, showing a u-shaped relation between sitting and upright face processing.

Though we found evidence of a human-face-specialization with age, not all of our findings are consistent with perceptual narrowing. For example, overall, with age there were increases in the number of species discriminated, as well as increases in the number of facial properties that can be used for discrimination. A model is needed that can also account for the fact that the facial properties that can be used for discrimination vary between primates and nonprimates, as well as between humans and other animals. Instead, learned attention models may be useful for understanding these results.

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 individual faces was systematically controlled. These findings are somewhat congruent with previous findings that older infants show no evidence of discriminating natural sheep faces (Simpson et al., 2011). However, the finding that 9- to 12-month-olds can behaviorally discriminate monkey faces is in contrast to some (e.g., Pascalis et al., 2002, 2005), but not all (e.g., Fair, 2009; Fair et al., 2012) previous findings. 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. One limitation of the present study is that the results would have been easier to interpret if we had presented natural faces, concurrently varying in all three facial properties (inner feature, outer features, and configuration), to determine whether our findings are due to our stimuli (varying in only one property at a time) or some other aspect of our procedure. Adults discriminated all species, with the exception of the sheep in the spacing condition. This result is consistent with other results that adults can discriminate natural animal faces (Simpson et al., 2011), and suggests that those who have failed to find discrimination by adults (Pascalis & Bachevalier, 1998; Pascalis et al., 2001, 2002) may not have employed sufficiently sensitive tests (e.g., they may have used an insufficient number of test trials).

Despite the fact that faces are one of the most important stimuli for humans and other vertebrate species (Little, Jones, & DeBruine, 2011), with evidence supporting an early evolutionary emergence of face recognition (Leopold & Rhodes, 2010), relatively little is yet known about the development of this impressive skill, already present in infancy. The present study contributes to knowledge of the development of human face perception in three ways. 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 that with an increase in age, there is an increase in the number of facial properties that can be used for discrimination, starting with at least two properties in later infancy (outer features and inner features), and expanding to at least three properties in adulthood (with the addition of discriminating based on the spacing among inner features). Finally, the present study demonstrates limitations in humans' discrimination of nonprimate faces (i.e., sheep faces), across all ages, suggesting primate faces may be privileged in their processing. Together, these findings can help answer questions regarding not only *what* develops, but also *how* face discrimination develops, such as through learned attention. It is only through this understanding that we can begin to devise early ways to identify and treat disorders of social recognition, such as prosopagnosia (e.g., Dalrymple, Corrow, Yonas, & Duchaine, 2012).

NOTES

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