Age Categorization of Conspecific and Heterospecific Faces in Capuchin Monkeys (*Sapajus apella)*

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Abstract

Across various species infant faces share various features referred to as "baby schema" (Lorenz, 1943). Assuming that these features are indeed shared among species, it is possible that non-human animals may perceive age information in conspecific and heterospecific faces. We tested whether tufted capuchin monkeys (*Sapajus apella)* would visually categorize age from faces. In Experiment 1, we trained four monkeys to discriminate adult and infant faces of conspecifics using a symbolic matching to sample procedure. We then tested whether their categorization transferred to faces of other species (i.e. dogs and human). In Experiment 2, we trained another two monkeys on age categorization of heterospecific (human) faces and tested them with conspecific and dog faces, to assess whether conspecific age categorization in Experiment 1 was specific. In Experiment 3, the four monkeys from Experiment 1 were trained with human faces while the two monkeys from experiment Experiment 2 were trained with conspecific faces; we then tested all six monkeys with faces of dogs and other species including New World monkeys, Old World monkeys, apes and carnivores. During training the monkeys quickly learned to categorize adult and infant faces of both conspecifics and humans. However, age categorization failed to transfer to different species in the test phase in all three Experiments.

Keywords: capuchin monkey, age categorization, operant learning, baby schema, face recognition

Recognizing the approximate age of other conspecifics is important for appropriate social interactions. For example, recognizing whether another individual is adult or not is crucial in reproductive contexts. Recognizing infants is also important for many species including humans in which alloparenting is common. Behavior directed toward infants and mature individuals usually needs to be different. Many primate species show high tolerance of infants (Alley, 1980). One common infant signal or set of signals is the “baby schema,” proposed by Lorenz (1943). The baby schema is a set of physical, especially facial features (e.g., large head, large eyes, protruding forehead, small nose and mouth) typical of infants in many species. In humans, such features (contained within “baby schema”) induce the perceptions of cuteness and facilitate caretaking behavior (Alley, 1981, 1983b, 1983a; Borgi, Cogliati-Dezza, Brelsford, Meints, & Cirulli, 2014; Glocker et al., 2009; Sternglanz, Gray, & Murakami, 1977). Several studies have indicated that baby schema in other species’ faces affect human perception (Borgi & Cirulli, 2013; Borgi et al., 2014; Golle, Lisibach, Mast, & Lobmaier, 2013; Little, 2012). For example, Borgi et al., (2014) found that in 3-6-year-old children, cuteness scoring and gaze patterns were affected by baby schema of humans, dogs and cats, suggesting a common mechanism for recognizing baby schema in human and animal faces.

The concept of baby schema - physical features likely shared across species - leads to the question of how it affects facial perception in other animals. However, few experimental studies have addressed age-related recognition in nonhuman primates. In one study (Sato, Koda, Lemasson, Nagumo, & Masataka, 2012), when shown pairs of visual stimuli Japanese macaques (*Macaca fuscata*) and Campbell’s monkeys

(*Cercopithecus campbelli*) looked at images of infant Japanese macaques for longer than adult images. Similaly, barbary macaques (*Macaca sylvanus*) looked at images of newborn conspecifis longer than they looked at adults (Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016). However, conspecific newborn faces did not capture the attention of two Japanese macaques (Koda, Sato, & Kato, 2013). As far as we know, there is no study investigating whether nonhuman animals explicitly categorize individuals' faces based on age.

The present study asked whether capuchin monkeys can form age categories from faces of conspecifics and heterospecifics. Like other primates, capuchin monkeys show strong attraction toward and tolerance of infants (Ottoni, de Resende, & Izar, 2005). As capuchin monkeys are highly social and have a large repertoire of facial expressions (Fragaszy, Visalberghi, & Fedigan, 2004), they should be sensitive to differences between faces. They have been shown to categorize individuals in photographs as in-group or out-group (Pokorny & de Waal, 2009) and to discriminate emotional facial expressions (Calcutt, Rubin, Pokorny, & de Waal, 2017). We focused on face instead of whole-body pictures because the face has multiple baby schema-related features. We employed a symbolic matching-to-sample procedure using faces of adults and infants. It is known that animals can easily learn to discriminate categories that are relevant to their natural concepts. For example, Real, Iannazzi, Kamil, & Heinrich (1984) trained four blue jays (*Cyanocitta cristata*) to discriminate between leaf damage caused by palatable and unpalatable caterpillars. They reported that the birds quickly discriminated and generalized to new instances after learning only one pair of each category. If age category is ecologically relevant for capuchin monkeys, they should also learn to categorize individuals quickly.

We first trained four monkeys to discriminate between faces of adult and infant conspecifics, and then tested for generalization to human and dog faces (Experiment 1). We used both a familiar primate species (humans) and an unfamiliar nonprimate species (dogs) as test stimuli to see whether familiarity would affect performance. If species-general infantile features like baby schema exist in both primates and non-primates, and animals perceive this age-related information, they may do so even with unfamiliar species. To test whether age categorization for conspecifics was restricted, we conducted a second experiment in which two naive capuchin monkeys first learned to discriminate between adult and infant heterospecific (human) faces, after which we tested them with faces of dogs and conspecifics (Experiment 2). To test the possibility that monkeys may require training with multiple species stimuli to form a general age category, in Experiment 3 and trained the four monkeys from Experiment 1 on human stimuli and the two monkeys from Experiment 2 on conspecific stimuli. Then we tested all six monkeys for generalization using the same dog stimuli as previously, as well as stimuli from another eight species of New World monkeys, Old-World monkeys, apes and carnivores (see Table 1 for summary of overall flow). The capuchin monkey subjects see human adults (students and staff) every day, so they were highly familiar with human adults. They also see squirrel monkeys housed in the same room. By contrast, they have never been exposed to human infants, dogs or other species. If the monkeys naturally recognize conspecific age categories from facial features, they should easily learn the conspecific discrimination. Moreover, if this categorization ability operates across species, they should also learn the heterospecific discrimination and show transfer to facial stimuli from different species.

Experiment 1

Methods

Subjects

Four group-living adult tufted capuchin monkeys (*Sapajus apella*) participated: one 21-year-old adult male ("Heiji"), two multiparous adult females ("Zilla" and "Theta", 21 and 19 years old, respectively), and a 12-year-old nulliparous female ("Zen"). All had participated in various noninvasive psychological experiments, including matching-to-sample tasks (e.g., Fujita, 2009; Hiramatsu & Fujita, 2015). The monkeys were neither food- nor water deprived. They received vegetables, monkey chows, eggs and fruit at the end of testing each day. The experiment was approved by the Committee for the Animal Experiments of the Graduate School of Letters, Kyoto University (application 17-21).

Apparatus

The monkeys were trained and tested in an operant box (45 × 45 × 45 cm) with a touch-sensitive LCD monitor (Mitsubishi, TSD-CT157-MN, 1024 × 768 pixels) and a universal feeder (Biomedica, BFU310-P100) installed. Two levers and lever lights were attached below the monitor. The lever light was illuminated whenever the lever was available. Stimulus presentation, response detection, and food delivery were controlled by a customized program written in Microsoft Visual Basic 2010 Express on a personal computer (CPU: Core (TM) i3-4130 3.40 GHz; Intel, Santa Clara, CA, USA). White noise masked external sounds during experimental sessions.

Stimuli

In the training phase we used 10 pairs of photos of unfamiliar adult and infant conspecific faces. We also prepared four adult and infant face pairs of humans (Japanese) and dogs (Labrador retriever) for the test phase. Most photos were obtained from the Internet; others were taken by one of the authors or provided by colleagues. Among the human adult stimuli there were two males and two females. The sex of most of the depicted dogs, capuchins, and some human infants was unknown. As each species has its own typical life history, controlling the age of infant stimuli is difficult. We collected pictures of infants that appeared to be younger than weaning age (e.g., carried by the mother). As we did not know the exact age of most of the stimulus individuals, we prepared a questionnaire for 10 human volunteers (5 males, 5 females, mean age 23.7 years, *SD* = 2.4) to rate the age of all stimuli used in Experiments 1 and 2 on a 5-point scale (1: “newborn”, 2:”infant”, 3:” toddler”, 4:”juvenile”, 5: “mature”). With one exception, all infant monkey stimuli (average = 2.1, *SD* = 0.37) were rated younger than all adult monkey stimuli (average = 4.26, *SD* = 0.39); the exception was judged as older (mean rating: 4.3) relative to the other infant monkeys. However, as we knew that this was a 4-month-old infant from information on the website of the zoo where it was born, we included the image as an infant stimulus. All four infant human test stimuli were scored younger (average =1.68, *SD* =0.19) than each of four adult human stimuli (average = 4.8, *SD* = 0.08). All four puppy test stimuli were scored younger (average =2.16, *SD* =0.67) than each of four adult dog stimuli (average = 4.14, *SD* = 0.23). Using

Adobe Photoshop CS6, we pasted each face into a square (300 × 300 pixel) with a 50% gray background. All stimuli were presented in grayscale (Figure 1).

Procedure

Monkeys were trained to discriminate between adult and infant conspecific faces in a zero-delay symbolic matching-to-sample procedure (Figure 1). A sample stimulus appeared on the center of the monitor when the monkey pressed the illuminated lever for 1 sec after a 3-sec ITI. Five touches on the sample resulted in its disappearance and two geometric figures (“icons,” open square and striped square, 150×150 pixel) appeared as comparison stimuli, one at each bottom corner of the monitor. One icon corresponded to “adult” and the other to “infant,” counterbalanced between subjects. The left-right position of the icons was counterbalanced within a session. Each session consisted of 100 trials. When the sample was an adult (or infant), touching the “adult” (or infant) icon was reinforced by delivery of a small piece of food (apple or sweet potato) via the universal feeder, accompanied by an electronic chime. Incorrect responses were followed by a buzzer, no food reward and a 10-sec timeout during which the house light was turned off. The monkeys were required to hold the lever down during the trials; releasing it aborted the trial, which re-started. Our training and testing procedures followed those in Adachi and Fujita's (2005) study of categorical discrimination of human faces from the other body parts in pigeons.

Training phase. For each subject training started with a pair of conspecific adult and infant faces randomly chosen from the set of 10. To test robustness of the adult vs. infant discrimination, whenever a subject scored higher than the 85% correct in 2 consecutive sessions we introduced a randomly chosen novel stimulus pair in probe test trials for two sessions. Sessions consisted of 32 probe trials and 68 baseline trials with learned stimuli. Rewards were delivered regardless of choice in probe trials but delivered only following correct choices in baseline trials. After two test sessions, we trained monkeys with their now-familiar stimuli along with the new ones. These after-test training sessions consisted of 50 trials with the new stimuli and 50 with the old ones. Training continued until the monkeys performed at above 80% correct for the new stimuli for two consecutive sessions. We repeated this procedure until they learned 10 pairs of adult and infant faces. The order of introducing the new stimulus pairs was counterbalanced across subjects.

Test phase. We tested generalization of age-category discrimination to dog and human faces in all-reinforced probe test trials following consistently good performance for conspecific stimuli in further baseline sessions. In the baseline sessions, all of the learned capuchin monkey faces (10 adults and 10 infants) were randomly presented at the same frequency for 100 trials. The criterion was over 90% correct in total and over 80% for each adult and infant stimulus for two consecutive sessions. In generalization test sessions, we used 16 stimuli consisting of four different photos for each of four stimulus types (4 human adults, 4 human infants, 4 adult dogs, and 4 puppy). We randomly divided the stimuli into 2 equal sets; one set was used in the first generalization test and the other in the second test, each comprising 4 sessions as a block. Each test stimulus appeared four times per session. Sessions consisted of 100 trials (32 test and 68 baseline). We confirmed the baseline performance again between the first and the second test blocks. Each stimulus was presented on 16 trials in total.

Statistical analysis

We measured the number of sessions to reach criterion for new stimulus pairs during the training phase. The number of correct responses in probe tests was analyzed using binomial tests with 50% as chance level.

To investigate whether age categorization transferred to novel species during the test phase, for each subject we used a logistic regression model with the number of “infant” responses as dependent variables, age category (adult, infant) as independent variable, and logit link function with binomial distribution as link function. We analyzed only the number of infant response because all the responses were either “infant” or “adult”. If monkeys recognized adult and infant correctly, then number of infant response should be significantly larger for infant stimuli than adult stimuli. For model fitting, we scored each adult stimulus as -1 and infant stimulus as 1. We also performed a group analysis using a Generalized Linear Mixed Model (GLMM) with the same fixed effects (age category) and link function (logit link function with binomial distribution) as the logistic regression analysis and random effect of subject. Significance of the effect was tested by the likelihood ratio test with chi-square test (type II tests). All statistical tests were run on R statistical language and environment version 3.30.32 (R Core Team, 2013) with “lme4” (Bates, Mächler, Bolker, & Walker, 2015) and “car” (Fox & Weisberg, 2011) packages.

Results and Discussion

Training phase

In each probe test, response accuracies were significantly higher than chance level ($p<0.05$) on 5 pairs out of 9 in three subjects (Zen, Heiji and Theta), and on 6 pairs in

Zilla, who scored above chance on all pairs after the 6th. These results showed that in all subjects the acquired conspecific age categorization transferred to novel stimulus pairs following training on a few exemplars; in other words, the monkeys did not have to learn each exemplar anew. This result suggest that monkeys may have an age category for conspecific faces.

Test phase

In the generalization test, a new species stimulus appeared in 128 trials (2 age categories × 4 faces × 16 trials) in total. Figure 2 shows the number of “infant” responses. In the dog condition, the logistic regression analyses revealed a significant main effect of stimulus age in Zen (p=0.001, odds ratio (OR) =0.52, Table 2); she selected the “infant” icon more frequently for adult stimuli than puppy stimuli. The logistic regression intercept analysis showed that all the monkeys chose the “infant” icon more frequently than “adult” (all: p<.001). This result is unlikely to reflect a bias for a particular icon because the correspondence between age category and icon was counterbalanced between subjects. We analyzed the number of infant responses for adult dogs and puppies at group level using GLMM (see Table 3 for detail results). “Infant” choices were significantly more frequent for adult dog faces than puppy faces ($\chi^2(1)$=12.7437, p<.001), indicating a strong tendency to categorize adult dog faces as “infant.”

In the human condition, the logistic regression analyses revealed no significant main effect of stimulus age in any monkey (Table2). The logistic regression intercept analysis showed that Heiji and Zen chose “infant” more frequently than “adult” (Heiji: p<.001, Zen: p=0.005); the other two monkeys showed no bias (Theta: p=0.078, Zilla:

p=0.859). The GLMM group analysis of the number of “infant” responses also showed no significant difference between human adult and infant faces ($\chi^2(1)= 0$, p=1).

<<<<<<<<<<<<<<<< Figure 2 will be located around here>>>>>>>>>>>>>>>>>>

In summary, following training with conspecific stimuli, the monkeys differentiated between adult dogs and puppies; however, they chose the infant icon more frequently than adult icon, and more so for adult dogs than puppies. This means that they were able to categorize adult dog and puppies on the basis of visual features, but the categorization was neither complete nor based on a species-general age category. Furthermore, the age category did not transfer to human stimuli. It is possible that the cues used by monkeys for categorization during the training were not available in the other species faces. In other words, features that differentiate between two age categories may not be shared by the three species. Another possibility is that the categorization formed through training was specific to own species. Specialized processing systems for own-species faces exist not only in humans (Dufour, Coleman, Cambell, Petit, & Pascalis, 2004; Pascalis, de Haan, & Nelson, 2002) but also capuchin monkeys (Dufour, Pascalis, & Petit, 2006). To test this possibility, in Experiment 2, we trained monkeys first to discriminate between heterospecific (human) faces based on age, and then tested whether performance transferred to conspecific and heterospecific (dog) faces.

Experiment 2

Method

Subjects

Two adult male tufted capuchin monkeys participated: Zinnia and Pigmon (15 and 18 years old, respectively). Neither had participated in Experiment 1, but they also had various laboratory experiences including matching to sample tasks. Their housing conditions were the same as those described for Experiment 1.

Apparatus

We used the same apparatus as Experiment 1.

Stimuli

We used 10 adult and infant faces of humans (Japanese) for training. In the test phase, we used 4 capuchin and 4 dog (Labrador retriever) faces from each age category. All dog stimuli and most human and monkey stimuli came from those used in Experiment 1. All human infant stimuli (average = 1.82, *SD* = 0.39) were rated younger than human adult stimuli (average = 4.67, *SD* = 0.21). Apart from the exception mentioned in Experiment 1, the infant monkey test stimuli were scored younger (average = 1.96, *SD* = 0.06) than the adult monkey stimuli (average = 4.45, *SD* = 0.53). All the stimuli were the same size (300 × 300 pixels) and presented in grayscale.

Procedure

Training phase. We trained the monkeys on age-based discrimination of human faces using the same procedure as in Experiment 1.

Test phase. After training, we tested for age categorization ability transfer to dog and capuchin monkey stimuli, using the same procedure as in Experiment 1.

Statistical analysis

We ran the same statistical analysis as in Experiment 1 except for the group analysis (GLMM).

Result and Discussion

Training phase

In probe tests, after the 4th pair the monkeys performed significantly above chance on age discrimination of all the novel pairs except Pigmon's 8th pair. Thus, they learned to categorize human faces according to age class and transferred this ability to novel human stimulus pairs, similar to the monkeys trained with capuchin faces in Experiment 1. The performance of the two monkeys was similar to that of the monkeys trained with conspecific faces in Experiment 1; monkeys can easily categorize adult and infant faces of not only conspecifics but also humans.

Test phase

In the generalization test, a new species stimulus appeared in 128 trials (2 age categories × 4 faces × 16 trials) in total. Figure 3 shows the number of "infant" responses. In the "dog" condition, the logistic regression analyses revealed no significant main effect of stimulus age in either subject (Pigmon: p=0.101, Zinnia: p=0.594, Table 4); the monkeys did not discriminate between adult dogs and puppies. The logistic regression intercept analysis showed that both subjects chose the "infant" icon more frequently than the “adult” icon (both: $p<.001$), the same result as in the dog condition in Experiment 1.

In the conspecific condition, the logistic regression analyses revealed a significant main effect of stimulus age for Pigmon ($p=0.031$, OR= 1.49, Table 4) but not for Zinnia ($p=0.415$). Although Pigmon discriminated according to age category, the logistic regression intercept analysis showed that he chose “adult” more frequently than the “infant” icon ($p=0.013$, OR=0.63). By contrast, Zinnia chose the “infant” more frequently than the “adult” icon ($p<.001$, OR=3.02).

<<<<<<<<<<<<<<<< Figure 3 will be located around here>>>>>>>>>>>>>>>>>>

In Experiment 2, the monkeys failed to discriminate according to age category of either dogs or humans despite training on heterospecific stimuli. Therefore failure in generalization of the age category in Experiment 1 is not explained by specialized learning for own-species faces. Monkeys showed an “infant choice bias” for dog stimuli, as did the monkeys in Experiment 1. The categorization might not have transferred to other species in both Experiments because monkeys have formed an age category limited to training species. If so, training with multiple stimuli may be required to form a more general age category. Another possibility is that the three stimulus species did not shared age-related cues. Therefore in Experiment 3 we trained the monkeys with another species stimulus set and then tested for transfer of categorization to a variety of novel species.

Experiment 3

Method

Subjects

The six capuchin monkeys from Experiments 1 and 2 participated in Experiment 3.

Apparatus

We used the same apparatus as Experiment 1.

Stimuli

We used 10 adult and infant faces of humans and conspecific stimuli for training. In the test phase, we used the same dog stimuli used in Experiments 1 and 2. For further generalization testing we prepared various species stimuli from four taxonomic groups including New World monkeys (white-headed capuchin monkeys, squirrel monkeys), Old World monkeys (anubis baboons, Japanese macaques), apes (gorillas, chimpanzees) and carnivores (domestic cats, wolves). The number of stimuli was 64 in total (4 different stimuli*8 species*2 age categories). All stimuli were the same size (300 × 300 pixels) and presented in grayscale.

Procedure

Training phase. We trained the four monkeys from Experiment 1 on age-based discrimination of human faces and trained the two monkeys from Experiment 2 on discrimination of conspecific faces. The procedure was the same as in Experiments 1 and 2.

Test phase. After training, we tested if age categorization transferred to dog stimuli. Generalization tests with the novel species were also conducted after confirming the baseline performance. The procedure was the same as in Experiments1 and 2.

Statistical analysis

We performed a group analysis on the number of “infant” responses using a Generalized Linear Mixed Model (GLMM) with age category (and species for the novel species test) as fixed effect, binomial distribution as link function, with random effect of subject.

Result and Discussion

Training phase

In each probe test of the training phase response accuracies of the monkeys trained with human stimuli were significantly higher than chance level on 6-9 pairs out of 9 (Theta: 6, Zen; 7, Zilla; 8, Heiji; 9). For the monkeys trained with monkey stimuli, response accuracies for Zinnia were significantly higher than chance on 8 pairs and for Pigmon on 5 pairs. As in Experiments 1 and 2, monkeys trained on human or monkey stimuli quickly transferred their acquired age categorization to novel stimulus pairs.

Test phase

Dog stimuli: The GLMM group analysis of the number of “infant” responses showed no significant difference between adult and infant faces ($\chi^2(1)= 0$, $p=0.06$, Table 3, Figure 4). Although we cannot conclude that the monkeys succeeded to differentiate adult dog and puppy faces, the opposite response (respond as “infant” to adult dogs) observed through Experiment 1 and 2 was disappeared.

Various species stimuli: We analyzed the number of infant responses for each of the four taxonomic groups at group level by using GLMM (Table 5). The monkeys made significantly more “infant” responses to infant stimuli than adult stimuli ($\chi^2(1)=14.78$, $p<0.001$). There was also a significant main effect of taxonomic stimulus group

($\chi^2(3)=20.48$, $p<.001$). Multiple comparisons with Bonferroni correction revealed significant differences between “apes” and “carnivores”, and “apes” and “New World monkeys” (both $p<0.001$). Performance for ape stimuli was better than that for other stimuli (at least carnivores and New-world monkeys). One possibility is that physical difference between adult and infant faces of apes were more salient, but morphological study is required to confirm this. Another possibility is that cues used by monkeys in training were salient in the ape stimuli. In general, the monkeys differentiated between infant and adult stimuli, but “infant” responses continued to predominate (“infant choice bias”, Figure 5).

<<<<<<<<<<<<<<<< Figure 4, 5 will be located around here>>>>>>>>>>>>>>>>>

Given that the “infant choice bias” for adult dog stimuli disappeared and monkeys differentiated age category of various species stimuli, their generalization performance can be said to have slightly improved following training on a second species in Experiment 3. However, there was no evidence of formation of a species-general age category; nor did they transfer age categorization to faces of New World monkey, despite belonging to the same taxonomic group. This is consistent with a previous study of Tonkean macaques (*Macaca tonkeana*) and brown capuchin monkeys (*Cebus apella*) suggesting that stimuli of conspecifics and phylogenetically close species do not necessarily provide similar results (Dufour et al., 2006).

General Discussion

This study investigated whether capuchin monkeys can categorize conspecific and heterospecific faces based on age. In Experiment 1 we trained four monkeys to discriminate between adult and infant faces of conspecifics, then tested whether their acquired categorization ability transferred to other species (dogs and humans). In Experiment 2 we trained another two monkeys on age category discrimination of heterospecific (human) faces, and tested transfer to conspecific and dog faces. In Experiment 3, all monkeys were trained on stimuli of a second species, after which they were tested with photos of dogs and other various species. In all experiments, age categorization failed to transfer significantly to different species in the test phase. However, it is noteworthy that during the training phase in three experiments, all monkeys quickly learned to differentiate “adult” and “infant” categories of conspecifics and humans.

The capuchin monkeys in this study learned to categorize conspecific and human faces on the basis of age. In previous studies of nonhuman primates’ use of visual information, chimpanzees and rhesus monkeys were shown to visually discriminate between unknown individuals (Parr, Winslow, Hopkins, & de Waal, 2000), while Japanese macaques can categorize sex of conspecifics (Koba & Izumi, 2006). It is also known that nonhuman primates can discriminate between faces of other species (Parr, Dove, & Hopkins, 1998; Parr, Winslow, & Hopkins, 1999). The results of the present study are not only consistent with previous research, but add age as a category within nonhuman primates’ discrimination abilities; furthermore, this applies to both conspecific and heterospecific (human) faces.

If the categorization established during the training phase was low-level features, we might have expected that many more stimulus pairs would have been necessary to complete the training. Moreover, we used “all reinforcement” for new stimuli during the training phase, meaning that even without feedback the monkeys still responded correctly. The rapid acquisition of categorical learning in training indicates that the discrimination was not based on only low-level features, although we cannot rule out the possibility that it was based on something other than age, for example, “cuteness”. Importantly, however, their performance matched the age category, and they extracted shared visual features within each age category immediately during the training.

Human raters quite easily correctly recognized the age categories of humans, capuchin monkeys and dogs. However, although the monkeys learned to categorize faces according to age during training, they failed to transfer to other species in the test phase. There are several possible reasons for this failure. First, categorizing age from faces may not be an automatic process. Generalization was tested by probe trials, which investigate spontaneous responses. Given that facial information is not the only available information in daily life, the ability to recognize age-related information and spontaneously categorizing age of faces reflect different things. The former but not the latter was observed in our capuchin monkeys. Second, we trained the monkeys using pictures of two species (humans and capuchins), but training with more species may be required to form species-general age categorization. Finally, monkeys failed to generalize possibly because certain cues used in one species was not available for another species. They did not use species-general features to categorize adults and infants, or there may be no set of common features that distinguish between adult and infant faces across the species we used. If so, we need to be careful before asserting that species-general infantile features like “baby schema” exist across species.

Interestingly, all six monkeys showed a consistent “infant choice bias” in the test phase in all Experiments. The reason for this bias is unclear; however, one possibility is that subjects may have formed a more specific prototypical “adult” face during training. This is because stimuli may include both younger and older infant/adult features as we could not fully control the age of stimuli. Because more marked morphological changes usually occur in early developmental than in adulthood, there may be greater variety within infant compared to adult stimuli.

In this study we used stationary, grayscale visual stimuli. In their daily life of course monkeys have a much richer array of information available to help them recognize other individuals, including color, body size, motion, vocalizations and odors. For example, infant vocalizations work as releasers of caretaking in common marmosets (*Callithrix jacchus*) (Barbosa & Mota, 2014). The impoverished visual stimuli used in our experiments might explain the failures to transfer the acquired discrimination ability to different species. A previous study revealed auditory-visual cross-modal perception in tufted capuchin monkeys (Evans, Howell, & Westergaard, 2005). These authors simultaneously presented monkeys with two videos of facial expressions along with one vocalization that matched one of the faces. The monkeys preferred to look at the face that matched the vocal stimulus. Age-related recognition should also be possible using cues in auditory or other modalities as well as visual.

Unfortunately, we are unable to specify which cues the monkeys used to discriminate age categories in this study; they might have used local cues (e.g. eye size), global cues (e.g. relative location of eyes) or some combination. Systematic manipulation of stimuli might help to reveal the key features of faces for age categorization and clarify the boundary between “adults” and “infants” for monkeys. Future studies should examine both morphological changes with development and the role of such changes in age category recognition in various species.

In summary, capuchin monkeys categorized adult and infant faces of both conspecifics and heterospecifics through training, which means they are sensitive to some features which convey age-related information. However, training with stimuli of two species did not result in clear generalization of the age categorization to different species. These results call for reconsideration of the “baby schema” from a comparative perspective.

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Table

Table1. The overall flow and stimuli used in Experiment 1,2 and 3

Phase	four monkeys; Heiji, Zilla, Theta and Zen	two monkeys; Zinnia and Pigmon
Experiment 1		
training	conspecific	-
test	human and dog	-
Experiment 2		
training	-	human
Test	-	conspecific and dog
Experiment 3		
training	human	conspecific
test	dog	
test	various species from four taxonomic groups	

Table 2. Summary of the result of logistic analyses for the number of “infant” responses in Test phase during Experiment 1

	Odds Ratio		*p*		95% Conf. Interval			
Subject	Intercept	age	Intercept	age	Intercept		age	
Dog								
Heiji	9.80	0.83	<.001	0.546	5.62	18.96	0.44	1.51
Theta	2.59	0.79	<.001	0.240	1.77	3.87	0.53	1.17
Zen*	**2.04**	**0.52**	**<.001**	**0.001**	**1.40**	**3.06**	**0.35**	**0.76**
Zilla	2.01	0.72	<.001	0.094	1.39	2.95	0.50	1.05
Human								
Heiji	14.02	1.45	<.001	0.309	7.36	31.72	0.73	3.21
Theta	1.37	0.94	0.078	0.720	0.97	1.96	0.66	1.33
Zen	1.67	1.14	0.005	0.466	1.17	2.41	0.80	1.64
Zilla	1.03	0.86	0.859	0.377	0.73	1.46	0.60	1.21

*Significant result is in bold.

Table 3. GLMM parameter estimate coefficients and confidence interval in Experiment 1 and 3.

Predicter variables	Estimate	SE	*Z*	*p*	95% Conf. Interval	
Exp.1 Dog stimuli						
(Intercept)	1.52	0.35	4.37	<.001	0.84	2.2
Infant	**-0.75**	**0.21**	**-3.57**	**<.001**	**-1.17**	**-0.34**
Exp1. Human stimuli						
(Intercept)	0.84	0.50	1.67	0.10	-0.15	1.82
Infant	<.001	0.20	<.001	1.00	-0.39	0.39
Exp3. Dog stimuli						
(Intercept)	1.62	0.43	3.80	<.001	0.78	2.45
Infant	0.38	0.20	1.91	0.06	-0.01	0.78

*Significant result is in bold.

Table 4. Summary of the result of logistic analyses for the number of “infant” responses in test phase during Experiment 2

	Odds Ratio		*p*		95% Conf. Interval			
Subject	Intercept	age	Intercept	age	Intercept		age	
Dog								
Pigmon	1.75	1.36	0.003	0.101	1.22	2.53	0.95	1.96
Zinnia	7.05	1.15	<.001	0.594	4.30	12.44	0.68	1.99
Monkey								
Pigmon*	**0.63**	**1.49**	**0.013**	**0.031**	**0.43**	**0.90**	**1.04**	**2.16**
Zinnia	3.02	1.18	<.001	0.415	2.05	4.59	0.79	1.78

*Significant result is in bold.

Table 5. GLMM parameter estimate coefficients and confidence interval in Experiment 3.

Predicter variables	Estimate	SE	*Z*	*p*	95% Conf. Interval	
(Intercept)	0.07	0.37	0.20	0.84	-0.64	0.79
Ape vs. New-world	**1.85**	**0.47**	**3.95**	**<.001**	**0.93**	**2.77**
Ape vs. Old-World	**0.62**	**0.31**	**1.99**	**0.05**	**0.008**	**1.22**
Ape vs. Carnivore	**1.11**	**0.29**	**3.80**	**<.001**	**0.54**	**1.68**
Adult vs. Infant	**1.15**	**0.33**	**3.54**	**<.001**	**0.51**	**1.79**
New-world: Infant	-0.97	0.69	-1.40	0.16	-2.32	0.39
Old-World: Infant	-0.23	0.48	-0.48	0.63	-1.16	0.71
Carnivore: Infant	**-0.91**	**0.43**	**-2.09**	**0.04**	**-1.75**	**-0.06**

*Significant result is in bold.

Figure

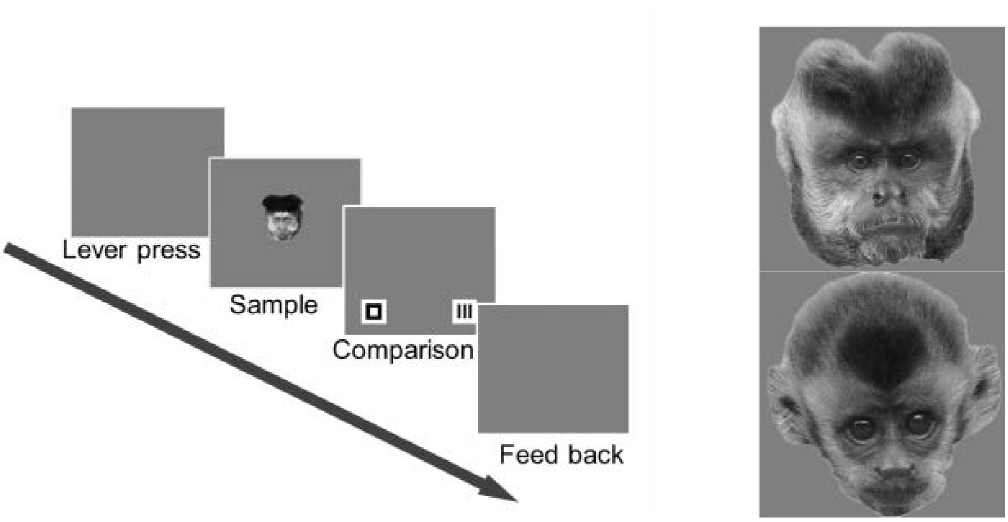

Figure 1. Experimental procedure (Symbolic matching to sample task) and examples of stimuli (top: adult capuchin monkey, bottom: infant capuchin monkey)

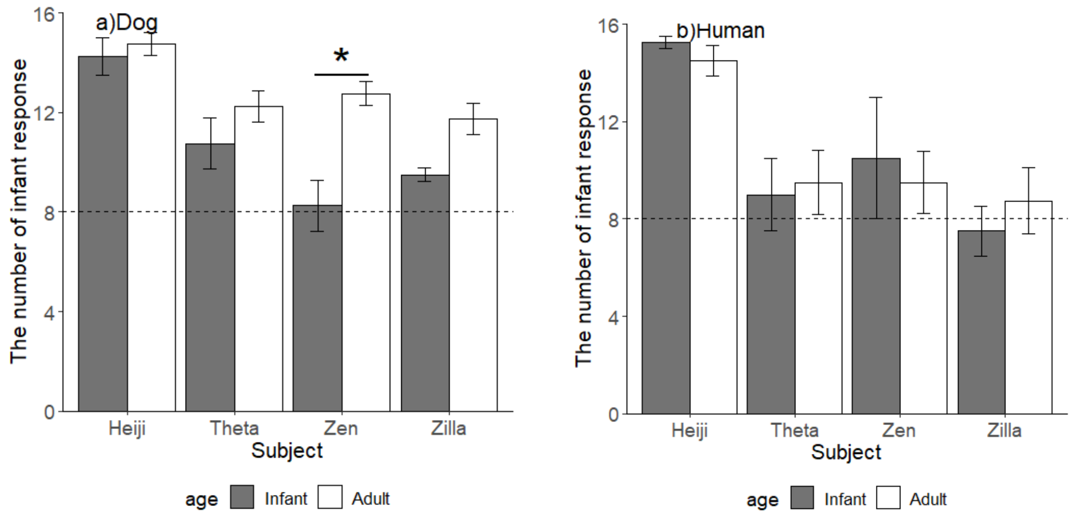

Figure 2. The mean number of “infant” responses in the generalization test for dog stimuli (a) and human stimuli (b) in four monkeys in Experiment 1. The dotted line represents chance level. The color of bar indicates age category of stimuli. Asterisk indicates significant difference between adult and infant stimuli, $p<.05$. Error bars represent standard errors.

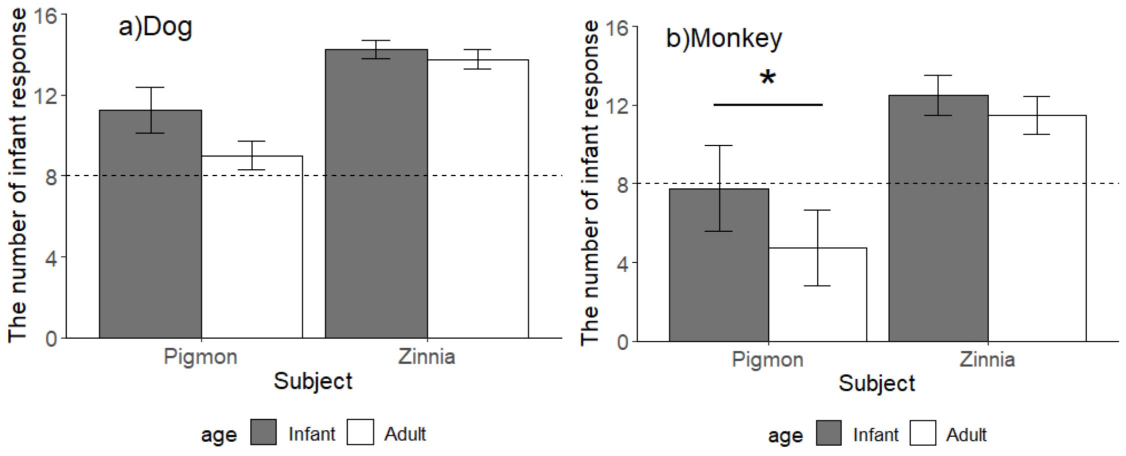

Figure 3. The mean number of “infant” responses in the generalization test for dog stimuli (a) and monkey stimuli (b) in two monkeys in Experiment 2. The color of bar indicates age category of stimuli. The dotted line represents chance level. Asterisk indicates significant difference between adult and infant stimuli, *p*<.05. Error bars represent standard errors.

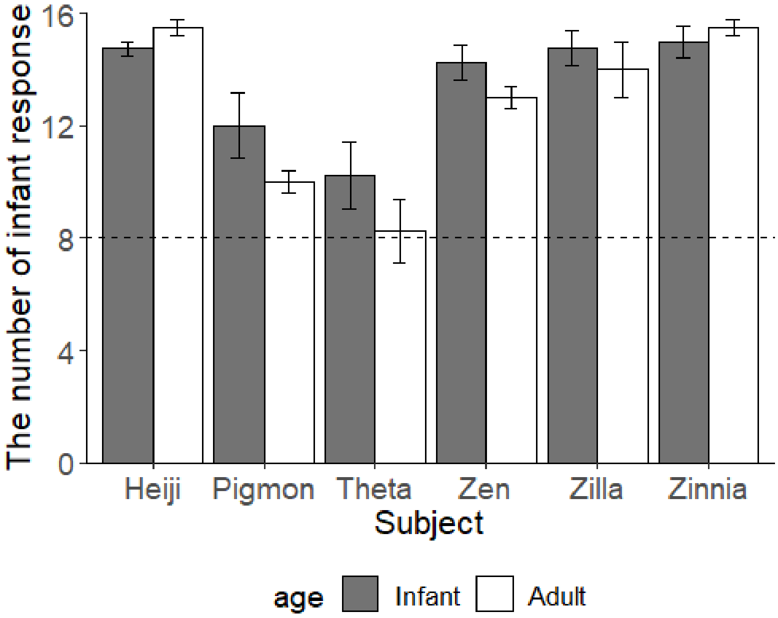

Figure 4. The mean number of “infant” responses in the generalization test for dog stimuli in all six monkeys in Experiment 3. The color of bar indicates age category of stimuli. The dotted line represents chance level. Error bars represent standard errors.

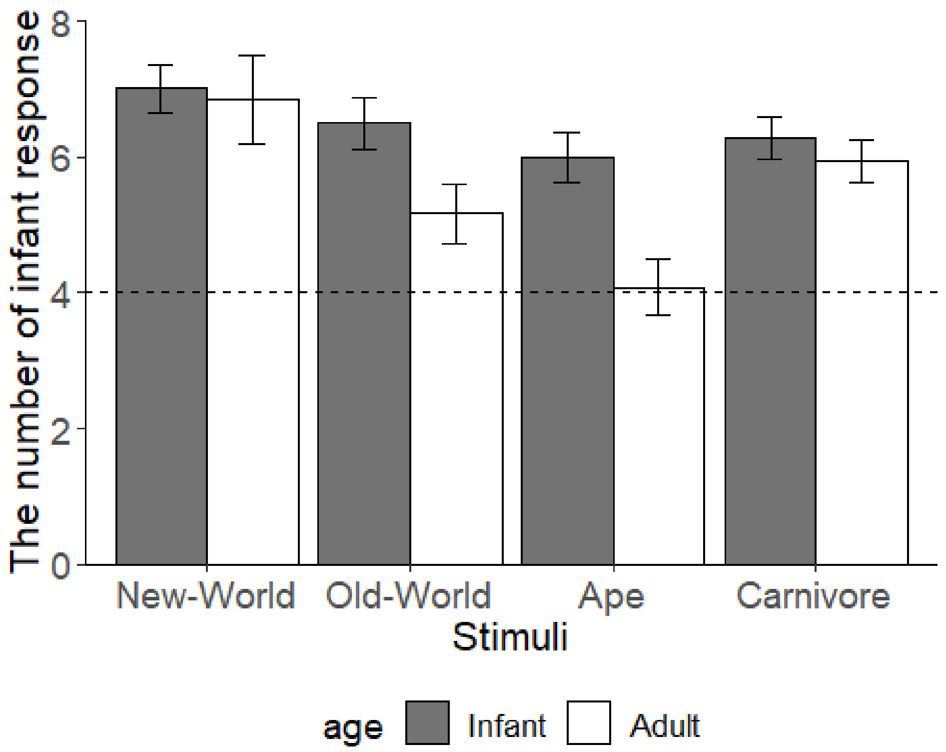

Figure 5. The mean number of “infant” responses in the generalization test for various species stimuli (New World monkeys, Old World monkeys, apes and carnivores) in Experiment 3. The dotted line represents chance level. The color of bar indicates age category of stimuli. Error bars represent standard errors.