

THE ROLE OF LEARNING IN CHUCK CALL RECOGNITION BY SQUIRREL MONKEYS (SAIMIRI SCIUREUS)

by

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Summary

This study explored the role of learning in the development of chuck call recognition in squirrel monkeys. We experimentally exposed subjects of four different age classes, under controlled conditions, to the chuck calls of genetically unrelated individuals of different social affinities. Using playback experimentation, we tested the hypothesis that subjects at different developmental stages respond preferentially to the chuck calls of genetically unrelated familiar social group companions when compared to those of unfamiliar individuals from outside of the social group. Results demonstrated that adults vocally respond preferentially to the chuck calls of familiar social group members. Subadults behaviorally respond preferentially to the chuck calls of close social associates within their social groups. Juveniles behaviorally responded more strongly to the playback of chuck calls arising from individuals within their colony when compared to the playback of 'silence.' Infants did not behaviorally or vocally respond preferentially to the chuck calls of close social associates or other social group members. These results demonstrate that learning plays a role in chuck call recognition in squirrel monkeys and may suggest that infants gradually learn to acoustically recognize social companions within their group.

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Introduction

The comparative approach to vocal development can offer valuable insights into the mechanisms of vocal learning such as the type, extent, and timing of vocal learning, including the different types of social and environmental factors that influence the developmental process (see Snowdon & Hausberger, 1997 for review). Additionally, the comparative approach allows us to investigate the socioecological parameters that might predict the presence of learning in a vocal system and thus may have contributed to the evolution of vocal learning in humans and other animals. Vocal learning can occur in the acquisition and modification of the acoustic structure of a signal, in the contextual use of signals, and in the comprehension or recognition of signals. The occurrence of one aspect of vocal learning is not requisite for the emergence of others nor is it the case that all vocalizations within a repertoire be learned for evidence of learning in one call type (Seyfarth & Cheney, 1997 for review). In addition, the timing of learning in each of these aspects can be disparate; for example, comprehension of calls can precede production of vocal signals as evidenced in human speech acquisition (see Locke & Snow, 1997 for review). Conversely, vocal production can precede comprehension or contextual use (Seyfarth & Cheney, 1997; Snowdon *et al.*, 1997).

Nonhuman primates provide an excellent model for the comparative study of vocal development and learning in nonhuman mammals. Nonhuman primates exhibit diverse but complex vocal behavior that varies in importance in fostering social interactions. While a role for learning in the production of calls has not yet been confirmed for any nonhuman primate (Hauser, 1989, 1992; Masataka & Fujita, 1989; Owren *et al.*, 1992; Snowdon *et al.*, 1997), the role of experience in the use and perception of species-specific vocalizations has been reported for several species and specifically for Old World monkeys such as vervets and macaques (Masataka, 1983a, 1985; Seyfarth & Cheney, 1986; Gouzoules & Gouzoules, 1989; Hauser, 1989). In vervet monkeys, the use and comprehension of predator alarm calls are gradually acquired (Hauser, 1988). Young animals tend initially to produce the specific alarm calls in inappropriate contexts and appear to overgeneralize the contexts of these calls. They apparently learn to produce these alarm calls in the appropriate contexts. They have also been reported to learn to respond appropriately to the different alarm call types (Seyfarth & Cheney, 1986). In pigtail macaques, similar developmental patterns are found. Young macaques tend

to produce the acoustically distinct agonistic screams in contexts inappropriate to their functions. Older individuals more often match these agonistic screams to their proper social contexts (Gouzoules & Gouzoules, 1989). In Japanese macaques, infants gradually develop the ability to recognize the calls of individuals within their social groups (Masataka, 1985).

In contrast to Old World monkeys, developmental modification in vocal use and perception for New World monkeys has remained relatively undocumented with the exception of a few notable species (Masataka, 1983b; Snowdon *et al.*, 1985; Heymann, 1990; Roush & Snowdon, 1994). This is surprising in view of the fact that vocal communication is widely regarded as essential in maintaining the social organization of small, arboreal primates.

Vocal communication in squirrel monkeys (*Saimiri* spp.) has been under detailed study for more than 20 years. Much of the earlier work suggested that the squirrel monkey vocal repertoire consisted primarily of vocalizations in which learning played little if any role (Winter *et al.*, 1973; Lieblich *et al.*, 1980). As a result, the squirrel monkey has been held as a classic model for vocal inheritance in nonhuman primates (Hauser, 1996; Seyfarth & Cheney, 1997). Nevertheless, one vocal type in squirrel monkeys, the chuck call, is acoustically different in infants and adults (Newman *et al.*, 1983), is emitted primarily by adult females during close affiliative interactions (Smith *et al.*, 1982b), and shows a strong degree of individuality in acoustic structure (Smith *et al.*, 1982a). In addition, adult females vocally respond differentially to chucks of familiar social companions over chucks of unfamiliar individuals (Biben & Symmes, 1991; Biben & Bernhards, 1994). That chuck structure is individually distinctive (Smith *et al.*, 1982b), changes with age (Biben & Bernhards, 1995), and occurs as dyadic exchanges ('dialogues' or 'duets') between familiar individuals (Smith *et al.*, 1982a; Biben *et al.*, 1986; Biben & Bernhards, 1994) all suggest that learning may play an important role in the maturation of this vocal subsystem.

As a part of a series of studies on the role of learning in squirrel monkey vocal development, this study was conducted to determine if young squirrel monkeys learn to recognize the chuck calls of individuals within their social groups. We experimentally exposed subjects of four different age classes, under controlled conditions, to the chuck calls of genetically unrelated individuals of different social affinities (stranger, unfamiliar, non-associate, close associate). Chuck calls from unrelated individuals were chosen deliberately to document the role of learning, not simply the developmental process, in

the vocal perception of chuck calls. We tested the hypothesis that subjects at different developmental stages respond preferentially to the chuck calls of socially familiar but genetically unrelated companions when compared to those of unfamiliar individuals from outside of the social group.

Methods

Subjects and living arrangements

Three social groups from the California Regional Primate Research Center consisting of 4-5 adult females housed with their offspring of 0-46 months of age were the subjects of this study. Groups were housed in an indoor room in standard living cages ($1.2 \times 1.2 \times 2.1$ m high), equipped with four parallel perches arranged in stepwise fashion. The three different social groups had acoustic contact but no visual or physical contact. Focal subjects included four infants less than 12 months of age (three males, one female), four juveniles between 12 and 30 months (two males, two females), four subadults between 30 and 60 months (all females), and five adults over 60 months (all females). All adult females within and across each social group were genetically unrelated to each other and to the infants, juveniles, and subadults (with the exception of their mothers).

Behavioral observations and analysis

Behavioral sampling was conducted in the indoor room using a focal animal sampling design (Altmann, 1974) and 15-s interval sampling. Focal individuals within each social group were observed for one 5-min period twice per week for 12 months. The order in which subjects and groups were observed was systematically varied. Behaviors collected on the interval included identification of individuals who were in proximity (within arm's reach) to the focal individual, identification of those in contact with the focal individual, and whether the focal individual was engaged in a social huddle. Social affinity or familiarity was measured by the amount of time focal individuals spent in proximity with genetically unrelated adult females within their social groups. The association index for each focal individual was calculated by taking the mean number of 15-s interval samples on which proximity occurred across all 5-min observation periods for each unrelated adult female. This calculation resulted in a measure of the mean proportion of time each focal individual spent in proximity to each unrelated adult female within the social group. The adult female companion with the highest association index for each focal individual was chosen as the 'close associate.' The adult female with the lowest association index was chosen as the 'non-associate' (see Table 1). In addition, the ratio of the close associate and non-associate association indices (CAI/NAI) was required to be equal to or greater than two (Table 1). It is important to note that the close associates and non-associates of infants, juveniles, and subadults were not necessarily identical to that of their mothers (see Table 1). Thus, the tests of close-associate and non-associate chuck call responses were independent for mothers and their offspring (but also see "*Dependency of behavioral responses between simultaneously tested subjects*" in the results section). For example, in only four of 12 mother-offspring pairs did mothers and offspring have the same genetically unrelated close associate within the social group.

TABLE 1. *Description of focal subjects and the association indices for close associates, non-associates and their ratios (CAI/NAI)*

Individual	Group	Sex	Age (months)	Age class	Close-associate association index	Non-associate association index	CAI/NAI
69	1	F	> 60	Adult	0.100	0.010	10
129	2	F	> 60	Adult	0.060	0.010	6
42	3	F	> 60	Adult	0.080	0.010	8
108	3	F	> 60	Adult	0.060	0.010	6
84	3	F	> 60	Adult	0.090	0.010	9
163	3	F	46	Subadult	0.060	0.030	2
165	3	F	43	Subadult	0.100	0.030	3
173	2	F	32	Subadult	0.060	0.030	2
181	1	F	30	Subadult	0.050	0.010	5
184	3	F	21	Juvenile	0.060	0.030	2
186	2	M	17	Juvenile	0.240	0.020	12
188	1	M	17	Juvenile	0.080	0.010	8
189	2	F	16	Juvenile	0.060	0.010	6
190	3	M	8	Infant	0.130	0.001	130
196	3	M	7	Infant	0.150	0.020	7.5
198	1	M	7	Infant	0.050	0.010	5
200	2	F	6	Infant	0.140	0.010	14

Experimental housing

A subset of animals from a single group was moved in transport cages to an indoor experimental enclosure in a separate building. The experimental enclosure provided a large area ($2.31 \times 3.84 \times 2.09$ m) with one perch (measured and marked in 0.3-m intervals) that spanned the entire length of the enclosure. An opaque wall was located in the middle of the enclosure with a window through which the monkeys could travel using the perch (see Fig. 1). Water was available to the subjects during each 45-min testing period. All subjects were housed with two other individuals (a subset consisted of one focal infant, juvenile, or subadult and two focal adult females, excluding group members from which playback exemplars were selected — see section entitled “*Playback exemplars*” below) during testing to reduce the group separation response (*e.g.* continuous isolation peeps) that frequently occurs when individuals are separated from the rest of their social group (Newman, 1985).

Playback exemplars

Multiple chuck exemplars were selected from a library of chuck calls from genetically unrelated adult females, differing in social association patterns, for each subject: close associates (Total exemplar $N = 15$), non-associates (Total exemplar $N = 15$), socially-unfamiliar individuals from another other social group within the colony (Total exemplar $N = 26$), and strangers from a different colony (NIH Animal Center, Total exemplar $N = 20$). These vocalizations were collected during observational recordings for a study

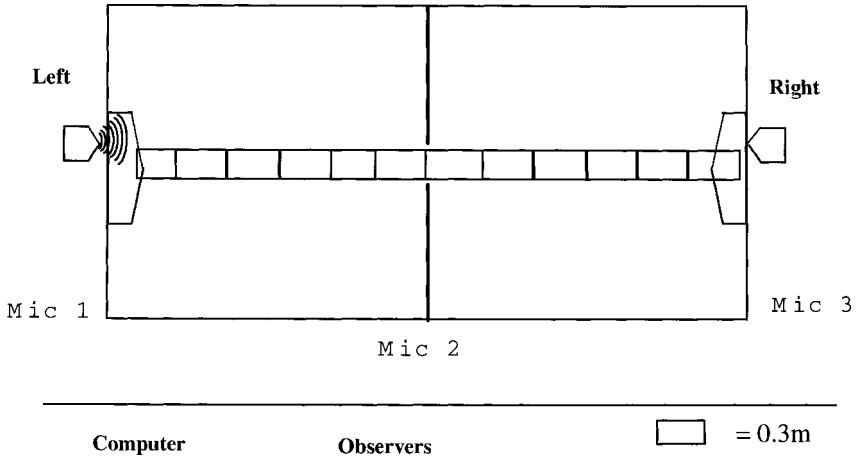


Fig. 1. Experimental enclosure (top view).

on chuck call development (B. McCowan & J.D. Newman, unpubl. data) and were processed for playback parameters (Biben, 1993; Biben & Bernhards, 1994). Both single and multiple chuck element exemplars were selected. Selection criteria for chuck playback stimuli was based upon high signal-to-noise ratio and at least 10 s of vocal silence to eliminate calls that were responses to other chuck calls. Previous research indicated that 70% of chuck responses occur within 4 s of chuck production (Biben & Bernhards, 1994) and thus the 10-s window of vocal silence was conservative.

'Sham' playbacks (500 ms of recorded silence) and playbacks of alarm peeps (Total exemplar $N = 48$) were randomly interspersed in the procedure to serve as controls. The object of the 'sham' control was to evaluate whether the incidence of response to chuck playbacks was greater than that which occurs under identical conditions but with no chuck stimulus presented. The purpose of the 'alarm peep' control was to distinguish the behavioral and vocal responses specific to chuck calls from those to other vocalization types and to determine at which point in development infants respond to chuck vocalizations as a category. Like chucks, alarm peeps were selected from our library of vocalizations for each social group and processed for playback parameters.

Playback collection methods

A six-month experimental period was conducted using a cross-sectional study design for age class (infants, juveniles, subadults, adults). Each focal subject was tested at least twice per month. A total of 133 sessions and 2660 trials was conducted during the experimental period. The order in which groups and subjects were tested was systematically varied. No individual or group of individuals was tested twice on one day.

Playbacks were broadcast using a Micron Pro 200 computer equipped with a SoundBlaster 32-wavetable sound board (sampling rate: 44.1 kHz) and Cool Edit Signal Software (Syntrillium Incorporated) through one of two Advent V270 computer speakers, mounted on platforms at opposite ends (termed 'left' and 'right') of the experimental enclosure (see Fig. 1).

The speakers were sufficiently hidden from the experimental subjects to closely mimic authentic vocal behavior. A playback list consisting of three different chuck calls each from the close associate, the non-associate, an unfamiliar individual, and a stranger, and a total of eight control stimuli was generated with a pseudorandom ordering of playback stimuli for each focal subject for each session. Thus, playback files consisted of a total of 20 playback stimuli (three close-associate chucks, three non-associate chucks, three unfamiliar chucks, three stranger chucks, four shams, and four alarm peeps). The ordering of playback stimuli was conducted such that no individual exemplar was repeated within a session and no two stimuli of the same type (*e.g.* chuck vocalizations from the same individual, alarm peeps) immediately followed another. Trials were conducted every two minutes (extremely conservative given an average calling rate of over 200 chucks per hour by squirrel monkeys; B. McCowan & J.D. Newman, unpubl. data) and the broadcast speaker ('left' or 'right') was determined by the location of the focal infant, juvenile, or subadult in the experimental enclosure (*e.g.* if the infant was in the 'right' partition of the enclosure then the playback stimuli was broadcast through the 'left' speaker). Each session began with a 5-min pre-session habituation period.

Five experimenters conducted each session. One experimenter ran the playback and recording procedures on the computer. The second experimenter collected focal behavioral data on the infant, juvenile, or subadult. The third and fourth experimenters collected focal behavioral data on the two adult females. Behaviors scored immediately prior to playback included the location of the individuals in the enclosure and the general activity of the individuals (*e.g.* locomoting *vs* stationary). Behavioral responses scored for 5 s after playback included two quantitative measures (in m) of approach to and/or withdrawal from the speaker. Initial approach was defined by the first movement toward or away from the broadcast speaker following playback. Overall approach was defined by the sum of each movement toward or away from the broadcast speaker within the 5-s post-playback period. Gaze toward or away from speaker was not used as a behavioral measure because it is an unreliable response variable for squirrel monkeys (B. McCowan, pers. obs.).

Recording of vocal behavior by the subjects prior to, during, and following playback was conducted using three microphones (Audio-technica AT 4071 (frequency response to 20 kHz); Sennheiser MP100 (frequency response to 20 kHz); and a AKG C 1000 S (frequency response to 20 kHz) connected through a Radioshack M460 mixer directly into a Micron Pro 200 computer equipped with a SoundBlaster 32-wavetable soundboard (sampling rate of 44.1 kHz) and Cool Edit Signal Software. For each trial, vocal behavior was continuously recorded directly onto the computer for 10 s prior to playback, during playback, and for 5 s after playback. Thus each trial generated a 15-s digitized sound file of the vocal behavior surrounding playback. The fifth experimenter determined the identity and order of vocalizers, including the type of vocalization produced, both prior to and following playback.

Because multiple observers were used to conduct sessions, inter-observer reliabilities were conducted by calculating a raw percentage of the correspondence between the observers' scoring on the same focal individual for a total of 5 sessions or 100 trials. Inter-observer scores ranged from 92-97% agreement.

Playback analysis methods

Behavioral responses

The relative movement toward or away from the broadcast speaker was analyzed both for the initial approach (first movement following playback) and a summed overall approach (each

movement toward or away from the broadcast speaker was scored and summed) during the 5-s period following playback. The distance (in m) from the speaker after the post-playback period of 5 s was also calculated as a third variable by adding the positive or negative value obtained for overall approach to the pre-playback distance from the broadcast speaker (determined by the location of individuals prior to playback). This third variable represented a measure of proximity to the broadcast speaker following the 5-s post-playback period.

Using unbalanced repeated measures ANOVA in BMDP Dynamic Statistical Software (Dixon *et al.*, 1990), the quantitative measures of initial approach, overall approach, and post-playback distance from broadcast speaker were analyzed for differences in the four categories of chuck calls (stranger, unfamiliar, non-associate, and close associate) and the two controls (shams, alarm peeps) for each age class (infants, juveniles, subadults, and adults). Although sex differences were tested where possible (infants and juveniles), no significant differences were found and thus this variable was removed from the final analyses. Unbalanced repeated measures ANOVA in BMDP Dynamic uses the maximum likelihood (ML) method. ML estimation of parameters uses the comparison of ML values in relation to elements of the estimated covariance matrix of parameter estimators. The likelihood ratio test, under the chi-square distribution, is used to compare the fit of selected models by comparing the ratio of ML values generated from the models to assess the significance in the change in ML values between models (Kleinbaum *et al.*, 1988). Individual was designated as the repeated measure in each analysis. To test for normality, regression diagnostics were evaluated and revealed the aptness of the model. Because neither initial approach nor overall approach showed significant differences among our chuck call categories, they were removed from the final analyses. Thus, results represented below only include the calculated variable of post-playback distance from the broadcast speaker. Where appropriate, pairwise comparisons using repeated measures ANOVA of chuck call categories and the controls were conducted to determine where the significance was found. For all tests, significance was evaluated at the 0.05 level. However, because we conducted multiple comparisons, we corrected our alpha levels for the pairwise comparisons using Holm's sequential Bonferroni test (Rice, 1988). In addition, because subjects were tested with one or two additional individuals, we tested for the dependency of behavioral responses to chuck call playback by infants, juveniles, and subadults on that by mothers and other adults. For each young subject, we calculated the proportion of responses in which younger individuals and their mother or the other adult female approached the same post-playback location (after the 5-s post-playback period) following chuck call and sham playback.

Vocal responses

Two categories of vocal responses were analyzed from the data collected on the subjects' vocal behavior surrounding playback. First, we examined for each focal individual whether a vocal response occurred after playback (measured as 'yes' or 'no' for each individual). However, because subjects were tested simultaneously, a given individual could have responded vocally as a result of other subjects' responding vocally to the playback. Thus, to control for this possibility, we also specifically examined the first vocal response after playback. In examining this first vocal response by an identified individual, we determined (1) the type of vocal response (adults: chuck call versus isolation peep; infants, juveniles, subadults: short peep, tuck, oink or chuck *versus* isolation peep) and (2) whether the first vocal response after playback was emitted within 2 s after playback. Thus, these variables were used as categorical measures of the type and the latency of first vocal response after playback when vocal

response occurred. We chose to analyze the latency variable as a categorical variable, rather than a continuous one, because after trying several transformations, the latency variable failed to fit the required assumptions of normal distribution.

These response categories were analyzed as outcome variables in relationship to two categories of chuck call playback stimuli (unfamiliar chucks from individuals outside of the social group but in the same colony, and familiar chucks which included both non-associate and close associate chuck calls from within the social group) and two control stimuli (shams, alarm peeps) for each age class (infants, juveniles, subadults, adults). We combined the non-associate and close-associate playback stimuli into one category termed 'familiar' for the final analyses because they showed no significant differences in any of our initial statistical analyses.

Because each of these vocal analyses were categorical and, more specifically, binary in structure, logistic regression was used as the statistical method (Egret, 1997). Logistic regression is the statistical method of choice for binary data, because unlike other tests such as chi-square, logistic regression indicates both significance as well as the magnitude of the association in the form of an odds ratio. Furthermore, logistic regression is free of a number of problematic distribution assumptions that affect other types of analyses. We used mixed effects logistic regression in Egret Statistical Software for the PC (Egret, 1997) with 'individual' (the identity of each monkey) designated as the random effect or repeated measure in each analysis (Searle *et al.*, 1992).

For all statistical tests, significance was evaluated at the 0.05 level unless indicated otherwise. Goodness-of-fit statistics for each logistic regression model were conducted using a likelihood-ratio chi-square statistic (Agresti, 1990). All models presented below exhibited appropriate goodness-of-fit.

Results

Dependency of behavioral responses between simultaneously tested subjects

Table 2 presents the proportion of responses in which younger individuals and their mother or the other adult female approached the same post-playback location (after the 5-s post-playback period) following chuck call and sham playback. The proportion of responses in which younger animals approached the same post-playback location as their mother ranged from 0.02 to 0.13. The proportion of responses in which younger animals approached the same location as the other adult female ranged from 0.02 to 0.07. No differences were found among subadults, juveniles, and infants. These data suggest that younger subjects did not appear to respond to chuck call playback as a function of their mother's or other adult's behavioral responses.

TABLE 2. *Dependency test of behavioral responses: proportion of trials in which young subjects and their mother or other adult female were found in the same post-playback location after chuck call and sham playback*

ID	Age class	Mother	Adult	Total	Trial N
163	S	0.05	0.05	0.10	162
165	S	0.04	0.02	0.06	172
173	S	0.02	0.03	0.05	172
181	S	0.07	0.04	0.11	162
184	J	0.04	0.02	0.07	159
186	J	0.03	0.07	0.10	170
188	J	0.09	0.05	0.14	184
189	J	0.13	0.03	0.16	183
190	I	0.07	0.04	0.12	156
196	I	0.03	0.02	0.05	119
198	I	0.09	0.02	0.11	167
200	I	0.07	0.04	0.11	167

Chuck call recognition

Behavioral responses

Figure 2 presents the post-playback distance from the broadcast speaker for each category of chuck calls and the two control conditions by age class. Juveniles and subadults showed a significant difference in this variable (see Table 3). Pairwise comparisons revealed that the significance was found between the chuck calls of close associates and every other category of playback stimuli (non-associate, unfamiliar, stranger, sham, and alarm peep) in subadults (Table 3). Therefore, subadults approached significantly closer to the broadcast speaker when the chuck call of a close associate was broadcast. Interestingly, juveniles were significantly closer to the broadcast speaker after playback of chuck calls emitted from individuals within the colony (unfamiliar, non-associate, close-associate) when compared to sham but not alarm peep controls (Table 3). Juveniles, however, did not show significant differences between any of the chuck call categories (Table 3).

To further evaluate the effect of age on behavioral response to close-associate chucks, we calculated a ratio of the mean post-playback distance of sham stimuli (MSHAM) divided by the mean post-playback distance of close-associate chuck stimuli (MCA) for each infant, juvenile and subadult. A larger value for this ratio (MSHAM/MCA) means closer proximity to the broadcast speaker after close-associate chuck playback than after sham

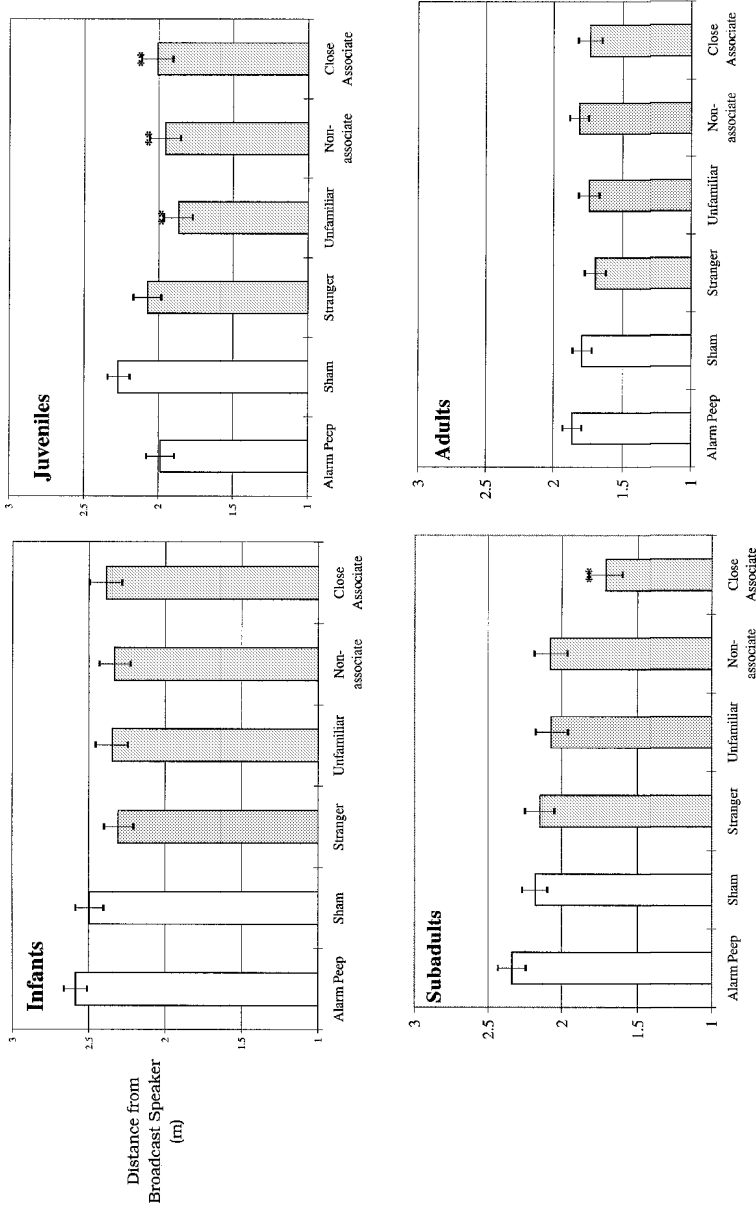


Fig. 2. Post-playback distance from broadcast speaker for the four chuck call categories and two controls in infants, juveniles, subadults, and adults (bars represent the mean and lines represent SEM). Double asterisks in the 'juvenile' panel indicate significant differences at the 0.05 level between the categories and the sham category. Double asterisks in the 'subadult' panel indicate significant differences at the 0.05 level between close-associate category and all other categories.

TABLE 3. *Repeated measures ANOVA (χ^2 likelihood ratio test) and significant pairwise comparisons on post-playback distance from broadcast speaker by age class for the four chuck call categories and two controls⁴⁾*

Age class	Model ¹⁾	χ^2	df	<i>p</i>	Rank ²⁾	Corrected alpha level ³⁾ $\alpha = 1 - [1 - \alpha]^{1/(1+k-i)}$
Infants	All	9.27	5	0.090		
Juveniles	All	14.44	5	0.013		
	SM-AL	6.69	1	0.009	3	0.017
	SM-UF	9.29	1	0.002	1	0.010
	SM-NA	9.13	1	0.002	2	0.013
	SM-CA	5.55	1	0.01	4	0.025
Subadults	All	16.69	5	0.005		
	CA-AL	14.12	1	0.0002	1	0.010
	CA-SM	11.60	1	0.0007	2	0.013
	CA-ST	6.14	1	0.013	4	0.025
	CA-UF	5.51	1	0.018	5	0.050
	CA-NA	9.79	1	0.0017	3	0.017
Adults	All	4.17	5	0.524		

¹⁾ AL = Alarm peep, SM = Sham, ST = Stranger, UF = Unfamiliar, NA = Non-associate, CA = Close associate.

²⁾ Rank = rank of *p*-value.

³⁾ Holm's sequential Bonferroni test for multiple comparisons (Rice, 1988). See text for explanation.

⁴⁾ Random effect individual (repeated measure) was significant ($p < 0.002$) for all tests (not shown); random effect interaction between random effect individual and fixed effect call type was insignificant for all tests and was therefore removed from the model.

playback (termed 'relative proximity'). We regressed MSHAM/MCA ratio on age of infants, juveniles and subadults to determine if a developmental trend could be found in the behavioral response to close-associate chuck calls. Regression revealed significance ($F_{1,10} = 6.36$; $p < 0.05$; $R^2 = 0.39$) for the effect of age (see Fig. 3). Age showed a positive linear relationship with relative proximity to speaker at the end of the 5-s period following close-associate chuck playback. Thus as squirrel monkeys develop they gradually appear to exhibit a differential behavioral response to the chuck calls of their unrelated close associates that becomes maximal and significant by the subadult stage.

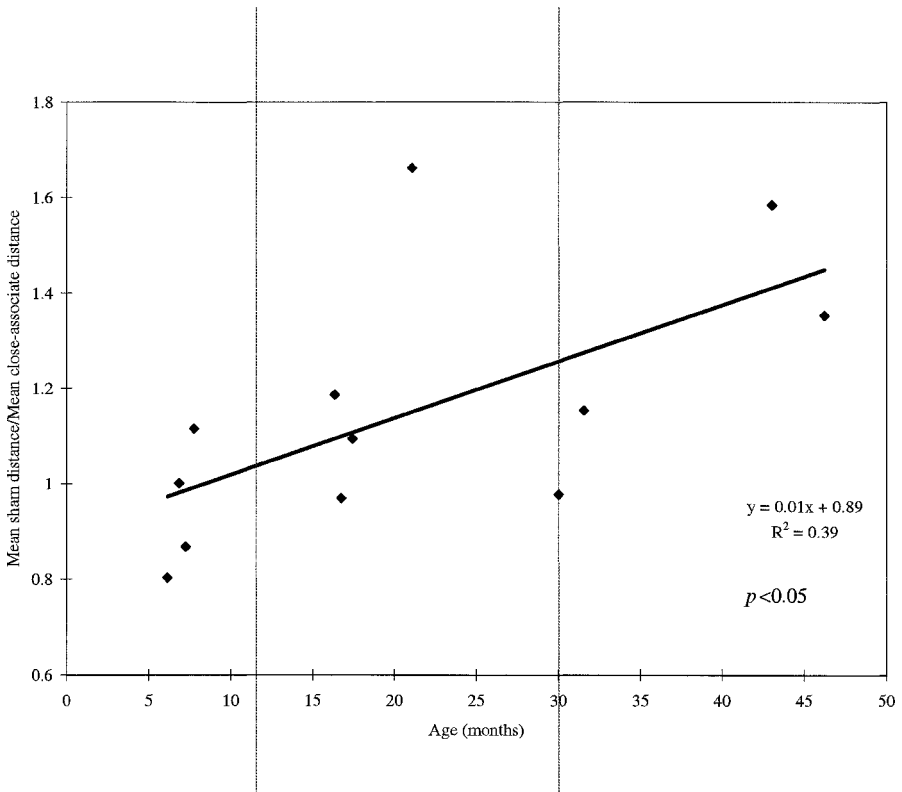
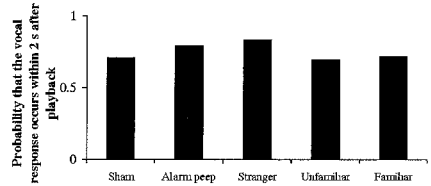
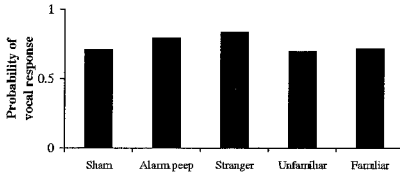


Fig. 3. Regression of mean sham distance/mean close-associate distance from broadcast speaker on age of subject for infants, juveniles, and subadults. Dotted lines indicate age class cutoff points.

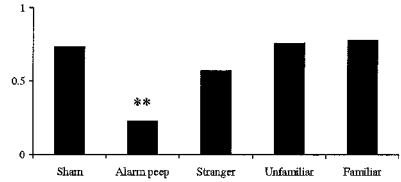
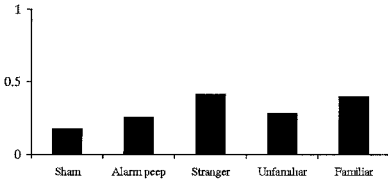
Vocal responses

Figure 4 presents the logistic regression models for both the presence and latency of vocal responses to the two controls (shams and alarm peeps) and the three experimental playback stimuli (chuck calls arising from genetically unrelated 'familiar', 'unfamiliar', and 'stranger' adult females) for each age class (adults, subadults, juveniles, and infants). For adults, vocal response after familiar chuck playback occurred significantly more often than after sham ($\beta = -0.74$, $df = 1263$, $p < 0.05$, Odds ratio = 0.48) and alarm peep ($\beta = -0.66$, $df = 1263$, $p < 0.05$, Odds ratio = 0.52) control playbacks but not after unfamiliar ($\beta = -0.08$, $df = 1263$, $p = 0.69$, Odds ratio = 0.93) or stranger ($\beta = -0.02$, $df = 1263$, $p = 1.03$, Odds ratio = 0.93) chuck playback. Similarly, in subadults, vocal response after

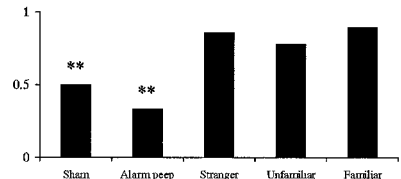
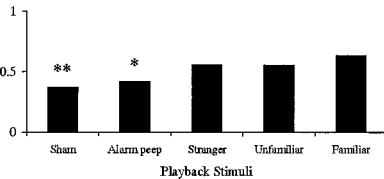
Infants



Juveniles



Subadults



Adults

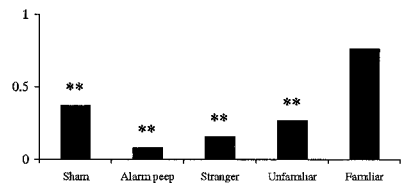
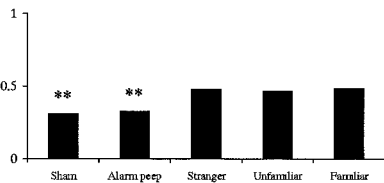


Fig. 4. Logistic regression models on the probability of vocal response (left panels) and the probability that the first vocal response occurred within 2 seconds after playback (right panels) for sham, alarm peep, stranger chuck call, unfamiliar chuck call, and familiar chuck call playback stimuli for infants, juveniles, subadults, and adults. Single asterisks indicate significant differences at 0.10 level and double asterisks indicate significant differences at the 0.05 level between the familiar category and the other categories.

familiar chuck playback occurred significantly more often than after sham playback ($\beta = -1.08$, $df = 197$, $p < 0.05$, Odds ratio = 0.34), and alarm peep ($\beta = -0.89$, $df = 197$, $p = 0.09$, Odds ratio = 0.41) playback (at the 0.10 level), but not after unfamiliar ($\beta = -0.33$, $df = 197$, $p = 0.49$,

Odds ratio = 0.72) or stranger ($\beta = -0.35$, $df = 197$, $p = 0.36$, Odds ratio = 0.65) chuck playback. Thus, adults and subadults, and not infants or juveniles, were more likely to vocally respond to chuck calls as a category than to either alarm peeps or sham controls (Fig. 4).

When only the first vocal response after playback was considered, adults vocally responded using chuck calls more often to chuck calls of both familiar and unfamiliar individuals within the colony in comparison to alarm peep ($\beta = -1.63$, $df = 240$, $p < 0.05$, Odds ratio = 0.20) and sham controls ($\beta = -1.88$, $df = 240$, $p < 0.05$, Odds ratio = 0.15). However, differential adult response using chuck calls to familiar chuck call stimuli significantly differed from unfamiliar chuck call stimuli only at the 0.10 level ($\beta = -0.98$, $df = 240$, $p = 0.08$, Odds ratio = 0.37) and did not significantly differ from chuck calls arising from strangers ($\beta = 0.11$, $df = 240$, $p = 0.86$, Odds ratio = 0.89). Infants, juveniles and subadults showed no significant differences in response call type to the different playback stimuli.

However, most importantly, when the latency of first vocal response after playback was considered with respect to playback stimuli and response call type, significant differences were found in all but the infant age class ($\beta = -0.105$, $df = 101$, $p = 0.87$, Odds ratio = 0.900; Fig. 4). Juveniles vocally responded significantly more often with shorter latency to chuck calls as a category in comparison to alarm calls ($\beta = -2.46$, $df = 57$, $p < 0.05$, Odds ratio = 0.08) but not sham controls ($\beta = -0.232$, $df = 57$, $p = 0.81$, Odds ratio = 0.79; Fig. 4). Subadult females vocally responded significantly more often with shorter latency to chuck calls as a category in comparison to alarm calls ($\beta = -2.83$, $df = 41$, $p < 0.05$, Odds ratio = 0.06) and sham controls ($\beta = -2.14$, $df = 41$, $p < 0.05$, Odds ratio = 0.12; Fig. 4). Adult females vocally responded more often, specifically using chuck calls, with shorter latency to the chuck calls of familiar individuals within their own social groups (Fig. 4) in comparison to the chuck calls from individuals outside of the social group or colony (unfamiliar: $\beta = -2.74$, $df = 240$, $p < 0.05$, Odds ratio = 0.06; stranger: $\beta = -2.86$, $df = 240$, $p < 0.05$, Odds ratio = 0.07) as well as in comparison to the two controls: shams ($\beta = -2.39$, $df = 240$, $p < 0.05$, Odds ratio = 0.09) and alarm peeps ($\beta = -3.61$, $df = 240$, $p < 0.05$, Odds ratio = 0.03). Therefore, adults vocally responded differentially to the chuck calls of their genetically unrelated social group members by responding with their own chuck calls

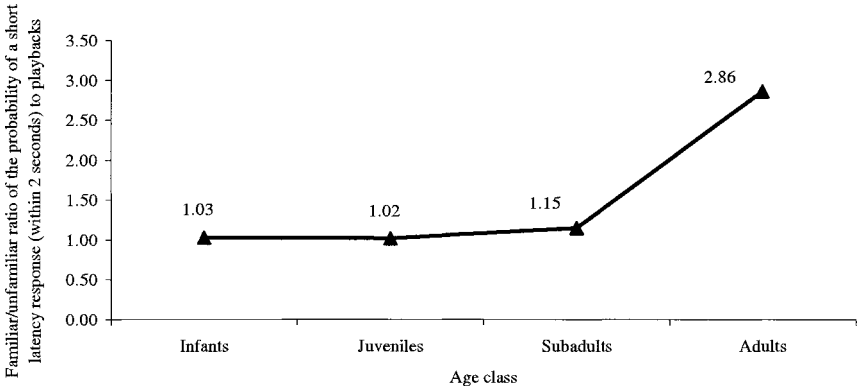


Fig. 5. A plot of the ratios of the probabilities generated from logistic regression analyses on the vocal response latency to familiar and unfamiliar chuck playback categories for infants, juveniles, subadults, and adults. A larger value for this ratio means that individuals are responding more often with shorter latency to the chuck calls of familiar individuals within social groups than to the chuck calls of unfamiliar individuals outside of social group within the colony.

with shorter latency than to chuck calls from individuals outside of their social group or colony (with whom they had no social contact).

To further evaluate the developmental trends in vocal responses to familiar chuck calls, we generated a ratio of the probabilities generated from the logistic regression analyses on the response to familiar *versus* unfamiliar chuck call categories for each age class. A larger value for this ratio would mean that individuals are responding more often with shorter latency to the chuck calls of familiar individuals than to the chuck calls of unfamiliar individuals. The results are plotted in Fig. 5. As indicated by Fig. 5, infants, juveniles and subadults exhibited little difference in their probabilities to vocally respond differentially to familiar chuck calls in comparison to unfamiliar chuck calls. Only adults showed a large value for this response ratio.

Discussion

A role for learning in chuck call recognition

Young squirrel monkeys at the subadult stage behaviorally responded preferentially to the playback of chuck calls from their close social associates

(Fig. 2) and vocally responded preferentially to chuck calls as a category in comparison to the controls (Fig. 4). A role for learning is clearly evidenced in this recognition system, specifically indicated by the subadults' behavioral response, because chuck call exemplars were chosen from genetically unrelated adult females within the social group. Interestingly, subadults did not behaviorally respond differentially to non-associates or vocally respond differentially to the chuck calls of social group members in comparison to the remaining chuck call categories. Perhaps, the motivation to respond behaviorally to social group members of low social affinity is absent and to respond vocally to social group members as a category of callers has not yet fully emerged in subadults.

In contrast to subadults, adults failed to respond behaviorally to the chuck calls of close associates. While this discrepancy is potentially confusing, it actually does not oppose a role for learning in this recognition system. As indicated by our results on the vocal responses to chuck call playback, adults responded vocally, and not behaviorally, to the chuck calls of social group members in comparison to other playback stimuli. These data are supported by past observational and experimental research (Biben & Symmes, 1991; Boinski & Mitchell, 1992; Biben & Bernhards, 1994). In fact, our results have replicated results from these past studies by demonstrating that the *latency* of specific types of vocal response, not necessarily just the *presence* of vocal response, is the measure that differentiates adult female response to different chuck call playback stimuli. In addition, the fact that subadult and adult females do not respond in a similar manner should not be viewed as evidence against the learning hypothesis. Different age groups can respond in different ways that are specifically adaptive for those age groups (Galef, 1981; Owings & Loughry, 1985; Hersek & Owings, 1994). While the acoustic aspects of chuck calls are near maturity in subadult females, they and other vocalization types are produced relatively infrequently (B. McCowan & J.D. Newman, unpubl. data). Thus, instead, subadult females behaviorally responded differentially to the acoustic structure of chuck calls from genetically unrelated close associates. In contrast, adult females vocally responded differentially to the acoustic structure of chuck calls from genetically unrelated individuals within their social groups. Perhaps, for adult females, the strategy to vocally respond is more efficient than behavioral response, especially given that one of the most important functions of chuck

calls is to maintain social group cohesion while foraging and travelling in wild arboreal populations of squirrel monkeys (Boinski & Mitchell, 1997).

Despite the use of alternative strategies, adults and subadults differentially responded to the calls of their genetically unrelated social group companions. Thus, the only viable explanation for the results found in adults and subadults is that both age classes must have learned to recognize the acoustic structure of calls from their genetically unrelated social companions.

In contrast to the adults and subadults, infants showed no differential response to chuck calls either vocally or behaviorally among specific chuck call categories or as an overall category when compared to sham and alarm peep controls. Juveniles did show some differential behavioral response to chuck calls emitted by individuals from within the colony in comparison to sham controls and differential vocal response to colony chuck calls in comparison to alarm peep controls. However, because juveniles showed no difference in behavioral or vocal response to chuck calls among the chuck call categories, we cannot be certain that they recognized chuck calls arising from individuals within their colony.

The lack of significance found for infant and juvenile behavioral and vocal responses could be due to two alternative explanations. First, learning to recognize the chuck calls of genetically unrelated social companions may occur at, or some point after, chuck call acoustic structure reaches maturity in young squirrel monkeys. Despite reports in past literature (Winter *et al.*, 1973; Liebllich *et al.*, 1980; Seyfarth & Cheney, 1997 for review), infant squirrel monkeys do not emit adult-like chuck calls at birth (Biben & Bernhards, 1995). Early in development infants produce the precursor components of chuck calls, *e.g.* 'short peeps', 'tucks', and 'oinks', but the assemblage of these components and maturation of chuck acoustic structure does not occur until well into the third year (B. McCowan & J.D. Newman, unpubl. data). Moreover, the relationship found between close-associate chuck call behavioral response and age (Fig. 3) suggests that infants gradually learn to recognize the calls of social group members, as reported for other nonhuman primates (Masataka, 1983a; Seyfarth & Cheney, 1986; Hauser, 1989). Furthermore, the vocal response data suggest that differential vocal responses to different call categories, and specifically chuck call categories, emerge over development (Fig. 5), becoming maximal at the adult stage. A longitudinal study design experimentally testing vocal recognition as infants mature should help to identify when this recognition

emerges in development. Even if such developmental tests fail to provide a positive result, however, we still cannot exclude the possibility that infants and juveniles acoustically recognize unrelated social group members; they simply may lack the motivation to behaviorally or vocally respond at these developmental stages to chuck calls as a category.

Taken together, the results from this cross-sectional study demonstrate that learning plays a role in chuck call recognition in adults and subadults and may suggest that infants gradually learn to recognize unrelated social companions. At first, this recognition seems to be exhibited through behavioral response as seen in subadult females, which eventually becomes replaced by vocal response as seen in adult females. These data are particularly important because they suggest that mature adult female squirrel monkeys are capable of learning to acoustically recognize genetically unrelated adult females, with whom they became later housed when adults. Further research is needed to determine when in development this learned vocal recognition emerges, whether there is a critical or sensitive period for this learned recognition system, and whether a sex difference is found in the chuck recognition system in squirrel monkeys. Such research can be conducted by examining both the behavioral and vocal responses to chuck calls of genetically unrelated adults by male and female infants as well as individuals from other age classes using a longitudinal and/or developmental study design.

Conclusions

This study has provided new evidence for vocal learning in a call recognition system in squirrel monkeys. As data accumulate on the importance of learning in the vocal perception, use and production of nonhuman primates, and nonhuman mammals in general, we must begin to examine the extent and process of vocal learning with respect to various socioecological parameters. Continued comparative research is necessary to determine the relevance of life history strategy, ecological variables, social organization, and social dynamics to the study of vocal learning and to develop effective theoretical models that help to predict the role, type and degree of learning in the vocal communication of different mammalian species (McCowan *et al.*, 1999).

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