

Vocalizations of Rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) Macaques Cross-Fostered between Species Show Evidence of Only Limited Modification

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Two rhesus and two Japanese macaque infants were cross-fostered between species in order to study the effects of auditory experience on vocal development. Both the cross-fostered and normally raised control subjects were observed over the first 2 years of life and their vocalizations were tape-recorded. We classified 8053 calls by ear, placed each call in one of six acoustic categories, and calculated the rates at which different call-types were used in different social contexts. Species differences were found in the use of "coo" and "gruff" vocalizations among control subjects. Japanese macaques invariably produced coos almost exclusively. In contrast, rhesus macaques produced a mixture of coos and gruffs and showed considerable interindividual variation in the relative use of one call type or the other. Cross-fostered Japanese macaques adhered to their species-typical behavior, rarely using gruffs. Cross-fostered rhesus subjects also exhibited species-typical behavior in many contexts, but in some situations produced coos and gruffs at rates that were intermediate between

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Received for publication 15 June 1992
Revised for publication 15 May 1993
Accepted for publication 27 May 1993

those shown by normally raised animals of the two species. This outcome suggests that environmentally mediated modification of vocal behavior may have occurred, but that the resulting changes were quite limited. © 1993 John Wiley & Sons, Inc.

In many avian species, song production by adults is affected by early auditory experience. In species that exhibit geographically based "dialects," individuals usually sing songs that most closely resemble those they were exposed to as nestlings. Nonetheless, song learning occurs within clear constraints. For example, although song sparrows (*Melospiza melodia*) can imitate the songs of other species, birds raised under natural conditions produce only species-typical sounds. Song sparrows reared in the laboratory preferentially learn these singing patterns when both conspecific and "alien" songs are presented (reviewed by Kroodsma, 1982; Marler & Peters, 1988).

The occurrence of vocal learning that is constrained by apparently innate predispositions suggests that a number of parallels exist between song development in certain avian species and human speech development (e.g., Gleitman, 1984; Gleitman & Wanner, 1982; Marler & Peters, 1981). However, it has been difficult to show an analogous role for early auditory experience in the ontogeny of vocal behavior in any nonhuman primate species. This outcome seems anomalous given the much closer evolutionary relationship between humans and nonhuman primates than between humans and songbirds.

Some studies of vocal development in squirrel monkeys (*Saimiri sciureus*) have indicated that neither vocal production nor appropriate responding to calls are dependent on auditory experience. Squirrel monkeys raised in acoustic isolation or deafened in infancy can show calls with apparently normal acoustic structure (Talmage-Riggs, Winter, Ploog, & Mayer, 1972; Winter, Handley, Ploog, & Schott, 1973). Young squirrel monkeys that are hybrids between the "Roman Arch" and "Gothic Arch" subspecies produce "isolation peeps" whose acoustic features coincide with visible markers of their dominant genetic makeup (Newman & Symmes, 1982). Adult females, moreover, respond only to distress calls from infants of their own subspecies (Snowdon, Coe, & Hodun, 1985). Rearing in social isolation also appears to have no effect on the ability of squirrel monkey infants to respond appropriately to predator alarm calls (Herzog & Hopf, 1984).

However, other data from both laboratory and field settings suggest that experience does play a role in nonhuman primate vocal development. At the most basic level, for instance, the emission of vocalizations appears to be at least partially under voluntary control in a number of species. Ten of 12 operant conditioning experiments reviewed by Pierce (1985) reported successful modification of call production, including production of calls under discriminative control and modification of duration and intensities of individual calls. Similarly, Masataka (1992) has described operantly conditioned vocal responding by provisioned Japanese macaques (*Macaca fuscata*) in response to being individually addressed by caretakers. Two studies of vervet monkeys (*Cercopithecus aethiops*), one conducted in the field and the other in captivity, indicate that members of this species can selectively withhold alarm calls when predators threaten, depending on the social context at the time (Cheney & Seyfarth, 1985).

In studies directly related to development, Newman and Symmes (1974) reported that even partial social isolation during infancy results in abnormalities in

call production by squirrel monkeys and rhesus macaques (*M. mulatta*). Green (1975a) examined tonal "food calls" produced by 3 geographically separated Japanese macaque groups and found differences in acoustic structure. He proposed that each group showed a distinctive, site-specific version of this call indicative of dialect variation and vocal learning. However, the possibility of genetic differences between groups due to "founder effects" could not be ruled out. Mitani, Hasegawa, Gros-Louis, Marler, and Byrne (1992) have also found evidence that is suggestive of dialects in geographically separated groups of chimpanzees (*Pan troglodytes*). In this case, the acoustic features of "pant hoots" (previously shown to be individually distinctive by Marler & Hobbett, 1975) were found to be distinguishable between sites. Masataka (1992) reported a shift in the peak frequency location of coo calls produced by two 1-year-old Japanese macaques over a 4-week period during which they were addressed by caretakers. This study strongly suggests malleability in call production, but it did not include contingencies designed to produce the vocal change or any control subjects. Hauser (1992) observed that "coo" calls produced by one group of matrilineally related rhesus monkeys within his study population produced "nasalized" versions of this normally tonal sound and suggested that learning might underly this altered mode of production in these animals. Again, however, the possible influence of hereditary factors could not be excluded.

Vocal development in vervet monkeys may resemble that of many songbirds in being the product of both innate predispositions and experiential factors. From a very early age, vervets produce acoustically distinct calls within various social circumstances—alarm calls that differ by predator type, "grunts" that vary according to social situation, and "wrrs" in interactions with both foreign groups and resident adult males (Cheney & Seyfarth, 1982; Hauser, 1989; Seyfarth & Cheney, 1986; Seyfarth, Cheney, & Marler, 1980). In young vervets, each of these sound types undergoes modification over time. Such modification can take the form of changes both in acoustic structure and the relationship between call-type and social context or external referent. Responses shown by an individual to the calls of others can also change (Hauser, 1988, 1989; Seyfarth & Cheney, 1986).

Overall, while the evidence is not entirely clear-cut, there are indications that modification can occur not only in responses to calls, but also in call use and acoustic structure. One of the strongest claims that auditory experience can affect vocal development in nonhuman primates is based on the last type of modification and has been presented by Masataka and Fujita (1989). Their evidence concerns food calls produced by infant rhesus and Japanese macaques that were cross-fostered onto different-species mothers at an early age. In this experiment, 2 rhesus infants were fostered onto Japanese macaque mothers and 1 Japanese macaque offspring was placed with a rhesus mother. Subjects were housed indoors in colony room cages as mother-infant dyads. Masataka and Fujita examined the maximum value of the fundamental frequency (F_0) of coos produced by cross-fostered offspring and control animals that were raised with their biological mothers in the same colony rooms. They found both that young, normally raised rhesus and Japanese macaques differ on this measure and that the cross-fostered subjects produced calls that were typical of their foster-mother's species rather than those of their own species.

We have also employed a cross-fostering preparation with these monkeys, both because macaques in general seem well suited to cross-fostering and because many similarities exist between these particular species. A number of experiments have been conducted in which various macaques have been successfully introduced both to congeneric and other nonhuman primate species (e.g., Bernstein & Gordon, 1980; Maple, 1974). Within the *Macaca* genus, rhesus and Japanese macaques may specifically be good candidate species for cross-fostering experiments. These animals are genetically closely related, readily interbreed, and can produce fertile hybrid offspring (Wolfe, 1981). Both species exhibit multimale, multifemale group structure with pronounced dominance hierarchies and similar rates of overall development among offspring (Melnick & Pearl, 1987). The vocal behavior of each species has been relatively well documented and, although call morphology can be quite variable, appears to be generally similar in both (compare for example, spectrograms in Green, 1975a with those in Hauser, 1991 and Peters, 1983).

Our preparation involved four groups of socially housed animals living in outdoor cages at the California Regional Primate Research Center. Four offspring, 2 of each species, were cross-fostered in the 1st week of life, received normal maternal care, gained weight normally, and were similar to normally raised conspecifics in interacting with their mothers, peers, and other cagemates (Owren & Dieter, 1989; Owren, Dieter, Seyfarth, & Cheney, 1992a, unpublished data).

Elsewhere (Owren, Dieter, Seyfarth, & Cheney, 1992b), we have examined the acoustic features of food calls in both the adult females, normally raised control subjects, and cross-fostered offspring in these groups. Like Masataka & Fujita (1989), we found that normally raised offspring in the two species differ with respect to the maximum F_0 value in their food calls. However, no species difference was found in the calls produced by adult females, suggesting that this particular vocalization does not present a good opportunity to test for the possibility of vocal modification based on auditory environment due to the lack of a distinctive, species-typical adult model (see Owren et al., 1992b, for further discussion).

In this article, we examine the possibility of vocal modification in our cross-fostered subjects based on changes in their rates of producing acoustically distinctive call types in various behavioral contexts. This approach seeks changes in call use rather than acoustic structure, analogous to the findings of modification in use of alarm calls, grunts, and wrrs described above for free-ranging vervet monkeys. Although rhesus and Japanese macaques are capable of producing acoustically similar calls, their use of such calls can differ markedly. In play, for example, young Japanese macaques typically produce a clear, tonal coo call whereas rhesus macaques use a harsh gruff. In our preparation, each situation of this sort offered an opportunity to examine whether cross-fostered individuals adhered to their species-typical vocal pattern or used calls similar to those of their adoptive species.

Method

Subjects

Two groups each of rhesus and Japanese macaques housed at the California Regional Primate Research Center (CRPRC, Davis, CA) served as subjects. Initially, each group consisted of a single adult male, 4 or 5 adult females, 2–5

offspring, and up to 4 unrelated juvenile males. Each group occupied a separate outdoor cage consisting of two corn cribs and a rectangular intercage unit (see Hoffman & Stowell, 1973).

The two groups within each species were housed in adjacent cages and were clearly visible to one another. The Japanese macaques used in our study were the only such animals at the CRPRC. The rhesus macaques, on the other hand, were part of a large, permanent population. In an attempt to maintain auditory separation between species, the Japanese macaques were situated behind a row of coniferous trees 60 m from the nearest rhesus group. The two rhesus study groups were semi-isolated from other animals by a wooden fence 2.5 m high and were approximately 100 m from the Japanese macaques. Members of the rhesus study groups (including the cross-fostered Japanese macaques) were effectively isolated from hearing Japanese macaque vocalizations due to distance, physical obstacles, and prevailing wind conditions. However, the Japanese macaque groups (including the cross-fostered rhesus) were able to hear the loudest calls produced by members of the general CRPRC rhesus monkey population. Quieter calls, however, like the coos and gruffs that are the focus of the present article, were not audible. Animal histories, kinship relations, and other maintenance conditions are described by Owren et al. (1992a).

All individuals born in the groups in the years 1986 through 1988 served as study subjects. Four infants, 2 rhesus and 2 Japanese macaques, were cross-fostered between species (described by Owren & Dieter, 1989). Each infant was placed with a foster mother within the 1st week of life. Due to the opportunistic manner in which cross-fostering had to be conducted, both Japanese macaques came to be placed with the same rhesus female, 1 year apart. One group of rhesus macaques therefore eventually included 2 Japanese macaques while each Japanese macaque group received a single rhesus infant. Coincidentally, both cross-fostered rhesus offspring were female while both Japanese macaque subjects were male.

The overall study population included the 4 offspring cross-fostered between species and 16 normally raised control individuals (9 rhesus and 7 Japanese macaques). Behavioral data and vocalizations were collected over the course of several years in order to maximize the number of individuals represented in the sample. However, the comparisons presented here involve only comparably aged individuals observed during the first 2 years of life, which are referred to as Years 1 and 2. Six other normally raised animals (3 rhesus and 3 Japanese macaques) were between 1 and 2 years old at the time that observations were terminated and were therefore excluded from calculations concerning Year 2. Two rhesus infants were also cross-fostered within their own species to determine whether cross-fostering in itself affected behavior. These offspring, living in the rhesus group without any Japanese macaques, showed no differences when compared with normally raised rhesus (Owren et al., 1992a) and are treated as control subjects in the present data analysis.

Behavioral Observations and Audio Tape-Recording

Audio tape-recording of vocalizations occurred simultaneously with focal animal observational sampling (Altmann, 1974) of behavior based on entry of numerical codes into a Radio Shack TRS-80 Model 100 or 102 portable computer (see

Owren et al., 1992a for further details). Most individuals were observed for one 10-min period each week while cross-fostered subjects and an equal number of age-matched control offspring were observed at twice this rate. Although vocalizations were routinely recorded from nonfocal individuals, only calls recorded from a subject while it was the focal animal are included here. Calls were tape-recorded using two microphones (Sennheiser ME88 directional heads with K3U power modules) positioned outside each half of the cage, which allowed recording of the focal subject's calls regardless of location. A lapel microphone allowed supplemental commentary on a third track of the Tascam 234 four-channel cassette deck used for recording. A 63-behavior ethogram was used along with identification and directionality-of-action codes to describe behaviors occurring both before and after each vocalization (see Owren et al., 1992a). This information was encoded as a series of time-stamped numerical computer entries that were supplemented as necessary through verbal comments recorded on the cassette deck. Following each observation session, vocalizations were transferred to quarter-inch audio tape using either a Uher 4200 Report Monitor or a Fostex A-2 reel-to-reel deck. Calls were separated, numbered, and annotated during this process using the encoded behaviors and commentaries.

Data Analysis

Our strategy in data analysis was as follows: First, we searched for any evidence of a species difference in vocal behavior between normally raised rhesus and Japanese macaques during their first 2 years of life. Species differences were crucial to our study because they provided the only unambiguous means of testing whether the calls of cross-fostered animals resembled calls of their own or their adoptive species. Second, in cases where a species difference was found in a particular social context, we then compared cross-fostered subjects with normally raised control animals of the two species.

Vocalizations were sorted by ear into six mutually exclusive acoustic categories: "coo" (coo), "gruff" (grf), "gecker" (gkr), "scream" (scr), "bark" (brk), and "creak" (crk). Despite variation within categories, each call type was distinguishable from the others. Wideband (300-Hz) spectrograms of typical calls from each acoustic category are shown in Figure 1.

The coo category consisted of tonal calls corresponding to the sound classes "coos" and "whistles and warbles" in Green's (1975b) description of the Japanese macaque vocal repertoire and to the sound class "basic coos" in Peters' (1983) description of the rhesus vocal repertoire (see also Hauser, 1991). Gruffs were predominantly quiet, atonal sounds comparable to the subtype of "gruff" sounds in the "growled sounds and roars" class described by Green and to the "basic grunt" described for stump-tail macaques by Bertrand (1969) and for rhesus macaques by Peters. Most gruffs consisted of a short series of iterated bursts of energy, with longer periods of silence between calls. Geckers were comparable to those described by Green (1975b), Rowell and Hinde (1962), and Peters (1983). These vocalizations consisted mostly of iterated sounds, but single-pulse calls could also occur. Geckers were usually atonal but brief tonal exclamations were also included in this category. Screams were of longer duration and were either atonal or harshly tonal. This category incorporated both the "shrieks and screams"

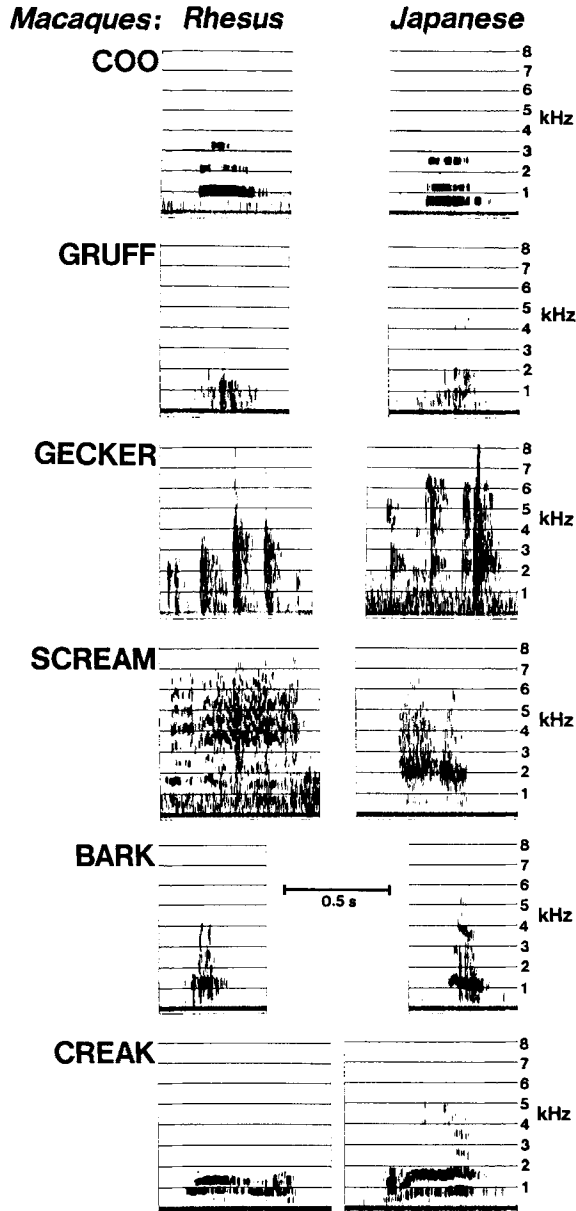


Fig. 1. Wideband (300 Hz) spectrograms of typical vocalizations in each of the six categories used in acoustic classification.

and “squeals and screeches” described for Japanese macaques by Green. Gouzoules, Gouzoules, and Marler (1984) analyzed a similar category of calls among rhesus macaques. Barks were comparable to sounds from the “chirps and barks” class in Green’s classification and the “shrill barks” described by Rowell and Hinde, and Peters. Creaks were characterized by a mixture of tonal and atonal components uttered in a continuous fashion and were reminiscent of strangulation

or choking. These calls included the “stops” of Green’s whistles and warbles class but had no apparent counterpart in other classification systems.

Calls were also sorted into eight broad, mutually exclusive behavioral contexts based on the detailed characterizations available for each through the 63-behavior ethogram and supplemental commentary. These were calm situations, including antiphonal and nondirected calls (calm); interactions with a cagemate that were not associated with play or agonism (cagemate); attending to the adult male in the absence of other overt interactions (α male); prior to food provisioning or during actual consumption of food in the absence of any particular social interactions (food); when interacting with the mother (mother); while experiencing distress related to nonagonistic interactions with other animals (e.g., inadvertent physical contact, rough-and-tumble play, or unwelcome affiliative interest), some mishap, or a frightening stimulus outside the cage (distress); while engaged in social play in the absence of any distress (play); and while involved in an agonistic interaction (agonism).

Results

A total of 8053 calls produced during the first 2 years of life were classified by acoustic type. Normally raised offspring accounted for 2402 and 1928 vocalizations for rhesus and Japanese macaques, respectively, while 1491 and 2232 calls were recorded from the cross-fostered rhesus and Japanese macaques, respectively. Overall, 88% of these calls could be classified using the behavioral contexts described above. All group comparisons involve percentage or ranked scores computed separately for individual subjects.

Vocalizations of Normally Raised Subjects

Figure 2 shows the proportion of calls used in each social context during Years 1 and 2 by normally raised animals of each species. Analysis of these data was complicated somewhat in that preliminary screening revealed both deviations from normality in the distribution of call frequencies in some contexts and heterogeneity of covariance matrices. Multivariate parametric testing could therefore be inappropriate for this data set (see Tabachnick & Fidell, 1989). On the other hand, a multivariate test was preferred to avoid repetitive testing and concomitant increases in the probability of Type I error. Both multivariate and nonparametric tests were therefore applied, producing virtually identical results. One-way MANOVA testing revealed no significant main effects of species or context in either of these 2 years. Within-cells correlations analysis did not indicate violations of multicollinearity and singularity criteria (Tabachnick & Fidell, 1989). Multiple Mann-Whitney two-sample tests (or Wilcoxon–Mann-Whitney tests, Siegel & Castellan, 1988) conducted separately for each context also failed to reveal species differences in either of the 2 years. This outcome indicates that immature rhesus and Japanese macaques produced vocalizations at similar rates in similar social contexts.

Figure 3 shows the proportion of calls by normally raised animals that fell into each of the six acoustic categories. Barks and creaks accounted for only 2% of all calls and were therefore not included in statistical comparisons. One-way

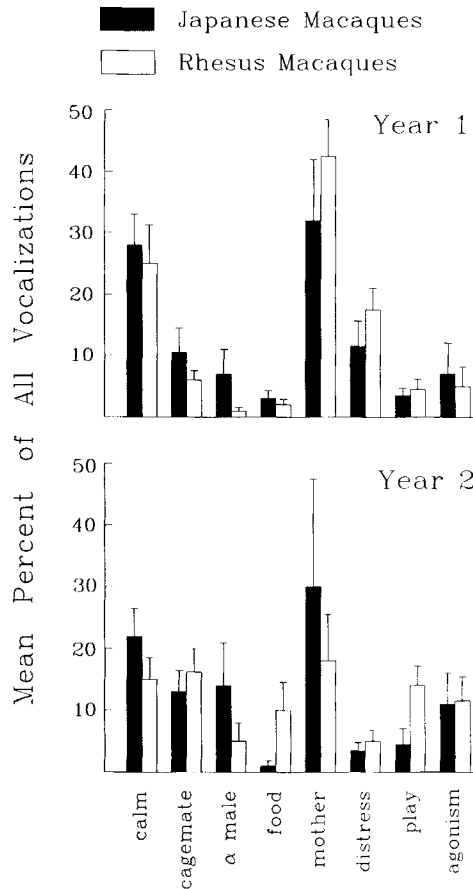


Fig. 2. Percentages of vocalizations produced by normally raised rhesus and Japanese macaques in various social contexts in the first 2 years of life. Means and standard errors are shown for each of the contexts used in classifying behavior. Year 1 comparisons include 1292 vocalizations produced by 11 rhesus (5 females, 6 males) and 1149 vocalizations from 7 Japanese macaques (2 females, 5 males). Year 2 data represent 816 vocalizations from 8 rhesus (3 females, 5 males) and 558 vocalizations from 4 Japanese macaques (2 females, 2 males).

MANOVA revealed significant effects of species and call type in both Year 1, $F(4,7) = 3.82$, $p < .05$, and Year 2, $F(4,7) = 4.83$, $p < .05$. Post-hoc univariate F tests revealed no significant differences between species with respect to the use of geckers and screams, which made up approximately 33% of the sample. Coos and gruffs, however, which made up over 65% of the sample, were produced at different rates by the two species. As shown in Figure 3, rhesus monkeys produced more gruff calls than did Japanese macaques, which used coos almost exclusively. Significant differences were found in the use of gruffs in Year 1, $F(1,16) = 8.58$, $p < .01$, and coos in Year 2, $F(1,10) = 8.73$, $p < .05$. Similar differences approached significance in Year 1 for coos, $F(1,16) = 4.45$, $p = .051$, and in Year 2 for gruffs, $F(1,10) = 4.15$, $p < .10$. Results from Mann-Whitney tests again confirmed this pattern of results, showing significant differences in gruff rates in both Years 1, $z = 3.17$, $p < .01$, and 2, $z = 2.55$, $p < .05$.

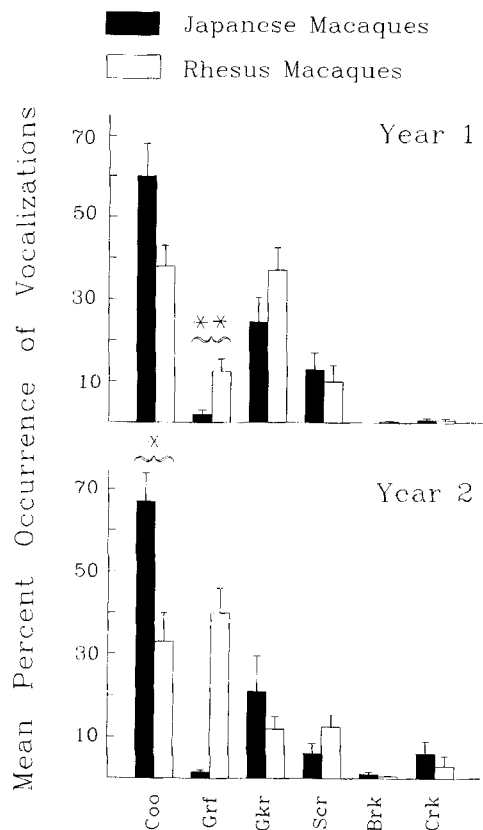


Fig. 3. Overall percentage occurrence of six acoustically distinctive vocalization types produced by normally raised rhesus and Japanese macaques of both species in the first 2 years of life. Means and standard errors are shown for each category used in acoustic classification. See Figure 2 for sample sizes. Year 1 comparisons include 1425 and 1259 vocalizations from rhesus and Japanese macaques, respectively, while 977 and 669 calls were used from the two species, respectively, in Year 2.

The difference in coo rates in Year 1 again approached significance, $z = -1.77$, $p < .10$. Nonparametric tests of gecker and scream rates revealed no significant differences in either year.

To further document this difference, we examined the relative proportions of coos and gruffs produced in each of the eight behavioral contexts. In these and subsequent comparisons, we measured the proportional use of either coos or gruffs by dividing each by the total number of coos and gruffs. A total of 16 possible comparisons (eight contexts in each of 2 years) could be used to test for species differences. However, we eliminated data from any animal with fewer than five calls in a given context and disregarded any contexts in which less than 3 animals from each species were represented. Ten contexts remained (four in Year 1 and six in Year 2) for species comparisons. Here, multivariate statistics were entirely inapplicable due to the varying numbers and identities of individuals representing the two species in each of the contexts. Based on the overall absence of gruffs among normally raised Japanese macaques (see Figure 3), it was expected

Table 1

Results of One-Tailed t Tests Comparing the Proportion of Coos Used in Eight Social Contexts by Normally Raised Rhesus and Japanese Macaque Offspring

Year	Social Context							
	Calm	Cagemate	α Male	Food	Mother	Distress	Play	Agonism
1	2.99**	3.30**	—	—	1.76	—	2.43*	—
2	2.30*	4.22**	8.67**	2.26*	1.29	—	17.8**	—

Note. Contexts are defined in the text. See Figure 2 for sample sizes of subjects and vocalizations. No test was possible because of sample size restrictions (see text).

* $p < .05$. ** $p < .01$.

that rhesus would produce fewer coos (hence more gruffs) in these contexts. One-tailed t tests revealed significant differences in this direction in 8 of these 10 cases, as shown in Table 1. Rhesus also showed significantly greater variation in the use of coos and gruffs than did Japanese macaques. Coefficients of variation corrected for sample size were calculated using Sokal and Rohlf's (1969, p. 59) procedure ($CV = (1 + 1/(4n)) * ((SD * 100)/X)$). In each context in which a species comparison could be made, variation in the proportion of coos produced was higher for rhesus macaques (ranges were from 4.8 to 195 and 0.0 to 13.4 for rhesus and Japanese macaques, respectively). However, there were no indications of gender differences in variability in either species.

In sum, a species difference in vocal behavior was most apparent in the use of coos and gruffs. In circumstances when Japanese macaques used coos almost exclusively with little variation among individuals, rhesus macaques used significantly more gruffs and showed significantly more interindividual variation. Because use of coos and gruffs provided the best opportunity to test whether cross-fostered monkeys adhered to their own or their adoptive species' pattern, these calls became the focus of subsequent analysis.

Vocalizations of Cross-Fostered Subjects

Figure 4 shows the relative use of coos and gruffs by cross-fostered and normally raised animals. Table 2 presents data on the proportion of coos used by each group. The latter data are drawn only from those social contexts in which we found a significant difference between the two species in the use of coos and gruffs (see Table 1).

The results indicated no modification of vocalizations by cross-fostered Japanese macaques, which continued to use almost only coos in their first 2 years of life (see Figure 4 and Table 2). In most circumstances, cross-fostered rhesus macaques also adhered to their own species' pattern. Both outcomes are apparent in Table 3, which shows the results of nonparametric statistical comparisons between coo rates from the 2 cross-fostered subjects of each species, their different-species cagemates, and same-species controls. The cross-fostered Japanese macaques always produced a significantly higher proportion of coos than did normally raised rhesus macaques and were indistinguishable from normally raised conspecifics. In Year 1, testing three social contexts, cross-fostered rhesus used

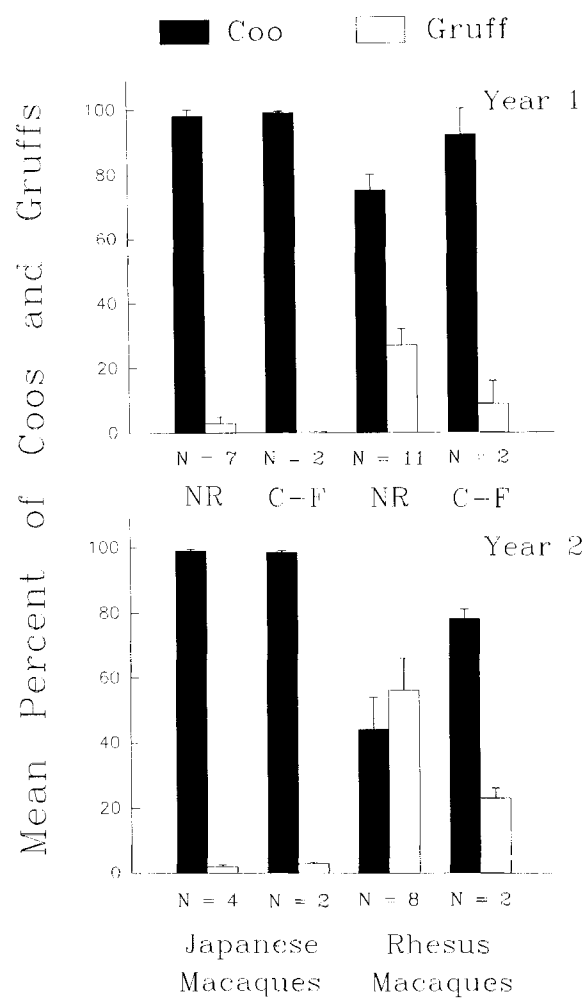


Fig. 4. Relative percentage use of coo and gruff calls by normally raised and cross-fostered rhesus and Japanese macaques in the first 2 years of life. Means and standard errors are shown for overall use across all social contexts.

significantly fewer coos than did normally raised Japanese macaques in one case and a second difference approached statistical significance. These animals were statistically indistinguishable from their own species in all three contexts. Data from Year 2 show a similar outcome in testing five different social contexts.

At the same time, however, there was some indication that vocal behavior in the cross-fostered rhesus offspring became more like that of Japanese macaques and differed from that of control conspecifics. As noted earlier, normally raised rhesus and Japanese macaques differed significantly in their use of coos and gruffs in the calm context in Year 1 (Table 1). The cross-fostered rhesus were intermediate in this context and could not be distinguished from control subjects of either species (Table 3). Overall, the mean proportion of coos produced by cross-fostered rhesus was higher than that for normally raised conspecifics in seven of eight

Table 2
Proportion of Coos by Normally Raised (NR) and Cross-Fostered Offspring (C-F)

		Rhesus macaques						Japanese macaques					
		NR			C-F			NR			C-F		
Year	Context	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
1	Calm	8	83.5	12.9	2	93.6	7.9	7	98.4	2.5	2	99.8	0.3
	Cagemate	7	68.1	23.5	2	89.0	4.7	6	100.0		2	100.0	
	Play	5	54.4	37.3	2	49.5	47.7	5	93.3	11.6	2	100.0	
2	Calm	7	65.3	29.6	2	94.8	1.4	4	100.0		2	98.6	2.1
	Cagemate	6	52.0	19.0	2	76.4	0.2	3	100.0		2	97.7	0.9
	α Male	4	81.8	4.2	2	95.6	6.2	4	100.0		2	99.4	1.3
	Food	5	76.3	21.0	1	100.0		4	100.0		2	100.0	
	Play	6	2.4	4.5	2	57.0	18.4	3	93.3	11.5	2	98.9	1.6

Note. Mean values are shown for social contexts in which normally raised individuals in the two species were significantly different (see Table 1).

n is the number of individuals in each category.

contexts that could be compared in the 2 years (Table 2). In five cases, the cross-fostered rhesus mean value was closer to that of normally raised Japanese macaques than to that of normally raised rhesus. The strongest evidence for modification was found in the calm context in Year 2, where cross-fostered rhesus macaques used coos at rates clearly intermediate between normally raised individuals of each species (Table 3).

The cross-fostered Japanese macaques might have failed to modify their use of coos and gruffs because they were raised in the same group by the same mother and could hear each other's calls. We tested this hypothesis by comparing these 2 individuals' use of coos and gruffs during their first year. The older of the 2

Table 3
Results of One-Tailed Mann-Whitney U Tests Comparing the Proportion of Coos Used by Cross-Fostered (C-F) and Normally Raised (NR) Individuals

		C-F rhesus macaques tested against		C-F Japanese macaques tested against	
Year	Context	NR rhesus macaques	NR Japanese macaques	NR rhesus macaques	NR Japanese macaques
1	Calm			*	
	Cagemate		*	*	
	Play		*a	*a	
2	Calm	*	*a	*	
	Cagemate		*	*	
	α Male			*a	
	Food				
	Play	*		*	

Note. Data are presented only for those contexts in which normally raised individuals in the two species were significantly different (see Table 1).

* $p < 0.05$. *a $p < 0.06$.

animals, "Swapo," spent his first year alone in a rhesus group while the younger one, "Switch," spent his first year in a rhesus group that included Swapo. The sample of calls was large, an average of 66 calls for Swapo and 36 calls for Switch in each context. However, the proportion of coos used by the 2 subjects was the same in each case.

As a partial test for gender-related effects on modification by the cross-fostered individuals, we examined the vocal behavior of normally raised rhesus males and females separately. No differences were found in their use of vocalizations or in individual variability within each gender.

Finally, cross-fostered rhesus were found to use gruffs in the same social contexts as normally raised conspecifics. Ranking the eight social contexts according to the mean proportion of gruffs produced by normally raised and cross-fostered rhesus revealed a positive correlation that was statistically significant in Year 1, Spearman $r_s = 0.690$, $p < 0.05$, one-tailed, and approached significance in Year 2, $r_s = 0.565$, $p < 0.10$, one-tailed.

Discussion

Normally raised rhesus and Japanese macaques differed in their use of coo and gruff vocalizations. These differences were consistent across a number of contexts, emerged early in life, remained stable for the animals' first 2 years, and were not gender related. Elsewhere, (Owren et al., 1992a, unpublished data) we have shown that the quality and quantity of social interactions did not differ between normally raised offspring of each species and that their overall rates of vocalizing were also the same. Therefore, the differences in calling found here can be specifically attributed to the use of a particular call type in a given behavioral context rather than differences in the likelihood of experiencing that context. In calm situations, when calling to or in proximity to a cagemate, when interacting with a dominant male, and when playing, Japanese macaques used coos almost exclusively and showed little variation among individuals. In contrast, rhesus macaques used a mixture of coos and gruffs with considerable individual variation.

Given these differences, the most striking result to emerge was the lack of modification in cooing and gruffing by cross-fostered animals. Cross-fostered Japanese macaques almost never used gruffs even though they lived in an environment in which gruffs were used at high rates. When these subjects vocalized in play, for example, they invariably used coos even as their rhesus playmates were producing gruffs. Similarly, cross-fostered rhesus macaques used gruffs during interactions with peers, when calling to a dominant male, and in play, despite not hearing this call from their Japanese macaque peers.

In some social contexts, cross-fostered rhesus macaques increased the proportion of coos and decreased the proportion of gruffs, showing vocal behavior that resembled that of Japanese macaques. However, such modification was very limited. It occurred in a small number of contexts and involved only a subtle shift in vocalization pattern. Typically, the cross-fostered rhesus macaques were intermediate between normally raised individuals of the two species but remained distinguishable from the Japanese macaques. Major changes in call use were not found. Rather, the cross-fostered rhesus offspring simply increased the use of a

call that was already in their repertoire. While their production of gruff calls did decrease, they used these sounds in the same contexts as did normally raised members of their own species.

However, the relatively greater modifiability found among cross-fostered rhesus macaques may be noteworthy inasmuch as this species always showed more individual variation in using coos and gruffs than did Japanese macaques. This outcome implies greater *a priori* difficulty in statistical documentation of changes shown by the cross-fostered rhesus than by the Japanese macaques. Nonetheless, modification appeared only in the former subjects and not the latter.

As both cross-fostered rhesus subjects were females while the cross-fostered Japanese macaques were males, the greater modifiability observed among cross-fostered rhesus may have been due to a difference related to gender rather than to species. For instance, the changes in vocal behavior shown by cross-fostered rhesus may have occurred because the vocalizations of females are more malleable and more easily affected by auditory experience than are those of males. In pigtail macaques, for instance, Gouzoules and Gouzoules (1989) have reported that juvenile females become proficient in the use and production of scream vocalizations earlier in development than do juvenile males. This hypothesis could not be tested directly. However, normally raised rhesus macaque females gave no indication of showing greater variability than normally raised males or of using calls in a different manner, as would be expected if the females' vocal behavior was in fact more malleable. Furthermore, the 2 cross-fostered rhesus females were not found to be more different from normally raised conspecific males than they were from normally raised females when separate comparisons were made.

These indirect arguments suggest that the limited modification occurring in the cross-fostered rhesus females would also have been found in conspecific males. Greater variability in the use of coos and gruffs by normally raised individuals and greater modification among cross-fostered subjects both suggest that vocal production may be somewhat more labile in rhesus than in Japanese macaques. This result is reminiscent of those from laboratory experiments with songbirds, where species with larger, more diverse song repertoires appear capable of learning more song types than do species with smaller, less variable repertoires (Kroodsma, 1982). There is, however, no indication of repertoire size differences in these monkey species.

The lack of modification in the vocalizations of cross-fostered animals cannot readily be explained on the basis of species differences in sound production capabilities. While control subjects clearly differed in their use of coos and gruffs, animals in each species were capable of producing both call types. In fact, a cross-fostered individual in this study could have acquired its adoptive species' pattern of vocalizations simply by modifying the use of calls already in its repertoire. On the whole, such modifications did not occur.

Our subjects' failure to modify their vocalizations can also not be accounted for on the basis of abnormalities in overall social experiences. Cross-fostered subjects continued to use their own species' vocalizations even though they were, by other measures, fully integrated into their adoptive groups (Owren et al., 1992a, unpublished data). Cross-fostered subjects could use different vocalizations than their adoptive cagemates when playing, for instance, but showed comparable rates of play behavior. Similarly, when interacting with their mothers, cross-fostered

rhesus individuals produced both coos and gruffs when these adult females would normally have heard only coos. Cross-fostered Japanese macaque offspring, on the other hand, used only coos to mothers who would normally have heard many gruffs. Nevertheless, there was no indication that any of the cross-fostered subjects received inadequate, or even different, maternal care.

The failure of cross-fostered subjects to alter their vocal behavior while showing otherwise normal social interactions suggests that vocal communication in these species may not be subject to significant environmentally induced change. This outcome may imply that calling is less malleable than other aspects of social behavior in these animals. In our experiment, however, very few species differences were actually found when we compared rates of social interaction such as aggression, grooming, and play (Owren et al., 1992a). Social integration of cross-fostered subjects may therefore not have required that these animals alter their behavior to any significant degree. The use of rhesus and Japanese macaques in this study may have led us to underestimate the extent to which nonhuman primate vocalizations can be modified as a result of experience. Given similarities in size, rates of development, and major features of social organization (e.g., Melnick & Pearl, 1987; Owren et al., 1992a), it may be possible for a rhesus or Japanese macaque to become fully integrated into a group of the other species without altering its vocalizations. Bernstein and Gordon (1980) suggest that similar integration without vocal modification may have occurred when they formed mixed-species groups of macaques. The present study's cross-fostered individuals might have modified their calling behavior had they been subjected to more challenging social circumstances. Developmental changes in the use of alarm calls, grunts, and wrrs by vervet monkeys, for instance, appear to be at least partially mediated by social reinforcement (Hauser, 1989; Seyfarth & Cheney, 1986). In the absence of such reinforcement contingencies, facultative learning capabilities may simply not have been expressed.

In sum, previous research has shown that immature nonhuman primates seem predisposed to use particular types of calls in certain broad contexts. In some species, age and experience bring changes in the acoustic features of vocalizations, their use in specific circumstances, and in responses to calls. Results of our study indicate, however, that predispositions to use particular call types in certain situations can be very strong. For rhesus and Japanese macaques, the predispositions appear to be so strong as to leave an individual basically unaffected by its auditory environment even when living in a group where others use the vocalizations differently.

The data presented here concern only the use of two acoustically distinct call types in particular social situations. In many circumstances, these species produce calls that sound alike but that may be found to have subtly different acoustic features. Variation in acoustic structure did occur, for instance, within each of our broad call-type categories. Masataka (1992; Masataka & Fujita, 1989) has reported evidence of both pitch contour and frequency peak location changes within the class of coo calls produced by these species. To the extent that these data and our data overlap, we have not corroborated this evidence of vocal modification (Owren et al., 1992a, 1992b). However, further analysis of both these and other calls may yet reveal cases in which cross-fostered animals modify the acoustic features of their vocalizations.

Notes

Research was supported by grant RR00169 from the Division of Research Resources, NIH to the CRPRC, Grant NS 19826 from the NICHD, and postdoctoral Fellowship 5 F32 HD06878-03 to Michael Owren. Special thanks to C. Cornelius and R. Henrickson whose initial support and encouragement made the project possible, and to A. Hendrickx and W. Mason for facilities and support. C. Mead contributed to the data collection and J. Adams, A. Cabrera, P. Telfer, and other members of the technical staff provided expert assistance. G. Barlow, L. C. Drickamer, and several anonymous reviewers provided helpful comments on previous versions of this article.

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