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Sources of Acoustic Variation in Rhesus Macaque (*Macaca mulatta*) Vocalizations

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Abstract

All species in the genus *Macaca* produce a set of harmonically rich vocalizations known as "coos". Extensive acoustic variation occurs within this call type, a large proportion of which is thought to be associated with different social contexts such as mother-infant separation and the discovery of food. Prior studies of these calls have not taken into account the potential contributions of individual differences and changes in emotional or motivational state. To understand the function of a call and the perceptual salience of different acoustic features, however, it is important to determine the different sources of acoustic variation. I present data on the rhesus macaques' (*M. mulatta*) coo vocalization and attempt to establish some of the causes of acoustic variation. A large proportion of the variation observed was due to differences between individuals and to putative changes in arousal, not to differences in social context. Specifically, results from a discriminant-function analysis indicated that coo exemplars were accurately assigned to the appropriate individual, but vocal "signatures" were more variable in some contexts than in others. Moreover, vocal signatures may not always be reliable cues to caller identity because closely related individuals sound alike. Rhesus macaque coos evidently provide sufficient acoustic information for individual recognition and possibly kin recognition, but are unlikely to provide sufficient information about an external referent.

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Introduction

Vocal signals have the potential to provide extensive information. There are, however, two fundamental constraints on the information conveyed: the sound-producing apparatus and the perceptual resolving abilities of the auditory system (e.g. NOWICKI & MARLER 1988; NELSON & MARLER 1990). Recent research on the vocal communication of nonhuman animals has focused on dissecting the stream of acoustic information into components that are likely to be correlated with an individual's internal state (e.g., aggression: DABELSTEEN & PEDERSEN 1990) and features of the socio-ecological environment (e.g., predators: KLUMP & SHALTER 1984; food: DITTUS 1988; for reviews, see CHENEY & SEYFARTH 1990; HAUSER & NELSON 1991). At the core of this research is an attempt to make sense of the

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sources of acoustic variation and the relative perceptual salience of different acoustic features of the signal. This paper examines some of the factors underlying acoustic variation and attempts to relate such variation to problems of perception.

Acoustic variation has a number of potential sources, including respiratory activity (e.g., SUTHERS et al. 1972; HAUSER & FOWLER 1991), mode of articulation (e.g., NOWICKI & MARLER 1988; OWREN & BERNACKI 1988; SUTHERS 1990), developmental stage (e.g., KROODSMA & MILLER 1982; HAUSER & MARLER 1991), emotional state (e.g., MORTON 1977, 1982; GOEDEKING 1988), caller identity (BROOKS & FALLS 1975; TYACK 1986) and social context (e.g., SMITH 1977; NARINS & CAPRANICA 1978; NELSON 1985; CHENEY & SEYFARTH 1990; MARLER et al. 1991). If one seeks the meaning or function of a given signal, it is therefore important to insure that sampling is appropriate and that the acoustic variation described is perceptually salient to the organism observed.

The purpose of this paper is to establish some of the sources of acoustic variation for one call type (i.e., "coos") in the repertoire of the rhesus macaque (*Macaca mulatta*) and thereby establish a foundation for subsequent perceptual studies. Analyses were restricted to coos for two reasons. Variation in the acoustic morphology of this call in closely related species appears to be associated with different social contexts (GREEN 1975; GRIMM 1976; LILLEHEI & SNOWDON 1978; HOHMANN & HERZOG 1985; DITTUS 1988; HOHMANN 1989). In the most detailed investigation of this problem, GREEN (1975) showed that Japanese macaques (*Macaca fuscata*) produce seven different types of coos that can be distinguished by their characteristic fundamental frequency (Fo) contours. Each type of coo is associated with different social contexts including mother-infant separation, dispersal, and consortship. However, GREEN's analyses did not consider other potential sources of variation such as that resulting from differences between individuals or affective state. Thus, it is not possible to evaluate the significance of the association between social context and acoustic structure. The same point applies to the other macaque studies, with one exception (LILLEHEI & SNOWDON 1978).

Second, a number of important perceptual studies on Japanese macaques (reviewed in MOODY et al. 1990) used insights from field research (GREEN 1975) to address such issues as species-specific acoustic cues (ZOLOTH et al. 1979; MAY et al. 1988), hemispheric lateralization (PETERSEN et al. 1984), and categorical perception (MAY et al. 1989). One of the primary conclusions to emerge from this work is that for Japanese macaques, but not other closely related species, the temporal location of the Fo contour's peak frequency is perceptually the most salient feature of the call; for the other species tested, the absolute frequency of the Fo contour was perceptually more salient. To place these results in a more appropriate comparative context it would be useful to have a better understanding of the sources of acoustic variation in both Japanese macaques and closely related macaque species.

Part I of this report provides analyses of an extensive calling bout by one adult female rhesus macaque in the context of group progression. The purpose of these restricted analyses is to reveal the extent of acoustic variation that may emerge from one individual within an apparently homogeneous context. Although such analyses must be treated cautiously, they can be used to gain insights into the relative stereotypy of a signal, when at least two important contributors to acoustic variation have been controlled for. In Part II of the paper, the role of contextual and individual sources of acoustic variation are explored based on analyses of approximately 550 vocalizations from over 30 different individuals. Thus, these analyses will provide a check on the generality of the results obtained from the first part of the paper.

Methods

Study Area

Observations were conducted from Nov. 1988 to Jun. 1989 and from Aug. to Oct. 1990 on adult female and adult male rhesus macaques living in one of the 7 social groups (groups L) on the island of Cayo Santiago, Puerto Rico. Cayo Santiago is a 15-ha island, located off the east coast of Puerto Rico (see RAWLINS & KESSLER 1987 for a detailed description of the island and its history). During the period of observation, the population consisted of approx. 1200 to 1400 individuals. The island consists of two smaller islets, a "small cay" and a "large cay" that are connected by a narrow isthmus. Three dispensers provide food (Purina monkey chow), one on the small cay and two on the large cay. For most of the groups on the island, chow comprises over 50 % of the diet with natural foliage, fruits (e.g., coconuts) and soil making up the remaining proportion. During periods of observation, group L (approx. 300 to 350 individuals) was the largest group on the island and had almost exclusive access to chow on the small cay. No other groups were seen on the small cay during the study although peripheral males were observed feeding on chow from the small cay's dispenser.

Behavioral and Acoustic Analyses

Data were collected by two observers, one recording data on socio-ecological behavior and the other tape-recording all vocalizations uttered by the focal animal and those individuals with whom it interacted. Vocalizations were recorded using a Sony TC-D5M cassette recorder and a Sennheiser ME88 or MKH816 directional microphone with zepplin windscreen. Observation and tape-recording occurred at a distance of approx. 0.5—2.0 m.

Behavioral data were collected onto prepared checksheets using a focal-animal sampling technique; ad libitum data were also collected. Over 1300 h of observation were made during the study. Focal samples were collected from a total of 12 adult males and nine adult females. Observations began at approx. 06.00—07.00 h and ended at approx. 14.30—15.00 h. When our focal animal called, a detailed description of the conditions leading to the call and those ensuing were provided. Such descriptions included, e.g., records of those individuals within 10 m, nonvocal displays, type of food eaten, general activity of the focal animal and the group.

Three contexts were explored as potential sources of acoustic variation: group progression (i.e., movement), food, and female-infant affiliative interactions; over 80 % of all coos recorded occurred in these three broad contexts. Group progression was defined as directed movement from one location on the island to another location. Behavior accompanying such movement was typically striking and included relatively long bouts of locomotion in one direction together with frequent scanning to see which, if any, animals were following.

Calls given in the context of food most frequently involved waiting for chow to be placed in the dispensers or possession of chow. Less frequently, calls were given to rare and highly preferred food items such as coconut. To avoid ambiguity, calls were excluded from the analyses if they were produced as the group was moving toward a corral with food still in the dispenser.

The final context included situations where females were attempting to initiate or maintain contact with an infant, typically their own. Such interactions included attempts to groom or carry, but not cases where a mother picked up her infant and moved with the group to another location. The latter was considered ambiguous because it potentially overlapped with the context of group progression.

Table 1: Data set for statistical analyses of coos by context and by individual

Type of analysis	#of subjects	Range of calls/subj.	Total# calls	Section of paper
Variation w/in one context for individual 480	1	—	72	A
Subj. 480 vs. others in group progression	6	5—27	145	B.1
Individual differences in context of food	6	8—88	256	B.1
Individual differences in the context of grp. prog.	5	6—63	137	B.1
Individual differences in the context of female-infant associations	6	7—74	134	B.1
Contextual differences	20	5—88	547	B.2

Calls selected for analyses were recorded from individually recognized members of group L. The initial data set included analyses of 943 coos from 43 individuals (32 adult females and 11 adult males). The final data set (Table 1), however, was reduced to 547 coos (16 adult females and 4 adult males) because for some calls the description of the socio-ecological context was relatively poor and, some analyses required a particular sample or distribution of exemplars across individuals or contexts. Thus, for example in analyses concerned with individual variation, only individuals with at least five calls were included.

Acoustic analyses were performed using the Signal digital sound analysis program (BEEMAN 1989) which operates on an IBM-compatible 80386 computer. Because the bandwidth of coos does not exceed 10 kHz and the fundamental frequency (Fo) range is 200 to 600 Hz in adults, all calls were low-pass filtered at 100 Hz, high-pass filtered at 10 kHz, and sampled at a rate of 25 kHz; using a 1024-pt fast fourier transform (FFT; with Hanning window), this set-up provided a frequency resolution of 24 Hz and a temporal resolution of 5 ms. To obtain better frequency resolution for analyzing the Fo contour, coos were reacquired using a 2000 Hz bandwidth, a sampling rate of 5000 Hz, and a 1024-pt FFT. This set of parameters resulted in a frequency resolution of 5 Hz.

Two types of acoustic analyses were performed on the Fo contour of each coo. First, based on the research of GREEN (1975) with Japanese macaque coos and of STEBBINS and his colleagues on the perceptual responses of Japanese macaques to natural and synthesized coos (e.g., reviewed in MOODY & STEBBINS 1989; MOODY et al. 1990), a suite of acoustic features was selected for analysis. The spectral features (Fig. 1) of the Fo contour were: Maximum frequency (MXF), Minimum frequency (MNF), Beginning frequency (BF), Middle frequency (MF), Ending frequency (EF), and Frequency of Peaks (PF) in the contour. The highest frequency (HF) value in the call (frequency of highest harmonic) was also measured. The temporal features were: Total duration of the call (CD), Duration from beginning of the call to: (1) Maximum frequency (BMXF), (2) minimum frequency (BMNF) and (3) peak frequency (BPF). Six composite features were also measured: Fundamental frequency bandwidth (FOBW = MXF-MNF), Median fundamental frequency (MEDFO = [MXF+MNF]/2), Bandwidth (BW = HF-MNF) and the Temporal location of the maximum (MXFLOC), minimum (MNFLOC) and peak (PFLOC) frequencies (calculated as, e.g., BMNF/CD).

Statistical Quantification

Discriminant-function analysis has been successfully used to distinguish the calls of nonhuman primates on the basis of individual and contextual variation (e.g., SMITH et al. 1982; SNOWDON et al. 1983; MACEDONIA 1986). This procedure was used with the rhesus macaque coo data set for the same

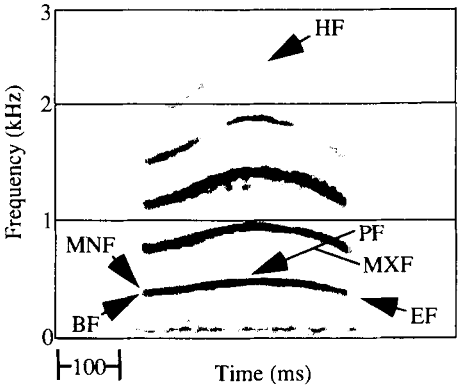


Fig. 1: Spectrogram of a rhesus macaque coo. Labels refer to the spectral measurements extracted: MXF = maximum frequency; MNF = minimum frequency; BF = beginning frequency; MF = middle frequency; EF = end frequency; PF = peak frequency; HF = highest harmonic frequency

purpose and the specific steps in the analysis were as described by GOUZOULES & GOUZOULES (1989) in their description of pigtail macaque scream vocalizations. The direct discriminant-function analysis in Systat (WILKINSON 1985) was used to classify coo exemplars on the basis of context or caller identity. Before running this analysis, all acoustic parameters measured were first examined for significant F ratios. Only those variables reaching a significance level of at least $p < 0.05$ were entered into the model.

The results from the discriminant analysis were then used in two ways. First, chi-square analyses revealed whether or not the classification of exemplars to contexts or individuals was significantly greater than chance. Second, the absolute magnitude of the standardized discriminant function coefficient weights were used to establish which predictor variables were most important in the classification procedure.

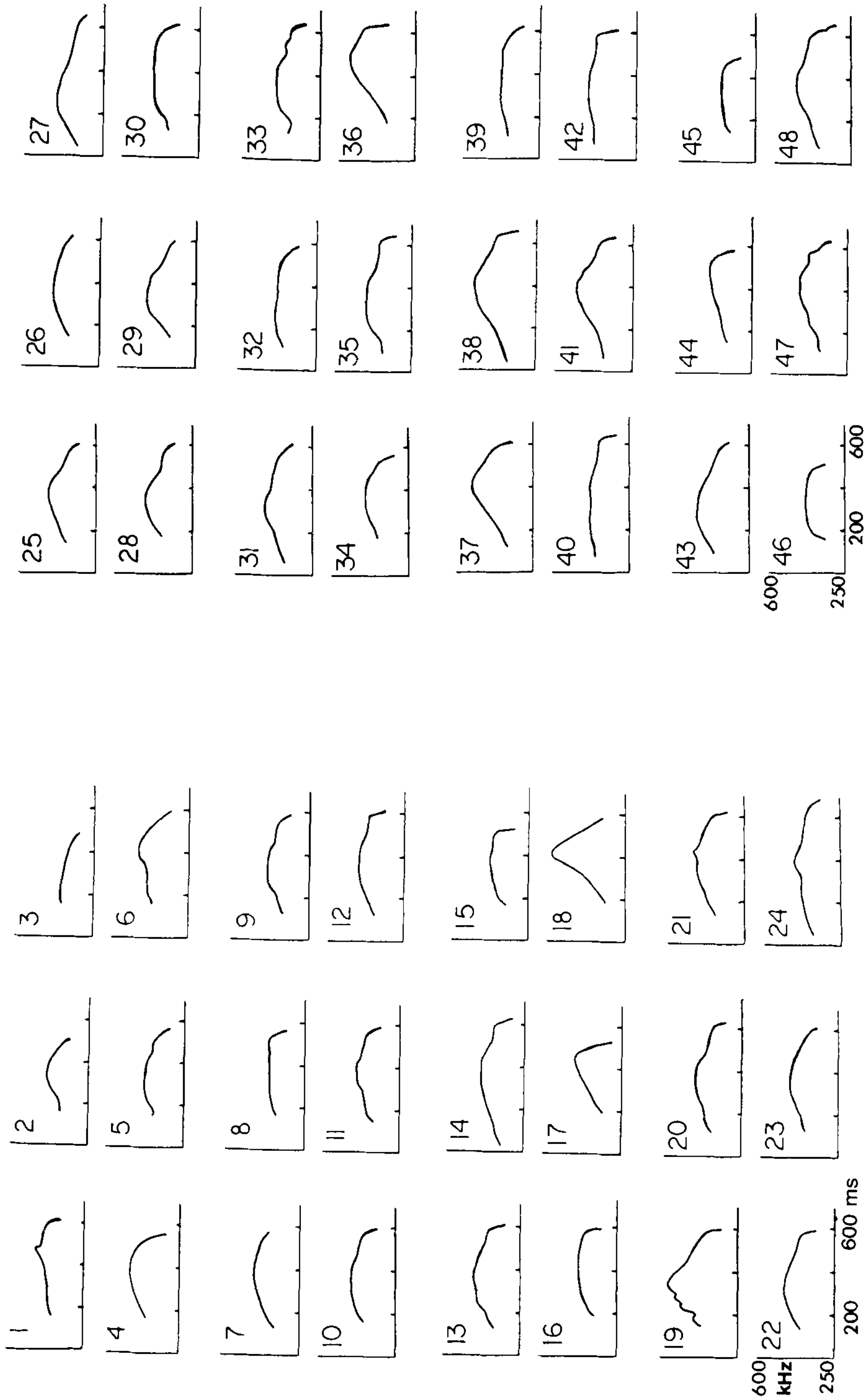
A second approach to characterizing the acoustic morphology of a call type (i.e., and thereby reducing observed variation) is the cross-correlation technique (see CLARK et al. 1987). One advantage of this technique is that it does not rely on parameter extraction but rather provides a full representation of the signal. Specifically, each call is described entirely by a frequency-by-time matrix with each cell representing root-mean-square (RMS) amplitude. The similarity between two calls is determined by correlating amplitude values of the two frequency-time matrices. One matrix is shifted relative to the other in successive time increments until the maximum cross-correlation is found. The result from each comparison is a correlation value (range of +/− 1.00) which is an estimate of similarity between two calls. Correlation values are then entered into a multi-dimensional scaling routine to establish whether significant clusters exist within the matrix.

The cross-correlation technique was used to evaluate the similarity between 70 coos produced by one adult female during group progression. Two calls from the original set of 72 were excluded because of the presence of environmental noise that interfered with the tail portions of these calls. Following CLARK et al. (1987), the matrix of correlation values was statistically analyzed using multidimensional scaling (MDS). Due to limitations of the statistical package (Systat, WILKINSON 1985), the MDS routine (Guttman-Lingoes coefficient of alienation and two dimensions) was first performed on one half of the matrix (i.e., 35 calls) and subsequently, on the second half of the matrix (i.e., 35 calls).

Results

Part I: Acoustic Variation Generated by One Individual in One Context

During a period of 87 min, subject 480 (middle-aged adult female) sat on the small cay within 1—10 m of other group members and called 79 times. All of these calls were coos. In general, observations suggested that 480's coos were directed toward other group members in an attempt to initiate a progression from the small cay to the large cay. At this time, none of the dispensers on the island had chow.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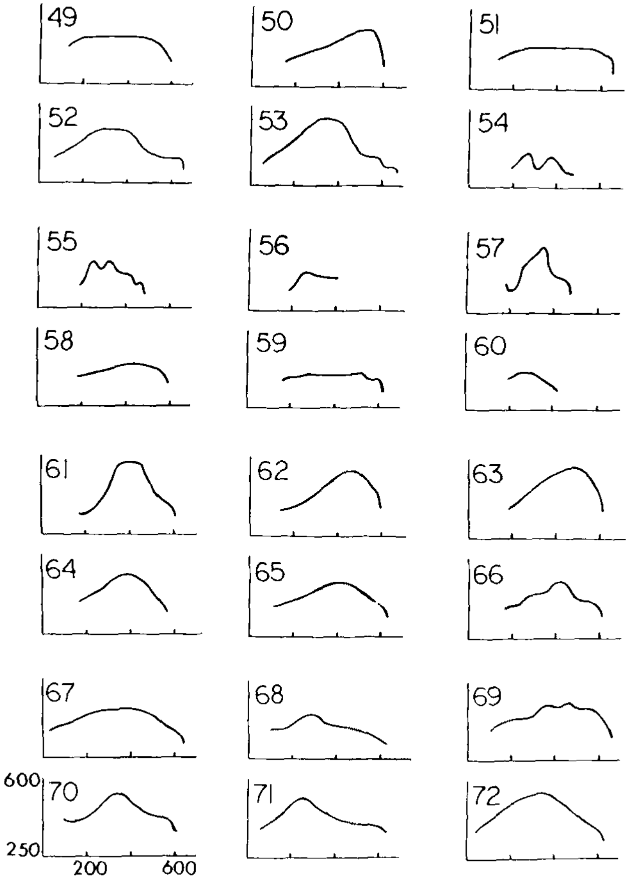


Fig. 2: Chronological sequence of the fundamental frequency contours of coos produced by subject 480 during group progression. Call 1 occurred at 11:01:09 and Call 72 occurred at 12:28:12

Table 2: Descriptive statistics on acoustic features of coos given by individual 480 during a group progression

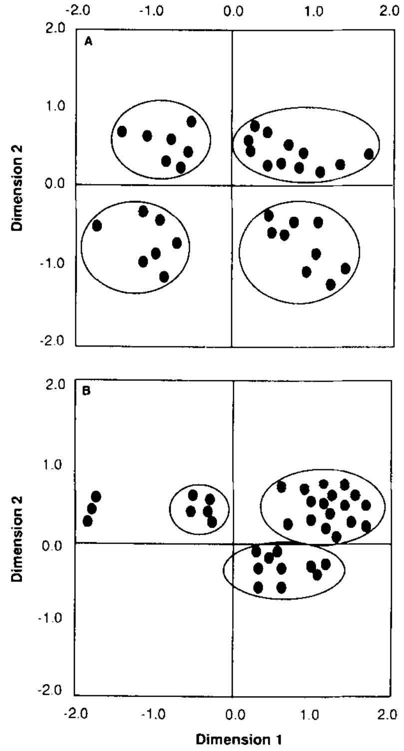
Variable	x	SE	CV	n	Min	Max
Max. freq.	495.8	6.7	10.7	72	280	670
Min. freq.	368.2	3.7	8.0	72	315	436
Begin freq.	407.4	3.0	5.9	72	326	438
Mid. freq.	487.6	6.7	10.9	72	280	624
End freq.	368.3	4.4	9.5	72	208	442
Peak freq.	497.0	6.9	10.8	70	280	670
Highest harmonic freq.	3946.4	83.8	14.2	72	3316	4229
Call duration	459.7	14.2	24.6	72	180	705
Max. freq. location	0.42	0.02	31.5	72	0.12	0.99
Min. freq. location	0.90	0.03	30.6	72	0.00	1.00
Peak freq. location	0.50	0.02	25.7	70	0.10	0.99

The reason 480's behavior is so interpreted is because of the repeated pattern of movement exhibited during the period of calling: 480 looked to her group, then to the large cay, then moved and then looked back toward the group. During this calling episode, 480 moved approx. 20 m and the only other detectable activity within a 25-m radius was occasional movement by other group members toward the large cay or toward 480. Approx. ½ h after 480's calling bout, group L moved to the large cay and 480 was one of the first to arrive.

Fo contours were accurately depicted for 72 coos (i.e., minimal interference from other calls or background noise; 7 coos rejected for this analysis). The Fo contours of these calls (Fig. 2) were extremely different. For example, some calls had a shallow arching contour whereas others began with a rapid frequency rise and then fell to a significantly lower terminal frequency. These calls were subjected to univariate acoustic analyses (Table 2). All of the spectral features analyzed had relatively low coefficients of variation, whereas most of the temporal features had relatively high coefficients of variation. In particular, measures of the location of frequency maxima and minima were highly variable even though these calls were recorded under reasonably constant contextual conditions (i.e. group progression) and from the same individual.

To determine whether the acoustic variation observed could be statistically reduced to a subset of call types, as documented by GREEN (1975) for Japanese macaques, MDS was implemented (Fig. 3A: results from the MDS analyses for the first set of 35 calls; Fig. 3B: results from the second set of 35 calls). For the second set of coos, the MDS routine was rerun, after three outlying points were removed (points in the upper left quadrat of Fig. 3B; they correspond to contour numbers 54, 55 and 57 in Fig. 2).

Fig. 3: Results from multidimensional scaling on 480's A) first set of 35 coos and on B) second set of 35 coos; coos given during group progression



Using the clusters generated by MDS, the contours for each cluster were entered into an averaging routine to generate "prototypical" contours (Fig. 4). With the exception of one additional contour-type, the contours generated from the first set of coos corresponded almost exactly to the contours generated for the second set. The four prototypical contours can be characterized as follows: (I) Rapid, short, frequency rise and fall from a central frequency plateau; (II) Gradual and shallow arching frequency contour; (III) Gradual frequency change up and down from a central frequency peak; (IV) Gradual frequency change up to a terminal frequency peak and then a rapid frequency fall.

The prototypical contours were next analysed in light of more detailed notes on the contexts in which each coo was produced. Four sub-contexts within the more general context of group progression were extracted for subject 480: (1) sitting and scanning toward other group members on the small cay and then in the direction of the group progression to the large cay; (2) sitting and observing other group members moving in the direction of the large cay; (3) moving alone in the direction of the large cay; (4) moving with other group members in the direction of the large cay.

Table 3 reveals the association between prototypical contour-type and sub-context. These data suggest that during this one calling episode, 480 produced exemplars with a relatively narrow bandwidth (contours I and II) when she was

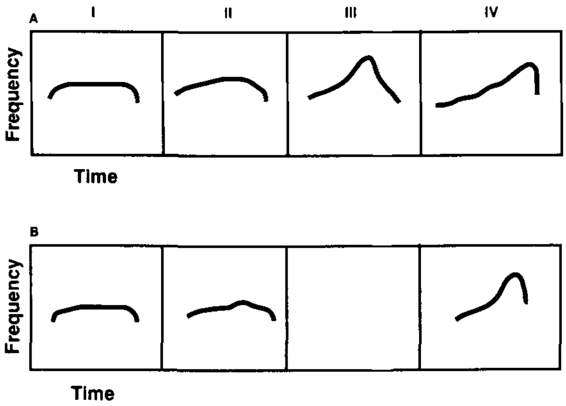


Fig. 4: Prototypical contours based on averaging routine using clusters from MDS analyses. Prototypes from A) first set of 35 coos and from B) second set of 35 coos

sitting and looking at stationary or moving group members. In contrast, calls with a relatively wide bandwidth (contours III and IV) were produced when she was moving alone or with other group members.

Part 2: Sources of Acoustic Variation

1. Acoustic Variation due to Differences between Individuals

The previous set of analyses raise two questions. First, is the acoustic variation exhibited by subject 480 during this one calling bout typical of other bouts in similar contexts? Second, is the pattern observed for 480 representative of other individuals in this population and for other contexts?

Regarding the first, it is currently not possible to assess whether the variation observed during this one bout is comparable to other bouts in the same context due to a lack of data. Although recordings of subject 480's coos in the context of group progression are available, the number of calls per bout is fewer than five.

Table 3: Association between contour type and social context

Social context	Contour type I	II	III	IV
Sit and scan toward other group members	28	9	2	1
Sit and watch other group members move toward direction of group progression	2	2	2	0
Move in direction of group progression	2	1	8	4
Move in direction of group progression with other group members	0	2	4	3

To explore the second question, data on coos (n = 144) produced by four adult females and one adult male in the context of group progression (Table 1) were statistically compared with subject 480's coos; each individual was treated as a single datum by taking the mean value for all calls recorded. Results show that for three acoustic features (CD, MNFLOC and BW), 480's group-progression coos were significantly different (t-tests, $p < .05$) from those of the other individuals examined. However, if one compares coefficients of variation for 480's coos to those of the other individuals, the magnitude of difference is small. That is, for all of the other individuals examined, coefficients of variation for spectral measures ranged between 8—15% whereas coefficients of variation for temporal measures ranged between 25—100 %. Thus, coos given in the context of group progression were highly variable even though 480's coos in this context were different from those of the other individuals sampled.

A discriminant-function analysis was carried out on a sample of 110 coos from four adult females and one adult male (a range of 5—27 calls per individual, evenly distributed across contexts) to determine whether each call could be correctly assigned to one of the sub-contexts of group progression: 1) waiting/anticipating group progression and 2) group progression in progress. The discriminant-function analysis model included three variables (CD, MNFLOC and BW) which, based on inspection of the cross-correlation matrix, failed to show evidence of multicollinearity or singularity. Results of this analysis indicate that coos were classified to the appropriate sub-context with only 32 % and 29 % accuracy, which is not statistically different from chance ($p > 0.05$). Thus, there were no detectable differences between coos produced in the context of waiting for a group progression and those produced during group progression when a larger sample of individuals is considered. This most likely indicates that the acoustic variation exhibited by 480's coos in the two sub-contexts of group progression reflect an affective or motivational response that is not species-specific. Rather, such variation either reflects a relatively consistent affective response to a given social context or, a response that is shared by group members not considered in the present analyses.

Results showed that 480's coos in the context of group progression were different from those of other individuals and overall the acoustic morphology of this call was highly variable in this particular context. Could such variation be due to distinct differences between individuals which are independent of the social context in which they were produced? To determine whether individuals differ in call structure, three separate discriminant-function analyses were run for the contexts of food, group progression, and female-infant affiliative associations.

In the context of food (Table 4A), the coos (n = 256) of five adult females and two adult males were correctly classified with between 35 to 88 % accuracy, which is significantly greater than chance (i.e., 14 %). In the context of group progression (Table 4B), the coos (n = 137) of five adult females were correctly classified with between 33—88 % accuracy which is, in general, greater than chance (i.e., 20 %). Finally, in the context of female-infant associations (Table 4C), the coos (n = 134) of six adult females were correctly classified with between 71—100 % accuracy which is significantly greater than chance (i.e., 17 %). Based on inspection of standardized discriminant-function coefficient weights, three variables (MXF, MNF, and HF) accounted for most of the differences between individuals.

A majority of misclassified cases were assigned to close kin (Table 4). For example, when subject 845 produced coos in the context of female-infant associations, 78 % of the calls recorded were correctly identified as her own productions whereas 17 % were assigned to her close kin. These results suggest that individuals could be recognized by voice alone even though classification mistakes might be made between close kin.

Table 4: Discriminant-function analysis on coos produced in different social contexts: classification by individuals

A. Context = food

ID	NA	405	480	660	845	A94	D14	F24	% Corr. class.	% Class. kin
405	14	13	0	1	5	0	0	0	39	15
480	38	0	31	1	1	3	11	3	35	13
845	1	0	0	7	0	0	0	0	88	0
A94	4	0	0	1	3	6	1	0	40	17
D14	12	0	8	0	1	1	28	0	56	16
F24	7	0	0	0	0	0	0	12	63	—

B. Context = group progression

ID	NA	405	480	660	709	845	% Corr. class.	% Class. kin
405	2	14	0	0	0	3	73	16
480	4	0	53	3	3	0	84	—
660	2	0	1	22	0	0	88	—
709	8	0	2	1	7	0	39	—
845	2	2	0	0	0	2	33	33

C. Context = female-infant affiliative associations

ID	NA	405	660	709	845	A94	H80	% Corr. class.	% Class. kin
405	0	23	0	0	0	0	0	100	0
660	0	0	12	0	3	2	0	71	—
709	0	0	0	4	0	1	0	80	—
845	1	8	0	2	58	5	0	78	17
A94	0	0	0	1	1	9	0	82	9
H80	0	0	0	0	0	0	7	100	—

NA: Calls that could not be assigned to any of the focal subjects sampled in this analysis.
Kin relationships: 405 is the mother of adult female 845 and the grandmother of adult female A94; 845 is the aunt of A94; 480 is the mother of adult male D14 who transferred out of his natal group one year prior to the current study and is currently a peripheral male.

It would be interesting to determine whether individuals retain their vocal "signatures" across contexts. This analysis is currently not possible, however, because only two individuals are represented in each of the three social contexts evaluated.

2. Acoustic Variation Due to Different Social Contexts

Are coos given in different contexts acoustically distinct, as suggested by research on closely related macaque species? To address this question, data on coos, given in known contexts and produced by 13 adult females and three adult males, were analysed for contextual differences. Using a discriminant-function analysis on a total of 282 calls ($n_{food} = 169$, $n_{group\ progression} = 113$), 66 % of food coos were correctly classified and 79 % of group-progression coos were correctly classified ($p < 0.001$). The standardized discriminant-function weights revealed that the call's bandwidth (BW) was the only variable to contribute significantly to the contextual differences, with food coos exhibiting a significantly greater BW than group progression coos.

How is the accuracy of the above classification affected by the addition of other contexts? The only context for which there was a sufficient sample size was affiliative associations between females and infants ($n = 146$). Results from the discriminant-function analysis indicated that classification accuracy was poor, even though the variables entered into the model were the same as when food and group-progression coos were evaluated. Specifically, coos were assigned to the context of food with 28 % accuracy, group progressions with 46 % accuracy and female-infant associations with 32 % accuracy. 49 % of all calls examined could not be assigned to any of the contexts entered into the model. A chi-square analysis for classification accuracy was not statistically significant ($p > 0.05$). Thus, it appears that the addition of other contextual parameters increases the overall acoustic variation within coos and thereby increases the difficulty of correctly assigning a particular call to a particular context.

Discussion

Summary of Results

Observations of all macaques species studied to date have suggested that the "coo" is a structurally variable call and that such variation is closely associated with the context in which it is given (ROWELL & HINDE 1962; GREEN 1975; GRIMM 1976; LILLEHEI & SNOWDON 1978; HOHMANN & HERZOG 1985; DITTUS 1988; INOUE 1988; HOHMANN 1989; MASATAKA & FUJITA 1989). Moreover, perceptual studies on Japanese macaques have shown that the temporal location of the fundamental-frequency peak is the most salient acoustic parameter in the classification of coos. In contrast, differences in absolute frequency were more important for other, closely related species (reviews in PETERSEN & JUSCZYK 1984; MOODY & STEBBINS 1989; MOODY et al. 1990).

Results presented here reveal that rhesus macaque coos are acoustically variable, even when one factors out variation due to individuals and to gross-level changes in context. Specifically, coos given by one adult female during group progression showed relatively high coefficients of variation with regard to the temporal location of different spectral features. Within the general context of group progression, however, more subtle differences in the social conditions eliciting coos emerged and these appeared to be associated with different prototypical contours. In particular, coos with a narrow bandwidth were associated with the caller's attempt to initiate group movement whereas coos with a wide bandwidth were more frequently associated with the caller's actual movement during group progression.

Data on a larger sample of individuals failed to support the finding of significant sub-contextual variation during group progression. Thus, changes in frequency modulation and bandwidth appear to represent an individually distinctive response to the contextual variation associated with group progression. Such variation may, however, be the result of fairly consistent and context-dependent changes in arousal that are shared by individuals not sampled in the present study.

Coos produced during group progression were acoustically different from those produced in the context of food. However, a discriminant-function analysis on coos given in the context of food, group progression and female-infant affiliative interactions showed that the acoustic variation in this call type is so great that coos cannot be reliably classified into discrete contexts based on call morphology alone. Because these three contexts represent over 80 % of the situations in which rhesus on Cayo Santiago produce coos, it is unlikely that other contexts will show acoustically distinct structural properties.

Although it was not possible to accurately classify coos by context it was possible to assign coo exemplars correctly to the appropriate individual. Thus, coos appear to provide sufficient information for individual recognition, a result that supports data on a variety of other nonhuman primates (e.g., MARLER & HOBBETT 1975; WASER 1977; LILLEHEI & SNOWDON 1978; SYMMES et al. 1979; SNOWDON et al. 1983; MACEDONIA 1986). What makes the results presented here different from previous studies is that the accuracy of classification by individual appeared to be affected by contextual variation and by the number of kin in the data set. Specifically, coos given in the context of female-infant associations were assigned to the appropriate individual with greater accuracy than coos given in the context of food or group progression. This suggests that the extent of acoustic variation between tokens of one individual's coos depends on the nature of the context eliciting the call and that some contexts, such as mother-infant separation, may select for greater stereotypy with regard to individual signatures. In addition, the discriminant-analysis procedure most often misclassified coo exemplars to a close relative, thereby indicating that kin sound alike.

The Potential Information in Rhesus Macaque Coos

As mentioned, none of the studies of macaque coo vocalizations have taken into account the relative contribution of contextual and individual variation. The only exception is LILLEHEI & SNOWDON's (1978) study on stumptail macaques which focused on a small sample of infants and yearlings. I have argued, based on the results presented here and those emerging from other studies (e.g., LILLEHEI & SNOWDON 1978; SMITH et al. 1982; SNOWDON et al. 1983), that such variation should be considered in order to evaluate properly the information contained in a call and its associated function. Given this claim, what can one conclude about rhesus macaque coos?

Analyses presented here suggest that for rhesus monkeys on Cayo Santiago, no statistically significant association exists between the acoustic variation in coos and the contexts that appear to elicit them. Consequently, coos do not appear to provide sufficient acoustic information for listeners to discern the external referent of the call. Results from the discriminant-function analysis, however, do suggest that there is sufficient acoustic information for caller identity to be classified reasonably accurately. In addition, of the individuals examined, the coos of close kin were acoustically similar. Thus, it may only be possible to establish that a given coo exemplar belongs to one matriline or another. Such information would be useful if the primary function of rhesus macaque coos is to maintain contact with kin or individuals who have recently been involved in affiliative social interactions.

The conclusions on individual- and kin-specific acoustic features should be treated with some caution. Specifically, the ability to recognize individuals by their calls will be affected by the number of individuals considered and thus the perceptual and memory constraints of the species in question. In general, most studies looking at individual signatures, including the present study, have sampled a small number of individuals (e.g., LILLEHEI & SNOWDON 1978; 6 stumptail macaques; MACEDONIA 1986; 8 ringtailed lemurs). Thus, it is currently unclear whether the classification accuracy of the discriminant-function analysis would be as high with a larger sample of subjects.

Acoustic Variation and the Study of Perception

The results discussed in this paper are directly relevant to two sets of data on the perception of coos by macaques: 1) psychophysical experiments claiming that Japanese macaques are sensitive to peak position in the fundamental frequency contour (reviews in PETERSEN & JUSCZYK 1984; MOODY & STEBBINS 1989; MAY et al. 1990) and 2) cross-fostering experiments which claim that the food coos of Japanese and rhesus macaques are perfectly discriminable and thus provide young with species-specific models for vocal learning (MASATAKA & FUJITA 1989).

Psychophysical experiments have shown that rhesus macaques, in contrast to Japanese macaques, attend less closely to the peak position of the fundamental than to variation in the absolute frequency of coos. This result, viewed in the context of the data presented here, provides a potentially more complete description of the perceptual system of macaques. That is, because the shape of the fundamental frequency contour of rhesus coos is highly variable, it is unlikely to represent a particularly salient feature in species recognition. In Japanese macaques, however, this contour appears to be associated with different social contexts and thus provides a salient feature for species recognition. It will now be important for studies to establish whether species-specific cues are associated with the coos of different macaque species.

Results presented by MASATAKA & FUJITA (1989) suggest that the maximum frequency of the first harmonic (i.e., Fo) is sufficient to discriminate cross-fostered Japanese and rhesus macaque food coos. Although they do not present data on adult coos, they assume, based on the cross-fostering results, that each species' coo provides a species-specific model for vocal learning. However, the data set presented in this paper shows that for rhesus macaques on Cayo Santiago, the maximum frequency of the Fo contour is highly variable, with an overall coefficient of variation of 53 % (n = 20 adults, 547 calls) and a range of 400 Hz. This variation, which exceeds the difference between species discussed by MASATAKA & FUJITA (1989), makes the possibility of a species-specific acoustic marker for coos less likely (OWREN et al. 1991).

In conclusion, this study supports the view, espoused by others, that several potential sources of acoustic variation exist (GREEN & MARLER 1979). Consequently, it is important to use an appropriate sampling regime. Of course, understanding the sources of acoustic variation only provides the first step in an analysis of vocal communication. Perceptual research is a necessary follow-up for understanding the complexities of call meaning and the mechanisms underlying species-specific auditory biases.

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