

Temporal and acoustic flexibility in vocal exchanges of
coo calls in Japanese macaques

ニホンザルのクー・コールによる鳴き交わしにおける
時間及び音響的特徴の可塑性

杉 浦 秀 樹

①

学 位 論 文

TEMPORAL AND ACOUSTIC FLEXIBILITY IN VOCAL EXCHANGES OF
COO CALLS IN JAPANESE MACAQUES

(ニホンザルのクー・コールによる鳴き交わりにおける時間及び音響的特徴の可塑性)

平成6年12月 博士(理学)申請

東京大学大学院理学系研究科
人類学専攻

杉 浦 秀 樹

CONTENTS

1. Introduction	3
2. Naturalistic observations of vocal exchange of coo calls	8
Methods	8
Subject groups	8
Data collection	8
Acoustic analysis	9
Results	11
Contextual and individual variability of coo calls	11
Temporal analysis	12
Similarity of first and second coos in DC sequence with short and long intervals	14
Discussion	17
3. Playback experiment with a group	19
Methods	19
Results	20
Discussion	21
4. Playback experiment with individuals	22
Preliminary experiment	22
Methods	22
Results	23
Main experiment	24
Methods	24
Results	26
5. General discussion	27
6. Summary	30
7. Acknowledgments	31
8. References	32
9. Figures and tables	36

1. INTRODUCTION.

Over the past two decades, considerable numbers of studies have been made on vocal communication of nonhuman primates. Many researches have shown that there are rudimentary parallels between nonhuman primates vocal communications and human language. Two different paradigms appeared in the study of nonhuman primate communication. One is to teach great apes sign or arbitrary symbol systems which is analogous to human language. The other is to study natural vocal communication of nonhuman primates (Snowdon, 1990). The "ape-language" projects demonstrated that great apes have surprising larger capacity of language than had ever been considered (reviewed by Seyfarth, 1986; Snowdon, 1990). Although the "ape-language" studies can tell us the ability of language by great apes, they do not tell how apes communicate in their natural environment. The study of natural vocal communication of primates is also important to know the evolutionary background of language. The attempts to decode natural communication systems have shown that rudimentary parallels to human language are found in their vocal behavior. For example, referential signals were found in some vocalizations of nonhuman primates. In the vervet monkey (*Cercopithecus aethiops*), they emit three different predator alarm calls against different predators (Seyfarth *et al.* 1980). Toque macaques (*Macaca sinica*) give food calls specifically when they find large and good food patches (Dittus, 1984). Although many researches have shown that there is apparent continuity between nonhuman primate vocal communication and human language, there still be many unresolved questions in primate vocalizations.

A central issue in the study of primate vocalizations concerns the extent of control over vocal production. Information on the ontogeny of vocal communication of nonhuman primates is limited and conflicting. Until recently, our primary data were from squirrel monkeys (*Saimiri sciureus*), focusing on infant isolation peeps. The major finding was that call structures were inherited, not learned (Newman & Symmes, 1982). The infants raised under acoustic isolation from their conspecifics could produce normal vocalization (Winter

et al., 1973). In addition, the calls were structurally stable and little modification occurred during development (Lieblich *et al.*, 1980). In other species, there are some studies suggesting that vocal production is genetically programmed. For example, Brockelman and Schilling (1984) studied loud calls of white-handed gibbons, pileatus gibbons and hybrids between them. Acoustic patterns of the hybrids were intermediate between the two species. A similar phenomenon is found in the hybrid of ruffed lemur (*Varecia variegata*) subspecies (Macedonia and Taylor, 1985). Again, in the squirrel monkey, Snowdon *et al.*, (1985) found that the infants' isolation peeps were different in two different populations, and that the adults showed stronger response to their own infant's vocalization. Failure to find evidence of learning is somewhat surprising given the influence of learning on other behaviors, and the fact that there are some clear parallels in the development of bird song and the development of human speech (Marler, 1970).

The study of development of vocal production requires research on two interrelated areas: how species-specific calls develop and whether animals can modify acoustic features of a given specific type of vocalization in particular circumstances. To answer the first question, Masataka and Fujita (1989) showed through cross-fostering experiments between Japanese macaques (*Macaca fuscata*) and rhesus macaques (*Macaca mulatta*) that production of one of species-specific call is learned by each species. In their study, cross-fostering was initiated within 24 hours after the birth of subjects. The monkeys were tested when one year old since the vocalization chosen for study, that labeled food related call, is not made by Japanese or rhesus macaques until they were close to this age. Food calls of Japanese and rhesus macaque infants reared by their biological mothers differed from each other in a single acoustic parameter. The calls of the Japanese macaque infant fostered by rhesus female at the age of 12 months differed from those of conspecifics reared by their biological mothers. Similarly, the vocalizations given by the two rhesus macaques fostered by Japanese macaque females were dissimilar to those of rhesus macaques reared by their biological mothers, but similar to those of Japanese macaques reared by their biological mothers. However, more recently, Owren *et al.* (1992) provide no evidence of vocal learning by cross-fostering study with the same species.

Concerning the second question, discriminative conditioning studies were conducted as a first step to examine whether there was a voluntary component in nonhuman primate vocalizations. Very simply, in such experiments, animals must learn to emit a call of given amplitude and duration in response to an arbitrary stimulus and withhold vocalizations in response to a second arbitrary stimulus in order to get food and in some instances to avoid punishment (Pierce, 1985). While some of the attempts to condition vocalizations failed (Myers, 1976), others, using the same species (rhesus macaques) have found that such discriminative vocal behavior is no more difficult to obtain under these training conditions than is a manual lever press response (Sutton *et al.*, 1981).

Additional evidence has been presented from a series of studies of squirrel monkeys living in captive groups. Under naturalistic circumstances, animals of this species live in large social groups and inhabit forests with dense vegetation. To maintain contact with group members, individuals utter a variety of vocalizations. One of these vocalizations, the "chuck" was studied intensively to determine whether there are "question" and "answer" chucks which are used to gain information regarding the dynamics of particular social relationship. In this species, mutually preferred partners exchanged chucks more often and responded with shorter latencies than other pairs. The acoustic features of the vocalizations that followed other vocalizations closely were more similar than those of vocalizations that followed a period of silence (Biben *et al.*, 1986). Masataka & Biben (1987) reported the presence of temporal "rules" that appeared to regulate vocal exchanges. Namely, if an animal is responding to a call given by a group member, it does so within 0.5 sec after the sound is heard; if an animal utters a call independently of the preceding call, the interval is greater than 0.5 sec. This temporal rule allowed the animals to determine whether the second vocalization was a response to the first or not, when two calls were heard consecutively. Squirrel monkeys therefore appear to use temporal "rules" to guide their vocal exchanges.

Recently, Elowson & Snowdon (1994) showed that pygmy marmosets (*Cebuella pygmaea*) modify acoustic features of contact calls. They placed two unfamiliar populations together in a common acoustic environment and recorded their vocalizations before and

after the contact. For each individuals of both populations, two frequency measures of the call shifted together after the acoustic contact.

Research presented below has been conducted to extend this previous study of temporal flexibility of vocal behavior, with respect of coo call of Japanese macaques (*Macaca fuscata*). Acoustically, the call has a basically tonal structure and a high degree of variability in the structure (Green, 1975a). In this species, most members of a troop utter these vocalizations in calm or relaxed situations. Coo calls are uttered in a variety of contexts except agonistic ones. Green (1975a) observed that coos were uttered in many social contexts that lack affiliative contact. The coo calls or similar homologous expressions have also been described in several macaque species (reviewed by Bauer and de Waal, 1991). In stump-tailed macaques, the function of the coo vocalization was studied by comparing the behavior of animals when they gave coo calls with that of control situation (Bauer & de Waal, 1991). The calls were uttered more often when the caller was alone than not. After they gave the vocalizations, more affiliative contact with group members occurred than in control situations. In free-ranging situations, the calls are emitted most often during foraging and group progression, but regardless of any other ongoing activity. The coo calls often occur in dense vegetation and the calls are often responded by group members. (Itani, 1963). Animals appear to maintain within-group contact vocally when visual contact is difficult to achieve. They also appear to recognize individuality of the vocalizations. Indeed, Pereira (1986) reported that Japanese macaque mothers were able to distinguish coos of their own juvenile from those of the other juveniles. Moreover, coos are often emitted consecutively by two or more group members (Sugiura, 1993). Mitani (1986) studied their "exchanges" and described a "network" of vocal exchange in a free-ranging troop. The vocalizations were found to be exchanged most frequently among females of the same kinship.

In this paper, the timing and acoustic properties of coo call exchanges in Japanese macaques are described and analyzed. The temporal patterns of occurrence of consecutive coo calls were studied to determine whether or not following coos could be considered a response to preceding coos. I also examined whether the acoustic features of following

coos were related to those of preceding coos. The observations suggested that part of the coos are uttered in response to preceding coos and that in those cases the acoustic features of following coos were similar to those of preceding coos. Therefore, a playback experiment with a group was performed to eliminate unobserved factors which could affect the result and to confirm the phenomenon experimentally. Moreover, a playback experiment with individuals was undertaken, to control the stimulus coo and response coo individually.

Subject groups.—Two populations of *Thalassidroma brevicauda* were studied: the Yachengshan P group and the Chikongshan group. The Yachengshan group was previously reported (1974) and consisted of 10 birds in the wild and 10 birds in the lab. Adults of the Yachengshan group were approximately 10% of the total birds in the Yachengshan Island, mostly in January. The group has been studied since April 1974 in a preliminary observation (1974), and since October of 1974 in a detailed study (Table 1). During the study period, the group consisted of 10 males (hereafter male 1, 2, 3, 4, 5, 6, 7, 8, 9, 10) and 10 females (female 1, 2, 3, 4, 5, 6, 7, 8, 9, 10) in the field, and 10 males and 10 females in the lab.

The Chikongshan group was originally a nonbreeding group. The original members of the group were caught in January or February 1974 in Yachengshan Island and transported to the Chikongshan Island. They were placed in the Yachengshan Island. Thereafter, they have been provided with the artificial feeding conditions. A majority of the group had the habit of feeding themselves. The group consisted of 10 adult females and 10 juvenile females (female 1, 2, 3, 4, 5, 6, 7, 8, 9, 10) and 10 adult males (male 1, 2, 3, 4, 5, 6, 7, 8, 9, 10) in the field, and 10 adult females and 10 juvenile females (female 1, 2, 3, 4, 5, 6, 7, 8, 9, 10) and 10 adult males (male 1, 2, 3, 4, 5, 6, 7, 8, 9, 10) in the lab.

Field collection.—Birds were caught in the Yachengshan Island. Collection of the Yachengshan P group was conducted between August and October, 1974 (10 birds), and during the Chikongshan group between January and February, 1975 (20 birds). The catching of birds is done once a month in the Yachengshan P group, and 2-3 times in the Chikongshan group. During the study period, 10 birds were caught in the Yachengshan P group and 10 birds in the Chikongshan group. All birds were kept in the lab for 10 days before the playback experiment. In each group, 10 birds were kept in the lab for 10 days before the playback experiment.

2. NATURALISTIC OBSERVATIONS OF VOCAL EXCHANGE OF COO CALLS

Methods

Subject groups. Two populations of Japanese macaques were studied: the Yakushima P-group and the Ohirayama group. The two have been geographically separated (>700 km) and without any contact for the past 33 years (Fig. 1). Animals of the Yakushima P-group range over approximately 40 ha of mountain forest on Yakushima Island, south of Kyushu. The group has been studied since 1973 without provisioning (Maruhashi, 1980). Age-sex structure of the two groups are shown in Table 1. During the study period, the group consisted of 5 adult females (≥ 6 yrs), 2 juvenile females (3-5 yrs), 1 immature female (0-2 yrs), 6 adult males (≥ 6 yrs), 3 juvenile males (3-5 yrs), and 1 immature male (0-2 yrs).

The Ohirayama group was originally a translocated group. The original members of the group were captured together in 1957 on Yakushima Island and immediately flown to Mt. Ohirayama, Aichi Prefecture, located in the Japanese mainland. Thereafter, they have been provisioned under semi-free-ranging conditions. A description of the group and its habitat is given by Kawai (1960). The group comprised 15 adult females (≥ 6 yrs), 5 juvenile females (3-5 yrs), 9 immature females (0-2 yrs), 11 adult males (≥ 6 yrs), 9 juvenile males (3-5 yrs), and 14-15 immature males (0-2 yrs) during the observation period.

Data collection. Data presented here were drawn from observations of the Yakushima P-group conducted between August and October, 1990 (62 days), and those of the Ohirayama group between January and February, 1991 (49 days). For recording of data, 5 females from the Yakushima P-group and 8 females from the Ohirayama group were chosen as target animals (all were 3 years or older, see Table 1). Mean ages were approximately 10 years (range: 3 ~ approximately 20 yrs) for the target females in the

Yakushima P-group and 8.3 years (range: 3 ~ 17 yrs) for those in the Ohirayama group. The ages did not differ significantly between the two populations (U-test, $U=17.5$, $N_1=5$, $N_2=8$, $p>0.72$).

Data were collected by the focal animal sampling method (Altmann, 1974), with a given observation session lasting for 60 min. In an observation session, the observer stood near the focal animal with a hand-held microphone (Sony ECM-672) aimed at it, and he recorded all the vocalizations (target and others), identities of callers and behavioral correlates with a tape recorder (Sony WM-D6C). The observations were conducted when most of the group members were located within visible or audible range. If an animal that emitted a vocalization could not be identified, the caller was treated as "unidentified" for the subsequent analysis. A total of 23 and 84 observation sessions were conducted with the Yakushima P-group and the Ohirayama group, respectively. Since, in general, the frequency of vocal emission varied considerably among individuals, data collection method was designed to provide a similar number of vocalizations for each individual per group. The observation sessions were distributed almost equally over the time between 8.00 and 17.00 h in the case of the Yakushima P-group and between 9.30 and 15.30 h in the case of the Ohirayama group.

Acoustic analysis. From the corpus of data described above, I extracted 5-min continuous recording segments where vocal exchanges were successfully recorded, then chose 43 and 42 segments at random for spectrographic analysis for the Yakushima P-group and the Ohirayama group, respectively. All the vocalizations included in the segment were analyzed, using a Kay DSP Sonagraph 5500 with a wide band filter (128 pts: 234 Hz), and a frequency scale of 0-8000 Hz. Time and frequency parameters were measured with an accuracy of ± 0.0032 sec and ± 40 Hz, respectively.

Green (1975a) defined coos as "continuous tonal sound". Although most vocalizations heard during vocal exchange were coo calls, there also occurred some calls which are acoustically similar to coos but do not satisfy his definition. Such vocalizations consisted of the calls that are predominantly tonal but contain a noisy component (noisy

coo) and/or contain a silent component (discontinuous coo, see appendix). As these calls occurred during vocal exchange, mingled with the continuous tonal coos, the calls were also treated as coos. Therefore, coo call is defined as a predominantly tonal vocalization.

The F_0 elements of these basically tonal calls are spectrographically distinct and are usually the most dominant frequency components (Fig. 2). Therefore, for each call, the duration, location of the maximum frequency in relation to the entire length of F_0 elements, start frequency, end frequency, minimum frequency, maximum frequency, and frequency ranges (maximum minus minimum frequency, maximum minus start frequency and maximum minus end frequency) were measured.

Green divided coos into 7 "subtypes" based on their acoustic structure. For example, he categorized coo calls into discrete classes by duration of call (≤ 0.19 sec and ≥ 0.20 sec) or maximum frequency location ($< 2/3$ and $\geq 2/3$). He also argued that each type of coo call was associated with a different social context. However, his findings have not necessarily been confirmed by subsequent studies. Hoop *et al.* (1992) studied the perception of coo call by Japanese macaques with reference to peak position in the laboratory. The results showed no evidence for categorical boundaries in the peak position of the vocalization. Recently, Owren & Casale (1994) measured peak positions of coo calls produced by captive adult Japanese macaques. If Japanese macaques discriminate the call into two categories, it is predicted that they would produce fewer calls with the peak position at the categorical boundary. However, the animals produced the calls with the peak location at the hypothesized boundary at rates equal to or higher than predicted by chance. The results indicate that coo call are not perceived categorically. Also from my data, no obvious discretable categorical boundary was found for any of the parameters measured. Therefore, coo calls were not divided into subtypes and their acoustic features were measured continuously.

When all the vocalizations were categorized, more than 85% of the total vocal sample consisted of coos. Because of their low incidence, call types other than the coos were excluded from the subsequent analysis. Whenever two coos were uttered consecutively, being uninterrupted by other call types, the inter-call interval was defined as the time from

the end of a call to the beginning of the next. If two or more coos occurred concurrently (e.g., the second coo overlapped the first), the inter-call interval was measured between the end of the n th call and the beginning of the $(n+1)$ th call and given a negative value. When three or more coos occurred consecutively, I measured the interval between the first and the second call, and then that between the second and the third. For example, if three calls occurred consecutively like $A \rightarrow B \rightarrow C$, I measured interval between A and B, and that between B and C. In such case, B was treated as the second call to A, and was also treated as the first call to C.

Results

Contextual and individual variability of coo calls

Other species of the genus *Macaca* are known to emit coo calls. Hauser (1991) recorded coo calls and contexts in which the vocalizations were given in free-ranging rhesus macaques (*Macaca mulatta*). The calls were highly variable even in the same context, and it was impossible to classify coos by contexts. However, it was possible to discriminate the caller by the acoustic features of the calls alone. He concluded that coos calls provide sufficient acoustic cues for individual recognition, but do not provide sufficient information about the context in which callers engage. Therefore, first of all, contextual and individual variability of coo calls were analyzed.

Number of coo calls by each caller in each contexts by callers were shown in Table 2. The contexts in which coos were recorded were feeding (68.5 % and 30.9 %), grooming (1.0 % and 29.0 %), moving (14.3 % and 5.4 %) and resting (13.6 % and 30.7 %) for the Yakushima P-group and the Ohirayama groups, respectively. The context was not recorded or uncertain in the 2.6 % and 4.0 % of the case for the Yakushima P-group and the Ohirayama groups, respectively. To test whether the acoustic properties of coos are different by the contexts or not, two-way analysis of variance was conducted with context and caller as two factors. Because the number of coos given while grooming in the

Yakushima-P group and those given while moving in the Ohirayama group were relatively few, these calls were eliminated from the analysis. The analysis was performed only for the animals with more than five coos in each context. If there were more than ten calls in one cell, ten calls were chosen randomly for the analysis. The result of analysis of variance is shown in table 3. Acoustic features of coos were significantly different among the contexts only for one parameter (maximum minus minimum frequency) in the Ohirayama group, and the other acoustic parameters did not differ among the contexts. However significant overall effect by caller was present for all the parameters except one (maximum frequency in the Ohirayama group).

There were no salient differences in the acoustic properties of coos in the different contexts. Therefore, it seems safe to pool the coos given in different contexts for the following analysis.

Temporal analysis

Sequences of two consecutive coos were classified into two categories as follows: (1) sequence of two consecutive coos where the second call was uttered by a different caller from the first (*DC* sequence) and; (2) sequence of two consecutive coos uttered by the same caller (*SC* sequence). A total of 244 and 140 intervals in *DC* sequence were analyzed for the Yakushima P-group and the Ohirayama group, respectively. Inter-call interval in *DC* sequence can be defined according to the identity of the first caller or the second caller. Median interval of *DC* sequence grouped by the first caller shown in Table 4 represents the interval between the coo of the target and the following coo by another group member when two coos were uttered consecutively. Table 5 shows the median intervals grouped by the second caller, which represents the interval between the coo of a group member and the following coo by the target animal. A total of 141 and 74 intervals in *SC* sequence were analyzed for the Yakushima P-group and the Ohirayama group, respectively. Median intervals in *SC* sequence are shown in Table 6. These values are the intervals between two coos by the same animal, uninterrupted by another group member.

Among the 244 and 140 intervals in *DC* sequence, 182 (74.5 %) and 124 (86.1 %) second coos occurred between 0-4 sec in the Yakushima P-group and the Ohirayama group, respectively. Of the 141 and 74 intervals in *SC* sequence, 83 (58.8 %) and 64 (86.4 %) intervals were shorter than 4 sec in the Yakushima P-group and the Ohirayama group, respectively. Median intervals in *DC* and *SC* sequence between 0-4 sec were calculated for each target female, to compare the duration of intervals in *DC* sequence with those in *SC* sequence individually. For the 13 target animals in the two populations, the median intervals in *SC* sequence were plotted against the median intervals in *DC* sequence, grouped according to the first caller (Fig. 3) and against those in *DC* sequence, grouped according to the second caller (Fig. 4). Compared with the median intervals in *DC* sequence where the first callers were target animals, those in *SC* sequence were statistically significantly longer for all individuals (Wilcoxon's signed ranks test: $N=13$, $p<0.01$). Also, the median intervals in *SC* sequence were longer than those in *DC* sequence where the second callers were target animals for all individuals (Wilcoxon's signed ranks test: $N=13$, $p<0.01$).

Because there were no significant individual differences in the intervals in *DC* sequence or in *SC* sequence within each population [Kruskal-Wallis test: the Yakushima P-group, $H=2.36$, $N=5$, $p=0.67$, (*DC* sequence where the first callers were target animals), $H=2.36$, $N=5$, $p=0.67$, (*DC* sequence where the second callers were target animals), $H=4.41$, $N=5$, $p=0.35$, (*SC* sequence); the Ohirayama group, $H=3.71$, $N=8$, $p=0.82$, (*DC* sequence where the first callers were target animals), $H=4.43$, $N=8$, $p=0.73$, (*DC* sequence where the second callers were target animals), $H=10.5$, $N=8$, $p=0.16$, (*SC* sequence)], pooling the data seems justified.

Overall distributions of intervals in *DC* sequence and *SC* sequence are shown in Fig. 5. Compared with the distribution of *DC* sequence between 0-4 sec and that of *SC* sequence between 0-4 sec, intervals of *DC* sequence were significantly shorter than those of *SC* sequence in the two populations (Mann-Whitney U-test: Yakushima P-group, $N_1=182$, $N_2=83$, $U=1923$, $p<0.001$; the Ohirayama group, $N_1=124$, $N_2=64$, $U=1471$, $p<0.001$). Median intervals of *SC* sequence between 0-4 sec were 1.1 sec and 1.0 sec in the Yakushima P-group and the Ohirayama group, respectively. In the Yakushima P-group,

88 % of second coos in *DC* sequence that were separated by intervals of 0-4 sec were distributed between 0 sec and 1.1 sec (the median intervals of *SC* sequence). Similarly, 87 % of second coos were distributed between 0 and 1.0 sec (median interval of *SC* sequence) in the Ohirayama group.

In summary, in both populations, most of the second coos in *DC* sequence occurred at shorter intervals and the remaining ones at relatively longer intervals. As a working hypothesis, we may assume that, if the second coo follows the first one after a short interval, it is more likely to be a response to the first coo than if it follows after a long interval. In the latter case the second call may have occurred independently of the first call, and thus be considered "spontaneous". This assumption is in line with the fact that the second coos in *SC* sequence rarely occurred during the periods in which most of the second coos in *DC* sequence occurred.

Similarity of first and second coos in *DC* sequence with short and long intervals

The question arises whether acoustic properties may differ between calls of *DC* sequence with short and long intervals. Acoustic features of the second coos given by different caller with short intervals, which may represent responses, might be dependent on those of the first. On the other hand, second coos with long intervals, which may be "spontaneous", might acoustically independent of the first coos. For example, one might hypothesize greater similarity between coos separated by short intervals than by longer intervals. Therefore, a correlation analysis was performed between the acoustic features of two consecutive coos made by different callers. The median intervals of *SC* sequence between 0-4 sec were 1.1 sec, when the data of the Yakushima P-group and that of the Ohirayama group were pooled. Therefore, the entire data set for each population was divided into two subsets according to the following criteria: (1) two consecutive coos that occurred at intervals of 0-1.1 sec and; (2) two consecutive coos that occurred at intervals longer than 1.1 sec.

As shown in above, acoustic properties of coo calls were significantly different among individual (Table 3). To exclude the effect of interindividual differences, data for the second

callers were standardized by transformation to the z score according to the formula: $z=(x-x_i)/s_i$ (x , raw value; x_i , mean of individual i ; s_i , standard deviation of individual i). The z score represents the relative deviation from the mean value for each individual. Z score conversion was carried out only for the data obtained when the second caller was the target animal and when the standard deviation was larger than zero. The data obtained when the second callers were other than target or unidentified, or when the standard deviation was zero were eliminated from the following analyses ($N=145$). Because the sample size were not large enough, the data of the Yakushima P-group and the Ohirayama group were pooled. The distribution of second coos by caller is shown in Table 7

When a correlation analysis was undertaken between two consecutive coos in *DC* sequence using these data (Table 8), 5 parameters (duration, maximum frequency, maximum minus minimum frequency, maximum minus start frequency and maximum minus end frequency) of the second coos in *DC* sequence that were separated by intervals of 0-1.1 sec showed significant positive correlations with those of the first coos. Among the 9 parameters of the second coos in *DC* sequence that were separated by intervals longer than 1.1 sec, one acoustic parameter (duration) of the second coos in *DC* sequence showed a significant positive correlation and 3 acoustic parameters (minimum frequency, start frequency and end frequency) showed significant negative correlations with that of the first coos. The second coos given by a different caller within 1.1 sec were likely to be similar in several acoustic parameters with those of first coos. This similarity was not seen in coos that occurred at intervals longer than 1.1 sec. The findings imply the possibility that Japanese macaques might alter their acoustic features of responding coo calls matching to those of preceding coos.

Although most vocalizations of nonhuman primates are emitted from very early stage of development, the ability to use particular types of the vocalizations in proper contexts is known to develop gradually in some species. For instance, vervet monkeys (*Cercopithecus aethiops*) emit "eagle alarm" in the presence of avian predators (Seyfarth *et al.*, 1980). Seyfarth & Cheney (1986) found that while adults gave the calls very strictly to avian predators, infants uttered the calls to a variety of birds including non-predators. Juveniles

(1-5 years old) were more restrictive than infants in the species toward which they directed the alarm calls, but were less restrictive than adults. Although infant vervet monkeys are able to emit alarm calls that are acoustically similar to those of adults from a very early age, their ability to use alarm calls properly in particular contexts develops gradually until they reach adulthood. Pigtail macaques (*Macaca nemestrina*) emit four types of screams and each type of scream is given in a different agonistic context with regard to relative rank of opponent and severity of aggression (Gouzoules & Gouzoules, 1989). However, each scream variant is often heard in improper context, too. The proportion of such "errors" is significantly higher in young animals (1-3 years old) than in adults, suggesting that the ability to use different types of screams in proper agonistic contexts is acquired as pigtail macaques develop.

Thus, in Japanese macaques, usage of coo calls during vocal exchanges might undergo similar developmental modifications. To test this possibility, I examined whether characteristics of vocal behavior of coo calls in Japanese macaques described above were influenced by callers' age. Namely, I compared (1) two consecutive coo calls where the second caller was an adult target (≥ 6 yrs); and (2) two consecutive coo calls where the second caller was a juvenile target (3-5 yrs). Correlation analyses were performed between two consecutive coos in *DC* sequences (Table 9). Results on adult animals indicated significant positive correlations for four acoustic parameters (maximum frequency, maximum minus minimum frequency, maximum minus start frequency and maximum minus end frequency) between the second coo uttered within 0-1.1 sec and the first coo. One parameter (maximum minus end frequency) of second coos of adult animals with the intervals longer than 1.1 sec showed a significant negative correlation with those of the first. For animals younger than 6 years, only one acoustic parameter (duration) of the second coo within 0-1.1 sec was significantly positively correlated with the first coo. No parameter of the second coo uttered by young animals with intervals longer than 1.1 sec revealed any correlation with those of the first coo.

Discussion

The results suggest that the second coos in *DC* sequence are of two different types, and that the second coos of two consecutive calls that are separated by shorter intervals occurs in response to the first coo, whereas the second call of two consecutive coos that are separated by longer intervals occurs independently of the preceding call. The phenomenon is quite similar to those that found in squirrel monkeys (Masataka & Biben, 1987). If Japanese macaques respond to coos given by members of their group, they appear to do so within a certain length of time.

In both populations, the second coos in *SC* sequence rarely occurred during the periods in which most of the second coos in *DC* sequence occurred. Most of the second coos in *DC* sequence occurred at intervals of more than the median intervals of *SC* sequence (1.1 sec in the Yakushima P-group and 1.0 sec in the Ohirayama group). These results suggest that when an animal gives a coo spontaneously, she remains silent during the period when the group members are likely to respond. And when no animals make any vocal response, she gives another coo again addressing the other animals.

The second call in a *DC* sequence given by adult animals with intervals of 0-1.1 sec were similar in several parameters with those of the first, and those with intervals longer than 1.1 sec were dissimilar to the first. On the other hand, there was no similarity between the second coo given by young animals and the first coo regardless of temporal separation.

Three acoustic parameters of second coos given both by adults and juveniles with intervals of longer than 1.1 sec showed negative correlations (Table 8). For these parameters, correlation coefficients where the second callers were juveniles were negative, while those where the second animals were adults were positive. The correlation coefficients tend to be different between adults and juvenile (minimum frequency; $z=1.93$, $p<0.06$, start frequency; $z=2.13$, $p<0.05$, end frequency; $z=1.83$, $p<0.07$). The negative correlation might due to the second coos given by juveniles. However, the reason why the correlation coefficients become negative is unclear because the sample size is too small.

The results suggest that adult Japanese macaques modify acoustic features of coos according to those of preceding coos when they respond, and that juvenile macaques do not. A possible explanation for the result is that the young animals can not alter the acoustic features of their coos. However, the standard deviations of all acoustic parameters of coos by young target animals were not significantly different from those of adult targets (Mann-Whitney U-test, $N_1=8$, $N_2=7$, for 9 acoustic parameters, $p>0.05$). Therefore, young animals are apparently to be able to emit various coo calls as adult animals do. Therefore this explanation can be discarded. Another explanation is that the juvenile animals more often responded to coos whose acoustic features were dissimilar to theirs. As my dataset is not large enough to control for the first callers, this explanation is possible. However, an alternative explanation is that the young animals are able to utter various calls, but they might not match the features of their coos to those of preceding coos. If this interpretation is correct, there is a possibility that the ability to match acoustic properties of coos might develop gradually.

3. PLAYBACK EXPERIMENTS WITH A GROUP

The observations of vocal exchange of coo calls suggest that response coos are similar acoustically to the first coos. I conducted playback experiments of recorded coo calls in an attempt to eliminate exogenous unobserved stimulation responsible for similarity in the structure of two consecutive calls. If the hypothesis is correct, broadcast coos should be followed by acoustically similar coos in cases where they occur within 1.1 sec after the playback, but dissimilar in cases where they occur after intervals longer than 1.1 sec.

Methods

The playback experiment with a group was conducted with the Ohirayama group in September and October, 1991. A choice was made of 14 tape-recorded coos as playback stimuli (2 coos from each of 7 target animals in the naturalistic observation described above). Each trial was conducted when most group members were within audible range of the experimenter. The experimenter stood about 5 meters away from the speaker and waited until all the animals within his audible range were vocally inactive, at least for a 5 sec period prior to the playback, to prevent any other vocalizations affecting the subsequent calls of the animals. Thereafter, a single coo call was produced from the tape recorder. In a given experimental trial, one of the 14 stimuli was broadcast from a tape recorder (Sony WM-F203) through a speaker (Sony SRS-77G). Playback stimuli and vocalizations from the animals during the 4-sec period after the playback were recorded, through two microphones (Sony ECM-672 directional microphone and Sony ECM-261 non-directional microphone) with a tape recorder (Sony WM-D6C). Whenever possible, identities of the animals that made vocalizations during the period were recorded. If any vocalization occurred during the 4-sec period after the playback, the attempt was regarded as successful regardless of which animal made the vocalization. Intervals in the *DC* sequence were measured from the

end of playback to the start of the first vocalization thereafter. If any coo vocalization occurred simultaneously with a stimulus or if the first vocalization was not a coo, the trial was ignored in the subsequent analysis (N=43). If the caller could not be identified, it was treated as "unidentified" for the subsequent analysis. The mean distance from the speaker to the animals that uttered coo calls following the stimuli was 8 meters. At that distance the mean sound pressure of the stimuli was 57 dB (range 56-58 dB; Quest Elemetrics sound level meter model 215, A weighting).

Results

Acoustic parameters of the stimuli are shown in Table 10. The number of entire and successful trials for each stimulus are shown in Table 11. Of the 329 broadcast coos, 57 (17 %) were successfully followed by coo calls with intervals of 0-4 sec. Of these 57 following coos, 35 (61 %) occurred within 1.1 sec after the presentation of the stimulus, and 22 (39 %) occurred after intervals longer than 1.1 sec. In the 57 successful trials, callers were identified in 14 (25 %) cases, and in 43 (75 %) cases the callers could not be identified. I observed one case that an animal followed her own stimulus (*i.e.*, a call recorded from the same animal) with an interval of 1.8 sec. The overall distribution of inter-call intervals between the stimuli and the subsequent coos is shown in Fig. 6. Correlation analyses were made between the stimuli and subsequent coos for the following two data sets: (1) coos that followed the stimuli at intervals of 0-1.1 sec; and (2) coos that followed the stimuli at intervals of 1.1-4 sec. Results indicate significant positive correlations between these stimuli and subsequent coos that occurred at intervals of 0-1.1 sec for two acoustic parameters (maximum minus minimum frequency and maximum minus start frequency) (Table 12). No parameters of the coos that followed the stimuli at intervals of 1.1-4 sec correlated significantly with those of the stimuli.

Discussion

In the Ohirayama group, the second coos given by a different caller within 1.1 sec were similar in several acoustic parameters with those of the first coos. This similarity was not seen in coos that occurred at intervals of longer than 1.1 sec. The phenomenon described in the naturalistic observations were confirmed experimentally. For these results, two explanations are possible. Greater similarity with shorter intervals might simply have been due to individuals with calls similar to the first caller being more likely to respond more often and more quickly. In this experiment, individuals whose acoustic features of coos were similar to the acoustic quality of the playback stimuli may have responded more often and more quickly. But alternatively, individuals might modify acoustic features of their coos under certain conditions, adjusting them to the acoustic features of the call they hear. To answer this question, I describe a playback experiment conducted with individuals in the next chapter.

4. PLAYBACK EXPERIMENT WITH INDIVIDUALS

The playback experiment with a group described above raised the question of whether individuals alter acoustic features of their coos, matching them to the preceding coos or not. The question can be answered if we undertake a playback experiment by directing prepared coo calls to a predetermined target adult and are able to evoke, an overt response by the animal. In the Ohirayama troop, the number of potential respondents were so great that it appeared to be very difficult to conduct such experimentation on a single predetermined target animal. On the other hand, in an unprovisioned group such as the Yakushima P-group whose group size is relatively small and whose members are more likely to spread out over relatively large distances, the study should be feasible. The results of the playback experiment carried out at the group level suggest the possibility that animals might alter some acoustic features (maximum minus minimum frequency and maximum minus start frequency) of their vocalizations according to those of preceding coos. If the subject animals indeed match the acoustic features of the calls with those of playback vocalizations, the acoustic parameters of the subjects' coos should be varied depending on the acoustic quality of the stimuli. To explore this possibility, I carried out the following playback experiment, testing individuals.

Preliminary experiment

Methods

The following experiment was conducted with the Yakushima S-group between August, 1992 and August, 1993. The Yakushima S-group inhabits an approximately 40 ha area neighboring the area of the Yakushima P-group. We started habituation of the group in

April, 1992, without provisioning, and individual identification of all adult animals was accomplished in May, 1992. At the beginning of the experimentation, the group consisted of 8 adult females, 8 adult males, at least 5 juveniles, and 1 infant.

Four adult females were chosen as target individuals. For each subject animal, a pair of stimuli was presented; they consisted of "high-pitched coo calls" with a relatively large frequency modulation range [maximum minus minimum frequency (mean=872 Hz) and maximum minus start frequency (mean=824 Hz)], and "low-pitched coo calls" with a relatively low maximum frequency (mean=152 Hz) and small frequency range (mean=120 Hz) (Figure 9). The stimuli were recorded from adult females of the same group. For each target animal, 1-2 pairs of high-pitched and low-pitched coos recorded from the same female were prepared. I did not present an animal with her own stimuli. A total of 5 coos (5 high-pitched stimuli and 5 low-pitched stimuli) was used. A speaker was hidden about 15 meters away from a predetermined target animal and the experimenter stood about 10 meters away from the speaker. At the distance of 15 meters, the mean sound pressure level of the stimuli was 42 dB (range 41.0-43.8 dB; Quest Elemetrics sound level meter model 215, A weighting). In a given experimental trial, one of the two stimuli was broadcast from a digital tape recorder (Sony NT-1) through a speaker. If any vocalization occurred simultaneously with a stimulus or if the first vocalization was other than a coo of the target animal, the trial was ignored in the subsequent analysis. Other experimental procedures and equipment used were same as playback experiment with a group described above.

Results

Representative sonagrams of the playback experiment are shown in Figure 7. The numbers of entire trials and successful trials are shown in Table 13. A total of 147 high-pitched coos and 158 low-pitched coos were played back. The 147 and 158 trials yielded 27 and 35 responses with intervals of 0-4 sec. Of these 27 coos following the high-pitched stimuli, 22 (81%) occurred within 1.1 sec after the playback and 5 (19%) occurred after

intervals longer than 1.1 sec. Of the 35 coos following the low-pitched stimuli, 25 (71%) occurred within intervals of 1.1 sec, and 10 (29%) occurred at intervals of 1.1-4 sec. Overall distribution of intervals in the playback experiment is shown in Figure 8. Acoustic parameters (maximum minus minimum frequency and maximum minus start frequency) of coos that occurred with intervals of 0-1.1 sec were analyzed by two-way analyses of variance. For the analysis, pitch of stimuli (high and low) and subject individual were chosen as two factors.

The 2×4 analysis of variance revealed significant effects for stimulus with regard to both of the two parameters (Table 14). There was no significant effect for subject individual with regard to the parameters. No significant Stimulus \times Subject individual interaction was present. The means of these two parameters were significantly greater for coos given in response to high-pitched stimuli to low-pitched stimuli (Figure 9). This means that the coos are more modulated when they are given in response to high-pitched stimuli than to low-pitched stimuli.

Main experiment

The results of the preliminary playback experiment strongly suggest that adult female Japanese macaques can modify acoustic features of their own coo calls and match them with the features of preceding coos to which they respond. Therefore, I conducted a playback experiment with more stimuli and trials for each subject individual.

Methods

The playback experiment with individuals was conducted with the Yakushima G-group between May and October, 1994. Naturalistic observations and recording of

vocalizations of the group members for playback stimuli were conducted between May and June in 1994, and the playback experiment was done between July and October in 1994. The Yakushima G-group inhabits approximately 70 ha area neighboring the area occupied by the Yakushima S-group. The group has been occasionally observed since 1986, and intensive habituation of the group was started in October, 1993. Individual identification of all adult members were accomplished before the start of vocal recording, and that of all group members was completed in August, 1994. At the beginning of the experimentation, the group consisted of 7 adult females, 8 adult males, 4 juvenile females, 3 juvenile males and 1 infant.

Four adult females of the group were chosen as target animals. Vocalizations for playback stimuli were recorded from the adult females of the same group. Coo calls of high quality recording, with different F0 pitch (maximum frequency) and frequency ranges (maximum minus minimum frequency and maximum minus start frequency) were chosen as stimuli. For each subject animal, 6-7 stimulus coo calls recorded from the same female were presented. In a given trial, a speaker (Sony, SRS-77G) was hidden approximately 15-20 meters away from a predetermined target animal, and the experimenter who stood about 10 meters away from the speaker played back one of the set of stimuli from a minidisk player (Sony, MZ-R2) through the speaker. Other experimental procedures and equipment used were the same as in the preliminary playback experiment with individuals described above.

Statistical procedure

To test the effect of acoustic features of stimuli on those of responses, regression analyses were performed for each subject, with the acoustic parameter of stimuli as the independent variable X and that of response calls as the dependent variable Y. As more than one response exists for each stimulus, the analysis was done according to the regression with multiple Y for each X, described by Sokal and Rohlf (1981). The stimuli with less than 5 responses with intervals of 0-1.1 sec were eliminated from the following analysis (stimulus MI-6 for subject Mdr and Tk-7 for Yn, see Table 15).

Results

Acoustic parameters of stimuli are shown in Table 15. The numbers of entire trials and successful trials are shown in Table 16. A total of 1366 trials were conducted and a total of 309 stimulus calls were successfully responded (23 %) by target animals. Mean numbers of entire trials and successful trials per target animal are 342 and 77 respectively. Of the 309 successful trials, 211 response calls (%) occurred within 1.1 sec after the presentation of stimuli, and 98 response coos occurred with intervals of 1.1-4 sec.

Overall distribution of intervals between the end of stimulus and the beginning of the response is shown in Figure 10. Acoustic parameters of response calls that occurred with intervals of 0-1.1 sec were analyzed by linear regression. The F values for fitness of acoustic parameters of response to the regression line are shown in Table 17. For the 3 subjects, regressions of maximum frequency of response coos on that of the stimuli are significant (Fig. 11). For all the subjects, regressions of maximum minus minimum frequency and maximum minus start frequency are significant. Therefore, the acoustic features of stimulus coo calls have a significant effect on those of response coos.

5. GENERAL DISCUSSION

The results of playback experiments demonstrated that the adult female Japanese macaques match the acoustic features of their coo calls to those that they respond to. The results of naturalistic observations and playback experiments indicate that they are able to modify especially frequency range of the calls. Therefore, their vocal production is more flexible than has ever been considered.

Although nine acoustic parameters were used to evaluate the acoustic features, they are not independent of each other. Thus, the parameters can be classified into a small number of groups and two groups are important. One is start frequency and minimum frequency. They are highly correlated and were the least variable within each individual. As the parameters are known to correlated with caller's age and body size (Inoue 1988), these features may physically constrained. Another is maximum frequency and three frequency ranges (maximum minus minimum frequency, maximum minus start frequency and maximum minus end frequency). They are also highly correlated with each other. In the contrast of the former parameters, these are the most variable within each individual. Therefore, Japanese macaques may be able to alter frequency modulation range easily. The most variable feature may be used for call matching.

Matching acoustic features might function as cues that the call is really a response to the preceding call. The coo call exchange is likely to be reciprocal communication that functions to maintain contact with one another. However, occasionally, two or more animals give coos concomitantly. In such case, acoustically matched calls may be more reliable response that the call is received and responded.

If this functional explanation is appropriate, there can be differences in the behavior of the first caller, whether her call was responded by an acoustically similar call or her call was responded by a dissimilar call. For example, the first caller may be likely to give another call when her first call was responded by a similar call but may not give another response when she is responded by dissimilar call. The problem should be studied by further research.

As the present study do not specify the context in which coo calls were responded, there is possibility that the acoustic similarity of coo calls might reflect contextual difference. Assume that the acoustic features of coo call was associated with some contexts, temporally succeeding coos may be acoustically similar reflecting the common context. However, the analysis of contextual and individual variability of coo call revealed that the acoustic features of coos did not differ by contexts. Moreover, in the playback experiment in the Ohirayama group, coos that followed with intervals of 1.1 - 4 sec were not acoustically similar to the stimulus coos. Four-sec period seems to be short enough to consider that the context remains the same one. If we can assume that a context did not change within 4 sec, the explanation can be discarded. However, if the contextual difference affect only a response coo followed with a short interval but not a coo followed with a relatively long intervals (e.g. >1.1 sec), this explanation is still considerable.

Anyway, to answer these problems, function of coo call exchanges should be studied, because the understanding the function of coo call exchange will help to classify the context properly. The primary function of coo call exchange seems to locate group members vocally. A possible function of coo call exchange may be regulation of interindividual distance. For example, in the Ohirayama group, coo call exchanges between two individuals were sometimes seen prior to the approach to each other. In the monkeys of Yakushima, coo call exchanges were often seen when they are feeding, especially entering into food patches. In free-ranging Japanese macaques, agonistic interactions often occur when they are feeding close to each other (Furuichi 1983). To examine this hypothesis, coo call exchanges need to be studied using various parameters, such as contexts, social relationship and interindividual distance.

The phenomena found in Japanese macaque vocal exchange are comparable with human conversation. Masataka (1993) reported conversational vocal behavior of the cooing of 3- to 4-month-old human infants with their mothers. When the three-month-old infant emitted cooing, the mother responded mostly within 0.5 sec after the infant's vocalization. While the mother did not respond to her infant experimentally, the infant was more likely to repeat another vocalization with intervals of 0.5-1.5 sec. When the infant was four months

old, the mother responded more slowly (mostly more than 0.5 sec) and the infant come to repeat cooing with longer intervals (1.0-2.0 sec) in the absence of mother's response. Interestingly, the intervals of repeated vocalizations by infants corresponded to the promptness of the mothers' response. The results imply that after vocalizing spontaneously, the infant tended to pause as if to listen for a possible vocal response from the mother. In the absence of a response, repeated vocalization occurred.

Matching the pitch pattern is also seen in human infants. Kessen and Levine (1979) reported that infants between 3 and 6 month of age could match the pitch of their vocalizations with the presented sung tones. Masataka (1992) reported that three- or four-month-old infants matched the frequency modulation patterns of their vocalization with those given by the mothers during the conversational turn-taking. The results found in human infants seems to be parallel to those I report here for Japanese macaques.

The present study also suggests that the ability to use the call properly might develop gradually by learning. Green (1975b) reported that food calls are structurally different among the three populations. Moreover, our preliminary acoustical analysis on coos between the two Japanese macaque groups (Tanaka and Sugiura, unpublished data) reveal acoustic features of the vocalizations *per se* that are strikingly different in terms of F_0 elements in the call: the presence of "dialects" could be indicated.

Remarkable similarities found between infant prelinguistic cooing and Japanese macaque cooing might suggest possibilities that further investigation on Japanese macaque vocal behavior could provide some important insights for understanding certain aspects of the origins of human language. As pointed out by Snowdon *et al.* (1982), to study vocal ontogeny in nonhuman primates, what is most urgent is to find a appropriate species to determine how flexibly primate vocalizations are produced. From the present study, vocal behaviors of Japanese macaques is more flexible with regard to its temporal and acoustic structures than has commonly been supposed. It is strongly suggest the Japanese macaque as a possible candidate.

6. SUMMARY

Vocal exchanges of coo calls in female Japanese macaques were observed in two populations under natural conditions. Temporal patterns of occurrence of these vocalizations during vocal interaction were studied by analyzing inter-call intervals between two consecutive coos. When the second call was uttered by a different caller from the first (*DC* sequence), most of the second calls occurred at intervals shorter and the remaining ones at longer intervals. These results indicate that the second coos of *DC* sequence are of two different types, and that second calls separated by short intervals may occur in response to the first call, whereas second calls separated by a relatively longer interval may occur independently of the preceding call. When two consecutive calls were uttered by the same caller (*SC* sequence), the second coos rarely occurred during the period in which most of the second coos in *DC* sequence occurred. These results suggest that, when an animal utters a coo spontaneously, it remain silent for a short intervals and that when no response occurs, she is likely to give further coos addressing group members.

Acoustic analysis of two consecutive coos in *DC* sequence showed that the second coos given by a different adult caller and occurring within 1.1 sec significantly correlated with those of first coos with respect to several acoustic parameters. This correlation was not observed when coos occurred at intervals longer than 1.1 sec. Second coos by different callers with short intervals were acoustically similar to the preceding coos. This similarity between two coos was observed when the second callers were adult animals. However the similarity was not seen when the second callers were juvenile animals. These results suggest that Japanese macaques alter their acoustic features of their responding coos, matching to those of the first coos. The results also suggest the possibility that this vocal matching behavior might develop during ontogeny. I conducted playback experiment with a group and with individuals to confirm the results observed under naturalistic condition and eliminate exogenous unobserved factors. The results of experiments confirmed that the animals match their acoustic features of coos in response to the first coos.

7. ACKNOWLEDGMENTS

I would like to thank Professor K. Aoki and Dr. N. Masataka for their invaluable advice and comments from the planning stage to final completion of this manuscript. I also wish to thank Drs. N. Agetsuma, S. Suzuki, Mr. T. Tanaka and the other researchers and residents of Yakushima Island for their help during the field research. I am grateful to Dr. S. Kodaera of the Japan Monkey Center for permission to study in the Inuyama Monkey Park, and Messrs. K. Sakurai, Y. Ishida, M. Takai and other members of the staff of the Japan Monkey Center for their assistance with the present research. I would like to express my gratitude to Dr. C. Saito, Ms. M. Hamai Mr. R. Oda and Dr. I. Tanaka for valuable discussion and help. This study was supported by Grant-in-Aid for JSPS Fellowships for Japan Junior Scientists and Cooperative Research Fund of the Primate Research Institute, Kyoto University.

8. REFERENCES

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, p. 227-267.
- Bauers, K. A. & de Waal, F. B. M., 1991. "Coo" vocalizations in stumptailed macaques: a controlled functional analysis. *Behaviour* 119, p.143-160.
- Biben, M., Symmes, D. & Masataka, N., 1986. Temporal and structural analysis of affiliative vocal exchanges in squirrel monkeys (*Saimiri sciureus*). *Behaviour* 98, p. 259-273.
- Brockelman, W. Y. & Schilling, D., 1984. Inheritance of stereotyped gibbon calls. *Nature* 312, p. 634-636.
- Dittus, W. P. J., 1984. Toque macaque food calls: semantic communication concerning food distribution in the environment. *Anim. Behav.* 32, p.470-477.
- Elowson, A. M. & Snowdon, C. T., 1994. Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Anim. Behav.* 47, p. 1267-1277.
- Furuichi, T., 1983. Interindividual distance and influence of dominance on feeding in a natural Japanese macaque troop. *Primates* 24, p. 445-455.
- Gouzoules, H. & Gouzoules, S., 1989. Design features and developmental modification of pigtail macaque, *Macaca nemestrina*, agonistic screams. *Anim. Behav.* 37, p. 383-401.
- Green, S., 1975a. Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study. In: "Primate Behavior, Vol. 4," L. A. Rosenblum, ed., Academic Press, New York, p. 1-102.
- Green, S., 1975b. Dialects in Japanese monkeys: vocal learning and cultural transmission of locale-specific vocal behavior? *Z. Tierpsychol.* 38, p. 304-314.
- Hauser, M. D., 1991. Sources of acoustic variation in rhesus macaque (*Macaca mulatta*) vocalizations. *Ethology* 89, p. 29-46

- Hopp, S. L., Sinnott, J. M., Owren, M. J. and Petersen M. R., 1992. Differential sensitivity of Japanese macaques (*Macaca fuscata*) and humans (*Homo sapience*) to peak position along a synthetic coo call continuum. *J. Comparative Psychol.* 106, p. 128-136.
- Inoue M., 1988. Age gradation in vocalization and body weight in Japanese monkeys (*Macaca fuscata*). *Folia Primatol.* 51, p.76-86.
- Itani, J., 1963. Vocal communication of the wild Japanese monkey. *Primates* 4, p. 11-66.
- Kawai, M., 1960. A field experiment on the process of group formation in the Japanese monkey (*Macaca fuscata*), and the releasing of the group at Ohirayama. *Primates* 2, p.181-255.
- Kessen W. & Levine J., 1979. The imitation of pitch in infants. *Infant Behav. Develop.* 2, p.93-99.
- Lieblch, A. K., Symmes, D., Newman J. D. & Shapiro, M., 1980. Development of the isolation peep in laboratory-bred squirrel monkeys. *Anim. Behav.* 28, p. 1-9.
- Macedonia, J. M. & Taylor, L. L., 1985. Subspecific divergence in a loud call of the ruffed lemur (*Varecia variegata*). *Am. J. Primatol.* 9, p. 295-304.
- Marler, P., 1970. Bird song and speech development: could there be parallels? *Am Sci* 58, p.663-669.
- Maruhashi, T., 1980. Feeding behavior and diet of Japanese monkey (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates* 21, p. 141-160.
- Masataka, N., 1993. Effects of contingent and noncontingent maternal stimulation on the vocal behaviour of three- to four-months-old Japanese infants. *J. Child Lang.* 20, p. 303-312.
- Masataka, N. & Biben, M., 1987. Temporal rules regulating affiliative vocal exchanges of squirrel monkeys. *Behaviour* 101, p. 311-319.
- Masataka, N. & Fujita, K., 1989. Vocal learning of Japanese and rhesus monkeys. *Behaviour* 109, p. 191-199.
- Masataka, N., 1992. Pitch characteristics of Japanese maternal speech to infants. *J. Child Lang.* 19, p.213-223.

- Mitani, M., 1986. Voiceprint identification and its application to sociological studies of wild Japanese monkeys (*Macaca fuscata yakui*). *Primates* 27, p. 397-412.
- Myers, R. E., 1976. Comparative neurology of vocalization and speech: Proof of a dichotomy. In: "Origins and Evolution of Language and Speech", Harnad, S. R., Steklis H. D. & Lancaster J. eds., Annals of the New York Academy of Science 280: p.745-757.
- Newman, J. D. & Symmes D., 1982. Inheritance and experience in the acquisition of primate acoustic behavior. In: "Primate Communication," C. T. Snowdon, C. H. Brown & M. R. Petersen, eds., Cambridge University Press, Cambridge, p. 259-278.
- Owren, M. J., Dieter, J. A. Seyfarth, R. M. & Cheney D. L., 1992. 'Food' calls produced by adult female rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques, their normally-raised offspring, and offspring cross fostered between species. *Behaviour* 120: p. 218-231.
- Owren, M. J. & Casale, T. M., 1994. Variation in fundamental frequency peak position in Japanese macaque (*Macaca fuscata*) coo calls.
- Pereira, M. E., 1986. Maternal recognition of juvenile offspring coo vocalizations in Japanese macaques. *Anim. Behav.* 34, p. 935-937.
- Pierce, J. D., 1985. A review of attempts to condition operantly alloprimate vocalizations, *Primates* 26. p. 202-213.
- Seyfarth, R. M. & Cheney, D. L., 1986. Vocal development in vervet monkeys. *Anim. Behav.* 34, p. 1640-1658.
- Seyfarth, R. M., Cheney, D. L. & Marler, P., 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Anim. Behav.* 289, p.1070-1094.
- Seyfarth, R. M., 1987. Vocal communication and its relation to language. In "Primate Societies", Smuts B. B., Cheney D. L., Seyfarth R. M., Wrangham, R. W. & Struhsaker, T. T eds. The University of Chicago Press.
- Snowdon, C. T., Brown C. H. & Petersen, M. R., 1982. "Primate Communication" Cambridge University Press, Cambridge.

- Snowdon, C. T., Coe, C. L. & Hodun, A., 1985. Population recognition of infant isolation peeps in the squirrel monkey. *Anim. Behav.* 33, p. 1145-1151.
- Snowdon, T. C., 1990. Language capacity of nonhuman animals. *Yearbook Physical Anthropoid.* 33, p. 215-243.
- Sokal, R. R., Rohlf, F. J., 1981. Biometry, second edition. Freeman.
- Sugiura, H., 1993. Temporal and acoustic correlates in vocal exchange of coo calls in Japanese macaques. *Behaviour* 124: p.207-225.
- Sutton, D., Trachy, R. E. & Lindeman, R. C., 1981. Vocal and nonvocal discriminative performance in monkeys. *Brain and Lang.* 14: p. 93-105.
- Winter, P., Handley, P., Ploog & Schott, D., 1973. Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour* 47, p. 230-239.

9. FIGURES AND TABLES



Figure 1. The location of study sites.

Table 1. Structure of the two groups by age-sex class. Number of target animals chosen are shown in parentheses.

Yakushima				Ohirayama			
Class	Age	N	(Target)	Class	Age	N	(Target)
Adult ♀	≥6	5	(3)	Adult ♀	≥6	15	(4)
Juvenile ♀	3 - 5	2	(2)	Juvenile ♀	3 - 5	5	(4)
Immature ♀	0 - 2	1	(0)	Immature ♀	0 - 2	9	(0)
Adult ♂	≥6	6	(0)	Adult ♂	≥6	11	(0)
Juvenile ♂	3-5	3	(0)	Juvenile ♂	3-5	9	(0)
Immature ♂	0-2	1	(0)	Immature ♂	0-2	14-15	(0)
Total		18	(5)			63-64	(8)

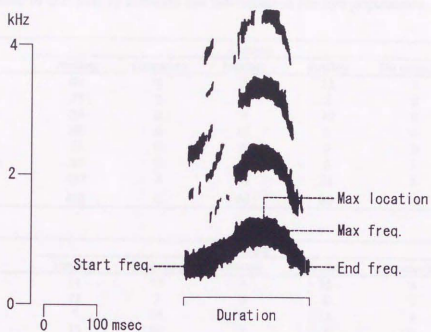


Figure 2. A representative sonagram of a Japanese macaque coo call, in which acoustic parameters measured for acoustic analyses are indicated.

Table 2. Number of coo calls by contexts and individuals in the two populations.

Yakushima

Caller	Context				Total
	Feeding	Grooming	Moving	No recording	
Hp	69	0	7	31	110
Ma	37	2	4	5	48
On	20	0	9	10	39
Ni	58	0	17	2	81
Ti	71	0	6	6	83
Other than target	30	0	5	5	40
Unidentified	117	4	36	21	186
Overall	402	6	84	15	587

Ohirayama

Caller	Context				Total
	Feeding	Grooming	Moving	No recording	
Bt	11	15	9	15	50
Nk	21	3	8	7	47
Tr	7	14	0	14	39
Bb	19	20	1	7	47
Bk	16	6	3	17	45
Nc	11	0	1	18	30
Tn	11	23	0	13	50
Ng	12	4	5	14	35
Other than target	28	15	6	14	63
Unidentified	57	81	1	72	219
Overall	193	181	34	192	625

Table 3. Results of two-way analyses of variance performed on the acoustic properties of coo calls.

Yakushima

Parameter	Context		Caller		Context x Caller	
	F	(df)	F	(df)	F	(df)
Duration	0.96	(2, 92)	4.22 **	(3, 92)	2.31 *	(5, 92)
Max location	1.85	(2, 92)	4.54 **	(3, 92)	3.49 **	(5, 92)
Min freq.	1.33	(2, 92)	29.08 ***	(3, 92)	2.08	(5, 92)
Start freq.	2.25	(2, 92)	69.63 ***	(3, 92)	5.11 ***	(5, 92)
Max freq.	2.63	(2, 92)	11.44 ***	(3, 92)	4.88 ***	(5, 92)
End freq.	1.87	(2, 92)	9.74 ***	(3, 92)	1.97	(5, 92)
Max-min freq.	2.13	(2, 92)	10.42 ***	(3, 92)	4.29 **	(5, 92)
Max-start freq.	2.25	(2, 92)	11.07 ***	(3, 92)	4.01 **	(5, 92)
Max-end freq.	0.89	(2, 92)	4.34 **	(3, 92)	2.34 *	(5, 92)

*, p<0.05, **, p<0.01, ***, p<0.001

Ohirayama

Parameter	Context		Caller		Context x Caller	
	F	(df)	F	(df)	F	(df)
Duration	0.78	(2, 117)	16.22 ***	(4, 117)	1.49	(8, 117)
Max location	0.03	(2, 117)	4.47 **	(4, 117)	0.83	(8, 117)
Min freq.	2.80	(2, 117)	43.09 ***	(4, 117)	2.13 *	(8, 117)
Start freq.	2.98	(2, 117)	45.22 ***	(4, 117)	2.47 *	(8, 117)
Max freq.	3.24 *	(2, 117)	7.28 ***	(4, 117)	2.01	(8, 117)
End freq.	2.06	(2, 112)	8.51 ***	(4, 112)	2.93 **	(8, 112)
Max-min freq.	2.71	(2, 117)	5.46 ***	(4, 117)	1.77	(8, 117)
Max-start freq.	2.59	(2, 117)	5.54 ***	(4, 117)	1.77	(8, 117)
Max-end freq.	2.06	(2, 112)	0.68	(4, 112)	0.73	(8, 112)

*, p<0.05, **, p<0.01, ***, p<0.001

Table 4. Median inter-call intervals in *DC* sequence grouped by the first caller.

1st caller	Yakushima			1st caller	Ohirayama		
	(Age)	Median (sec)	(N)		(Age)	Median (sec)	(N)
Hp	(>15)	0.416	(56)	Bt	(17)	0.428	(12)
Ma	(>15)	0.377	(18)	Nk	(15)	0.453	(13)
On	(6)	0.569	(13)	Tr	(9)	0.466	(7)
Ni	(5)	0.534	(26)	Bb	(8)	0.534	(16)
Ti	(3)	0.512	(39)	Bk	(5)	0.550	(18)
				Nc	(5)	0.242	(6)
				Tn	(4)	0.509	(11)
				Ng	(3)	0.512	(9)
Other than target		0.661	(18)	Other than target		0.186	(11)
Unidentified		0.431	(74)	Unidentified		0.500	(37)
Overall		0.478	(244)	Overall		0.514	(140)

Table 5. Median inter-call intervals in *DC* sequence grouped by the second caller.

2nd caller	Yakushima			2nd caller	Ohirayama		
	(Age)	Median (sec)	(N)		(Age)	Median (sec)	(N)
Hp	(>15)	0.488	(54)	Bt	(17)	0.556	(12)
Ma	(>15)	0.947	(17)	Nk	(15)	0.516	(13)
On	(6)	0.678	(11)	Tr	(9)	0.397	(9)
Ni	(5)	0.494	(32)	Bb	(8)	0.539	(12)
Ti	(3)	0.373	(40)	Bk	(5)	0.312	(13)
				Nc	(5)	0.456	(5)
				Tn	(4)	0.594	(11)
				Ng	(3)	0.402	(10)
Other than target		0.569	(19)	Other than target		0.847	(10)
Unidentified		0.387	(71)	Unidentified		0.500	(45)
Overall		0.478	(244)	Overall		0.514	(140)

Table 6. Median inter-call intervals in *SC* sequence by the caller.

Caller	Yakushima			Caller	Ohirayama		
	(Age)	Median (sec)	(N)		(Age)	Median (sec)	(N)
Hp	(>15)	9.250	(27)	Bt	(17)	0.812	(7)
Ma	(>15)	1.204	(30)	Nk	(15)	1.420	(6)
On	(6)	12.000	(26)	Tr	(9)	1.107	(6)
Ni	(5)	1.825	(21)	Bb	(8)	1.278	(7)
Ti	(3)	2.252	(20)	Bk	(5)	1.539	(14)
				Nc	(5)	1.086	(6)
				Tn	(4)	0.688	(6)
				Ng	(3)	1.023	(10)
Other than target		1.603	(13)	Other than target		1.181	(7)
Unidentified		1.462	(4)	Unidentified		0.809	(5)
Overall		1.744	(141)	Overall		1.139	(74)

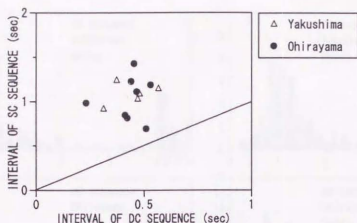


Figure 3. Distribution of 13 target animals with regard to median intervals in *DC* sequence between 0-4 sec, grouped according to the first caller (target individuals — group members), and median intervals in *SC* sequence between 0-4 sec. If an animal were plotted on the line, it would mean that mean intervals in *DC* sequence and that in *SC* sequence were the same for the animal.

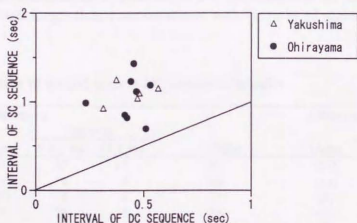


Figure 4. Distribution of 13 target animals with regard to median intervals in *DC* sequence between 0-4 sec, grouped according to the second caller (group members — target individuals) and median intervals in *SC* sequence between 0-4 sec. If an animal were plotted on the line, it would mean that mean intervals in *DC* sequence and that in *SC* sequence were the same for the animal.

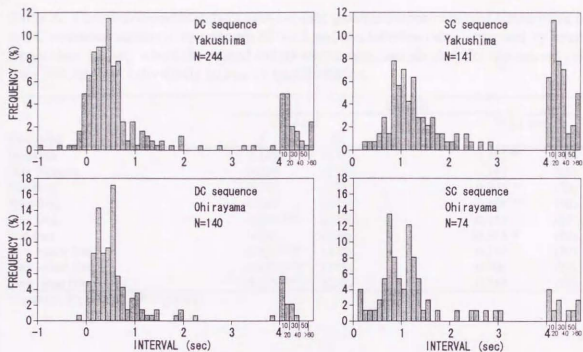


Figure 5. Overall distributions of intervals in *DC* sequence and *SC* sequence in the two populations. Intervals longer than 4 sec are shown with the reduced scales in Y axis.

Table 7. Distribution of second coos in *DC* sequence by caller.

Yakushima				Ohirayama			
Caller	(Age)	Interval		Caller	(Age)	Interval	
		0-1.1 sec	>1.1 sec			0-1.1 sec	>1.1 sec
Hp	(>15)	37	13	Bt	(17)	9	3
Ma	(>15)	9	8	Nk	(15)	12	1
On	(6)	6	4	Tr	(9)	9	0
Ni	(5)	26	5	Bb	(8)	10	2
Ti	(3)	26	10	Bk	(5)	10	3
				Nc	(5)	5	0
				Tn	(4)	9	2
				Ng	(3)	9	1
Other than target		11	7	Other than target		7	3
Unidentified		46	16	Unidentified		33	11
Overall		161	63	Overall		113	26

Table 8. Correlation coefficients of nine acoustic parameters between two consecutive coos in DC sequence separated by intervals of 0-1.1 sec and between those separated by intervals longer than 1.1 sec, where the second callers were target animals; data for the second callers were standardized individually by z score transformation.

Parameter	Interval			
	0-1.1 sec		>1.1 sec	
	r	df	r	df
Duration	0.149 *	(175)	0.343 *	(50)
Max location	0.018	(175)	0.101	(50)
Min freq.	-0.088	(175)	-0.301 *	(50)
Start freq.	-0.047	(175)	-0.358 **	(50)
Max freq.	0.250 ***	(175)	-0.013	(50)
End freq.	0.101	(170)	-0.343 *	(50)
Max—min freq.	0.317 ***	(175)	0.210	(50)
Max—start freq.	0.327 ***	(175)	0.206	(50)
Max—end freq.	0.247 **	(170)	0.252	(50)

*, $p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$

Table 9. Correlation coefficients of nine acoustic parameters between two consecutive coos in DC sequence separated by intervals of 0-1.1 sec and between those separated by intervals longer than 1.1 sec, where the second callers were adult target animals (≥ 6 yrs) or juvenile target animals (3-5 years); data for the second callers were standardized individually by z score transformation

Parameter	Age							
	≥ 6 yrs				3-5 yrs			
	Interval		Interval		Interval		Interval	
	0-1.1 sec		>1.1 sec		0-1.1 sec		>1.1 sec	
	r	df	r	df	r	df	r	df
Duration	0.028	(90)	-0.204	(29)	0.291 **	(83)	0.420	(19)
Max location	0.145	(90)	0.187	(29)	-0.154	(83)	0.303	(19)
Min freq.	-0.163	(90)	0.171	(29)	-0.007	(83)	-0.389	(19)
Start freq.	-0.124	(90)	0.217	(29)	0.072	(83)	-0.400	(19)
Max freq.	0.375 ***	(90)	-0.117	(29)	0.126	(83)	-0.049	(19)
End freq.	0.161	(87)	0.096	(29)	0.063	(81)	-0.427	(19)
Max—min freq.	0.427 ***	(90)	-0.012	(29)	0.194	(83)	0.286	(19)
Max—start freq.	0.458 ***	(90)	-0.160	(29)	0.178	(83)	0.328	(19)
Max—end freq.	0.389 ***	(87)	-0.449 *	(29)	0.109	(81)	0.388	(19)

*, $p < 0.05$, **, $p < 0.01$, ***, $p < 0.001$

Table 10. Acoustic parameters of 14 stimuli used in the playback experimental at the group level.

Parameter	Mean	SD
Duration (ms)	200.2	51.3
Max location (%)	69.5	26.1
Min freq. (Hz)	470	66.0
Start freq. (Hz)	480	64.0
Max freq. (Hz)	840	430.0
End freq. (Hz)	740	390.0
Max—min freq. (Hz)	370	430.0
Max—start freq. (Hz)	360	430.0
Max—end freq. (Hz)	100	120.0

Table 11. The numbers of successful trials and total number of trials (in parentheses) with 14 different stimuli in the playback experiment with a group.

Stimulus	Interval between stimulus presentation and response		(Total number of trials)
	0-1.1 sec	1.1-4 sec	
1	0	1	(16)
2	2	1	(17)
3	3	4	(33)
4	2	1	(10)
5	3	2	(27)
6	2	0	(24)
7	3	3	(30)
8	1	0	(11)
9	2	1	(42)
10	2	2	(14)
11	2	2	(28)
12	7	1	(24)
13	4	0	(34)
14	2	4	(19)
Total	35	22	(329)

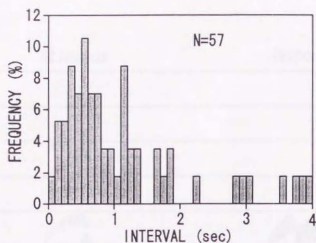


Figure 6. Overall distribution of intervals in the playback experiment with a group.

Table 12. Correlation coefficients of nine acoustic parameters between stimuli and following coos in the playback experiment at the group level.

Parameter	Interval between stimulus presentation and response	
	0-1.1 sec <i>r</i> (df=28)	1.1-4 sec <i>r</i> (df=25)
Duration	0.247	0.083
Max location	-0.061	-0.268
Min freq.	-0.204	-0.033
Start freq.	-0.225	0.051
Max freq.	0.154	0.100
End freq.	0.210	0.043
Max-min freq.	0.491 **	0.156
Max-start freq.	0.542 ***	-0.043
Max-end freq.	-0.195	-0.196

: $p < 0.01$, *: $p < 0.001$

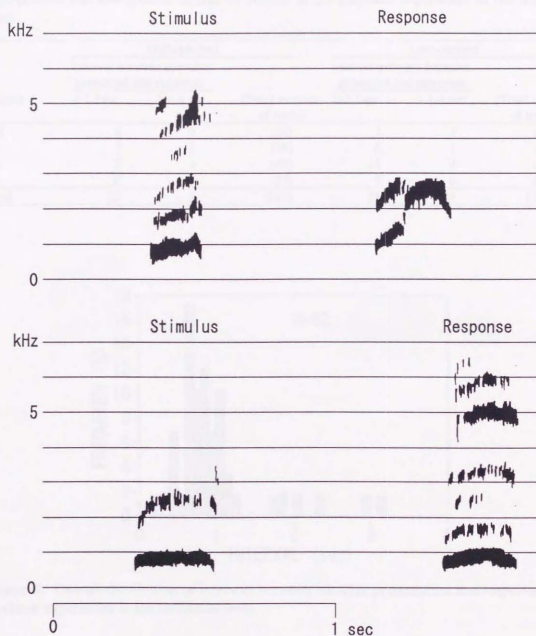


Figure 7. Representative sonograms of playback stimuli (upper: a high-pitched stimulus, lower: a low-pitched stimulus) and responding coos.

Table 13. The numbers of successful trials and total number of trials (in parentheses) with high-pitched and low-pitched stimuli by subject in the playback experiment at the individual level.

Subject	High-pitched			Low-pitched		
	Interval between stimulus presented and response		(Total number of trials)	Interval between stimulus presented and response		(Total number of trials)
	0-1.1sec	1.1-4 sec		0-1.1sec	1.1-4 sec	
Aoi	6	0	(26)	3	1	(23)
Tg	7	1	(18)	6	1	(18)
Ak	3	3	(48)	11	2	(51)
Nr	6	1	(55)	5	6	(66)
Total	22	5	(147)	25	10	(158)

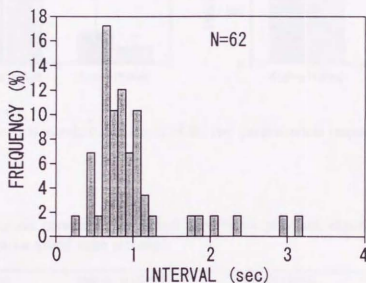


Figure 8. Overall distribution of intervals between stimulus presentation and response in the playback experiment at the individual level.

Table 14. Results of two-way analyses of variance performed on the acoustic properties of responding coos in the playback experiment at the individual level.

Parameter	Stimulus F (1, 39)	Subject individual F (3, 39)	Stimulus \times Subject individual F (3, 31)
Max—min freq.	6.59 *	2.20	1.76
Max—start freq.	6.95 *	2.10	1.83

*: $p < 0.05$

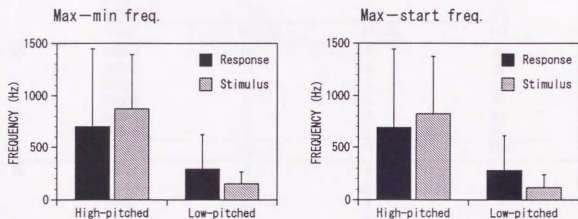


Figure 9. Means and standard deviations of the two parameters in response coos and stimuli.

Table 15. Acoustic parameters of stimuli used in the playback experiment by individuals from which stimulus sound were recorded.

Stimulus	Mdr-1~6 (N=6)		Ml-1~6 (N=6)		Tk-1~7 (N=7)	
Parameter	Mean	(Range)	Mean	(Range)	Mean	(Range)
Duration (ms)	332	(173 - 538)	308	(159 - 575)	294	(177 - 394)
Max location (%)	73.9	(57.4 - 91.0)	44.7	(0 - 69.1)	57.3	(35.4 - 84.9)
Min freq. (Hz)	410	(360 - 440)	413	(360 - 480)	497	(440 - 560)
Start freq. (Hz)	420	(400 - 440)	447	(400 - 480)	509	(480 - 560)
Max freq. (Hz)	727	(400 - 1340)	890	(400 - 1420)	894	(500 - 1380)
End freq. (Hz)	443	(360 - 480)	447	(360 - 640)	537	(440 - 640)
Max-min freq. (Hz)	317	(40 - 940)	477	(0 - 940)	397	(60 - 860)
Max-start freq. (Hz)	307	(0 - 940)	443	(0 - 940)	386	(20 - 860)
Max-end freq. (Hz)	283	(40 - 860)	443	(0 - 880)	357	(40 - 820)

Table 16. The numbers of entire trials and successful trials by subject and stimulus.

Subject	Stimulus	Interval between stimulus and response		Total number of trials
		0-1.1 sec	1.1-4 sec	
Mdr	MI-1	10	3	78
	MI-2	11	4	43
	MI-3	9	5	47
	MI-4	7	2	92
	MI-5	6	4	91
	MI-6*	2*	2*	63
	Total	45 (43)	20 (18)	414
MI	Mdr-1	10	4	63
	Mdr-2	10	8	68
	Mdr-3	8	3	36
	Mdr-4	9	9	55
	Mdr-5	6	7	61
	Mdr-6	7	3	56
	Total	50	34	339
Tk	MI-1	6	7	61
	MI-2	9	6	59
	MI-3	12	8	55
	MI-4	7	6	65
	MI-5	7	2	63
	MI-6	9	3	55
	Total	50	32	358
Yn	Tk-1	12	2	32
	Tk-2	10	2	27
	Tk-3	14	1	34
	Tk-4	10	2	34
	Tk-5	7	2	73
	Tk-6	9	3	35
	Tk-7*	4*	0*	20
	Total	66 (62)	12	255
Overall		211 (205)	98 (96)	1366

*: Trials with an asterisk were eliminated from the following analyses. Total numbers without these trials are presented in parentheses

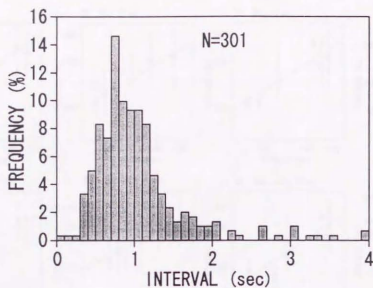


Figure 10. Overall distribution of intervals between stimulus presentation and response in the playback experiment with individuals.

Table 17. Results of linear regression analyses of acoustic parameters of stimuli on that of response.

Subject	Mdr	Ml	Tk	Yn
Parameter	F(1,3)	F(1,4)	F(1,4)	F(1,4)
Duration	3.66	36.73 **	1.19	0.15
Max location	2.20	1.33	0.01	0.45
Min freq.	0.00	0.77	0.05	2.28
Start freq.	33.19 *	0.01	0.95	0.63
Max freq.	28.38 *	42.49 **	13.60 *	7.42
End freq.	0.06	5.38	0.45	3.26
Max-min freq.	20.06 *	25.87 **	11.44 *	10.84 *
Max-start freq.	27.04 *	33.22 **	25.88 **	24.56 **
Max-end freq.	22.31 *	7.02	8.83 *	1.09

*: $p < 0.05$, **: $p < 0.01$

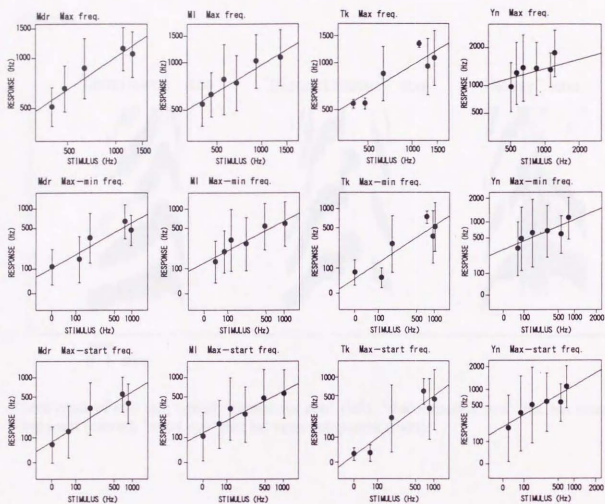
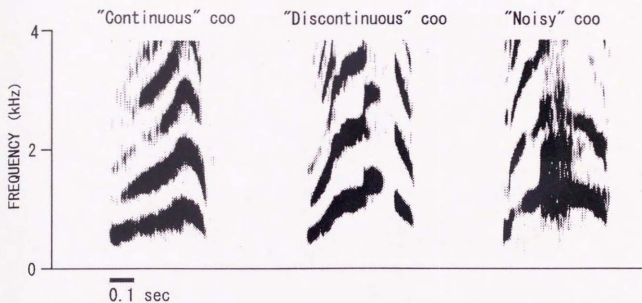


Figure 11. Regressions of acoustic parameters of response coos on those of stimuli by subject animals.

Appendix



Three types of coo call; typical "continuous coo" (left), "discontinuous coo" that has silent component (center), "noisy coo" that has noisy component (right).

