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## Individual vocal differences of the coo call in Japanese monkeys

Miyuki Ceugniet <sup>\*,1</sup>, Akihiro Izumi <sup>2</sup>

Primate Research Institute, Kyoto University, Inuyama, Japan

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### Abstract

We investigated individual vocal characteristics of the coo call in Japanese monkeys. The goal of the study was to determine which parameters are individual discriminators (for individuals of different ages and sexes) and to test whether those differences were similar for individuals of same age and sex. A discriminant analysis realized on eight individuals pointed out that three parameters (call duration, start and end frequencies of the fundamental component) differentiated individuals efficiently and was validated by a second discriminant analysis realized on three same-age females. **To cite this article:** M. Ceugniet, A. Izumi, *C. R. Biologies* 327 (2004).

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### Résumé

**Différences vocales individuelles du cri de recherche de contact chez les macaques japonais.** Nous avons étudié les caractéristiques vocales individuelles du cri de recherche de contact chez les macaques japonais. Le but était de déterminer quels paramètres étaient les discriminateurs individuels (pour des individus d'âges et de sexes différents) et de tester si ces différences étaient similaires pour des individus de mêmes âge et sexe. Une analyse discriminante englobant les huit individus a fait ressortir que trois paramètres (durée du cri, fréquences de début et de fin du cri de la fondamentale) différenciaient les individus efficacement, et a été validée par une seconde analyse discriminante réalisée sur trois femelles du même âge. **Pour citer cet article :** M. Ceugniet, A. Izumi, *C. R. Biologies* 327 (2004).

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**Mots-clés :** cri de recherche de contact ; différences vocales individuelles ; *Macaca fuscata* ; singes

### Version française abrégée

La structure sociale des macaques, qui repose sur une hiérarchie de dominance chez les mâles mais aussi chez les femelles, implique une reconnaissance individuelle. Afin de reconnaître un congénère, un singe peut utiliser plusieurs indices : visuels, acoustiques et olfactifs. Étant donné que les interactions sociales entre individus peuvent s'effectuer très rapidement et

\* Corresponding author.

E-mail addresses: [miyuki\\_ceugniet@yahoo.fr](mailto:miyuki_ceugniet@yahoo.fr) (M. Ceugniet), [izumi@pri.kyoto-u.ac.jp](mailto:izumi@pri.kyoto-u.ac.jp) (A. Izumi).

<sup>1</sup> Present address: 14, rue Jean-Baptiste Clément, 77330 Ozoir-la-Ferrière, France.

<sup>2</sup> Present address: Department of Behavioral and Brain Sciences, Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan.

que les individus bougent souvent simultanément dans une végétation susceptible de constituer des obstacles visuels, l'acoustique constitue un moyen de communication rapide non interrompu par la végétation. De plus, les échanges acoustiques présentent l'avantage de pouvoir s'effectuer à de grandes distances.

La reconnaissance vocale individuelle nécessite des différences dans les caractéristiques acoustiques individuelles. De nombreux auteurs ont analysé les caractéristiques vocales d'espèces chez les Primates et ont montré qu'il existait des différences individuelles chez le ouistiti pygmée *Cebuella pygmaea*, le maki catta *Le-mur catta*, le saïmiri jaune *Saimiri sciureus*, le tamarin pinché *Saguinus oedipus*, le singe vert *Cercopithecus aethiops*, le singe magot *Macaca sylvanus* et chez le chimpanzé sauvage *Pan troglodytes*.

La présente étude concerne les différences vocales individuelles du cri de recherche de contact chez le macaque japonais *Macaca fuscata*. Le but de l'étude est de déterminer quels paramètres acoustiques différencient les individus. De plus, nous avons voulu tester si les différences individuelles pour un groupe d'individus d'âges et de sexes différents étaient similaires pour un groupe d'individus de même âge et de même sexe. Une telle comparaison n'a pas encore été étudiée dans la mesure où les études précédentes concernaient généralement un groupe d'individus d'âges et de sexes différents. Le cri de recherche de contact est utilisé comme tentative de contact dans des contextes sociaux variés (maternel, sexuel, agonistique, d'épouillage, de mouvements de troupes et de fourragement). Il présente une structure harmonique avec l'énergie focalisée principalement sur les basses harmoniques.

Les enregistrements ont été effectués sur des macaques japonais du Primate Research Institute de l'université de Kyoto. Les huit individus comprennent deux mâles et six femelles âgés de 2 à 15 ans. Les cris ont été analysés au niveau temporel (durée du cri, durée comprise entre le début du cri et la fréquence maximale de la fondamentale, ci-après désignée par « position de *F*-max ») et fréquentiel (fréquences de début et de fin du cri, bande de fréquences de la fondamentale). Une première analyse discriminante a été réalisée sur les huit individus. Cette analyse a été réalisée sur 60% des cris de chaque individu, afin que l'on puisse vérifier les fonctions de classification avec les 40% de cris restants (qui n'ont pas été utilisés pour élaborer ces fonctions). L'analyse significative a mon-

tré plusieurs paramètres discriminant les individus. La durée du cri était le paramètre discriminant le plus efficace. Les fréquences de début et de fin du cri de la fondamentale intervenaient également dans la séparation individuelle des cris. En revanche, la bande de fréquences de la fondamentale ainsi que la position de *F*-max ne différaient pas suffisamment entre individus et n'ont pas été incluses dans le modèle. Les fonctions de classification de l'analyse discriminante ont permis une classification individuelle correcte des cris de 89,23%. Ces fonctions appliquées aux 40% de cris restants (validation croisée) ont permis d'obtenir une classification correcte des cris s'élevant à 83,72%. Le pourcentage de classification correcte de la validation croisée était élevé et similaire à celui de l'analyse des 60% de cris. Les cris étaient attribués de manière correcte à leurs émetteurs à un taux supérieur à celui du hasard (12,5%). Ceci indique que le modèle est fiable et que les trois paramètres sont des marqueurs individuels efficaces.

Une seconde analyse discriminante a été réalisée sur trois individus de même âge et de même sexe : des femelles de deux ans. De même que pour la première analyse, cette analyse a porté sur 60% des cris des individus afin que l'on puisse vérifier la fiabilité du modèle avec les 40% de cris restants. L'analyse significative a identifié trois paramètres discriminant les cris des individus. Ces paramètres étaient la durée du cri et les fréquences de début et de fin du cri de la fondamentale, paramètres identiques à ceux qui discriminaient les cris des individus dans l'analyse englobant les huit individus. Cependant, l'importance relative de ces trois paramètres dans la séparation individuelle des cris était différente de celle de la première analyse. En effet, c'est la fréquence de début de cri qui était le meilleur paramètre discriminant dans cette analyse des trois femelles de même âge. La fréquence de fin du cri ainsi que la durée du cri intervenaient également dans la séparation individuelle des cris, mais avec une importance moindre. La bande de fréquences de la fondamentale ainsi que la position de *F*-max n'ont pas été suffisamment différentes entre individus pour être incluses dans le modèle. Les fonctions de classification ont permis une classification individuelle correcte des cris de 94,74%, confirmée par la validation croisée (92,31%). Les cris étaient attribués de manière correcte à leurs émetteurs à un taux supérieur à celui du hasard (33,33%), indiquant la fiabilité du modèle et

l'efficacité des trois paramètres comme marqueurs individuels.

L'analyse discriminante englobant tous les individus a montré un taux important de classification correcte des cris. Les macaques émettent donc des cris qui présentent des caractéristiques différentes et sont différenciables. D'autres études, utilisant également l'analyse discriminante, ont montré que les individus étaient différenciables par leurs caractéristiques vocales chez le saïmiri jaune, le tamarin pinché, le maki catta et le singe araignée. Notre analyse a également montré que trois paramètres vocaux permettaient une séparation individuelle significative des cris. Ces paramètres sont la durée du cri et les fréquences de début et de fin du cri de la fondamentale. Ces paramètres ont déjà été mis en évidence en tant que marqueurs individuels chez d'autres espèces, telles que le singe araignée, le tamarin pinché et le singe rhésus.

L'analyse concernant les trois femelles de deux ans a également montré que les cris présentaient suffisamment de différences dans leurs caractéristiques pour être différenciables individuellement. De plus, les marqueurs individuels correspondaient aux mêmes trois paramètres que précédemment (durée du cri, fréquences de début et de fin du cri de la fondamentale). L'importance relative de ces trois paramètres différait entre l'étude englobant tous les individus et l'étude concernant les trois femelles de deux ans. Cependant, il a été montré que les mêmes trois paramètres semblent être de bons marqueurs vocaux individuels.

Par la présente étude, nous avons démontré que les macaques japonais émettaient des cris présentant des caractéristiques différentes et que ces cris étaient donc différenciables individuellement. Nous avons également montré l'importance de certains paramètres (durée du cri, fréquences de début et de fin du cri de la fondamentale) dans cette différence individuelle. En nature, ces caractéristiques vocales individuelles peuvent constituer un bon moyen de reconnaître un congénère lorsque l'on sait que les macaques évitent de regarder le visage des autres individus et que le milieu naturel peut être encombré de nombreux obstacles visuels, tels que la végétation. Cependant, des expériences de diffusion de signaux naturels et synthétiques sont nécessaires avant que l'on puisse affirmer que les macaques sont capables d'utiliser ces différences acoustiques pour la reconnaissance individuelle et spécifier quels en sont les paramètres effectivement utilisés.

## 1. Introduction

The existence of complex social behaviors implies that monkeys are able to recognize individually other monkeys. Imanishi [1] described the social organization of Japanese monkeys. The social structure is based on a dominance hierarchy that exists not only within males, but also within females. Dominance rank may be related to age order of individuals but not always, and it is generally linear. The access to food of a monkey is highly dependent on his rank in the group. Therefore, individuals involved in those dynamic phenomena have to recognize each individual to adapt their behavior.

In order to recognize individually each monkey, individuals may use visual, acoustic and/or olfactory cues. The acoustic means of recognizing individuals have some advantages compared to the two other informative cues. Indeed, since some social interactions (such as quarrels between individuals) develop very rapidly, with many individuals moving simultaneously among trees, which may constitute obstacles to see each others, the acoustic cues present a rapid mean of communication, which is not interrupted by visual clutters, such as vegetation. Moreover, vocal sounds can be used at great distances between individuals, contrary to olfactory signals.

The individual vocal recognition requires acoustical individual differences. Several studies have demonstrated different voice characteristics among individuals in various classes of vertebrates such as amphibians (green frogs [2]), birds (emperor penguins [3], sandwich terns [4]) and mammals (timber wolves [5]). Many authors analyzed the acoustic characteristics of calls in primates and some studies demonstrated also individual differences. This was the case for contact calls (the closed mouth trill and the J-call) of pygmy marmosets *Cebuella pygmaea* [6], for cohesion calls emitted by ringtailed lemurs *Lemur catta* [7], for isolation peeps of squirrel monkeys *Saimiri sciureus* [8], for quiet and normal long calls emitted by cotton-top tamarins *Saguinus oedipus* [9], for two types of calls of vervet monkeys *Cercopithecus aethiops* [10], for vocalizations (cry sequences and dusk calling) of young Barbary macaques *Macaca sylvanus* [11], and for the pant-hooting vocalization emitted by wild chimpanzees [12].

The present study focused on the existence of vocal differences between Japanese monkey individuals concerning the coo call. The goal of the study was to point out which vocal parameters are the individual discriminators. Moreover, we intended to test whether individual vocal differences for individuals presenting different sex and ages are similar to those for individuals of the same sex and of a single class age. Such a comparison has not been realized yet, since other studies usually focused on groups including the two sexes and many age individuals. The coo call is used as contact attempts in various social contexts (maternal, sexual, agonistic, grooming, troop movements and foraging) [13]. Green described coos as calls presenting a harmonic structure, with the lower harmonics being emphasized. In the present study, call characteristics were determined precisely in temporal and frequency domains for eight individual monkeys. Then, a discriminant analysis on all individuals was performed in order to identify the acoustic parameters that differ among individuals. Another discriminant analysis was performed on the three individuals of the same sex and age class. We chose the two-year-old females, since we disposed of three individuals for that sex and age class, contrary to other sex and age classes. Results of the second analysis were compared to those of the first analysis.

## 2. Material and methods

### 2.1. Call recordings

Recordings were performed in spring and summer 2001 on eight monkeys at the Primate Research Institute, Kyoto University. Monkeys comprised two males and six females, aged from 2 to 15 years old. They are housed in groups of two to five in cages. Recordings were performed at the end of the morning before food distribution since monkeys vocalize often when expecting food. A total of 108 coo calls were recorded from eight individuals. Calls were digitally recorded at a sampling rate of 48 kHz using a microphone (Sony, ECM-672) connected to a digital audio tape recorder (DAT Sony, TCD-D100). Signals were captured through a Yamaha DS-2416 acquisition card connected to a computer.

### 2.2. Acoustic measurements

Signals were examined through the Syntana signal processing software [14]. The analysis took into account various temporal and frequency parameters (Fig. 1). In the temporal domain, we measured the call duration and the position of the maximum frequency ( $F$ -max) of the fundamental component in the call (i.e., the time from the beginning of the call to  $F$ -max, expressed as a percentage of call duration). In the frequency domain, we determined the start frequency, the end frequency and the frequency band (i.e., the width between the minimum frequency and the maximum frequency) of the fundamental component.

### 2.3. Statistical analysis

Various call parameters that have been studied were included in a discriminant analysis. This analysis in-

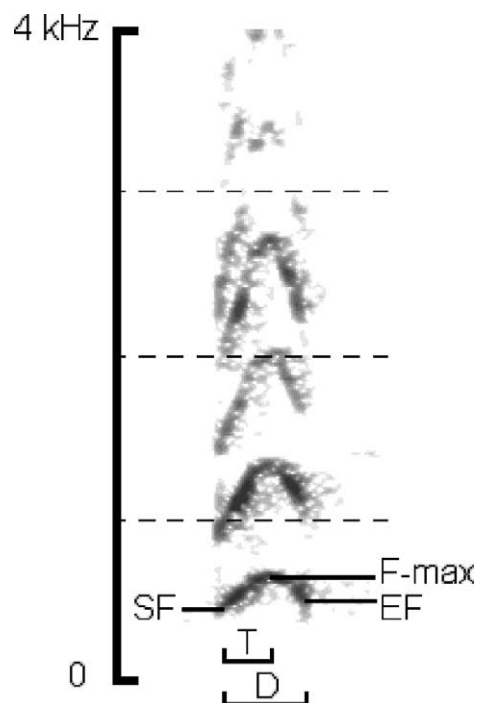


Fig. 1. Sonogram of a coo call emitted by a Japanese monkey. For the analysis, we measured the call duration ( $D$ ), the position of the maximum frequency ( $F$ -max) in the call ( $T$ , in percentage of call duration), the start frequency ( $SF$ ), the end frequency ( $EF$ ) and the frequency band of the fundamental component, which is the difference between  $F$ -max and the lowest frequency (which corresponds to the  $SF$  or to the  $EF$  depending on the call).

cluded many variables in order to identify those that discriminated between several groups, in our case between different individuals. We used a backward step-wise analysis. It means that at first, the program included all variables in the model and then, at each step, eliminated the variable that contributed least to the prediction of individual membership. In discriminant analysis,  $F$  ratios were calculated for each variable. These ratios indicated the contribution of different variables to the prediction of individual membership. We required an  $F$  ratio of 4.0 or greater for a variable to be retained in the analysis once entered ( $F$  to remove). This requirement excluded variables that were less efficient discriminators. The analysis created several discriminating functions using some optimal combinations of variables. Canonical correlation was performed in order to transform the discriminating functions into classification functions that are used to classify the cases. The classification matrix showed the number of cases that were correctly classified and that of cases that were misclassified. However, the classification matrix included calls that were used to derive the classification functions. Therefore, in order to verify the accuracy of the classification functions, we performed a cross-validation. We divided the call samples into two groups: 60% of calls (chosen randomly) of each individual were used to perform the discriminant analysis and to build the classification functions, whereas the remaining 40% of calls of

each individual were used to test the validity of the model.

Such discriminant analysis was performed for the total of eight individuals, on one side, and for the three two-year-old females, on the other side.

Correlations between parameters and age of individuals were evaluated using Spearman correlation coefficients. For those correlations, we used the mean values of each parameter for each individual.

Statistical analyses were performed using STATISTICA software (version 5.1).

### 3. Results

Means and standard deviations of all acoustic parameters studied as well as sex and age of the eight monkeys are presented in Table 1.

Discriminant analysis results including all monkeys are presented in Table 2. The discriminant analysis is significant ( $F(7, 57) = 37.91$ ,  $p < 0.001$ ) and identifies several parameters by which calls of different individuals can be discriminated. The  $F$  ratios show the discriminating power of each variable. These ratios show that call duration is the most efficient discriminator of individuals. Start and end frequencies of the fundamental also play a role in separating calls of individuals. Frequency band of the fundamental and position of  $F$ -max were not sufficiently different among

Table 1

Means  $\pm$ SD of various temporal (call duration and position of the maximum frequency in the call) and frequency (start and end frequencies and frequency band of the fundamental component) parameters of calls, sex and age for the eight recorded monkeys

Monkeys	Sex	Age	$n$	Call duration (ms)	Position of $F$ -max (%)	Start frequency (Hz)	End frequency (Hz)	Frequency band (Hz)
A	F	15	15	345.47	47.34	472.87	451.53	166.73
				$\pm 56.85$	$\pm 10.00$	$\pm 28.81$	$\pm 88.14$	$\pm 26.18$
B	F	7	15	800.27	44.58	448.80	465.80	78.00
				$\pm 93.37$	$\pm 16.24$	$\pm 32.75$	$\pm 44.59$	$\pm 25.35$
C	M	11	13	609.53	34.27	363.15	358.85	78.54
				$\pm 112.75$	$\pm 5.67$	$\pm 25.60$	$\pm 36.73$	$\pm 32.76$
D	F	2	15	644.40	68.47	706.47	847.53	194.47
				$\pm 89.87$	$\pm 6.53$	$\pm 44.83$	$\pm 78.62$	$\pm 89.69$
E	F	4	15	547.13	54.69	577.87	546.87	121.93
				$\pm 79.77$	$\pm 11.22$	$\pm 39.98$	$\pm 28.35$	$\pm 32.86$
F	M	3	18	552.06	49.59	805.72	814.22	194.28
				$\pm 52.84$	$\pm 13.61$	$\pm 96.00$	$\pm 107.06$	$\pm 129.42$
G	F	2	9	338.33	65.29	523.78	593.67	89.00
				$\pm 72.78$	$\pm 10.80$	$\pm 32.09$	$\pm 30.83$	$\pm 26.00$
H	F	2	8	310.25	45.19	611.75	603.50	60.13
				$\pm 64.27$	$\pm 14.18$	$\pm 26.42$	$\pm 32.19$	$\pm 27.06$

Table 2

Discriminant analysis including all monkeys (top) and classification results (bottom) of 60% of calls of each of the eight individuals. The *F* ratios (top) show the discriminating power of each variable. The classification matrix (bottom) shows the number of cases that were correctly classified and that of cases that were misclassified

Variables in analysis		<i>F</i> ratios of discriminating variables									<i>F</i> to remove
Call duration											29.97
Start frequency of the fundamental											14.81
End frequency of the fundamental											14.46
Individuals		Classification matrix									Percent correct
<i>n</i>	Predicted classifications										
	A	B	C	D	E	F	G	H			
A	9	8	0	0	0	0	0	1	0	88.89	
B	9	0	9	0	0	0	0	0	0	100.00	
C	8	1	0	7	0	0	0	0	0	87.50	
D	9	0	0	0	7	0	2	0	0	77.78	
E	9	1	0	0	0	7	0	0	1	77.78	
F	11	0	0	0	0	1	10	0	0	90.91	
G	5	0	0	0	0	0	0	5	0	100.00	
H	5	0	0	0	0	0	0	0	5	100.00	
Total	65	10	9	7	7	8	12	6	6	89.23	

Table 3

Classification results for cross-validation using the remaining 40% of calls (not used to build the classification functions) of the eight individuals. The cross-validation aims at verifying the validity of the model

Individuals		Classification matrix for the cross-validation									Percent correct
<i>n</i>	Predicted classifications										
	A	B	C	D	E	F	G	H			
A	6	3	0	0	0	0	0	3	0	50.00	
B	6	0	6	0	0	0	0	0	0	100.00	
C	5	0	0	5	0	0	0	0	0	100.00	
D	6	0	0	0	4	0	2	0	0	66.67	
E	6	0	0	0	0	5	0	0	1	83.33	
F	7	0	0	0	1	0	6	0	0	85.71	
G	4	0	0	0	0	0	0	4	0	100.00	
H	3	0	0	0	0	0	0	0	3	100.00	
Total	43	3	6	5	5	5	8	7	4	83.72	

individuals to be included in the model. The discriminant analysis created functions discriminating individual calls. Three classification functions derived from the discriminating functions permitted correct identification of the caller for 58 calls out of 65. The accuracy of reclassification was 89.23%. The cross-validation results are shown in Table 3. The mean classification accuracy for the remaining 40% of calls not used to build the classification functions was 83.72%, ranging from 50 to 100%, depending on the individ-

ual. The accuracy of call classification in the cross-validation was high and similar to that in the discriminant analysis. Calls were correctly attributed to their emitter at a rate higher than the chance level of 12.5%. This indicated that the model was reliable and that the acoustic parameters studied were effective individual markers.

Discriminant analysis results for the two-year-old females are presented in Table 4. The discriminant analysis is significant ( $F(2, 16) = 21.82, p < 0.001$ )

Table 4

Discriminant analysis of various acoustic parameters (top) and classification results (bottom) of 60% of calls of each of the three two-year-old females. The  $F$  ratios (top) show the discriminating power of each variable. The classification matrix (bottom) shows the number of cases that were correctly classified and that of cases that were misclassified

$F$ ratios of discriminating variables	
Variables in analysis	$F$ to remove
Start frequency of the fundamental	9.44
End frequency of the fundamental	6.17
Call duration	4.60

Classification matrix					
Individuals	$n$	Predicted classification			Percent correct
		D	G	H	
D	9	9	0	0	100.00
G	5	0	4	1	80.00
H	5	0	0	5	100.00
Total	19	9	4	6	94.74

and identifies several parameters by which calls of different individuals can be discriminated. The  $F$  ratios show that in that case start frequency is the most efficient discriminator of individuals. End frequency of the fundamental and call duration also play a role in separating calls of individuals. Frequency band of the fundamental and position of  $F$ -max were again not included in the model. Three classification functions permitted correct identification of the caller for 18 calls out of 19. The accuracy of reclassification was 94.74%. The cross-validation results are shown in Table 5. The mean classification accuracy for the remaining 40% of calls not used to build the classification functions was 92.31%, ranging from 75 to 100%, depending on the individual. The accuracy of call classification in the cross-validation was high and similar to that in the discriminant analysis. Calls were correctly attributed to their emitter at a rate higher than the chance level of 33.33%. This indicated that the model was reliable and that the acoustic parameters studied were effective individual markers.

Correlations between parameters and monkey's age were evaluated. Results are as follows:  $r_S = 0.29$ ,  $p = ns$  for call duration,  $r_S = -0.61$ ,  $p = ns$  for position of  $F$ -max,  $r_S = -0.68$ ,  $p = ns$  for start frequency,  $r_S = -0.85$ ,  $p < 0.01$  for end frequency,  $r_S = -0.05$ ,  $p = ns$  for frequency band of the fundamental component. Only end frequency was correlated signifi-

Table 5

Classification results for cross-validation using the remaining 40% of calls (not used to build the classification functions) of the three two-year-old females. The cross-validation aims at verifying the validity of the model

Classification matrix for the cross-validation					
Individuals	$n$	Predicted classification			Percent correct
		D	G	H	
D	6	6	0	0	100.00
G	4	0	3	1	75.00
H	3	0	0	3	100.00
Total	13	6	3	4	92.31

cantly negatively with age of monkeys. Results show that the older the monkey, the more it emits coo calls with lower end frequency of the fundamental component.

#### 4. Discussion

We demonstrated a negative correlation between end frequency of the fundamental component and the age of the callers. The older the individual, the more it emits calls with a lower fundamental component. Similar results have been obtained also for coo vocalizations of the rhesus macaque *Macaca mulatta* during their early development [15]. Those observations of the relation between pitch of calls and age of callers are in accordance with the well-known rule that a larger body size is associated with a bigger vocal tract that will produce sounds with lower frequencies [16].

The discriminant analysis demonstrated that calls of the eight different individuals can be quite well differentiated by their acoustic characteristics, and the cross-validation verified the accuracy of the model. Different individuals emitted calls that are different in their acoustic structures. The accuracy of call reclassification was 89.23% in the analysis (83.72% for the cross-validation). This reclassification percentage was lower than that of the chuck vocalization of the squirrel monkey *Saimiri sciureus* (95% [17]), but higher than those obtained for the quiet long call, the normal long call and the combination long call of the cotton-top tamarin *Saguinus oedipus* (68% and 57% [9], 77% [18]), for the cohesion call of the ring-tailed lemur *Lemur catta* (74% [7]) and for the long-

range vocalization of the spider monkey *Ateles geoffroyi* (44% [19]). The accuracy of classification obtained in this study is higher than the one obtained by Mitani in his study of wild Japanese monkeys [20], for which he could identify the vocalizer in two-thirds of the adults. However, his acoustic measurements differed from those of our study, since he took into account the fundamental component, the duration and formants of calls.

The discriminant analysis revealed that duration, start and end frequencies were the parameters that permit the separation of individuals. Chapman and Weary [19] also demonstrated that duration was a good discriminator of individuals for long-range vocalizations in spider monkeys (in their case, duration of the middle and last elements). Start frequency has also been found to differentiate individuals significantly in cotton-top tamarins (start frequencies of first and last syllables of normal long calls [9]). Moreover, Hauser [21] found that the minimum frequency was one of the parameters accounted for most of vocal differences between rhesus macaque individuals. The importance of the minimum frequency as a discriminating factor (which corresponded sometimes to start frequency and some other times to end frequency in our study) agrees with our results, since we have demonstrated that both the start and end frequencies were good acoustic variables separating individuals.

We found in our study that position of  $F$ -max was not a parameter that differentiated individuals. Other studies have used the temporal location of peak frequency to categorize different subtypes of coo calls, as smooth early high and smooth late high calls defined by Green [13]. Those categorizations of coo calls have been shown to depend on different social situations. Other authors also trained monkeys to discriminate those two types of coo calls, in order to demonstrate categorical perception of peak frequency related to functional situations [22,23]. Those studies showing that position of peak frequency was related to social situations and not to individual identity agreed with our study where we demonstrated that the position of  $F$ -max was not an individual marker. On the contrary, another study showed that position of peak frequency varied more consistently between individuals than by behavioral context [24]. These results do not agree with ours.

Results of the discriminant analysis realized on the three same age females present some similarities with those of the principal discriminant analysis, but also some differences. Indeed, the two analyses indicated that the same three parameters (call duration, start and end frequencies) were the ones that differed mostly among individuals. Even when sex and age were ignored, those three parameters were the individual markers. However, we can notice that the importance of those parameters as individual markers is lower for the three two-year-old females than for the eight individuals (values of  $F$  ratios indicate the contribution of different variables to the prediction of individual membership). Moreover, the relative importance of each of those three parameters is different for the eight individuals and for the two-year-old females. Call duration, which is the most salient parameter for individual differentiation, become less useful when individuals are of the same sex and age. End frequency has been demonstrated to be highly negatively correlated with age of monkeys. However, this parameter still plays a role in differentiating individuals of same sex and age. Although call duration, start and end frequencies present different relative importances in discriminating individuals of various ages and sexes and individuals of same sex and age, the present study demonstrated that those three parameters seem to be the best individuals markers out of the five tested.

In our study, we demonstrated that some parameters present more differences among individuals than others. Other studies also showed that particular vocal parameters are implicated in the individual discrimination or recognition by monkeys. However, vocal sounds constitute complex multidimensional stimuli that are perceived by monkeys as a whole and complete sound. Even if some parameters are more salient than other for individual discrimination, this process may be complex and may involve many parameters with different weights.

In the field, such vocal differences among individuals may constitute a good means for individual recognition since it has been demonstrated that, on one side, monkeys avoid looking at other individual faces [25] and, on the other side, the natural environment may be overgrown with obstacles for visual communication. However, even if individual vocal characteristics are different from one individual to another, this does not prove that monkeys can use those cues for individ-



ual recognition. Other playback experiments using not only natural signals but also synthetic ones (as Kojima and we already performed with chimpanzee [26]) remain to be investigated in order to demonstrate vocal individual recognition on one side and to determine precisely which parameters are used by monkeys for this recognition on the other side.

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