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Age- and sex-dependent contact call usage in Japanese macaques

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Abstract The question of the flexibility of nonhuman primate vocal communication remains open today, especially due to early evidence of innately guided vocal production. However, socially determined flexibility can be found when the debate is moved from vocal structure to vocal usage. While increasing evidence shows that the audience quality influences the vocal behaviour of nonhuman primates, the impact of the caller's characteristics has been far less studied. Here, we tested the influence of an individual's sex and age on the usage style of contact calls. We recorded contact calls of male and female Japanese macaques and compared the vocal usage styles of approximately 1-year-old juveniles with those of adults at various ages. We found, first, important differences in call usage style between juveniles and adults, the latter forming temporally ruled vocal exchanges respecting an interindividual turntaking principle. Moreover, sex differences were substantial in adults but nonexistent in juveniles. Finally, age continued to influence female vocal behaviour during adulthood, whereas dominance rank explained differences between adult males. Two nonexclusive mechanisms can explain this phenomenon, that is, a socially guided development of the appropriate form of calling versus an emotional maturation to control call emission, opening new lines of research on nonhuman primate vocal development of appropriate usages.

Keywords Vocal communication · Sex differences · Vocal development · Call usage · Nonhuman primates

Introduction

From an evolutionary perspective, songbirds are intriguingly considered as the best animal taxa to model the development of human language (Snowdon and Hausberger 1997). Both bird songs and human speech go through several comparable stages of social learning when youngsters learn the appropriate acoustic structure from adult models. For many decades, nonhuman primates, although closer anatomically and phylogenetically to humans, have progressively been excluded from comparative human–animal vocal development investigations, probably due to the early discovery of a strong genetic determinism of species-specific vocal repertoires (reviewed by Hammerschmidt and Fischer 2008). However, recent discoveries provided evidence of vocal flexibility capacities in adult nonhuman primates (Lemasson et al. 2011a; Candiotti et al. 2012). For instance, socially guided vocal convergence and innovation in several monkeys and apes have been reported (see Lemasson 2011 for a review). Vocal flexibility is even more striking when the debate is moved from vocal production (i.e., acoustic structure) to vocal usage (i.e., context

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and pattern of call emission; Seyfarth and Cheney 1999). A well known example is audience effect. Adult female chimpanzees produce more or fewer copulation calls (Townsend et al. 2008) and "pant-grunt" greetings (Laporte and Zuberbühler 2010) according to the sex, number and dominance rank of the individuals present in their environment.

Regardless of the audience quality, the characteristics of the caller are also a potential source of flexibility (Bouchet et al. 2010, 2012). Variability of nonhuman primate vocal usage is well illustrated by the differences between the calling behaviour of adult males and females. Traditionally, authors distinguish nonhuman primate species that display sex-specific call types (e.g., male intergroup-spacing loud calls vs. female copulation calls; Gautier and Gautier-Hion 1977), from species including males and females that share the same vocal repertoire but that present sex-specific call rates (e.g., males emit higher rates of threat calls, females emit more contact calls; Greeno and Semple 2009; Bouchet et al. 2010). Recent studies showed that, even for the species thought to display sex-specific vocal repertoires, the border between sexes is not as strict as previously reported. On some rare occasions, adult females have been observed to produce sounds previously thought to be male-specific (Geissmann 1983; Ouattara et al. 2009; Bouchet et al. 2012), suggesting that male–female differences cannot be due only to morpho-anatomico-physiological reasons, but could also be due to different social usages. Studies focused on the ontogeny of these male–female differences are now crucially needed.

The fact that macaque species live in large multi-male, multi-female groups and both males and females share the same repertoire to deal with affiliative vocal communication makes them an appropriate nonhuman primate model to study age and sex differences of vocal usage. Japanese macaques in particular are interesting for several reasons. First, their reproduction is seasonal so we can easily compare same-age juveniles. Second, it is considered as a relatively despotic species with a sex-determined dominance system (Kutsukake 2000; Thierry 2000), so we can assess the role played by particular social factors, like the position in the dominance hierarchy, on vocal usage. Third, Japanese macaques are known for their adults' high rates of affiliative contact calls, the so-called "coos", which have been well analysed (Koda and Sugiura 2010). These calls are usually emitted in peaceful social circumstances and appear very early after birth (Itani 1963; Green 1975; Owren et al. 1992). The fact that coo call rates differ between juveniles and adults may suggest that communication styles change depending on life histories (Koda et al. 2008). Moreover, these calls are usually produced by female adults within temporally ruled vocal exchanges, that is, group members respond to each others' calls by

respecting a minimum and a maximum delay, and by calling one after the other and respecting turn-taking rules (Sugiura and Masataka 1995; Sugiura 2001). Whether this particular vocal usage pattern is sex- and/or age-dependent remains an unresolved question. Flexibility has been found at the vocal structure level: an adult can respond to another individual by producing a call with an acoustic structure matching the call of the group member they are responding to (Sugiura 2001). Also, when a caller does not get a vocal response, it will later produce a second call with an exaggerated acoustic structure (duration, frequency modulation) and will then usually be more successful in getting a response (Koda 2004). The fact that vocal exchange plays a key role in a group's social life makes it a potential candidate for age and sex differences of the appropriate form of call usage.

Here, we investigated differences in coo call usage styles (i.e., isolated vs. repeated vs. exchanged calls) between juveniles and adults, focusing particularly on sex differences at both ages. We also evaluated the potential influence of the age and hierarchical status of individual adults on their vocal usage. The maturational and social factors which could guide the observed differences are then discussed.

Methods

Study group and housing conditions

One captive social group of Japanese macaques (*Macaca fuscata*), housed at the Primate Research Institute (Kyoto University), was studied between February and May 2009. The group included 8 adult males (average age: 9.75 years; range: 6–13 years old), 18 adult females (average age: 14.5 years old; range: 6–29 years old) and 10 juveniles (5 males, 5 females; average age: 8–10 months old). All group members were born and stayed in this captive group (Table 1). For breeding and sanitary reasons, 1 year prior to our study, juveniles present at that time were removed from the group. The group lived in a 960 m^2 outdoor enclosure enriched with several metal perches and shelters. Water was available ad libitum. the monkeys were provisioned with chow twice a day and with sweet potatoes twice a week. These animals have been habituated for several years to the presence of human observers.

Data collection

Sound recordings

Macaques were observed (M.G.) between 8:30 and 11:00 and between 13:30 and 16:00, because we wanted to avoid

feeding contexts (provisioning times were fixed at 11:30 and 16:30). All contact (so-called coo) calls from adults were recorded following the all-occurrence sampling method and each individual caller was identified (Altmann 1974), which was possible given the relative low call rate in our captive group and given the loudness of adult voices. Juvenile calls were recorded following a 10-min focal animal sampling method (Altmann 1974). Recordings were performed with an ECM-672 Sony© directional microphone (frequency response: 50–16 000 Hz) connected to a PMD-660 Marantz© professional digital recorder (.wav format; sampling rate: 48 kHz; resolution: 16 bit; frequency response 20–20 000 Hz). In all, each juvenile was observed for 25 focal sessions ($N = 250$ min/individual) following a predetermined randomised time schedule, whereas adults were observed for a total of 41 h. Monkeys were constantly recorded during focal and all occurrence samplings. Recording distance was less than 5 m for focal sampling (recording of soft infant calls) but variable (up to 20 m) for all occurrence sampling (recording of loud adult calls).

Nonvocal observations

One observer (R.) recorded submissive interactions using the all-occurrence sampling method (Altmann 1974) for a total of 226 h. Submissive behaviour of a subordinate towards a dominant was indicated by either a silent bared-teeth display, a grimace, running away or a fear scream (de Waal and Luttrell 1985). The dominance rank order of group members was deduced from the asymmetric patterns of submissive behaviour (Table 1). All dyadic submissive signals were used to build three separate dominance matrices: for adult males, adult females and juveniles of both sexes. We collected a total of 365 submissive signals among adult females, 205 among adult males and 155 among juveniles. We then used MatMan 1.1 software to analyse the matrices and to estimate dominance rank orders (for methodological details, see: de Vries et al. 1993; de Vries 1995).

Data analysis

Based on the exploration of spectrograms using Avisoft™ software, call utterances were divided into three usage styles (as defined by Koda 2004; see examples in Fig. 1):

- Isolated call: a given individual emits a single coo call, with no other call heard 2 s before or after it.
- Repeated sequence: a given individual emits a series of coo calls trailing each other by less than 2 s.
- Exchange sequence: two (or more) individuals call in a row with their respective calls trailing each other by

Table 1 Group structure

Group member	Age (years)	Dominance rank	Mother's name
AF1	6	17	d
AF2	17	10	d
AF3	7	5	d
AF4	8	15	d
AF5	9	16	d[1]
AF6	10	7	d
AF7	20	1	d
AF8	14	8	d
AF9	27	18	d
AF10	13	4	d[2]
AF11	7	13	d
AF12	7	6	AF10
AF13	8	3	AF7
AF14	21	12	d
AF15	29	14	d
AF16	13	11	AF15
AF17	19	9	d
AF18	26	2	d
AM1	11	5	d[2]
AM2	7	2	AF9
AM3	13	1	d
AM4	7	3	d
AM5	6	4	AF2
AM6	12	7	AF14
AM7	13	6	d[1]
AM8	9	7	d
JM1	<1	6	AF1
JM2	<1	5	AF2
JM3	<1	9	AF4
JM4	<1	10	AF5
JM5	<1	2	AF10
JF1	<1	4	AF6
JF2	<1	1	AF7
JF3	<1	7	AF11
JF4	<1	8	AF16
JF5	<1	3	AF17

Group members were named as follow: *AM* adult male, *AF* adult female, *JM* juvenile male, *JF* juvenile female, *d* the mother is dead and is different for all individuals (except *d[1]* and *d[2]*: same mother)

less than 2 s, regardless of the interindividual spatial distance.

Concerning the vocal behaviour, we selected several variables which were comparable between adults and juveniles despite the difference in the sampling regimes. The frequency per minute of the three different call usage styles were compared within age–sex classes with Friedman tests
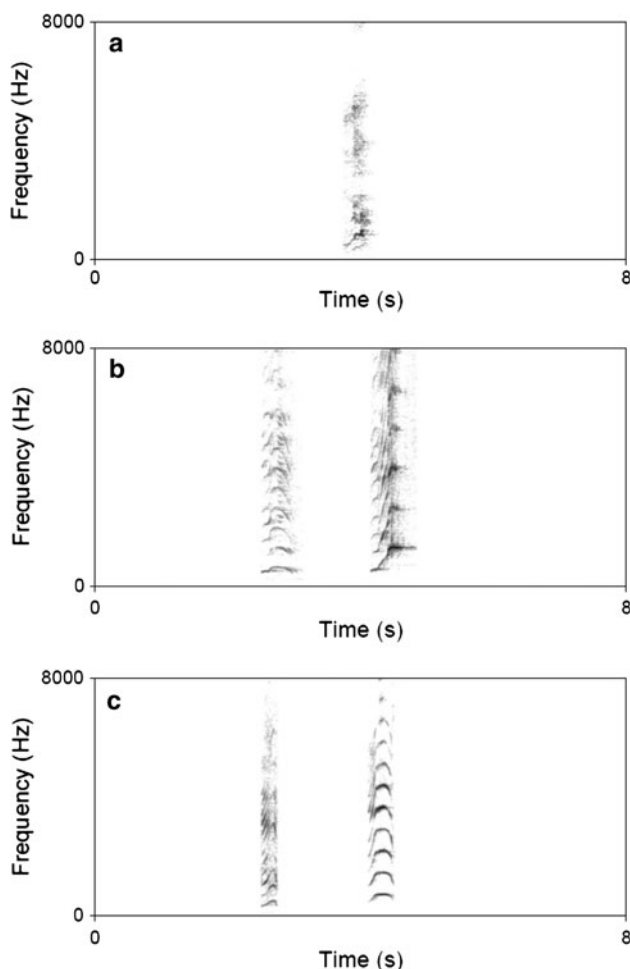
Fig. 1 Illustration of the three different vocal styles. **a** Isolated call. **b** Repeated sequence composed of two calls uttered by the same caller. **c** Exchange sequence between two different callers. Spectrogram setting: fast Fourier transform function, Gaussian window; frequency step: 20 Hz; time step: 0.005 s

and post hoc Wilcoxon signed-rank tests, and between age and sex classes with Kruskal–Wallis tests and post hoc Mann–Whitney tests. Kruskal–Wallis tests and post hoc Mann–Whitney tests were also used to compare the "response" proportions (= proportion of all coo calls from a given individual produced in response to another caller) and the "repetition within exchange sequences" rates [= frequency of coo calls emitted in consecutive series (intercall delay: less than 2 s) by the same individual within exchange sequences] between age and sex classes. Bonferroni correction was applied when multiple testing occurred. Spearman tests were used for adults to evaluate: (1) the relation between call usage styles and the caller's age or dominance rank and (2) the relation between an adult's age and its chance to receive a vocal response after calling.

Results

Frequency rates of call usage styles

Vocal usage styles were clearly age-dependent as well as sex-dependent in adults (Kruskal–Wallis tests, isolated calls: $H = 28.76$, $P < 0.0001$; exchanged sequences: $H = 24.93$, $P < 0.0001$; repeated sequences: $H = 25.53$, $P < 0.0001$; Fig. 2). Both male and female juveniles produced significantly (alpha threshold after applying Bonferroni correction: $0.05/6.0 = 0.0083$) more isolated calls, repeated sequences and exchange sequences than both male and female adults (Mann–Whitney tests, for all comparisons: $105 \geq W \geq 55$, $0.0043 \geq P \geq 0.0009$), with the exception of exchange sequence rates that did not differ between juvenile females and adult females ($W = 90$, $P = 0.027$). No significant difference was found in call rates between male and female juveniles whatever the call usage style (isolated: $W = 29$, $P = 0.835$; repeated: $W = 30$, $P = 0.676$; exchanged: $W = 29$, $P = 0.835$). Nevertheless, adult females produced more isolated calls ($W = 39.5$, $P < 0.001$), repeated sequences ($W = 291$, $P < 0.01$) and exchange sequences ($W = 312$, $P < 0.001$) than adult males.

Moreover, the predominance of a particular call usage style appeared to be clearly age-dependent as well as sex-dependent in adults only (Friedman tests, juvenile males: $N = 5$, $\chi^2 = 7.6$, $P < 0.05$; juvenile females: $N = 5$, $\chi^2 = 7.6$, $P < 0.05$; adult females: $N = 18$, $\chi^2 = 16.67$, $P < 0.001$; adult males: $N = 8$, $\chi^2 = 10.83$, $P < 0.01$). Both male and female juveniles produced isolated calls, repeated and exchange sequences at rates that did not differ significantly (Wilcoxon signed-rank tests; isolated vs. repeated/exchange: $N = 5$, $Z = 2.023$, $P = 0.043$ in all comparisons; repeated vs. exchange: $N = 5$, $Z = 0.674$, $P = 0.50$ in both comparisons; alpha threshold after applying Bonferroni correction: $0.05/3 = 0.017$). Both adult males and females produced more isolated calls than repeated sequences (males: $N = 8$, $Z = 2.027$, $P = 0.0117$; females: $N = 18$, $Z = 3.724$, $P = 0.0002$). Also, adult females, but not adult males, produced significantly more exchange sequences than isolated calls (females: $N = 18$, $Z = 2.604$, $P = 0.0092$; males: $N = 8$, $Z = 1.68$, $P = 0.093$) and repeated sequences (females: $N = 18$, $Z = 3.724$, $P = 0.0002$; males: $N = 8$, $Z = 2.521$, $P = 0.043$).

Although adults were less vocally active than juveniles in general, they restricted their calling to responses to the calls of other group members. Focusing the analysis on the proportions of coo calls given as a vocal response within vocal exchanges (Kruskal–Wallis tests: $H = 17.74$,

Fig. 2 Rates of isolated calls, repeated sequences and exchange sequences. Comparisons between age and sex classes. Isolated call: a given individual emits a single coo call. Repeated sequence: a given individual emits a series of coo calls. Exchange sequence: two (or more) individuals call in a row. $N_{\text{juvenile males}} = N_{\text{juvenile females}} = 5$, $N_{\text{adult males}} = 8$, $N_{\text{adult females}} = 18$. Mann–Whitney tests: $^{\text{NS}}P > 0.0083$, $*P \leq 0.0083$ (alpha threshold after Bonferroni correction: $0.05/6.0 = 0.0083$)
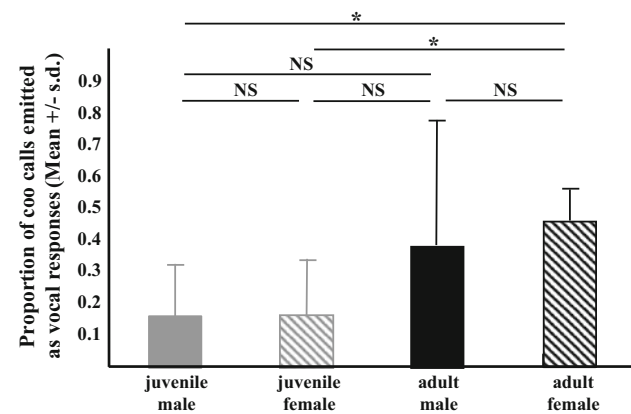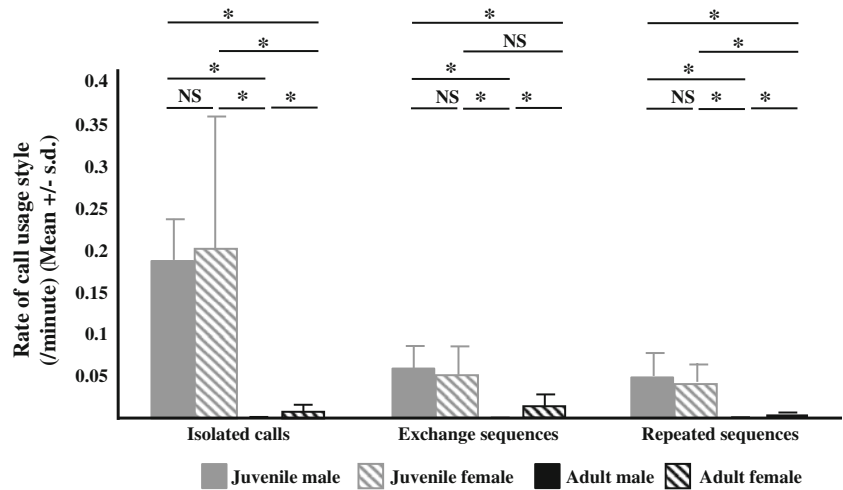
Fig. 3 Vocal response proportions. Comparisons between age and sex classes. Response proportion: proportion of all coo calls from a given individual produced in response to another caller. $N_{\text{juvenile males}} = N_{\text{juvenile females}} = 5$, $N_{\text{adult males}} = 8$, $N_{\text{adult females}} = 18$. Mann–Whitney tests: $^{\text{NS}}P > 0.0083$, $*P \leq 0.0083$ (alpha threshold after Bonferroni correction: $0.05/6.0 = 0.0083$)

$P < 0.01$; Fig. 3) revealed that coo call response rates of adult females were higher than those of both male ($W = 16$, $P = 0.0012$) and female ($W = 15$, $P = 0.0009$) juveniles, but did not differ significantly from those of adult males ($W = 265.5$, $P = 0.267$). Adult male emission rates did not differ from both juvenile rates (females: $W = 21$, $P = 0.048$, males: $W = 24$, $P = 0.124$), which also did not differ from one another ($W = 26$, $P = 0.835$).

The general principle of interindividual vocal exchanges is for each individual to produce one call, one after the other, respecting some kind of turn-taking rule. The propensity to break this rule (estimated by the "repetition within exchange sequences" rate) appeared to be age-dependent (Kruskal–Wallis tests: $H = 12.84$, $P < 0.01$). Adult males were never observed producing several consecutive calls within a vocal exchange. Male and female juveniles did not differ from one another ($W = 25.5$,

$P = 0.754$) but, when combining both sexes, juveniles emitted significantly more repetitions of several successive coo calls within vocal exchanges than adult females (juvenile rate: 0.038 ± 0.026; Adult female rate: 0.003 ± 0.004; $W = 188.5$, $P = 0.0005$).

Influence of chronological age and dominance rank

Contributions to exchange sequences were positively correlated with adult female age (Spearman, $n = 18$, $r = 0.834$, $P < 0.001$; Fig. 4a), but not with adult male age ($n = 8$, $r = 0.578$, $P = 0.134$), meaning that the older the female was, the more she contributed to vocal exchanges. Age did not influence other call usage styles, that is, frequency of isolated calls (males: $n = 8$, $r = -0.460$, $P = 0.252$; females: $n = 18$, $r = 0.455$, $P = 0.06$) and repeated sequences (males: $n = 8$, $r = 0.128$, $P = 0.763$; females: $n = 18$, $r = 0.003$, $P = 0.99$) whatever the caller's sex.

Rates of repeated sequences were however positively correlated with dominance score (score 1 being attributed to the highest ranking male) in adult males (i.e., the lowest ranking males produced the more repeated sequences; $n = 8$, $r = 0.760$, $P < 0.05$) but not in adult females ($n = 18$, $r = 0.084$, $P = 0.741$) or in juveniles ($n = 10$, $r = -0.285$, $P = 0.425$). Dominance rank did not influence the rates of the other call usage styles, that is, isolated calls (adult males: $n = 8$, $r = 0.599$, $P = 0.117$; adult females: $n = 18$, $r = 0.032$, $P = 0.899$; juveniles: $n = 10$, $r = -0.370$, $P = 0.293$) and exchange sequences (adult males: $n = 8$, $r = 0.117$, $P = 0.782$; adult females: $n = 18$, $r = -0.234$, $P = 0.351$; juveniles: $n = 10$, $r = -0.073$, $P = 0.841$).

In addition, not all adults received an equal amount of vocal responses. The propensity for an adult female to receive a vocal response was positively correlated with the caller's age, whether the respondent was a female
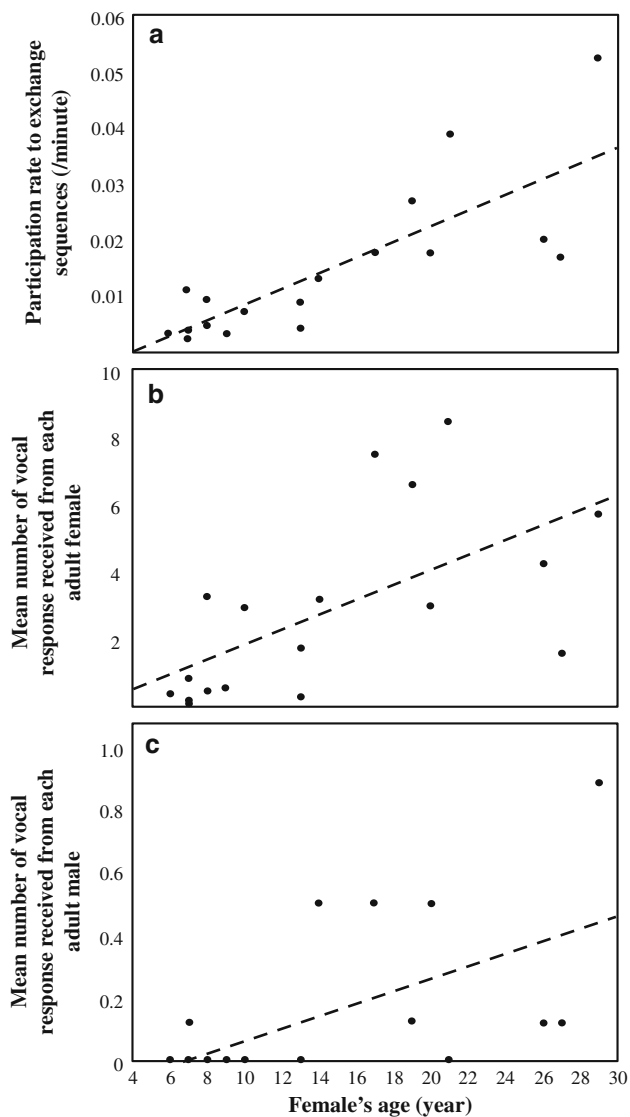
Fig. 4 Adult female's age in relation to **a** her participation in exchange sequences and her propensity to elicit a vocal response from **b** other adult females or **c** adult males. To calculate the number of vocal responses within a vocal exchange following the pattern ABC (A, B and C being three individuals), we considered that B responded to A and C responded to both A and B (as in Lemasson et al. 2010)

(Spearman: $n = 18$, $r = 0.703$, $P < 0.01$; Fig. 4b) or a male ($n = 18$, $r = 0.625$, $P < 0.01$; Fig. 4c). A similar correlation was found for adult males with female respondents ($n = 8$, $r = 0.713$, $P < 0.05$), but not with male respondents ($n = 8$, $r = 0.114$, $P = 0.788$).

Discussion

Japanese macaques' contact call usage styles clearly appeared to be age- and sex-dependent. Juveniles differed from adults both by their higher global vocal activity and

by the fact that they produce similar rates of isolated calls, repeated sequences (the same individual calls several times in a row) and exchange sequences (the individual responds vocally to or receives a response from a group member). Also, juveniles contributed to vocal exchanges by producing several calls in a row more often than adults, who usually called one after the other. Whereas none of the parameters we analysed revealed differences between juvenile males and females, adult males and females differed substantially. Adults of both sexes rarely produced several calls in a row, neither in isolation nor within a vocal exchange, but adult females were more vocally active than males in general and they contributed more frequently to vocal exchanges. Interestingly, the age of the adult was an important parameter for females. While they grew older, adult females' contributions to vocal exchanges increased and their position as privileged interactants also developed: they received increasingly more vocal responses from other group members of both sexes. However, data from adult males did not reveal a similar trend. In adult males, dominance rank was the decisive factor influencing their call usage style, with lower ranking males producing more repeated sequences than higher ranking males.

Whereas young Japanese macaques display different contact call usage styles, adults use contact calls preferentially to form temporally organised interindividual vocal exchanges, to the detriment of isolated calls and even more of repeated sequences. Even within vocal exchanges, juveniles differ from adults by breaking more often the turn-taking rule. Several authors (Snowdon and Cleveland 1984; Hauser 1992; Masataka 2003; Lemasson et al. 2010) have proposed that turn-taking is a key principle shaping nonhuman primate vocal exchanges. In humans as well, turn-taking rules affect the conversations of different cultures (Stivers et al. 2009). Among the human interlocutors who happen to break this rule we find children at early stages of language development (Bruner 1975; Levinson 1983). A recent study confirmed that Campbell's monkey juveniles break the turn-taking principle more often than adults do (Lemasson et al. 2011b). Using playback experiments, these authors showed that adults paid more attention to appropriate than to inappropriate vocal exchanges (i.e., respecting or not the turn-taking rule) whereas juveniles did not.

At this stage, at least two nonexclusive hypotheses can be raised regarding the underlying processes. First, an emotional maturation is likely to occur here as we know that the production of vocalisations in monkeys is strongly related to the limbic system and to areas associated with emotion (Jürgens 1995). Although difficult to test, it is possible that juveniles differ from adults in their affective and motivational states, resulting in a higher rate of repeated calls. Second, a more cognitively complex mechanism

based on learning from same-sex adult models of the appropriate form of calling certainly occurs. An increasing amount of primate studies supports this mechanism by showing that juveniles learn the appropriate form of emission of alarm, agonistic and food calls. For instance, immature vervet monkeys learn the appropriate context of emission of their species' eagle alarm call type, by alerting, first, about any flying item at early stages and then, later, about their real bird predators (Cheney and Seyfarth 1990). Moreover, adult vervets play an active role by calling just after the infant's call but only when the context of emission is appropriate (Cheney and Seyfarth 1990). Such reinforcement by adults may guide the vocal development of young vervets. In our study, juveniles did not get vocal responses systematically. Although it is much harder to clearly understand what context is appropriate for producing a contact call than an alarm call, it remains a plausible explanation in our study too. Also, young pigtail macaques produce agonistic calls in inappropriate social contexts at first (Gouzoules and Gouzoules 1989). Specific vocal sequences of adult tamarins in a food transfer context create an opportunity for infants to learn not only what food is appropriate but also which vocalisations are appropriate in feeding contexts (Roush and Snowdon 2001). Moreover, a recent neurobiological study revealed that coo call emissions optionally activate the macaque's ventral premotor cortex depending on the context of communication, suggesting that both emotional and voluntary control are involved (Coudé et al. 2011). More comparative research is needed to clearly sort between the social and the motivational hypotheses. Strong evidence in favour of social learning would require investigating more deeply individual variations and seeing whether they might be explained by matching differences in social models.

Interestingly, whereas sex did not influence significantly call usage styles of our less than 1-year-old juveniles, sex differences were strongly marked in adults. This could again suggest a socially guided ontogenesis. The sex differences we observed in adults match the social roles of both sexes within the group. In this species, as in many other nonhuman primate species, females form the social core of the group (Muroyama 1991; Nakamichi and Shizawa 2003; Lemasson et al. 2006). As contact call exchanges strengthen social bonds and maintain social cohesion (Marler 1977; Lemasson et al. 2005), the higher vocal activity of females and in particular the more frequent exchanges among females than among males is not surprising (Greeno and Semple 2009). We found that the participation of females in vocal exchanges increased with age; this result corroborates the fact that older, more experienced and socially integrated females play a crucial role in monkey societies (Fairbanks 1988). We also observed that females elicited increasing interest by

becoming preferred vocal partners as they grew older, a trend previously described in Campbell's monkeys (Lemasson et al. 2010) and well documented for human traditional oral societies (Bascom 1942; Albert 1964; Calame-Griaule 1965). We found that rank, but not age, influenced adult males' call usage styles. In macaques, male dominance hierarchy is clearly less predictable than that of females (Kutsukake 2000). Surprisingly, the lowest-ranking adult males behaved as juveniles, producing frequent repeated sequences. One hypothesis is that repeated sequences may reveal the motivation of less socially integrated male callers as well as particularly emotive juvenile callers to elicit a vocal response. In line with this, macaques are known for their ability to modify the acoustic parameters of their second call in order to increase their chances to receive a vocal response when the first call fails (Koda 2004).

We acknowledge that only one captive group, with a composition that does not perfectly match the social structure of wild groups (absence of older juveniles and male migration), has been studied here using a nonlongitudinal cross-sectional approach. Only comparative studies with other captive and wild groups will allow more definitive conclusions. Moreover, further investigations of juvenile macaques at different ages are now necessary to understand clearly the different steps of the sociogenetic process leading to important sex differences in adults. Eaton et al. (1985) showed that sex differences in Japanese macaques emerged progressively during the first year of life; notably juvenile females, conversely to males, display an increasing amount of allogrooming and spatial proximity. Social changes thus precede the vocal changes observed here and might thus be determining in vocal development. Also, macaque mothers seem to play a key role in controlling and guiding to some extent these social changes in young juveniles (Eaton et al. 1985). Similarly, mother–infant vocal interactions would be crucial for the juveniles' vocal development. Japanese macaque mothers display human-like "motherese" when interacting with their infant (Koda and Masataka 2002). This suggests new lines of research investigating the influence of mothers on the vocal-social co-development of nonhuman primates, to compare it to that of humans (Goldstein et al. 2003).

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