

Attention to elders' voice in non-human primates

Alban Lemasson^{1,*}, Enora Gandon²
and Martine Hausberger¹

¹*Ethologie animale et humaine, EthoS, UMR6552–CNRS, Université de Rennes 1, Station Biologique, 35380 Paimpont, France*

²*Faculté des Sciences du Sport, Institut des Sciences du Mouvement E7 Marey, UMR6233–CNRS, Université de Aix-Marseille 2, 13009 Marseille, France*

*Author for correspondence (alban.lemasson@univ-rennes1.fr).

The observed respect and attention to elders' speech in traditional cultures appears to have a 'universal' component which questions its possible biological bases. Animals present differential attention to the vocalizations of other individuals according to their characteristics but little is known about the potential propensity to pay more attention to vocalizations of elders. On the basis of several hundreds of vocal exchanges recorded, here we show that aged female Campbell's monkeys (*Cercopithecus campbelli*), despite being significantly less 'loquacious' than their younger adult counterparts, elicit many more responses when calling. These findings show that attention to elders' vocal production appears in non-human primates, leading to new lines of questioning on human culture and language evolution.

Keywords: intergenerational; vocal exchange; primate

1. INTRODUCTION

In traditional human societies (e.g. Dogon, Kirundi, Yoruba ethnic groups), ageing is a sign of wisdom and the speech of an elder elicits specific respect and attention (Bascom 1942; Albert 1964; Calame-Griaule 1965). Intergenerational conversations in modern societies are regulated by several factors, including culture (Giles *et al.* 2002), age-difference (Hummert *et al.* 1998; Williams & Garrett 2002) and the context of the interaction (Ervin-Tripp 1964). Even though it is not true in all contexts, at the workplace, younger people are particularly respectful to elders regardless of their eastern/western culture (McCann & Giles 2006). Children respect more turn-taking rules and respond more to their mothers than to other individuals, probably a solid necessary basis for respect to elders when older (Fitch 2004).

Learning to respond to the appropriate interlocutor is a key feature in language development, particularly visible during turn-taking exchanges. Animals, too, are sensitive to their interlocutors. Barnacle geese (*Branta leucopsis*) females' decision to respond to their mate depends on the pair's age (Bigot *et al.* 1995). Vervet monkeys' (*Cercopithecus aethiops*) vocal responses to others' calls depend on the caller identity (Seyfarth & Cheney 1997). Adults or older individuals especially elicit attention. Younger chickens tend to follow older ones (*Gallus gallus domesticus*;

Adret-Hausberger & Cumming 1987); young vervets have a more appropriate alarm response after having looked at an adult (Seyfarth & Cheney 1997). Conversely, young vervets are interrupted or 'neglected' more often during alarm call production (Hauser 1992; Seyfarth & Cheney 1997). Adults are essential for canalizing and guiding sociogenesis and communication in the young (Slotow *et al.* 2000; Bertin *et al.* 2007; Bourjade *et al.* 2009).

However, could this attention to older animals be maintained at later stages, i.e. between younger and older adults? Is attention to elders a purely human cultural characteristic? Elders represent an essential reservoir of information for group survival (Maxim 1979). Old female chimpanzees (*Pan troglodytes*) contribute to the community by having a stabilizing role (de Waal 1982). It would therefore make sense that they receive more attention.

We investigate whether adult female Campbell's monkeys (*Cercopithecus campbelli*) are more attentive and responsive to older adults. Vocal exchanges are common in this species (Lemasson *et al.* 2005, 2006). Encoding of age in primates' calls through specific parameters is a common phenomenon and therefore the emitter's age, which is not systematically although often related to body size, can immediately be perceived (Ey *et al.* 2007; Chen *et al.* 2009). A previous investigation using isolation experiments indicates the ability to respond differentially to older and younger individuals in marmosets (*Callithrix jacchus*; Chen *et al.* 2009). We observed spontaneous interactions within the group, in order to understand the normal functioning of an undisturbed social group. We expected elders to receive more attention, and therefore more responses, than younger adults which would indicate important parallels with human cultures.

2. MATERIAL AND METHODS

We observed female Campbell's monkeys living in a group composed of one male (13 years old), seven adults (3–15 years old) and one subadult (2 years old) females. Females belonged to two matriline and were nulliparous apart from the older one. The group composition matched the ones observed in the wild (Quattara *et al.* 2009). The group was housed in an indoor (21 m² × 3 m)—outdoor (21 m² × 4 m) enclosure enriched with litter and perches. Monkeys were fed two meals per day (fruits, vegetables, pellets). Water was available ad libitum.

The vocal repertoire of Campbell's monkeys is composed of several, acoustically and contextually distinct, call types including combined-harmonic (CH) affiliative calls (Lemasson 2003). CH calls, also named cohesion-contact calls, are usually produced in bouts by several group members interacting peacefully (Lemasson *et al.* 2005).

The data collection was divided into two steps. In order to investigate 'who was responding to whom?', we first conducted observations during three 12-day periods (March, April, October 1999). We performed two daily 5 min focal samples per female and noted each CH call production and social interaction of the focal subject and the identity of the exchange partner. Preliminary observations suggested that a vocal exchange was composed of calls separated by less than 1 s. The male never took part in these exchanges. We collected 823 vocal exchanges for the eight females who were each observed for 6 h. Individual call production was evaluated by adding the calls produced during vocal exchanges and those produced isolated. In order to confirm the temporal organization of these exchanges quantitatively, we secondly performed recordings using a Sennheiser MKH815 microphone connected to a Tascam DA-P1 recorder. Recordings were digitized using customized ANA software, which allowed measuring intercall durations between the calls of two subsequent individuals. Ten sessions of 90 min continuous recording were conducted over a period of two weeks in August 2001. We recorded 702 calls (isolated and exchanged).

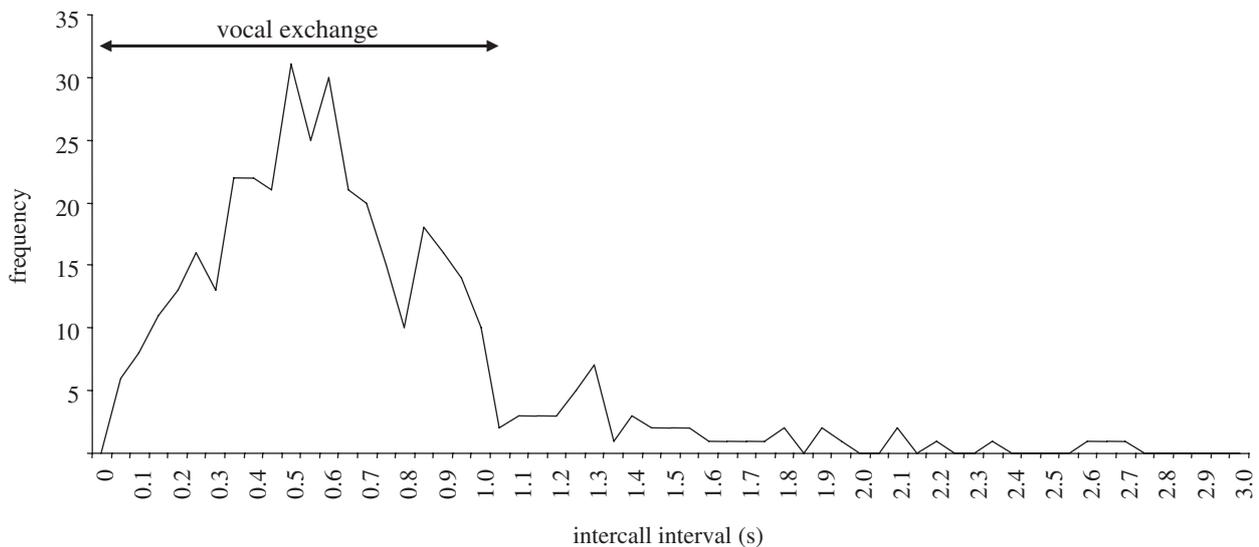


Figure 1. Frequency distribution of intercall intervals. The consecutive calls emitted by two different females typically trailed each other with a 0.5 s duration (peak submit). Using the Anderson–Darling normality test, we saw that our peak fitted a normal distribution ($n = 342$, $p = 0.013$) when we fixed the maximum threshold delay of response to 1 s.

Using data from observations, we tested the correlation between the emitter's (i) age (averaged over the study duration) or (ii) dominance index (see Lemasson & Hausberger 2004 for index calculation) and (a) her vocal behaviour (call rate h^{-1}) or (b) the vocal behaviour of the receiver (% of the emitter's calls that initiated a vocal response). Recordings were used to define the response latency threshold.

3. RESULTS

Vocal exchanges corresponded to series of successive calls from different females (2 or 3, 43–31%; sometimes 4 or 5, 15–5%), since 74% of the exchanges were composed of one call from each individual and the same individual almost never produced two consecutive calls (0.48%). The individuals who emitted several calls within a given exchange were the youngest (five times more for the female under 5 years old). Recordings confirmed that vocal exchanges were characterized as series of calls given by different individuals typically trailing each other with short intercall intervals of up to 1 s (figure 1). No call overlap was observed and individuals responded to each other with a latency rarely (7.7%) less than 260 ms (average contact call duration). Age appeared as a major factor in the contribution of individuals to vocal exchanges. In nulliparous females ($n = 7$), call production was negatively correlated with age (Spearman test: $r = -0.893$, $p = 0.0068$; figure 2a), indicating that elders were less 'loquacious' than younger individuals. Despite that, they received more responses from their younger conspecifics. Age was positively correlated with the rate of responses received ($r = 0.929$, $p = 0.0025$; figure 2b). Elders called less but when they called, they almost always received a response. The oldest individual, who was the mother of some of the nulliparous females, for some reason presented a particular profile with a high call production (figure 2a). Including this female in the analysis cancelled the 'call rate–age' correlation ($n = 8$, $r = -0.57$, $p = 0.14$). But, interestingly, including this female did not change the significance of the

correlation between age and rate of responses received ($n = 8$, $r = 0.857$, $p = 0.0065$; figure 2b). Call rate and response rate were not correlated with dominance status, with or without the mother ($-0.5 < r < 0.57$, $0.13 < p < 0.32$).

4. DISCUSSION

Observations of spontaneous vocal exchanges in a group of Campbell's monkeys revealed that, like other species, they perform temporally well-organized interactions, respecting turn-taking rules (Hauser 1992; Hausberger *et al.* 2008). More interesting still is the finding that age is an important regulating factor, with elders, regardless of dominance status, eliciting more responses from their younger counterparts despite a lower call production. Obviously, elders received more attention than younger adults. As delays were very short, age identification was probably related to the observed changes of sound structure with age (Lemasson 2003) as also found in marmosets (Chen *et al.* 2009), although here sight identification cannot be excluded. Only hypotheses can be raised at this stage to explain the high call rate of the old mother (particular social status/hormonal profile, re-increase of loquacity after a certain age-threshold, idiosyncrasy). This is an interesting question deserving further investigation. But these results show for the first time that 'attention to elders' constitutes an integral part of the daily social life of a non-human primate species and suggest that this may be more than a purely cultural human product.

One can wonder whether this can be the result of developmental and/or evolutionary history. Like children who respond more to their mother, young vervets who are attentive to adults' responses or young chickens who follow older peers, adult monkeys here replied more to elders, a result of the early mother–young relationship (Seyfarth & Cheney 1997; Fitch 2004) and/or of the social development (Hausberger *et al.* 2008). Campbell's monkeys displayed

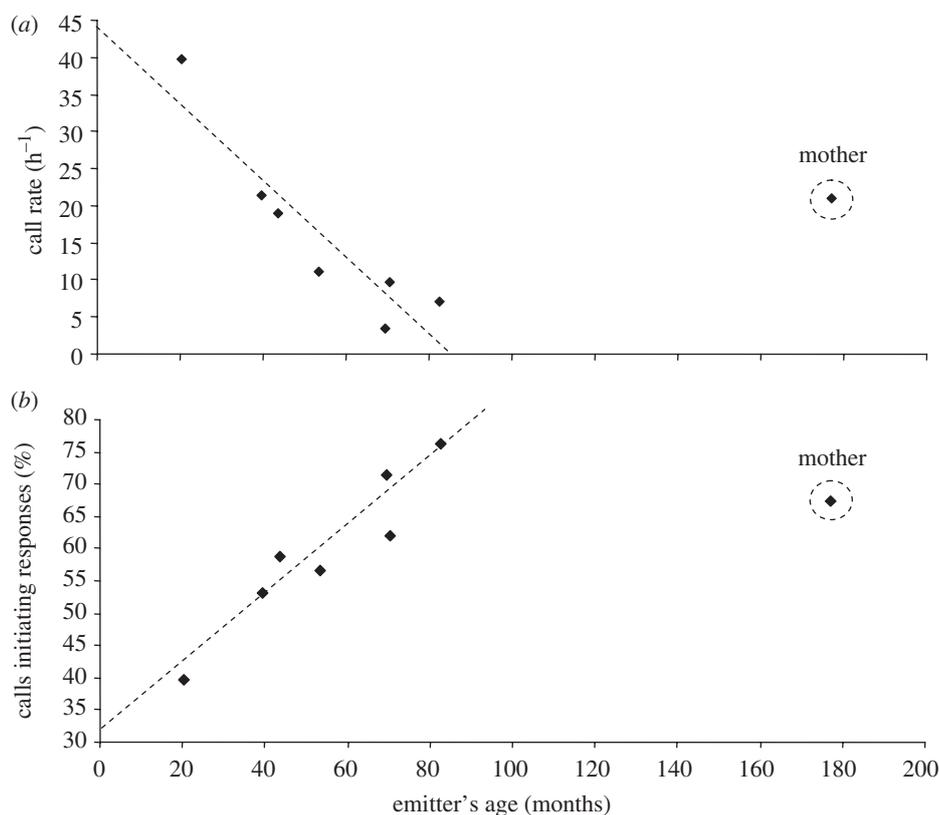


Figure 2. Relationship between the age of an emitter and (a) her call rate, (b) her propensity to elicit vocal responses.

temporal 'rules' when exchanging vocally, notably by avoiding call overlap and respecting turn-taking. Younger animals interfered more often in the exchanges, suggesting that the respect of exchange 'rules' was acquired with age. On the other hand, the fact that marmosets respond more to calls of isolated conspecifics if they are older, even if not originating from the same social group (Chen *et al.* 2009), suggests some evolutionary mechanism that leads to more attention towards elders' productions. We know from the study of alarm calling in vervets that individuals are more attentive to older monkeys' signal because they are produced in a more reliable context (Seyfarth & Cheney 1997). The increased 'credibility' or popularity with age in Campbell's monkey calls could explain the correlation between ageing and the propensity to elicit a response.

This first demonstration that elders' calls elicit more attention and responses from other adults in the daily functioning of a primate social group certainly leads to new and potentially fruitful lines of questioning on the origins of some traits of human culture and evolution of language.

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