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EDITOR'S NOTE

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1 Collaboration history

1 Nobuo Masataka is the head of the Cognition & Learning section of the Primate Research Institute (University of Kyoto, Japan). Alban Lemasson is the head of the Animal & Human Ethology lab (University of Rennes 1, France). Hiroki Koda and Hélène Bouchet are their former PhD students. Both our teams decided to engage in a long-term collaboration a decade ago, as we shared a common interest in nonhuman primates' vocal communication and in the evolutionary origins of human language.

2 The collaboration started when Lemasson was hosted by Masataka as a post-doctoral fellow at the Primate Research Institute in Japan in 2004/2005. Upon Lemasson's return to France, where he took a position as Lecturer at the University of Rennes 1, the two maintained strong bonds. Over the last decade, regular visits at each site have taken place, and several French and Japanese students and young researchers have taken part in the collaboration with co-supervised research programs (Assistant Professor: Hiroki Koda; Postdoctoral fellows: Hélène Bouchet, Malgorzata Arlet; PhD students: Chisako Oyakawa, Muriel Basile, Anna Sato; Bachelor and Master students: Manon Guilloux, Kévin

Remeuf, Ludivine Glas). Research programs received financial support from the Japan Society for the Promotion of Science ("Postdoctoral Fellowship for Overseas Researchers" and "Young Researcher Overseas Visits" programs), the French Ministries of Foreign Affairs and of Higher Education and Research (Partenariat Hubert Curien "Sakura"), as well as the French National Centre for Scientific Research ("Projet International de Coopération Scientifique").

3 Below, we first review the theoretical framework of research on vocal communication in nonhuman primates and its impact on the debate about the origins of human language, with illustrations from lab and field studies conducted independently by Masataka and Lemasson, and their colleagues. We then present our common research achievements along three axes: vocal flexibility under social influences in adults, vocal development in juveniles, and perceptual abilities.

2 Theoretical research framework: Separate contributions of the French and Japanese teams

4 Language plays a pivotal role in human societies, and the question of its origins is a hotly debated topic. Like any complex biological trait, it is unlikely to have evolved *de novo*, and it probably has a long evolutionary history. However, it is nearly impossible to find direct fossil-based evidence of the evolutionary path of language properties because they are of a behavioural nature. One alternative way to address this question is to examine the anatomical features, communicative mechanisms and cognitive abilities of humans compared to those of more or less phylogenetically related animals. Nonhuman primates, our closest relatives, are prime candidates for such a comparative approach. To look for the roots of human language, which is primarily of an acoustic nature with a social function, it is valuable to investigate the characteristics of vocal communication in nonhuman primates and the underlying cognitive and social mechanisms; this is the approach taken by both Masataka's and Lemasson's teams.

5 However, a few decades ago, the classic way to think of nonhuman primates' vocalizations was to consider them as reflex-driven expressions of the caller's internal state (Jürgens, 1995). Both our teams have conducted studies confirming the acoustic encoding of arousal, a phenomenon also described in humans (Breitenstein *et al.*, 2010). For example, in squirrel monkeys, isolation calls given by all group members have a longer duration when infants are separated further away from their natal group (Masataka and Symmes, 1986). Similarly, in three species of Old World monkeys, a separation-reunion experimental paradigm provided evidence of affect-induced changes in the use of contact calls (higher call rates) and their structure (longer and higher-pitched calls) (Lemasson *et al.*, 2012). But we now know that this is only part of the range of messages encoded acoustically, and that nonhuman primates have some degree of control over their vocal production. In line with this, studies using operant conditioning experiments and vocal adjustment during helium exposure have shown that white-handed gibbons can control their call emission and structure (Koda *et al.*, 2007, 2012).

6 Some nonhuman primates' calls also function as referential signals conveying information about external stimuli, a function analogous to semantics in human language. In Goeldi's marmosets, the acoustic structure of alarm calls provides reliable information about predator type (aerial *versus* terrestrial); this is used by listeners to

decide whether to climb down and freeze (aerial danger) or to climb up and respond with warning calls (terrestrial danger) (Masataka, 1983). In Campbell's monkey males, alarm calls are produced in complex sequences whose composition (call types and order of call delivery) and rhythm of emission, as well as the acoustic structure of the calls itself (temporal and frequency parameters), encode information about the type of danger (e.g. tree fall, intergroup encounter, predator encounter and whether it is aerial or terrestrial) and the level of urgency (Ouattara *et al.*, 2009a, 2009b; Lemasson *et al.*, 2010c). By analysing the multi-level structure of monkeys' vocal emissions, these latter studies even revealed call combinations akin to affixation and syntax in human language (Zuberbühler and Lemasson, 2013; Coye *et al.*, 2015). Also, by comparing populations living in habitats with different predator pressures, "lexical" dialects were found (Schlenker *et al.*, 2014).

7 The parallel with human language goes even further, with clear demonstrations of acoustic plasticity. In several primate species, contact calls have been found to function as "social badges". For example, acoustic analyses of contact coo calls in Japanese macaques revealed habitat-related population differences (Sugiura *et al.*, 2006), socially-driven "phonological" dialects (Tanaka *et al.*, 2006), and individual identity coding (Ceugniet and Izumi, 2004). In Campbell's monkeys, females produce several variants of their contact CH (combined harmonic) calls, some of which are shared by close affiliative partners (Lemasson and Hausberger, 2004). This remarkable phenomenon is dynamic (long term vocal convergence), as vocal sharing parallels the changes in social networks over time (Lemasson and Hausberger, 2004; Lemasson *et al.*, 2011b). Interestingly, by screening the entire vocal repertoire of Campbell's monkeys and other Old World species (red-capped mangabeys and De Brazza's monkeys), identity coding has been found to be more reliable in calls mediating inter-individual social interactions (e.g. contact calls) than in socially less-targeted calls (e.g. food calls, alarm calls) (Lemasson and Hausberger, 2011; Bouchet *et al.*, 2012b, 2013a). Identity coding is thus call type-dependent, but also varies with the context. For instance, Diana monkeys produce more stereotyped (individually distinctive) calls when travelling in dark compared with bright habitats, to facilitate spatial cohesion in the forest (Candiotti *et al.*, 2012). An interesting parallel can be drawn with human language, as the amount of identity cues in speech is adjusted according to the audience design (vocal accommodation theory: Giles *et al.*, 1991).

8 The inter-individual (social interaction) level of analysis has also revealed some interesting parallels with human language. Vocal exchanges in nonhuman primates have been found to resemble primitive forms of conversations, as they follow a number of interaction rules that are universal across human cultures (Sugiura and Masataka, 1995; Henry *et al.*, 2015). For example, Campbell's monkeys, Japanese macaques and marmosets respect a minimum and maximum inter-speech delay (to avoid calling simultaneously and ensure the continuance of the interaction) as well as a turn-taking principle (i.e. the two interlocutors alternate their calls) (Sugiura and Masataka, 1995; Lemasson *et al.*, 2010a; see also Takahashi *et al.*, 2013). Interestingly, social factors influence the organisation of vocal exchanges: in Campbell's monkeys, elders are more likely to receive a vocal response (Lemasson *et al.*, 2010a; see also for marmosets: Chen *et al.*, 2009), while in squirrel monkeys, closely-affiliated partners are preferred interlocutors (Biben *et al.*, 1986). Nonhuman primates are even capable of elaboration and persistence (two markers of intentional communication in humans) to increase their chances of getting a vocal response (Koda, 2004). They are also able to acoustically copy (immediate vocal convergence) their partner during a vocal exchange, by producing a response call that

structurally matches the one produced by their interlocutor (Sugiura, 1998); this phenomenon of "call matching" has also been observed in Diana monkeys and chimpanzees (Mitani and Brandt, 1994; Candiotti *et al.*, 2012).

9 The above-mentioned studies relate to adult plasticity, but human language is socially learnt at very early stages of development. Since the earliest works in the 1970s and 1980s, vocal development in nonhuman primates has been considered to be under strong genetic control. Social deprivation, deafening, hybridizing, and infant cross-fostering experiments revealed that nonhuman primates possess adult calls since birth and that they display little to no acoustic variability throughout their life (see Hammerschmidt and Fischer, 2008, for a review). But more recently, technical progress in acoustic analyses and a renewal of interest in vocal variability revealed some degree of acoustic variability during development (see Snowdon, 2009, for a review), and even a remarkable phenomenon of babbling in marmosets (Snowdon and Elowson, 2001).

10 In addition to the ontogeny of acoustic structure, a growing number of studies have provided evidence for social learning of the appropriate context of calling (see Seyfarth and Cheney, 1997; or Snowdon, 2009, for a review). For instance, any kind of flying object elicits an alarm call in young vervet monkeys, but through observation of adults' behaviour, they learn to become more selective and to use this call type only if they have spotted real aerial predators (Seyfarth and Cheney, 1997). In Japanese macaques, the appropriate use of greeting calls, notably the choice of specific receivers, is acquired in the course of development, probably under the social influence of group members (Katsu *et al.*, 2014). These studies have to some extent challenged the view of primate vocal behaviour as innate and inflexible, and they have highlighted the value of investigating vocal development in conjunction with the social environment.

11 To have a complete understanding of the mechanisms and functions underlying primate communication, as well as vocal production and usage, another important dimension to study is auditory perception. For a message to be conveyed, receivers must be able to discriminate between the fine acoustic variations described above. Thus, the cognitive abilities and neuropsychological mechanisms underlying nonhuman primates' perceptual capacities are an important area of research. Studies have provided evidence that various species of primates are able to perceive contextual variants and individual differences. For example, playback experiments have shown that monkeys, notably Japanese macaques, are able to discriminate between contextual variants of coo calls (Le Prell and Moody, 2000), girneys (Masataka, 1989) and screams (Le Prell *et al.*, 2002), and that they are capable of vocal recognition of individuals (intra-group: Ceugniet and Izumi, 2004b; Lemasson *et al.*, 2008 – inter-group: Briseño-Jaramillo *et al.*, 2015 – inter-species: Candiotti *et al.*, 2013), including mother-offspring pairs (Masataka, 1985; Shizawa *et al.*, 2005), and both maternal (Rendall *et al.*, 1996) and even paternal kin (Pfefferle *et al.*, 2014). Playback studies in different guenon species revealed that individual signatures are memorized for at least four years (Lemasson *et al.*, 2005) and that referential alarm calls are decoded at both conspecific and heterospecific levels (Zuberbühler, 2000; Coye *et al.*, 2015).

12 The assessment of nonhuman primates' perceptual abilities can provide insights regarding the evolutionary origin of language processing. For example, although the left cerebral hemisphere is known to play an essential role in the processing of speech in humans, there is also evidence of some task-sharing between the two hemispheres, with the left hemisphere specializing in processing of syntactic and semantic activities, and the right hemisphere attending preferentially to the prosody or novelty of a signal

(Friederici and Alter, 2004). No clear consensus about the phylogenetic origin of this hemispheric specialization has yet been reached, although there is some evidence for the importance of familiarity with the speaker as well as the emotional valence of the interaction on brain asymmetry in both human and nonhuman primates (Basile *et al.*, 2009).

3 Contributions of the France-Japan collaboration: A further step toward understanding primate communication

3.1 Vocal flexibility under social influences

13 To learn more about vocal flexibility in nonhuman primates, our teams have collaborated on two studies of the use of contact coo calls by adult Japanese macaques, with a special focus on the impact of the social characteristics of the caller and its interlocutor.

14 First, Lemasson and Masataka investigated sex differences in usage style of contact calls (Lemasson *et al.*, 2013a). They studied a group containing 8 adult males and 18 adult females, housed at the Primate Research Institute (University of Kyoto). Adult females were found to be more vocally active than males, and they also contributed more frequently to conversation-like vocal exchanges respecting the turn-taking rule. Interestingly, age was an important parameter: older females received increasingly more vocal responses from other group members. In males, however, dominance rank was the determining factor influencing call usage style, with lower-ranking males producing more repeated (juvenile-like) sequences than higher-ranking males.

15 Sex differences in nonhuman primates' calls can take the form of acoustic discrepancy (e.g. lower-pitched and longer calls in males) mostly related to differences in size and body weight (Ey *et al.*, 2007). But differences in call usage (e.g. higher call rates, preferential usage of certain call types) are thought to be related to sex-specific social roles (Bouchet *et al.*, 2010, 2012a). Females form the social core of the group in Japanese macaques, notably because they do not emigrate at puberty (Nakamichi and Yamada, 2010). They are thus often involved in mediation of intra-group social relationships, hence the frequent use of affiliative calls especially within socially ruled vocal exchanges. In addition, the order of participation within a vocal exchange is age-dependent, elders coming first, a pattern already known for other monkeys and in the conversations of most traditional oral, and some modern, human societies (Lemasson *et al.*, 2010a). Age is socially important in Japanese macaques, with older matriarchs possessing a particular social status (Nakamichi and Yamada, 2010). Males, by contrast, are more socially peripheral, acting mostly as group protectors and playing a role in social vigilance and inter-group spacing, hence the lesser use of social calls. Their hierarchical rank is nevertheless a critical determinant of their position, with dominant males being more integrated within the troop (Horiuchi, 2005). Interestingly, conversely to females, whose dominance rank is stable as it is determined by age and kinship (Nakamichi and Yamada, 2010), male inter-troop transfers cause frequent rank changes among resident males (Suzuki *et al.*, 1998).

16 A subsequent study asked whether vocal exchanges might parallel the social network, given that affiliative calls are used in mediating social interactions (Arlet *et al.*, 2015). Two

captive groups of Japanese macaques were studied, including 17 and 28 adult females respectively, housed at the Primate Research Institute in two very different enclosures (one relatively small with open visibility, and one large and forested). We tested whether affiliative relationships (measured through dyadic spatial proximity and grooming scores), kinship, dominance rank and age differences could predict the distribution of dyadic vocal exchanges. We found that contact call rates between two given females correlated only with the time spent grooming each other, regardless of the group. Interestingly, contact calls were mostly exchanged between females when they were distant from each other. Lastly, dyads presenting a higher level of grooming reciprocity also initiated vocal exchanges in a more balanced way.

17 These findings support the idea that social factors outweigh environmental factors in explaining flexibility in social call usage. Furthermore, this study provided empirical evidence for the predictions of the social bonding hypothesis developed by Dunbar (1996). This theory argues that vocal exchange rates evolved together with group size in primates, in order to facilitate the maintenance of cohesion between spatially-distant affiliated partners. Thus, once it became impossible to allocate enough time to physically interact with all affiliated group members, vocalizations replaced manual grooming as a form of "vocal grooming-at-a-distance", a step towards the emergence of conversations in the primate lineage.

3.2 Vocal development

18 The existence of vocal flexibility in adult nonhuman primates raises questions about how this variability emerges during ontogeny; there is a need for more studies in this domain. Our teams have collaborated on four studies investigating various aspects of vocal development in three nonhuman primate species.

19 One study, conducted at the Primate Research Institute, investigated the development of contact call use in Japanese macaques (Lemasson *et al.*, 2013a). This study (already mentioned above) provided evidence of sex differences in vocal usage in adults. However, observations of 10 juveniles (5 males, 5 females, average age: 8–10 months old) revealed no sex differences at this early age. Overall, juveniles differed from adults by their higher overall vocal activity, and by their production of 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); adults, by contrast, called mostly within temporally ruled vocal exchanges. Also, when juveniles contributed to vocal exchanges, they respected the turn-taking rule far less than adults.

20 Higher levels of vocal activity and absence of sex differences in juveniles have also been observed in other species, for example De Brazza's monkeys (Bouchet *et al.*, 2012a). This suggests that appropriate use of calls emerges through experience and social integration. As they grow older, individuals acquire more distinct social roles (Eaton *et al.*, 1985) and their vocal activity evolves accordingly. This process is hypothesized to be based on social learning from same-sex adult models. Our findings add to the growing literature showing that juveniles learn appropriate contexts of call emission from adults (Seyfarth and Cheney, 1997; Snowdon, 1997; Roush and Snowdon, 2001).

21 A second study focused on the turn-taking rule in another monkey species, again by comparing the appropriateness of call patterns between adults and juveniles, and also by testing the cognitive relevance of this rule in both age-classes (Lemasson *et al.*, 2011a).

Observations of 7 adult females and 7 youngsters, housed at the Station Biologique de Paimpont (University of Rennes 1), revealed that juveniles spontaneously break the turn-taking rule twelve times more often than adults. Furthermore, playback experiments showed that adult females discriminated between call exchanges that respected the turn-taking between callers and those that did not, whereas youngsters did not.

22 In a third study, using similar playback experiments based on the violation-of-expectation paradigm, Bouchet *et al.* (2013b) tested whether adult and juvenile Japanese macaques equally paid attention to the call-matching rule. As mentioned earlier, during vocal exchanges, adult female Japanese macaques acoustically copy their partner's calls (Sugiura, 1998). Observations revealed that sub-adults (aged 3-5 years old) were less efficient than adults at respecting the call-matching rule (Sugiura, 1998; Masataka, 2003). Here, we tested the ability of 10 adult females and 10 one-year-old females, housed at the Primate Research Institute, to discriminate between vocal exchanges that respected the call-matching rule or not. Again, only adults displayed different levels of interest for the two types of stimuli.

23 All of the above findings suggest that experience and social learning are involved in the emergence of different conversational rules. In fact, a recent study in marmosets provided empirical evidence that the turn-taking rule is learned during ontogeny under adult tutoring: adults reinforced their offspring by responding to calls that followed the species-typical temporal pattern, but remained silent following interrupted calls (Chow *et al.*, 2015). Interestingly, in human infants too, turn-taking and vocal imitation improve within the first few months of life, supported by feedback from the mother during vocal interactions (Masataka, 1992, 1993, 2003).

24 Finally, to better our understanding of maternal roles in monogamous primates, Koda and Lemasson investigated the development of wild gibbons' singing behaviour based on field data collected in Sumatra (Indonesia) (Koda *et al.*, 2013b). Pairs of adult gibbons produce complex duets during which male and female sing synchronously. As part of those duets, adult females produce great calls which are individually distinctive (Oyakawa *et al.*, 2007). Juveniles do not produce adult-like great calls, but sub-adult daughters are regularly involved in synchronized and overlapping great call interactions with their mother. We observed 6 female agile gibbons and their sub-adult daughters at different stages of development (inferred from co-singing rates). First, we found acoustic matching between mothers and daughters at the time of co-singing, which suggests abilities in immediate copying. Second, mothers were found to produce songs in a more stereotyped manner during mother-daughter interactions, especially at early stages of development, possibly to facilitate synchronization and their daughters' learning of the appropriate acoustic structure. Lastly, during development, the degree of acoustic resemblance between mother (but not other adult females) and daughter increases, along with the precision of synchronization in the duet.

25 This study provides evidence of a complex mechanism of song acquisition in sub-adult female gibbons, and highlights the maternal influence on offspring vocal development. Empirical evidence of social learning under parental influences and maternal tutoring is still very scarce. A recent study in marmosets demonstrated that infant calls undergo dramatic changes during the first two months of life, transforming from cries into mature adult-like phee calls. The timing of this transition was partly attributable to maturation but was also strongly influenced by contingent parental vocal feedback (Takahashi *et al.*, 2015).

3.3 Perceptual abilities

26 To know whether the acoustic variability observed is salient for the nonhuman primates themselves requires experiments. Playback experiments offer the possibility to investigate which characteristics of the acoustic stimuli subjects are sensitive to. Masataka's and Lemasson's teams have conducted two studies on the relevance of social and non-social acoustic stimuli in Japanese macaques and Campbell's monkeys, as well as a study testing for the pertinence of social visual stimuli in the same two species.

27 One study was conducted to explore the effects of sound specificity and familiarity on auditory laterality in Japanese macaques (Lemasson *et al.*, 2010b). Six adult females, housed at the Primate Research Institute, heard 10 categories of familiar and non-familiar nonhuman primate contact calls (familiar: calls of chimpanzees and gibbons housed at the same facility *versus* unfamiliar: calls of Campbell's monkeys, De Brazza's monkeys and red-capped mangabeys housed at the Station Biologique de Paimpont), bird calls (familiar: Japanese crows *versus* unfamiliar: French geese), and non-biological sounds (familiar: sound of pellets being poured into a bucket *versus* unfamiliar: piano melodies). Interestingly, familiarity, and not specificity, influenced auditory laterality but only for nonhuman primate calls, and not for other types of sounds. Experiments using the head-turn paradigm revealed a left-side head orientation (i.e. right cerebral hemisphere processing) bias at the group level for familiar nonhuman primates of the same or other species.

28 This finding confirms that the left-hemisphere dominance for communication processing in the primate lineage may have been over-emphasized, and that more studies investigating task-sharing between hemispheres are needed, "social" familiarity between interlocutors being an important factor to take into account. This finding also suggests that individual recognition is possible at the heterospecific level (see also Candiotti *et al.*, 2013), a potentially important ability for primates that share habitats with other species.

29 A second study asked whether there was a preference for consonant over dissonant sounds in Campbell's monkeys (Koda *et al.*, 2013a). An earlier study showed that Japanese macaques were able to discriminate between consonant and dissonant chords (Izumi, 2000). The distribution of this perceptual ability across the primate lineage is particularly interesting for unravelling the phylogenetic origin of musicality in humans, who spontaneously prefer consonant over dissonant sounds from early infancy (Zentner and Kagan, 1998). Musical ability, and the underlying cognitive mechanisms, have been hypothesized to constitute an intermediate stage in the evolution of language in the order Primates (Masataka, 2007, 2009). In our study, 6 adult female Campbell's monkeys, housed at the Station Biologique de Paimpont, were tested in an experimental paradigm that enabled monkeys to express their auditory preferences. We applied a sensory reinforcement paradigm based on the spontaneous spatial positioning of the subject, free to move in its habitual enclosure, which was divided into two identical sections. As soon as the monkey moved to one side, the corresponding loudspeaker played one of the paired-comparison sounds until the monkey crossed the central line and moved to the other side, resulting in the other paired-comparison sound being immediately broadcast from the opposite speaker. Monkeys showed no preference for consonant over dissonant stimuli, even though the experimental paradigm was verified as monkeys displayed a preference for soft over loud white-noise control stimuli.

30 In another study using the same experimental paradigm, tamarins did not show any preference for consonant chords (McDermott and Hauser, 2004). Only one human-reared infant chimpanzee has been reported to exhibit this preference (Sugimoto *et al.*, 2010); enculturation and previous experience of hearing music may account for its peculiar sensitivity to consonance. As very few music-based studies have been conducted comparing human and nonhuman primates, at present it is possible to conclude only that sensitivity to musical harmony has not been established in the latter; further investigations are needed.

31 Lastly, on a topic unrelated to the evolution of language but related to sensory and social preferences, our teams conducted a study of visual recognition of age-class and preference for infantile features in two species of Old World monkeys (Sato *et al.*, 2012). In humans, infantile features are innately perceived as cute (Sanefuji *et al.*, 2007); it is thought that attraction to "babyness" motivates caretaking behaviour. We tested 11 female Japanese macaques housed at the Primate Research Institute and 10 female Campbell's monkeys housed at the Station Biologique de Paimpont. Visual paired comparison tasks were conducted to test for the ability to discriminate between infant and adult images (of Japanese macaques) of their own species (Japanese macaque subjects) or of another species (Campbell's monkey subjects). Japanese macaques strongly discriminated, exhibiting a preference for infant over adult images. At the heterospecific level, Campbell's monkeys produced a weaker response, but still looked longer at infant *versus* adult images of Japanese macaques, suggesting that the attractiveness of infant images transcends species differences.

32 Nonhuman primate societies, like human society, are based on complex interactions between individuals who differ in their social roles. Age is a key determinant of social status, thus visual recognition of age-class, as with the perception of identity cues in vocal signals, might be critical for social group functioning. Humans can perceive not only conspecific but also heterospecific "babyness" (Sanefuji *et al.*, 2007). Our study provides evidence that this may also be the case in nonhuman primates, although additional studies in a wider range of species are needed.

4 Conclusion

33 The France-Japan collaboration has enabled both our teams to share their knowledge of experimental paradigms and some methodological (e.g. acoustic analysis) tools, to get access to research facilities for primate behaviour studies in each country, and to conduct comparative studies on a wide range of socially varied primate species. Together, Masataka's and Lemasson's teams have contributed significantly to the current debate about vocal flexibility in nonhuman primates and the evolutionary origins of human language. Their studies highlight the critical influence of social factors on the emergence of acoustic variability in nonhuman primates with some key results as follows: 1) vocal activity is determined by the subject's social status within the group; 2) the network of vocal exchanges parallels the network of affiliative interactions; 3) the appropriate acoustic structure of calls and the appropriate context of calling are to some extent subject to social learning; 4) parental feedback shapes offspring vocal ontogeny; 5) perceptual abilities for discriminating between various social acoustic and visual stimuli are related to social functioning and experience.

34 Over the years, our teams have gained extended knowledge, from both field and captive studies, about the communicative behaviour of two species notably: the Japanese macaque, a species endemic to Japan that lives in large multi-male multi-female groups, and the Campbell's monkey, an African guenon species that lives in harems. Comparative studies in these two, now well-known, key species whose social systems differ might allow us to further test the hypothesis of a co-evolution between social life and communicative abilities in the primate lineage (Dunbar, 1996; Masataka, 2008; Lemasson, 2011). This opens new lines of investigation regarding the factors which led to the emergence of the highly complex communication system that is human language (Zuberbühler *et al.*, 2009; Lemasson *et al.*, 2013b; Bouchet *et al.,* 2016).

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ABSTRACTS

Nobuo Masataka (University of Kyoto, Japan), Alban Lemasson (University of Rennes 1, France) and their colleagues have been collaborating for over a decade on projects investigating nonhuman primates' vocal behaviour and tackling the issue of the evolutionary origins of human language. They have worked together on topics including vocal flexibility under social influences in adults, the development of communicative abilities during ontogeny, and auditory and visual perception of social and non-social stimuli. In this paper, we review this work within the theoretical framework of language evolution.

Nobuo Masataka (Université de Kyoto, Japon), Alban Lemasson (Université de Rennes 1, France) et leurs collègues collaborent depuis une décennie à des projets s'intéressant au comportement vocal des primates non-humains et contribuant à élucider la question des origines évolutives du langage. Ils ont travaillé ensemble sur des sujets variés incluant la flexibilité vocale sous influences sociales chez l'adulte, le développement des capacités communicatives au cours de l'ontogénie, et la perception auditive et visuelle de stimuli sociaux et non-sociaux. Dans cet article, nous passons en revue ce travail en l'inscrivant dans le cadre théorique de l'évolution du langage.

INDEX

Geographical index: Japan, France
Mots-clés: communication vocale, plasticité acoustique, développement vocal, perception auditive, préférence visuelle, primates non-humains, langage
Keywords: vocal communication, acoustic plasticity, vocal development, auditory perception, visual preference, nonhuman primates, language

AUTHORS

HÉLÈNE BOUCHET

Université de Lyon – Université Jean Monnet Saint-Etienne, UMR 9197 Neuro-PSI / ENES – CNRS, Saint-Etienne, France.
Author for correspondence : helene.bouchet@yahoo.fr

HIROKI KODA

University of Kyoto, Primate Research Institute, Cognition and Learning Section, Japan.
Email: koda.hiroki.7a@kyoto-u.ac.jp

NOBUO MASATAKA

University of Kyoto, Primate Research Institute, Cognition and Learning Section, Japan.
Email: masataka.nobuo.7r@kyoto-u.ac.jp

ALBAN LEMASSON

Université de Rennes 1, UMR 6552 EthoS – CNRS, Station Biologique de Paimpont, Rennes, France.
Email : alban.lemasson@univ-rennes1.fr