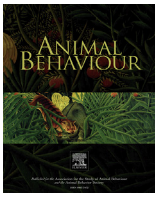
Animal Behaviour 115 (2016) 97–105

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Morphologically structured vocalizations in female Diana monkeys

Camille Coye [a, b, c, *], Klaus Zuberbühler [b, c, d], Alban Lemasson [a]

[a] *Université de Rennes 1, Ethologie animale et humaine–EthoS, U.M.R 6552-C.N.R.S, Station Biologique, Paimpont, France*
[b] *University of St Andrews, School of Psychology and Neuroscience, St Andrews, Fife, U.K.*
[c] *Centre Suisse de Recherches Scientifiques, Taï Monkey Project, Adiopodoumé, Abidjan, Côte d'Ivoire*
[d] *Université de Neuchâtel, Institut de Biologie, Neuchâtel, Switzerland*

ARTICLE INFO

Article history:
Received 2 June 2015
Initial acceptance 16 July 2015
Final acceptance 22 February 2016

MS. number:15-00472R

Keywords:
acoustic playback
call combination
field experiment
guenons
morphology
social communication

Social complexity is often thought of as a driving force in the evolution of communication and cognition, but this is at odds with the fact that nonhuman primates generally display only very limited flexibility in vocal production. Some primates partially overcome their limited vocal flexibility by combining two or more acoustically inflexible calls into complex sequences. Equally relevant is that some primate calls consist of separable morphological elements whose combinations create different meanings. Here, we focus on the vocal system of wild female Diana monkeys, *Cercopithecus diana*, which produce three call units (R, L, A) either singly or merged as RA or LA call combinations. Previous work has shown that R and L convey information about external events, while A conveys information about caller identity. We tested this hypothesis experimentally, by broadcasting artificially combined utterances to eight adult females. To test the significance of the R and L 'event' units, we merged them with the A 'identity' unit of a group member. To test the significance of the 'identity' unit, we merged an R 'event' unit with an 'identity' unit from a group member or a neighbouring individual. Subjects responded in ways that suggested that both event and identity units were relevant, suggesting that Diana monkeys' social calls possess morphosemantic features. We discuss this finding in relation to the coevolution of communication and social complexity in primates.

The evolution of vocal complexity in animals appears to be largely driven by social complexity as well as by visually difficult and ecologically challenging habitats (Bouchet, Blois-Heulin, & Lemasson, 2013; Dunbar, 1993, 1998; Marler, 1967; McComb & Semple, 2005). Many vertebrates and most primates live in social groups with complex and dynamic social networks and long-term social bonds (de Waal, 1987; Lehmann, Korstjens, & Dunbar, 2007; Wrangham, 1987). As a result, primates are constantly challenged to maintain cohesion during travel and other activities to optimize foraging, to compete with neighbouring groups and to protect themselves against predators (Dunbar & Shultz, 2007; Lehmann et al., 2007; van Schaik, 1983; van Schaik & van Hooff, 1983). To this end, many species have evolved specific vocalizations to maintain cohesion and synchronize within-group activities (Gautier & Gautier, 1977; Oda, 1996; Uster & Zuberbühler, 2001). Calls are often individually distinct and function to advertise individual identity or membership to specific social units (Bouchet, Pellier, Blois-Heulin, & Lemasson, 2010; Crockford, Herbinger, Vigilant, & Boesch, 2004; Dunbar, 2003; Neumann, Assahad, Hammerschmidt, Perwitasari-Farajallah, & Engelhardt, 2010; Rendall, Rodman, & Emond, 1996).

In light of this, it is surprising that nonhuman primates are thought to have relatively limited, species-specific vocal repertoires with a fixed set of call types that remain largely unchanged throughout adult life (review by Bouchet et al., 2013) and little sign of flexibility or voluntary control in call production (Hammerschmidt & Fischer, 2008). However, a more recent line of research has continued to demonstrate a previously underdescribed source of communicative complexity, namely the ability of individuals to assemble fixed acoustic units of their repertoire into more complex utterances. There is now good evidence that several nonhuman primate species produce calls in nonrandom sequences, with the information changing depending on the order or temporal structure of call sequences (vervet monkeys, *Chlorocebus aethiops*: Seyfarth, Cheney, & Marler, 1980; Campbell's monkeys, *Cercopithecus campbelli*: Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010; Ouattara, Lemasson, & Zuberbühler, 2009a; Zuberbühler, 2001; white-handed gibbons, *Hylobates lar*: Clarke, Reichard, & Zuberbühler, 2006; bonobos, *Pan paniscus*, and

---

[*] Correspondence: C. Coye, Station Biologique de Paimpont, 35380 Paimpont, France.
E-mail address: camille.coye@univ-rennes1.fr (C. Coye).

http://dx.doi.org/10.1016/j.anbehav.2016.03.010
0003-3472/© 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

chimpanzees, *Pan troglodytes*: Clay & Zuberbühler, 2011; Slocombe & Zuberbühler, 2005; Diana monkeys, *Cercopithecus diana*: Zuberbühler, 2000). One argument has been that these combinatorial capacities evolved in primates to enable more complex communication (Zuberbühler & Lemasson, 2014).

So far, however, most examples of call combinations are from studies on male primate alarm calls, which is surprising because social events may be at least as complex as dealing with predator encounters. Hence, if complex vocal abilities have evolved to deal with social complexity, we should find combinatorial phenomena in vocal behaviour during social interactions and also in females, the social core of primate species (Buzzard & Eckardt, 2007; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987).

One particularly promising candidate is the contact call of some forest-living female guenons. In Campbell's monkeys, for instance, adult females produce a short, low-pitched contact call, either as a single unit or merged with a second long, arched and frequency-modulated unit to form multi-unit utterances (Lemasson & Hausberger, 2011). The acoustic structure of the first unit varies depending on the degree of arousal experienced by the caller (Lemasson, Remeuf, Rossard, & Zimmermann, 2012) and contains fewer identity cues than the second, arched unit, which strongly relates to the caller's identity (Lemasson & Hausberger, 2011; Lemasson, Hausberger, & Zuberbühler, 2005; Lemasson, Ouattara, Petit, & Zuberbühler, 2011). The second unit is never uttered alone but functions as an affix to the first unit, which can also be uttered alone.

A second relevant example is the contact calls of female Diana monkeys, an arboreal forest-dwelling primate living in groups of one adult male and several adult females with their offspring (McGraw, Zuberbühler, & Noë, 2007). As in most primates, the females are the philopatric sex and constitute the social core of the group (Candiotti et al., 2015). They produce, among others, three acoustically distinct social calls (L, R and A) depending on context (Candiotti, Zuberbühler, & Lemasson, 2012a, 2012b; Uster & Zuberbühler, 2001): L calls are mostly given in sociopositive and neutral events (e.g. foraging, affiliative interactions). R calls are mostly given in socionegative events and mild danger (e.g. conflict within or between groups, walking on the ground), suggesting that these calls relate to the external events or emotional valence experienced by the caller. Finally, A calls are produced in unspecific ways to a large variety of events, but here the acoustic structure varies substantially between individuals, suggesting they function to signal the caller's identity, similar to what has been found in Campbell's monkeys. The three call types can be produced alone (A, L, R) or merged as two combined utterances, either LA or RA. Combined structures thus contain information about the external event (L or R) and the caller's identity (Candiotti et al., 2012a, 2012b), with some interesting parallels to the function of morphemes in human speech (Collier, Bickel, Schaik, Manser, & Townsend, 2014; Hurford, 2008; Tellier, 2008; Veselinovic, Candiotti, & Lemasson, 2014).

Here, we tested experimentally whether the information conveyed by contact calls of female Diana monkeys is compositional, i.e. whether the combined calls relate linearly to the information conveyed by the units given singly, as suggested by Candiotti et al.'s (2012a) observational data. To this end, we broadcast artificially combined calls to different subjects, eight female Diana monkeys belonging to a study group habituated to human presence. We created experimental stimuli by manipulating either the initial or final call unit, using recordings from group members, neighbours or completely unfamiliar individuals. Our goal was to test the significance of the L and R 'event' and A 'identity' units. To this end, we merged L and R 'event' units with A 'identity' units from familiar group members or neighbouring individuals. We predicted that, if combinations of call units were meaningful to receivers, L and R units should cause significant behavioural differences, particularly in terms of vocal responses, vigilance and exploratory behaviours. Because Diana monkeys are highly territorial, we also predicted different behavioural responses to the identity-encoding A units, depending on whether they originated from a group member or neighbour.

METHODS

Study Site and Subjects

Field experiments were conducted between June and September 2014 in Taï National Park, Ivory Coast (5°50′N, 7°21′W). The experimenter (C.C.) and two field assistants (F.B. and F.G., see Acknowledgments) conducted playback experiments with a free-ranging group of Diana monkeys with individually known subjects habituated to human presence for more than 20 years. At the time of the experiments, the group consisted of one adult male and eight adult females with their offspring. All adult females served as subjects in the experiments.

Playback Stimuli

All calls (stimuli and subject's reaction to the playbacks) were recorded using a Sennheiser K6/ME66 directional microphone connected to a Marantz PMD660 recorder (sampling rate 44.1 kHz, resolution 16 bits, WAV sound format). Calls from group members were recorded in May 2014; calls from unfamiliar and neighbouring individuals were recorded in June–July 2013 and February–June 2010. All calls were recorded under similar environmental conditions and distances to ensure high quality, low background noise and no overlap with other relevant sounds.

When creating the playback stimuli, we followed Candiotti et al.'s (2012a) classification (Fig. 1), defining L call units as 'continuous low-pitched trills with a general ascending frequency modulation' (duration ± SD: 409 ± 106 ms; minimum fundamental frequency ± SD: 247 ± 84 Hz; maximum fundamental frequency ± SD: 654 ± 354 Hz), R call units as 'rapid repetitions of one to four short atonal units separated by brief periods of silence' (duration ± SD: 82 ± 29 ms; minimum fundamental frequency ± SD: 331 ± 170 Hz; maximum fundamental frequency ± SD: 429 ± 199 Hz; first unit duration ± SD: 28 ± 11 ms; first interunit silence ± SD: 46 ± 18 ms) and A call units as tonal, arch-shaped frequency modulations (duration ± SD: 298 ± 105 ms; minimum fundamental frequency ± SD: 324 ± 233 Hz; maximum fundamental frequency ± SD: 3090 ± 696 Hz).

We created 24 different playback stimuli to generate the following three categories (Fig. 2): LA$_G$: combination of an unfamiliar individual's L merged with an A from an adult female group member ($N = 8$); RA$_G$: combination of an unfamiliar individual's R merged with an A from an adult female group member ($N = 8$); RA$_N$: combination of an unfamiliar individual's R merged with an A from an adult female from a neighbouring group ($N = 8$).

Each of the eight subjects received its own set of LA$_G$, RA$_G$ and RA$_N$ call combinations. Within a given set, we systematically used the same R call unit and the same A call unit to create paired stimuli (i.e. L**A$_G$**–R**A$_G$** and **R**A$_G$–**R**A$_N$) to allow the comparison of the changes in subject's reaction due to changes in only one part of the call. L and R call units were systematically extracted from naturally produced LA and RA call unit combinations. We further made sure that all unfamiliar L and R call units came from different individuals by using recordings from a different group. Only R calls composed of double units were used. A call units were from identified and habituated adult females of the focal