Morphologically structured vocalisations in female Diana monkeys

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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 non-human 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 diana*), who 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 morpho-semantic features. We discuss this finding in relation to the co-evolution of communication and social complexity in primates.

INTRODUCTION

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; Dunbar, 1998; Marler, 1967; McComb & Semple, 2005). Many vertebrates and most primates live in social groups with complex and dynamic social networks and long-term 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 optimise 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 evolved specific vocalisations to maintain cohesion and synchronise 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 non-human 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 signs of flexibility or voluntary control in call production (Hammerschmidt & Fischer, 2008). However, a more recent line of research has continued to demonstrate a previously under-described 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 non-human primate species produce calls in non-random sequences, with the information changing depending on

57 the order or temporal structure of call sequences (vervet monkeys *Cholorocebus aethiops*:

58 Seyfarth, Cheney, & Marler, 1980; Campbell's monkeys *Cercopithecus Campbelli*: Lemasson,

59 Ouattara, Bouchet, & Zuberbühler, 2010; Ouattara, Lemasson, & Zuberbühler, 2009a;

60 Zuberbühler, 2001; white-handed gibbons *Hylobates lar*: Clarke, Reichard, & Zuberbühler,

61 2006; bonobos *Pan paniscus* and chimpanzees *Pan troglodytes*: Clay & Zuberbühler, 2011;

62 Slocombe & Zuberbühler, 2005; Diana monkeys *Cercopithecus diana diana*: Zuberbühler,

63 2000). One argument has been that these combinatorial capacities evolved in primates to enable

64 more complex communication (Zuberbühler & Lemasson, 2014).

65

66 So far, however, most examples of call combinations are from studies on male primate alarm

67 calls, which is surprising because social events may be at least as complex as dealing with

68 predator encounters. Hence, if complex vocal abilities have evolved to deal with social

69 complexity, we should find combinatorial phenomena in vocal behaviour during social

70 interactions and also in females, the social core of primates species (Buzzard & Eckardt, 2007;

71 Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987).

72

73 One particularly promising candidate is the contact call of some forest living female guenons.

74 In Campbell's monkeys, for instance, adult females produce a short, low-pitched contact call,

75 either as a single unit or merged with a second long, arched, and frequency-modulated unit to

76 form multi-unit utterances (Lemasson & Hausberger, 2011). The acoustic structure of the first

77 unit varies depending on the degree of arousal experienced by the caller (Lemasson, Remeuf,

78 Rossard, & Zimmermann, 2012) and contains fewer identity cues than the second, arched unit,

79 which strongly relates to the caller's identity (Lemasson & Hausberger, 2011; Lemasson,

80 Hausberger, & Zuberbühler, 2005; Lemasson, Ouattara, Petit, & Zuberbühler, 2011). The

81 second unit is never uttered alone but functions as an affixation to the first unit, which can also

82 be uttered alone.

83 A second relevant example is the contact calls of female Diana monkeys, an arboreal forest-

84 dwelling primate living in groups of one adult male and seven to thirteen adult females with

85 their offspring (McGraw, Zuberbühler, & Noë, 2007). As in most primates, the females are the

86 philopatric sex and constitute the social core of the group (Candiotti et al., 2015). They produce,

87 amongst others, three acoustically distinct social calls (L, R and A) depending on context

88 (Candiotti, Zuberbühler, & Lemasson, 2012a, 2012b; Uster & Zuberbühler, 2001): L calls are

89 mostly given in socio-positive and neutral events (e.g., foraging, affiliative interactions). R calls

90 are mostly given in socio-negative events and mild danger (e.g., conflict within or between

91 groups, walking on the ground), suggesting that these calls relate to the external events or

92 emotional valences experienced by the caller. A calls, finally, are produced in unspecific ways

93 to a large variety of events, but here the acoustic structure varies substantially between

94 individuals, suggesting they function to signal the caller's identity, similar to what has been

95 found in Campbell's monkeys. The three call types can be emitted alone (A, L, R) or merged

96 as two combined utterances, either LA, or RA. Combined structures thus contain information

97 about the external event (L or R) and the caller's identity (Candiotti et al., 2012a, 2012b), with

98 some interesting parallels to the function of morphemes in human speech (Collier, Bickel,

99 Schaik, Manser, & Townsend, 2014; Hurford, 2008; Tellier, 2008; Veselinovic, Candiotti, &

100 Lemasson, 2014).

101

102 Here, we tested experimentally whether the information conveyed by complex calls of Diana

103 monkeys is compositional, i.e., whether the combined calls relate linearly to the information

104 conveyed by the units given singly, as suggested by Candiotti et al.'s (2012a) observational

105 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 and 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 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 identity-encoding A units, depending on whether they

originated from a group member or neighbour.

MATERIAL AND 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 (CC) and two field assistants (FB and FG)

conducted playback experiments in a free-ranging group of Diana monkeys (*Cercopithecus*

diana diana) with individually known subjects habituated to human presence for more than

twenty years. At the time of the experiments, the group consisted of one adult male and eight

adult females with their offspring. The experiment involved all the adult females of the

habituated group.

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) in Taï National Park. Calls from group

130   members were recorded in May 2014; calls from unfamiliar and neighbouring Diana monkeys

131   were recorded in June-July 2013 and February-June 2010. All calls were recorded under similar

132   environmental conditions and distances to ensure high quality, low background noise, and no

133   overlap with any other sound.

134

135   When creating the playback stimuli, we followed Candiotti et al., (2012a) classification (Fig.

136   1), who define L call units as continuous low-pitched trills with a general ascending frequency

137   modulation (duration±SD: 409±106 ms, Minimum fundamental frequency±SD: 247±84 Hz,

138   Maximum fundamental frequency±SD: 654±354 Hz), R call units as rapid repetitions of one to

139   four short atonal units separated by brief periods of silence (duration±SD: 82±29 ms, Minimum

140   fundamental frequency±SD: 331±170 Hz, Maximum fundamental frequency±SD: 429±199 Hz,

141   First unit duration±SD: 28±11 ms, First inter-unit silence±SD: 46±18 ms) and A call units as

142   tonal, arch-shaped frequency modulations (duration±SD: 298±105 ms, Minimum fundamental

143   frequency±SD: 324±233 Hz, Maximum fundamental frequency±SD: 3090±696 Hz).

144

| Ab	LAb	RAb
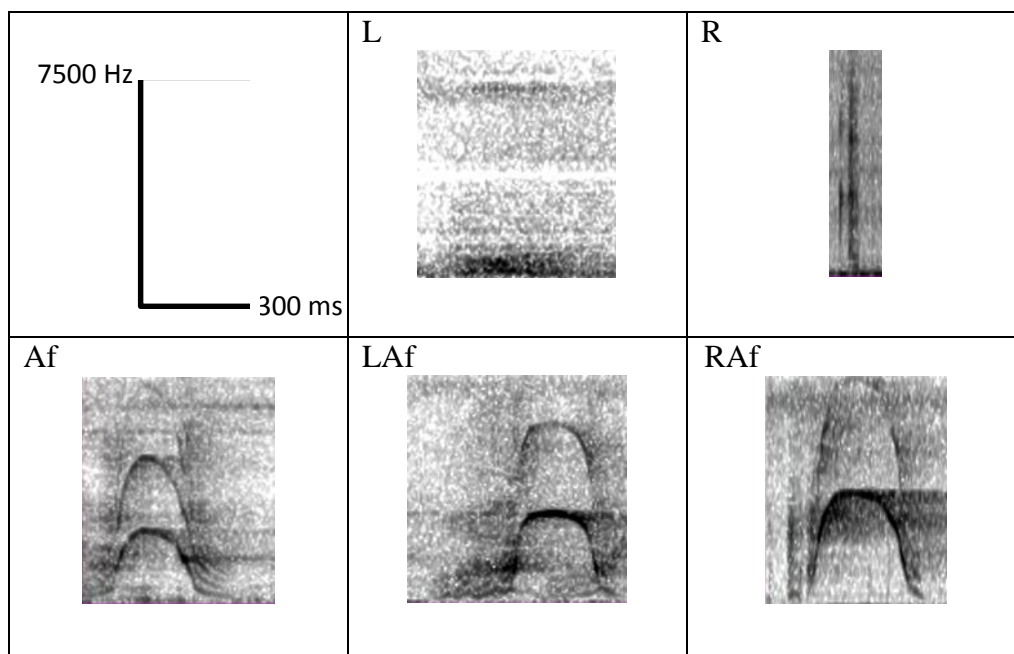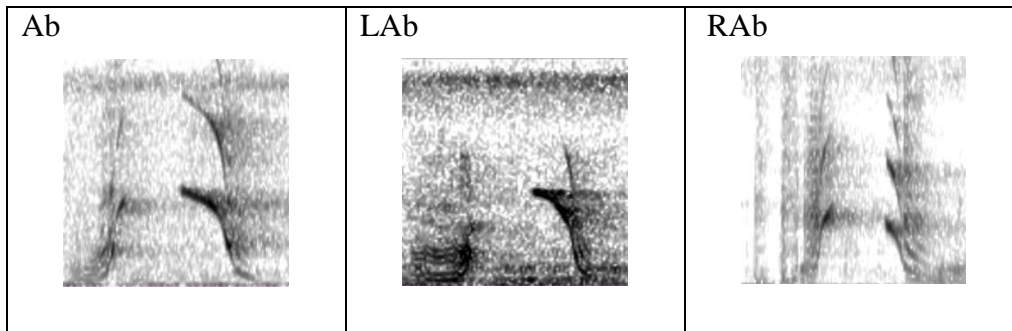
Figure 1: A, L and R call exemplars from female Diana monkeys emitted alone or merged into combined calls LA and RA (Ab and Af being two sub-types of A call).

We created twenty-four 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).
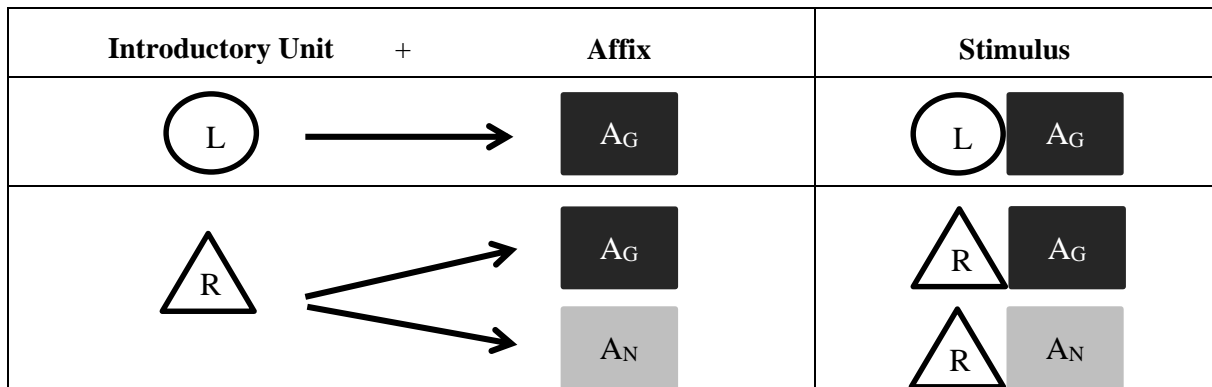
Figure 2: Stimulus creation. The geometric shapes indicate the valence of the call. Circle and triangle represent context-dependent units, respectively L (associated with positive and neutral events) and R (associated with negative events). Rectangles represent identity-dependent units A. The shading indicates the origin of the call recorded: white: unfamiliar individuals; black: group-members; grey: neighbouring individuals.

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., LA_G-RA_G and RA_G-RA_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

164 extracted from naturally produced LA and RA call unit combinations. We further made sure

165 that all unfamiliar L and R call units came from different individuals by using recordings from

166 a different group. Only R calls composed of double units were used. 'A' call units were from

167 identified and habituated adult females of the focal group (A_G) or the neighbouring group (A_N).

168 For each focal female, group or neighbour identities were pseudo-randomly attributed. This

169 was done to avoid complete pair-matching between group members: if the call from female A

170 was used as a stimulus for female B, then the call from female B was not selected to serve as

171 stimulus for female A, to prevent any particular social relationship between two individuals to

172 be over-represented. 'A' call units can be subdivided into full arches (Af subtype) or broken

173 arches (Ab subtype) (Fig. 1). Females differ in how they make use of this feature, with some

174 females mainly using 'Af' or 'Ab' subtypes (Candiotti et al., 2012a). When editing playback

175 stimuli, we used a group-member's most typical A subtype which was then matched with the

176 corresponding subtype for the neighbouring female stimulus.

177

178 Playback stimuli were created using Raven Pro 1.4 Software. Call exemplars were selected

179 based on recording quality and call duration (in seconds: mean ± *SE*: L = 0.170 ± 0.012 s, R =

180 0.108 ± 0.002 s, A = 0.293 ± 0.014 s). We amplified stimuli when necessary to obtain a

181 naturalistic intensity. Final tests of broadcast intensity were made in the Taï National Park to

182 make sure that stimuli's intensity was homogeneous and appropriate according to the natural

183 background noise.

184

185 *Experimental protocol*

186 Three observers followed the study group from 9:00 to 17:00 local time. Before the first

187 experiment, we ran a habituation phase on several consecutive days during which the equipment

188 was installed underneath the middle of the group in an open area so that it was fully visible to

189   the subjects. We repeated this until the subjects stopped giving alert calls and lost interest in the

190   equipment. Before starting an experimental trial, we ensured that the group was not travelling

191   or foraging 30 m or higher, that no neighbours were in the vicinity and that no male loud calls

192   had been produced for at least 15 min. The experimenters then selected the subject and

193   positioned the playback equipment at an elevation of 4 to 6 m above ground using a telescopic

194   perch, either in periphery of the group (stimuli made from neighbouring female calls) or within

195   the group. For within group trials, we kept the speaker about 5 m to 10 m away from the A call

196   unit providing female. We did not wait for the subject to move to a specific position within the

197   group and tested her where she was. Hence, playbacks of intra-group calls have been given

198   from varied positions (more or less peripheral) in the group, without any obvious consequence.

199   For each playback, CC continuously observed the subject, while FB and FG followed the call

200   provider (in-group trials) and handled the equipment, respectively. Before initiating a trial, we

201   ensured that (1) the subject was fully visible, (2) the call provider was 5 to 10 m away from the

202   speaker, and (3) no call was given by any group member for at least 8 s.

203

204   Playback stimuli were broadcast from a Marantz PMD660 solid-state recorder connected to a

205   Nagra DSM speaker/amplifier and a Bose 151 Environmental speaker that had been mounted

206   to a telescopic perch. We recorded the behaviour of the subject for 30 s and the group's vocal

207   behaviour for 60 s following each trial.

208

209   We never performed more than two trials per day and never for more than two days in a row.

210   We ensured that we never broadcast two combined calls of the same category within the same

211   day and we did not test the same individual in two consecutive experiments. Each day, we

212   performed one to three "mock" experiments (even on days when no experiment was scheduled)

213 by executing the full experimental protocol, but no sound diffusion, to prevent subjects from

214 anticipating a trial.

215

216 *Dependent variables*

217 During the 30 s post-playback period, we described the behaviour of the subject as the total

218 duration (s) and frequency (i.e., the number of times a behaviour was observed) of its posture

219 (i.e., sitting, standing or in vigilance posture), locomotion (i.e., immobile, walking, running or

220 jumping) and direction of gaze (i.e., looks at the speaker, above, under, at a conspecific, at the

221 observer and scans the environment). We also scored the latency in seconds for four behaviours:

222 adopting a vigilance posture, sitting, walking and looking at the speaker. Overall, this resulted

223 in 32 variables to describe each subject's behavioural response.

224

225 During the 1 min post-playback period, we also quantified the group's vocal activity using the

226 following variables: the latency to give first call (any call type), the number of social calls

227 (Coye, Ouattara, Zuberbühler, & Lemasson, 2015), the number of alert calls (Coye et al., 2015),

228 the number of calls given during vocal exchanges (a sequence of any calls separated by less

229 than 3 s of silence), the number of isolated calls (any call given more than 3 s before or after

230 another call), as well as the number of vocal exchanges (involving any call type) and the average

231 number of calls involved in a vocal exchange.

232

233 *Statistical analysis*

234 We expected the subjects' responses to differ in several subtle behavioural indicators

235 simultaneously (notably locomotion, vocalizations and direction of gaze), suggesting that

236 multivariate testing was most appropriate to deal with the potential co-variation of the variables.

237 Any pair of variables with an R Pearson's correlation coefficient above 0.7 was considered

colinear in case of which we systematically deleted one member of the colinear pair (Dormann et al., 2013; Katz, 2011). Then, we used a Linear Discriminant Analysis as a preliminary guide for variables selection but did not use this method for further statistical analysis due to repeated measures present in our data (see Mundry & Sommer (2007) for details on LDA and discussion of the case of repeated measures). This first, exploratory, step led to the selection of a subset of seven biologically relevant variables susceptible to represent subjects' reaction (group's vocal behaviour, subject locomotion and gaze direction) across the experimental conditions. We used five quantitative variables: Number of isolated calls (given more than 3 seconds before or after another call), Latency to give first call (s), Time spent walking (s), Latency before locomotion (s), Duration of first look to the speaker (s), and two binary variables: Presence/absence of Look towards the observer, and Presence/absence of Visual scanning of the environment (Fig. 3).

We calculated Gower's dissimilarity index between samples in the dataset (daisy{cluster}, R statistical software, Maechler et al., 2015). This index "summarises" the difference between two samples into a measure of distance, based on the samples' values for each variable included in the analysis. Gower's distance is a common method which allows the use of various types of variables (binary, ordinal, nominal and quantitative variables) (Gower, 1971; Oksanen et al., 2007; Podani, 1999). The two binary variables were treated as symmetric variables and no standardisation of variables was applied.

To study the impact of the introductory unit (L or R units) and the impact of the affix (A units from a group-member or a neighbour), we performed two separate non-parametric MANOVAs (Adonis{vegan}, R statistical software, Oksanen et al., 2007) on the matrixes of Gower's dissimilarity index, giving the distance between trials in LA_G-RA_G and RA_G-RA_N conditions respectively. Both NPMANOVAs were two-tailed, included the type of stimulus and the

263 identity of the subject as factors and were conducted using free permutation of the distance

264 matrixes, as suggested by Anderson (2001) and Gonzalez and Manly (1998) for small datasets.

265

266 NPMANOVA is a non-parametric multivariate method involving the calculation of an F-ratio

267 on an index of distances between samples. The computation of a p-value, like any other

268 permutational test, involves a comparison of the test value (i.e., the F-ratio) obtained on the

269 original dataset (i.e., the distance matrix) with test values computed on random permutations of

270 the same dataset. See Anderson (2001) for detailed explanation of the method and equations,

271 as well as Adams and Anthony (1996) for a discussion of the use of permutational tests on

272 behavioural data.

273

274 We completed the analysis with graphic representation of the results to describe the nature of

275 the behavioural changes (Fig. 3). We computed effect size for each variable included in the

276 multivariate testing. We used Cliff's delta for the quantitative (i.e., count and continuous)

277 variables (cliff.delta{effsize}, R statistical software, (Torchiano, 2015) using the original

278 formula proposed by (Cliff, 2014). And we used risk difference (riskdifference{fmsb}, R

279 statistical software (Nakazawa, 2015) with a 95% confidence interval for the binary variables.

280

281 *Ethical note*

282 Ethics approval was given by the St Andrews' University Ethics Boards; the research protocol

283 was authorised in Côte d'Ivoire, by the Minister of Scientific Research and the 'Office Ivoirien

284 des Parcs et Réserves' (OIPR). This study does not raise major issues regarding animal welfare.

285 Study groups have been habituated to human presence and followed on a regular basis since

286 1990 while the continued presence of researchers and field assistants has had a significant

287 impact on decreasing firearms-based poaching activities in the area. The habituation to the

288   playback equipment was conducted smoothly. Moreover, the call types broadcast during the

289   playbacks are naturally given at relatively high frequency: LA calls: 19.8 calls per hour, RA

290   calls: 2.7 calls per hour (Candiotti et al. 2012a). Intergroup encounters, as simulated by

291   playbacks of RA_N combinations (involving A calls from a neighbour), occur on average once

292   every three days (McGraw et al., 2007 p59). No playback enhanced male alarm calling

293   behaviour or triggered any sign of group panic or other abnormal behaviour.

294

295   RESULTS

296   *Impact of the Introductory Unit on subjects' reaction:*

297   When analysing the impact of the introductory unit, the NPMANOVA showed a significant

298   impact of the type of stimulus ($F_{1,7}$= 3.37, *P*=0.043) and no significant effect of the subject's

299   identity ($F_{7,7}$= 1.71, *P*=0.142). Graphic representation of the variables measured, combined

300   with measures of effect size, show that test subjects expressed distinct behavioural patterns in

301   the different experimental conditions (Fig. 3). Playbacks of LA_G ('positive' introduction, A

302   from a group member) and RA_G ('negative' introduction, A from a group member) stimuli

303   caused differences in locomotion, vocal behaviour and gaze direction (Fig. 3). Latency before

304   locomotion appears shorter after playbacks of RA_G than LA_G (medium effect size: *N*= 16, *Cliff's*

305   *delta*= -0.47), although we found no clear difference in the time spent walking (negligible effect

306   size: *N*= 16, *Cliff's delta*= -0.125). The group gave more isolated calls (i.e., calls not part of a

307   vocal exchange) in the RA_G than in the LA_G condition, with a medium effect size (*N*= 16, *Cliff's*

308   *delta*= -0.47).The latency to give a first call was shorter and much less variable in the RA_G than

309   in the LA_G condition although only a negligible effect was detected (*N*= 16, *Cliff's delta*=

310   0.125). Finally, the duration of the first look towards the speaker (*N*= 16, *Cliff's delta*= -0.031,

311   negligible effect) and the presence of looks towards the observer (*N*= 16, *RD*= -0.125, *P*= 0.285)

312   did not change between LA_G and RA_G conditions (0% of the LA_G trials, 12.5% of the RA_G

313   trials), but subjects scanned the environment more after the playback of the negative (i.e., RA_G)

314   stimulus (37.5% of the trials) than after playbacks of LA_G (0% of the trials; $N= 16$, $RD= 0.375$,
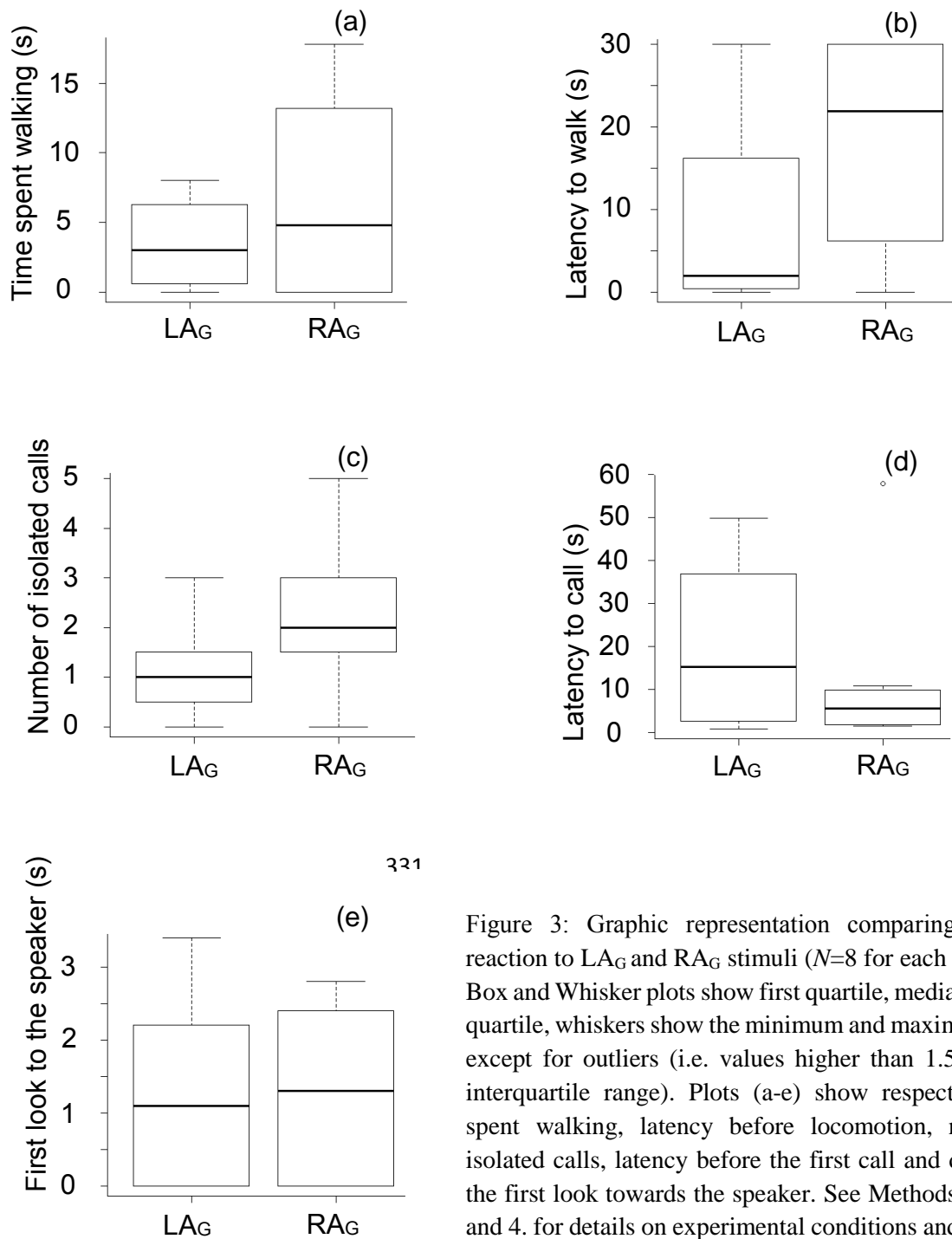
315     $P= 0.028$).

Figure 3: Graphic representation comparing subjects' reaction to LA_G and RA_G stimuli ($N=8$ for each condition). Box and Whisker plots show first quartile, median and third quartile, whiskers show the minimum and maximum values except for outliers (i.e. values higher than 1.5 times the interquartile range). Plots (a-e) show respectively time spent walking, latency before locomotion, number of isolated calls, latency before the first call and duration of the first look towards the speaker. See Methods section 2. and 4. for details on experimental conditions and variables.

343   *Impact of the affix on subjects' reaction:*

344   When analysing the impact of the affix, the NPMANOVA showed a significant impact of the

345   type of stimulus involved ($F_{1,7}$= 4.29, *P*= 0.02) and no significant role of subject's identity

346   ($F_{7,7}$= 1.66, *P*= 0.155). Graphic representation of the variables, combined with measures of

347   effect size, show that test subjects expressed distinct behavioural patterns in the experimental

348   conditions (Fig. 4): Comparison between responses to RA_G ('negative' introduction, A from

349   group member) and RA_N ('negative' introduction, A from a neighbour) stimuli highlighted

350   differences in locomotion, vocal behaviour and gaze direction but with a different pattern from

351   the one found for the impact of the introductory unit (Fig. 4). Subjects spent less time walking

352   (*N*= 16, *Cliff's delta*= 0.31, small effect size) and had a greater latency before locomotion (*N*=

353   16, *Cliff's delta*= -0.38, medium effect size) after playback of RA_N than RA_G stimuli. The

354   results also suggest slight differences in group's vocal behaviour: groups gave fewer isolated

355   calls (*N*= 16, *Cliff's delta*= 0.33) and displayed slightly greater and more variable latencies

356   when giving the first calls (*N*= 16, *Cliff's delta*= -0.23) after playbacks of RA_N than RA_G

357   stimuli. Finally, the pattern of gaze direction differed strongly between RA_G and RA_N stimuli:

358   after playbacks of RA_N stimuli, subjects' first looks to the speaker were longer (*N*= 16, *Cliff's*

359   *delta*= -0.73) with a large effect size. Subjects looked more at the observer (*N*= 16, *RD*= -0.375,

360   *P*= 0.077) in the RA_N condition (50% of the RA_N trials vs 12.5% of the RA_G trials) but visual

361   scanning of the environment did not seem to differ strongly between the playback of RA_G

362   (37.5% of the trials) and RA_N (12.5% of the trials) stimuli (*N*= 16, *RD*= 0.25, *P*= 0.23).
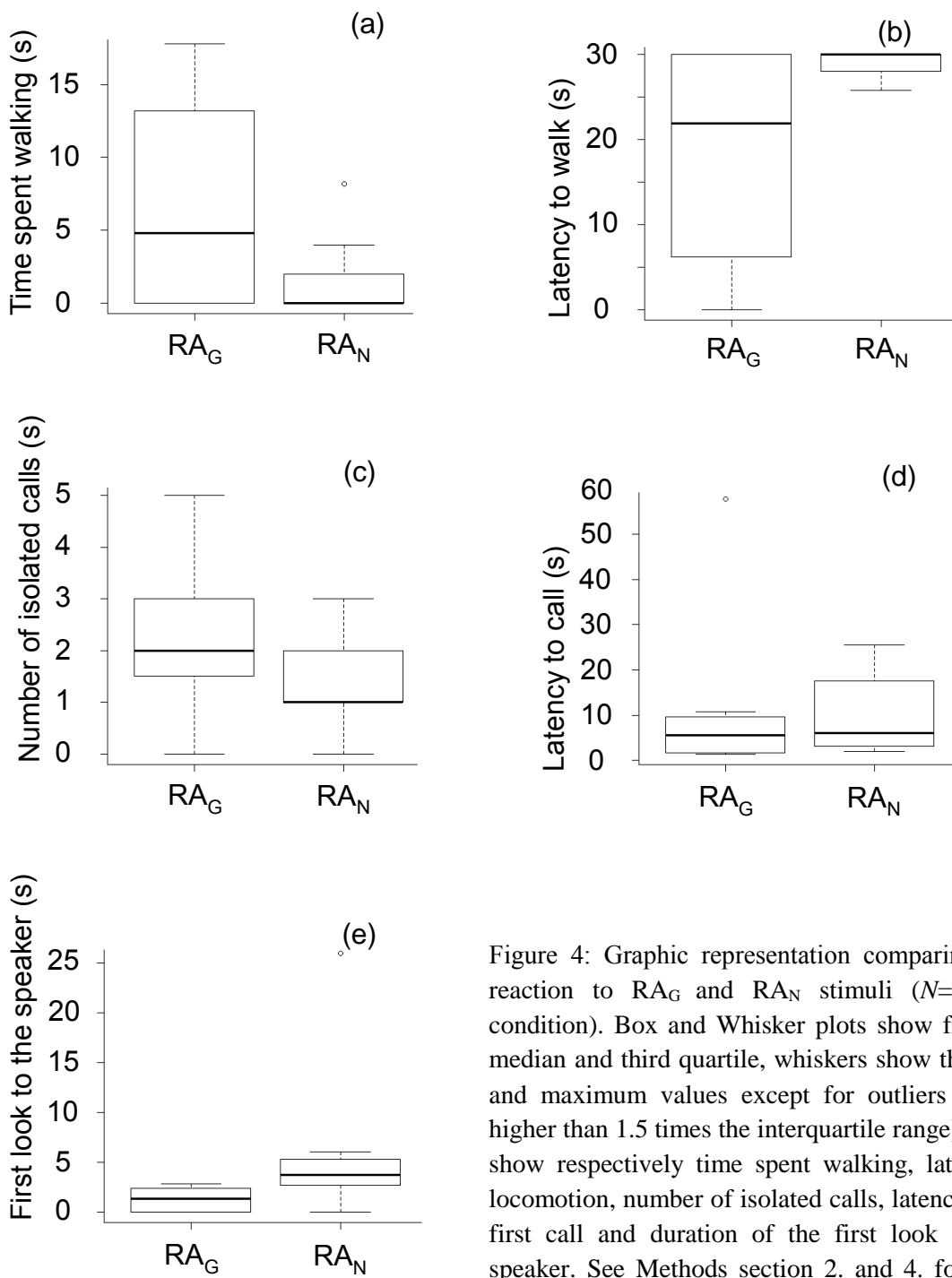
363

Figure 4: Graphic representation comparing subjects' reaction to RA_G and RA_N stimuli (N=8 for each condition). Box and Whisker plots show first quartile, median and third quartile, whiskers show the minimum and maximum values except for outliers (i.e. values higher than 1.5 times the interquartile range). Plots (a-e) show respectively time spent walking, latency before locomotion, number of isolated calls, latency before the first call and duration of the first look towards the speaker. See Methods section 2. and 4. for details on experimental conditions and variables.

DISCUSSION

In this study, we demonstrated experimentally that Diana monkeys responded differently to social calls composed of different morphological units in ways that suggested that at least two levels of information were conveyed. Morphological compounds consisted of L or R units, which related to different external events experienced by the caller (Candiotti et al., 2012a), and of A units, which related to caller identity. Response pattern suggested that recipients attended to these different levels of information conveyed by the call compounds. Specifically, our findings supported the idea that the initial morphemic unit of a combined call (L or R) encodes information about the social context experienced by the caller. R call units are typically associated with negative events, such as the detection of mild danger. Here, subjects responded with isolated social calls, prolonged latency before locomotion and scanning of the environment compared to L call units (typically associated with neutral and positive events) Overall, these results suggest that recipients associated the R and L call units with distinct socio-environmental contexts and adapted their behaviour accordingly.

The ability to reveal one's motivational states is a well-known function of animal communication (Briefer, 2012; Lemasson et al., 2012; Schehka & Zimmermann, 2009; Taylor & Reby, 2010), although it is often difficult to make a compelling argument about the exact nature of the underlying inner processes. Interestingly, the acoustically homologous call of Diana's monkey L unit in Campbell's monkeys increases in duration and frequency according to presumed differences in arousal (Lemasson et al., 2012). Here, we confirm the importance of this acoustic component to convey information about the emotional context, but we also show a different use in Diana monkey, whose social calls (L vs R) relate to the general valence of the external world as perceived by the caller. Importantly, L and R call units can be emitted singly or, more often, combined with A units into a compound call. More detailed contextual

420   analyses are required to determine which social situations are associated with single or

421   combined calls. For example, it is possible that the distance between the caller and the receiver

422   determines whether an A unit is affixed. Another possible explanation lies in variations in the

423   degree of visibility in the habitat (Candiotti et al., 2012a, 2012b).

424

425   Call compounds that contained A units from a neighbouring individual ('RA_N') triggered a high

426   decrease of locomotion, a slight decrease of vocal activity and an increased visual scanning

427   towards the presumed caller compared to call compounds that contained A units from a group-

428   member ('RA_G'). This pattern is similar to what has been in observed in other primates reacting

429   to unexpected stimuli (Bergman, Beehner, Cheney, & Seyfarth, 2003; Briseño-Jaramillo,

430   Estrada, & Lemasson, 2014; Zuberbühler & Wittig, 2011). These behavioural patterns suggest

431   that both RA stimuli were perceived as urgent but that subjects based decisions on differences

432   in the Affix.

433

434   Individual acoustic variations and auditory discrimination by receivers have been reported in

435   many primate species (putty-nosed monkeys *Cercopithecus nictitans*: Price, Arnold,

436   Zuberbühler, & Semple, 2009; marmosets *Callithrix jacchus*: Miller & Thomas, 2012; Olive

437   baboons *Papio hamadryas anubis*: Lemasson, Palombit, & Jubin, 2008; Japanese macaques

438   *Macaca fuscata*: Ceugniet & Izumi, 2003; squirrel monkey *Saimiri sciureus*: Kaplan, Winship-

439   Ball, & Sim, 1978), suggesting that providing identity cues in primate calls is of considerable

440   biological importance (Blumstein, Verneyre, & Daniel, 2004; Lemasson et al., 2007; Seyfarth

441   et al., 2010; Seyfarth & Cheney, 2010).

442   This is likely so in this species in which vocal exchanges play an important role to ensure social

443   cohesion and in which females differ in their vocal activity depending on their social integration

444   within the group (Candiotti et al., 2015). In line with this, a previous study on Campbell's

monkeys found that familiar calls (using homologous calls of Diana monkeys' LA) elicited more affiliative calling and vocal responses than unfamiliar calls (Lemasson et al., 2005). Taken together, the responses given by the subjects to the different types of stimuli suggest that the first unit (i.e., L or R) allows the receiver to get information about the direct social and physical environment –probably by associative learning- while the identity conveyed by the second unit (A) may influence receiver's decision regarding the behaviour to adopt in line with their respective positions in the social network. For example, receivers may have different reactions depending on the identity of the caller when hearing an RA call which signals that a given individual has spotted something disturbing. But it seems premature to draw stronger conclusions about the relative importance of both types of information conveyed as here no playback of LA_N call was done. In future experiments, it would therefore be necessary to test subjects' reaction to L call units combined with A call units from neighbours as well as L call units combined with A calls from immature or more or less affiliated group members.

Our study has high external validity because the data are from spontaneous reactions of untrained and free-ranging animals living in their natural habitat. The results obtained here suggest that the main social calls given by the adult females are linear combinations of different morphological units that convey information about the social context and the identity of the caller. In a related study based on analysis tools from formal linguistics (Veselinovic et al., 2014), call sequences of wild adult females Diana monkeys were analysed which revealed non-random patterns in terms of the order and type of calls units that were merged. The authors concluded that calls consisting of combinations of call units functioned as single calls rather than rapid sequences of independent units (Veselinovic et al., 2014).

469   Nevertheless, this study remains only a first step towards understanding the use of complex

470   calls and combinatorial abilities. Several technical and conceptual limitations must be

471   acknowledged. Firstly each combined stimulus was created from call units taken from two

472   distinct individuals and we do not know if the same reactions would be observed if we combined

473   calls from the same caller. This choice was based on evidence in Campbell's monkey, a closely

474   related species, that calls homologous to L and R calls in Diana monkeys (i.e., SH and RRC

475   calls) relate to a much lesser extent to caller's identity than the arched structure homologous to

476   Diana monkeys' A calls (i.e., *CH*) (Lemasson and Hausberger, 2011). Hence, if those data

477   suggest that receivers discriminate caller's identity mostly from the arched part of the call, its

478   actual importance in L and R calls remains to be tested in Diana monkeys. However, the fact

479   that LA_G did not trigger any reaction showing that subjects were disturbed supports our

480   hypothesis.

481

482   Moreover, in our experimental design, the L and R units of stimuli were taken from combined

483   calls but A units were taken from calls emitted alone (i.e., not combined to another unit). The

484   question remains whether the acoustic structure of A calls (when combined or not) differs

485   slightly. But again, the fact that LA_G (socio-positive calls) did not trigger disturbed reactions in

486   subjects suggests that this question may remain peripheral for the results obtained here. Testing

487   this question could generate an interesting comparison with males Campbell's monkeys in

488   which previous work found similar responses to natural Krak calls and artificial Krak calls

489   created from Krak-oo calls (Coye et al., 2015).

490   An alternative solution to determine both the potential of the first unit (i.e., L or R) to signal

491   caller's identity, and the influence of a possible variation in the structure of A calls' between

492   combined and single calls would be to develop a playback experiment comparing sets of

493   artificial stimuli. Notably a set of artificially combined calls created from single calls (i.e., L, R

494   and A calls combined in LA and RA complex calls) and a set of artificial 'single calls' taken

495   from complex calls (i.e., breaking down LA and RA calls into L, R and A units), using either

496   calls from a group-member or calls from a neighbour.

497

498   Interestingly, combinatorial abilities have been found in several animal species both at the call

499   level and at the sequence level, in both males and females, and notably in species where males

500   are more integrated socially (Bouchet et al., 2013; Bouchet, Laporte, Candiotti, & Lemasson,

501   2014; Bouchet et al., 2010; Coye et al., 2015; Lemasson, 2011; Ouattara, Lemasson, &

502   Zuberbühler, 2009b). Although most studies based their conclusions on contextual and acoustic

503   (non-experimental) analyses, they all suggest that combinatorial phenomena are an

504   evolutionary adaptive response to an increased need for complex communication, which may

505   be more widespread than initially thought. Whether the combinatorial abilities of non-human

506   and human primates originated in an ancestral capacity or result from convergent evolution

507   remains unclear and will require further comparative studies, notably to investigate

508   phylogenetic and cognitive aspects of the evolution of combinatorial phenomena.

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