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The function of non-linear phenomena in meerkat alarm calls

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Abstract: Non-linear vocal phenomena are a ubiquitous feature of human and non-human animal vocalisations. Although we understand how these complex acoustic intrusions are generated, it is not clear whether they function adaptively for the animals producing them. One explanation is that non-linearities make calls more unpredictable, increasing behavioural responses and ultimately reducing the chances of habituation to these call types. Meerkats (*Suricata suricatta*) exhibit non-linear subharmonics in their predator alarm calls. We specifically tested the “unpredictability hypothesis” by playing back naturally occurring non-linear and linear medium-urgency alarm call bouts. Results indicate that subjects responded more strongly and foraged less after hearing non-linear alarm calls. We argue these findings support the unpredictability hypothesis and suggest this is the first study in animals or humans to show that non-linear vocal phenomena function adaptively.

DOI: <https://doi.org/10.1098/rsbl.2010.0537>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-42046>

Journal Article

Accepted Version

Originally published at:

Townsend, S W; Manser, M B (2011). The function of non-linear phenomena in meerkat alarm calls. *Biology Letters*, 7(1):47-49.

DOI: <https://doi.org/10.1098/rsbl.2010.0537>

1 The function of non-linear phenomena in meerkat alarm calls

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15 SUMMARY

16

17 Non-linear vocal phenomena are a ubiquitous feature of human and non-human animal
18 vocalisations. Although we understand how these complex acoustic intrusions are generated, it is
19 not clear whether they function adaptively for the animals producing them. One explanation is
20 that non-linearities make calls more unpredictable, increasing behavioural responses and
21 ultimately reducing the chances of habituation to these call types. Meerkats (Suricata suricatta)
22 exhibit non-linear subharmonics in their predator alarm calls. We specifically tested the
23 “unpredictability hypothesis” by playing back naturally occurring non-linear and linear medium-
24 urgency alarm call bouts. Results indicate that subjects responded more strongly and foraged less
25 after hearing non-linear alarm calls. We argue these findings support the unpredictability
26 hypothesis and suggest this is the first study in animals or humans to show that non-linear vocal
27 phenomena function adaptively.

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29

30 **1. INTRODUCTION**

31

32 Non-linear phenomena in vocalisations, complex intrusions into the normal spectral structure of
33 calls, have received considerable recent interest (Fitch et al. 2002). Consequently, it is now
34 obvious that these irregularities pervade the vocal systems of a huge range of animal species;
35 from the screams of humans (Herzel & Wendler 1991) to the ultrasonic calls of frogs (Suthers et
36 al. 2006). Furthermore, by combining acoustic analysis (Riede et al. 2007), excised laryngeal
37 experimentation (Brown et al. 2003) and computer modeling, we also better understand why non-
38 linearities (from hereon “NLP”) arise and the various forms they can assume (see Fitch et al.
39 2002). However, this is only part of the puzzle, as, it still remains unclear what function, if any,
40 non-linearities serve for the species producing them.

41

42 A number of theories exist to explain the potential adaptive significance of NLP. NLP could act
43 as an honest signal, transferring information regarding vocal apparatus symmetry and hence,
44 mate quality (Riede et al. 2007). Alternatively, NLP may facilitate individual discrimination
45 (Volodina et al. 2006), provide cues regarding the movement direction of the caller (Miller 2002)
46 or confuse predators by mimicking the fundamental frequency of a larger animal during normal
47 phonation (Fitch et al. 2002). Lastly, the unpredictability generated by NLP may be difficult to
48 ignore, inducing a heightened behavioural response, ultimately preventing receivers from
49 habituating to certain call types, (the “unpredictability hypothesis”, Fitch et al. 2002; Blumstein
50 & Recapet 2009). This adaptive function would be particularly plausible for calls that influence
51 the survival of individuals, such as screams or alarm calls and indeed it has been shown that baby

52 and animal screams containing NLP are more evocative to human listeners than vocalisations
53 without (Mende et al. 1990; Belin et al. 2008).

54
55 However, no study in humans or animals has convincingly shown that, within the same call type,
56 naturally occurring non-linearities are meaningful for receivers. This approach is critical to
57 elucidate whether such integral components of animal vocalisations function adaptively, and are
58 not mere byproducts emanating from the physical properties of the sound production system
59 (Fitch et al. 2002).

60
61 Here, we test the “unpredictability hypothesis” of NLP using meerkat alarm calls. Meerkats
62 exhibit predator-type and urgency-specific alarm calls (Manser 2001) and further spectrographic
63 analyses indicated the clear presence (and absence) of subharmonic non-linear intrusions, within
64 a single alarm call variant (Townsend and Manser unpublished data; Fig 1.). We conducted
65 playback experiments exposing meerkats to non-linear (test) and linear (control) medium-
66 urgency aerial alarm call bouts (Manser 2001). In line with the unpredictability hypothesis, we
67 predicted that meerkats should be more aroused by alarm calls possessing subharmonic NLP than
68 those without, and subsequently exhibit stronger behavioural responses.

69 70 **2. METHODS**

71 72 *(a) Study site and subjects*

73 Playback experiments were carried out on eight groups of meerkats at the Kalahari Meerkat Project (KMP), South
74 Africa (Manser 2001) from August-November 2009. As part of the KMP’s long-term data collection, all animals
75 were tagged with sub-cutaneous transponders and with dye markings for individual identification. All subjects were
76 habituated to a level that allowed close observations within 1m.

77

78 ***(b) Call selection***

79 We selected 9 medium-urgency aerial alarm call bout stimuli, 4 possessing subharmonic non-linear intrusions
80 (average proportion of non-linear elements 46% (range 33%-62%)) and 5 without, following the protocol outlined by
81 Fitch et al. (2002), from a data pool of 38 call bouts, using Cool Edit Pro 2000 (see fig 1, see ESM). Only 9 stimuli
82 in total were pre-selected, because we wanted to use natural alarm call bouts, of the same urgency and predator-class,
83 with good signal-to-noise ratio, which were also matched in temporal parameters (see ESM). An acoustic analysis on
84 the available calls further indicated that structurally, and statistically, calls of the control and test categories did not
85 differ (see ESM).

86

87 ***(c) Playback protocol***

88 Playback experiments were conducted on dominant male meerkats in 8 different groups. Because of the specificity of
89 the stimuli needed, all four non-linear stimuli and 3 of 5 linear stimuli were tested in 2 groups, whilst the remaining 2
90 linear stimuli were tested in only 1 group. Subjects were followed for at least 30minutes (range +3 hours) prior to
91 playbacks; to control for sensitization effects we recorded all occurrence data on alarm call frequency. Call bouts
92 were played back from an iPod-touch connected to a JBL loud-speaker at a volume adjusted to match the amplitude
93 measured for call bouts elicited during natural predator encounters (Digital sound-pressure meter: Voltcraft SL-100).
94 Playbacks were only conducted on foraging meerkats, at least 50m from their sleeping burrow and 10m from any
95 boltholes, at a distance of 12-15m from the focal individual. Experiments were only performed if there had been no
96 disturbance (predator encounter, group encounters) during the previous 10minutes of observation. Playback subjects
97 were filmed for at least 30s before and 1minute after using a JVC solid-state digital video camera (JVC-everio GZ-
98 MG150). To control for differential responses to playback conditions due to satiation, after playbacks, each male was
99 weighed to estimate foraging success (Δ Experimental weight-Morning weight/foraging time). Finally, to avoid
100 order-effects we ensured that 50% of the subjects received non-linear playbacks first (N=4) and 50% received linear
101 playbacks first (N=4). Playbacks on the same male were separated by at least 7 days.

102

103

104

105 *(d) Behavioural responses*

106 We analysed videos frame-by-frame using Observer XT 7.0. We quantified the strongest behavioural response to the
107 playbacks by grading the behaviours observed in the following minute into 5 response categories of increasing
108 strength: 1) No response, 2) Vigilant, 3) Standing guard (GA), 4) Running, 5) Running to a bolthole. We allocated
109 each playback 1 response category, representing the strongest response exhibited in the 1minute after playback and
110 this value was then used in analyses. Furthermore we looked specifically at the strongest behavioural category
111 “running to a bolthole” to determine if this behaviour was employed differentially between playbacks. We made a
112 binary distinction between running to a bolthole (1) and all other behaviours (0). Finally, we also wanted to obtain an
113 estimate of time to relaxation. Unfortunately we could not use the absolute time to relax, because this behaviour was
114 automatically confounded by the running to a bolthole response category, given that once at the bolthole (the
115 strongest response category) and safe, individuals would immediately relax. To circumvent this, we took foraging
116 time in the minute after playback as a proxy measure of time to relax, as the decision to return to normal foraging
117 suggests the threat is no longer perceived. To ensure accurate coding of video tapes, a second observer blind-coded
118 75% of trials (12 trials) (see ESM).

119

120 *(e) Statistical analyses*

121 Due to the non-normal distribution of the data, we employed exact non-parametric tests to analyse the categorical
122 and continuous response variables. To determine if there were differences in the utilization of the strongest response
123 category (Running to a bolthole), we used a Generalized Linear Mixed Effects Model (GLMM) with a binomial error
124 structure (see ESM).

125

126 **3. RESULTS**

127 Meerkats responded differentially to the playback conditions. They responded more strongly after
128 hearing non-linear than linear playbacks (Exact Wilcoxon signed rank test, $N_{\text{non-linear}} - N_{\text{linear}} = 8$,
129 $Z = -2.23$, $p = 0.031$) and spent less time foraging (Mean \pm SD: Linear = 30 \pm 24secs, Non-linear =
130 18 \pm 19secs; $N_{\text{non-linear}} - N_{\text{linear}} = 8$, $Z = -2.52$, $p = 0.008$, fig 2). Meerkats employed the strongest
131 response category, running to a bolt-hole, significantly more often after hearing non-linear than

132 linear playbacks (Non linear = 62.5% of trials, Linear=0% of trials, GLMM, LR=9.28, df=1,
133 p=0.017).
134 There was no difference between experimental and control conditions for the additional factors
135 analysed: alarm call number/hour before playback (mean+-SD: Non-linear = 0.48 +-0.48,
136 Linear = 0.49 +-0.36, N=8, Exact Wilcoxon signed rank test, Z= -0.420, p= 0.742) or foraging
137 success (Mean Weight gain/hour: Non-linear = 2.16 +- 3g, Linear = 2.7 +-2.34g, N=6, Z=-0.674,
138 p=0.625).

139

140 **4. DISCUSSION**

141

142 Non-linear phenomena pervade the vocal systems of species across the animal kingdom.
143 However, until now, the idea that such complex intrusions can function adaptively has not been
144 clearly demonstrated. Previous attempts have been complicated by variation in call-type used
145 (Mende et al. 1990), or, the artificial synthesizing of non-linear intrusions during playbacks
146 (Blumstein & Recapet 2009).

147

148 In meerkats, we show that naturally occurring subharmonic NLP induce a stronger behavioural
149 escape response than a control sequence without non-linearities. Probably as a result of this more
150 intense behavioural response, we additionally found that, when exposed to non-linear alarm call
151 bouts, individuals generally needed longer to relax. Because the reaction exhibited by subjects
152 could be driven by sensitization to alarm calls or satiation, we recorded prior alarm call exposure
153 and foraging success. However, neither variable differed significantly between the two playback
154 conditions, indicating that NLP were responsible for the observed behavioural changes.

155 We suggest that our results support the unpredictability hypothesis (Fitch et al. 2002; Blumstein
156 & Recapet 2009) which postulates that non-linearities make calls less predictable and thus more
157 evocative to listeners, preventing receivers from ignoring such calls. This makes particular sense
158 with regards to meerkat alarm calls. Meerkats inhabit open desert environments, where the threat
159 of predation is extremely high (Manser 2001). This, combined with the fact that their vision is
160 compromised by their tendency to forage in the sand, means that alarm calls play a central role in
161 the survival and ultimate fitness of meerkats. Experimental manipulations have shown that
162 habituation to alarm calls can occur in meerkats (Schibler & Manser 2007); given the detrimental
163 effect such habituation could have on survival, meerkats may well have evolved NLP as a
164 mechanism to temper this.

165
166 As animals exposed to danger may become highly aroused and temporarily lose control of their
167 vocal membranes, it has additionally been suggested that receivers may perceive NLP as
168 communicating risk or urgency (Blumstein et al. 2008; Blumstein & Recapet 2009; Blumstein et
169 al. 2010). However, in meerkats, this explanation seems less plausible, as exemplars were taken
170 from within the same call-type and hence except for the subharmonic intrusion, were matched
171 structurally in urgency levels (see Manser 2001). Furthermore, preliminary data suggests non-
172 linearities only occur at low rates (20%) in their medium urgency aerial alarm calls (Townsend
173 and Manser unpublished data), a level that is unlikely to allow reliable perception of urgency or
174 risk levels.

175
176 To our knowledge this is the first study indicating that non-linearities function adaptively,
177 initiating a change in behavioural response. The comparative study of animal communication

178 strives to elucidate whether facets of our own language system are unique or whether they have a
179 more deeply rooted evolutionary history (Hauser et al. 2002). Our results support the notion that
180 there is some form of underlying phylogenetic continuity to NLP in humans (Belin et al. 2008).
181 Whether non-linearities generally function in contexts where unpredictability and ultimately
182 habituation-prevention, is of advantage still remains to be confirmed, though further systematic
183 habituation-dishabituation studies within the same call-type, with and without NLP, will help to
184 clarify this. We hope our work will stimulate much-needed additional research into the function
185 of animal and human non-linearities.

186

187 Acknowledgements

188 Thanks to Tim Clutton-Brock, for KMP research permission, Tecumseh Fitch and Roman Furrer
189 for discussions and Klaus Zuberbuhler, Dan Rankin and two anonymous reviewers for
190 manuscript comments. University of Zurich provided funding.

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238 enhance individual recognition in the Dhole, *Cuon alpinus*. *Ethology* 112, 815—825.

239 Figure 1: Spectrogram showing a linear and a non-linear call from a medium-urgency aerial alarm call bout. a) the
240 fundamental frequency of the call, b) harmonic overtones associated with this tonal call type, c) and d) non-linear
241 subharmonic intrusions into the call's spectral structure.
242

243 Figure 2: Error-bar plot indicating the effect of playback type on foraging time (s) in the minute after playbacks.