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The Sound of Arousal: The Addition of Novel Non-linearities Increases Responsiveness in Marmot Alarm Calls

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Abstract

Vocal structure should reflect vocal function. While much attention has focused on quantifying attributes of harmonic vocalizations, the vocalizations of many species also may contain non-linear phenomena such as warbles, subharmonics, biphonation, and deterministic chaos or noise. The function of these non-linearities remains enigmatic. In some species, harmonic vocalizations abruptly become 'noisy' when individuals are physiologically aroused and the sudden onset of these non-linearities could signal arousal or fear to receivers. One untested functional hypothesis is that vocalizations containing non-linearities are more variable from one rendition to the next, and thus are harder to habituate to. In some situations, reducing the likelihood of habituation could be important. Signals that are highly evocative are more difficult to habituate to. Thus, we conducted playback experiments to foraging yellow-bellied marmots (*Marmota flaviventris*) to determine whether the addition of white noise (a non-linear acoustic phenomenon) to alarm calls elicited a greater response than control calls without the non-linearity or control calls with silence, rather than noise, added to them. Marmots spent less time foraging after hearing calls that included noise than after normal or control calls. This result is consistent with the unpredictability hypothesis and suggests that the adaptive value of non-linearities is to prevent habituation.

Introduction

Much attention has focused on tonal and harmonic sounds that animals produce, while less attention has focused on the production or function of atonal, non-harmonic sounds, despite these non-linear vocal phenomena being easily identified on a spectrogram (Fitch et al. 2002). Formally, only pure tones have no non-linear attributes because harmonics are one type of non-linearity. In this study, we focus on other types of non-linearities because they have received relatively less study. They include (but are not limited to Wilden et al. 1998; Fitch et al. 2002): subharmonics (additional tonal components below the fundamental frequency), biphonation (the production of a second fundamental frequency), deterministic chaos (broadband components of low dimensional or non-random noise), and noise (broadband hissing, whispering, or white noise). In addition, bifurcations (and to a lesser extent warbles) are abrupt frequency changes caused by a sudden change in the vibrations of the vocal folds and are broadly included in the class of non-linear vocal phenomena. Indeed, these non-linear phenomena are a common feature of vocalizations in more than 30 mammals (Wilden et al. 1998; Tokuda et al. 2002; Facchini et al. 2003; Riede et al. 2004; Mann et al. 2006; Tyson 2006; Volodina et al. 2006; Tyson et al. 2007), birds (Fee et al. 1998; Beckers & ten Cate 2006), and amphibians (Suthers et al. 2006).

Because many vertebrate vocal systems that are normally linear, can become non-linear and produce non-linear vocal phenomena, these non-linearities have been viewed as non-adaptive products of vocal production (Wilden et al. 1998; Fitch et al. 2002). In mammals, non-linearities can be produced if there is an asymmetry in the size or muscular control of the left and right vocal fold. Consistent with this non-adaptive hypothesis is the occurrence of non-linearities in human pathological phonation (Herzel & Wendler 1991).

By contrast, several functional hypotheses may explain the addition of non-linear vocal phenomena to mostly tonal or harmonic vocalizations. First, because individual vocal tracts vary, non-linearities may provide a source of individual discrimination (Volodina et al. 2006; but see Owren & Rendall 2001). Second, because the production of non-linearities may result from asymmetries in vocal tracks, they could provide information about vocal tract symmetry to choosy females (Fitch et al. 2002), and thus be under sexual selection (Parsons 1990). Third, producing subharmonics may lower the perceived frequency and thus make signalers appear larger than they are (Fitch et al. 2002). Finally, abrupt frequency changes or the sudden introduction of non-linearities in a tonal call will generate unpredictability, and this unpredictability may function to prevent others from ignoring calls and screams (Fitch & Hauser 1995; Fitch et al. 2002).

The hypothesis that unpredictability enhances responsiveness is consistent with the observations that vocalizations containing chaotic noise are more arousing than those not containing such noise (e.g., in human singers and infants [Mende et al. 1990;]). Newborn human cries contained more noise as the pain created by taking a blood sample increased (Facchini et al. 2005). Furthermore, noise is seen in nonhuman vocalizations that elicit a strong response in conspecific perceivers (Tokuda et al. 2002), such as in domestic dog barks (*Canis familiaris*), Japanese macaque screams (*Macaca fuscata*), and piglet screams (*Sus scrofa domestica*). Noisy vocalizations from nonhumans are also particularly evocative to humans (Belin et al. 2008).

If the addition of non-linearities to 'normal' harmonically structured calls prevents habituation, their addition may function by increasing receiver arousal and we should expect them to characterize extremely fearful vocalizations. This expectation may contradict Morton's (1977) 'motivation-structure rules' hypothesis that predicts aggressive signals should be low frequency because body size is associated with the lowest possible frequency an individual can produce, and, in mammals, may become noisy from the vibrations of a membrane surrounding the glottis (Hauser 1993). By contrast, scared animals are expected to produce the antithesis of aggressive signals (Darwin 1872) higher frequency, tonal calls (Morton 1977). Alternatively, increasing the bandwidth of calls to create broadband vocalizations is consistent with calls designed to recruit conspecifics (e.g., mobbing calls). There is some support for the motivation-structure rule hypothesis. August & Anderson (1987) found aggressive mammalian signals were relatively lower frequency than fearful sounds. In primates, Hauser (1993) found that aggressive vocalizations were generally low frequency, and a greater proportion of aggressive calls was low frequency while fearful calls were high frequency. However, Hauser noted that this finding was somewhat taxonomically confounded. Additionally, Hauser (1993) focused on frequency, rather than precisely quantifying the presence of noise in both aggressive and fearful vocalizations.

It is also important to study how noisy/non-linear vocalizations are perceived. We directly tested the hypothesis that non-linearities function to enhance responsiveness by manipulating the simple harmonically structured alarm calls emitted by adult yellow-bellied marmots by adding either 5 ms of white noise or 5 ms of silence and comparing the responses elicited by these calls to normal adult alarm calls. Adult alarm calls do not contain obvious non-linearities, but adults sometimes produce a noisy 'chuck' (Blumstein & Armitage 1997). However, screams from marmot pups contain a variety of non-linearities, and these are more evocative than normal pup alarm calls (Blumstein et al. 2008). Thus, non-linearities may be produced in our experimental system – yellow-bellied marmots – but not in the types of calls we added them to. By doing so, we have a powerful assay to test the function of non-linear vocal phenomena.

Methods

We conducted playback experiments from 7 June to 15 July 2007 between 07:00 and 12:00 h in the upper East River Valley, in and around the Rocky Mountain Biological Laboratory (Gunnison County, CO, USA; Blumstein et al. 2006). Marmots were trapped in walk-in live traps, and marked (with ear tags and fur dye) to facilitate observations (detailed methods of trapping and marking are in Blumstein et al. 2008).

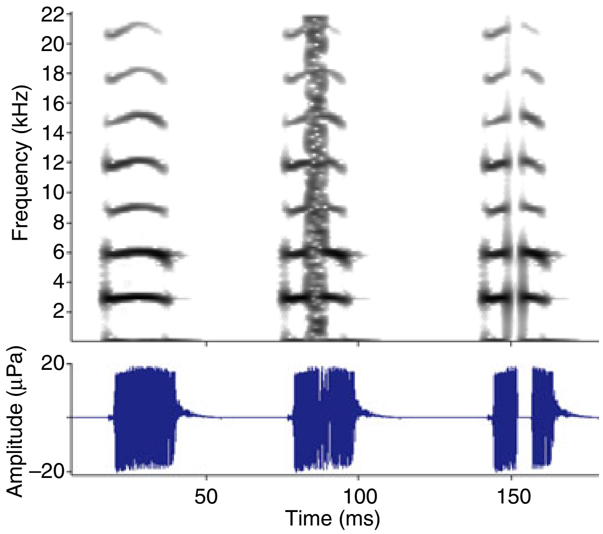

Fig. 1: Spectrograms of the three calls used to construct the playback tracks: normal alarm call (call 1), call including random noise (call 2), call including silence (call 3).

We recorded alarm calls from eight adult females in four colonies: Marmot Meadow, Picnic, River, and Stonefield. Three versions of each call were then produced by inserting 5 ms of white noise or 5 ms of silence into the middle of the call [i.e., 10–15 ms after the start of the call (Fig. 1)]. Each playback was composed of four exemplars of the same call separated by 300–500 ms inter-note intervals. The tracks were stored as uncompressed AIF files on an iPod (Apple Computer, Cupertino, CA, USA).

By inserting white noise into the centre of a call, we created a novel call that contained a non-linearity. We acknowledge that it was difficult to create a novelty control for this experiment. We elected to insert 5 ms of silence into the middle of the call and justify this as a novelty control because the addition of anything other than silence created another type of non-linearity (abrupt frequency shifts are considered by some to be a non-linear vocal phenomena). Playing back 5 ms of noise alone was an inadequate control because it addressed the evocativeness of a click, rather than the key question of the evocativeness of the addition of a non-linearity to a tonal call. An untested alternative control might have been to slowly increase the amplitude of the burst of white noise, but this was not practical given the short duration of the pulse of sound. Five milliseconds of silence may not be perceptually meaningful if the sound was too brief to be detected. Gap detection depends on frequency and amplitude (Syka et al. 2002; Recanzone & Sutter 2008). Rats (*Rattus norvegicus*) and gerbils (*Meriones unguiculatus*) can detect 1–3 ms gaps in relatively loud sounds (Syka et al. 2002; Hamann et al. 2004), and we assumed that marmots (a rodent) could detect short gaps embedded in loud alarm calls. To our ears, the three stimuli sounded different and the call with noise inserted in it sounded 'raspy' or 'harsh'.

The three stimuli (normal adult alarm call, alarm call with noise, alarm call with silence) were broadcast to 22 different subjects (11 adult females, five adult males, four yearling females, two yearling males) in six colonies (Bench, Gothic Townsite, Horse Mound, Marmot Meadow, River, Stonefield). Three individuals (one adult male, one adult female and one yearling female) from the same burrow did not obviously respond to any of the three stimuli and were excluded from subsequent analysis (including them reduced significance levels but did not otherwise change the pattern of response). Thus, our final data set consists of 19 subjects.

We ensured that marmots heard calls from unfamiliar animals (i.e., from acoustically isolated colonies). Each individual was exposed to all three stimuli (each from the same unfamiliar animal), typically no more than one playback per day ($x \pm SD = 37.67 \pm 37.34$ h between playback, $\tilde{x} = 23.75$, range = 0.15–146.17 h). Stimulus presentation order was balanced, thus our results were not confounded by order effects. Moreover, because each subject heard calls originally from the same unfamiliar individual, variation in response could not be attributed to idiosyncratic differences in the basic call. We aimed to have each subject hear only playbacks directed to that individual, but subjects sometimes heard playbacks directed to other individuals. On average, subjects heard 1.91 (± 1.48 SD) playbacks, including their own previous playbacks, prior to each specifically directed playback ($\tilde{x} = 2$, range = 0 – 5), including an average of 0.17 (± 0.41 SD) playbacks on the same day ($\tilde{x} = 0$, range = 0 – 2).

Marmots exhibit site-specific habituation to humans. Thus, observers sat in the open at distances (20–100 m) that did not otherwise modify marmot behavior at those sites. Marmots were baited with Omolene 300 horse feed (Ralston Purina Inc., St. Louis, MO, USA) to a distance 8–12 m from the speaker (Advent AV 570, Recoton Home Audio, Benicia, CA, USA). Playback amplitude was set to 95 dB SPL measured 1 m from the speaker (with a SPER Scientific 840029 digital sound level meter, accuracy ± 0.7 dB SPL, weighting level A, peak response). This amplitude was lower than the loudest marmot alarm calls, but has been proved to work well as an experimental assay (e.g., Blumstein & Daniel 2004; Blumstein et al. 2004, 2008). Although we aimed to focus on solitary subjects, other individuals were sometimes present either at the bait or within 50 m of the subject during the playbacks. There were on average 0.27 (± 0.48 SD) non-targeted animals at the bait during the minute following the calls ($\tilde{x}$ = 0, range = 0–2). There was an average of 0.83 (±0.90 SD) others present within 50 m including those at bait ($\tilde{x}$ = 1, range = 0–4). Once animals were foraging at the bait, we broadcast the 3-min tracks. Each track started with 1-min of silence, in order to determine baseline behavior for each individual. We then broadcast a four-call playback, followed by 2 min of silence. Subjects were video recorded using a Canon GL-1 mini-DV digital video recorder. The experimenter was far enough away not to obviously affect their behavior, a distance that depended upon the group, individual and landscape features (range: 20–120 m).

Video recordings were scored, by one observer (C.R), with an event recorder (JWatcher 1.0; Blumstein & Daniel 2007). The observer trained until correlation coefficients of time allocation between pairs of the same were >0.95 and re-scored any experiments that were ambiguous. We scored the onset of bouts of vigilance (standing quadrupedally and looking, rearing up bipedally and looking, lying and looking), hiding (time spent in burrow), movement (walking, running), foraging, self-grooming and social interactions. Because of the heterogeneous terrain and because of vegetative growth during the summer, our subjects may occasionally have been out-of-sight. Thus, all calculations are based on the proportion of time in sight. We calculated the proportion of time allocated to: foraging; heightened vigilance (rear-looking) combined with time spent in burrow; and total vigilance (lie-looking, stand-looking and rear-looking). After a comprehensive visual exploration of our data, we analyzed time allocation in the first minute following the start of the calls because the greatest heterogeneity of response occurred in that minute.

To determine whether marmots responded to the stimuli, we subtracted time allocation during the baseline period from the minute following the calls thus obtaining time reallocation for each playback. We calculated 95% confidence intervals of this difference and interpreted those responses that did not include zero as a significant response to playback.

We then fitted a repeated-measures general linear model to explain variation in the time spent in each of the three behaviors (foraging, heightened vigilance plus in burrow, total vigilance) during the first minute following the calls. We set our significance level at 5%. Age, sex, and maternity were subsequently examined as between-subjects factors. We tested for sphericity using Mauchly's test (Keppel 1991). When we could not assume sphericity, we report the Hynn–Feldt corrected p-values and degrees of freedom. We measured effect size calculating partial η^2 for general linear models and Cohen's d for pair-wise comparisons, using the pooled standard deviation (Cohen 1988). We tested order effects by fitting a repeated-measures general linear model where the playback order, instead of the stimulus, was the within-subjects factor. We also regressed the number of playbacks previously heard, the maximum number of adults at bait and the total number of adults within 50 m of the subject against our dependent variables. All analyses were calculated with SPSS 11.0 (SPSS Inc. 2002, Chicago, IL, USA).

Results

Marmots responded to all stimuli by significantly decreasing the proportion of time spent foraging during the minute following the playback. The 95% confidence intervals for difference from baseline were −0.365 to −0.088 for the normal calls, −0.520 to −0.295 for the calls that included noise, and −0.378 to −0.132 for the calls that included silence.

Marmots responded differently to the three stimuli in the proportion of time spent foraging (Fig. 2; $F_{2,17}$ = 3.560, p = 0.039, partial η^2 = 0.165), but not

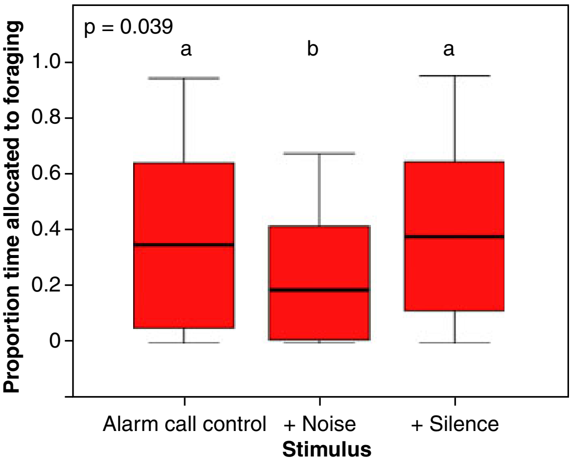

Fig. 2: Response of yellow-bellied marmots in proportion of time spent foraging to three different playbacks (normal alarm calls, calls including noise and calls including silence). Identical letters above box plots (which illustrate the median, inter-quartile range, and 95% confidence intervals) illustrate non-significant (p > 0.05) differences.

in the time spent engaged in total vigilance ($F_{2,17} = 0.618$, $p = 0.544$, partial $\eta^2 = 0.033$), nor in the time spent in high vigilance plus in burrow ($F_{2,17} = 1.565$, $p = 0.223$, partial $\eta^2 = 0.080$). Marmots foraged significantly less after hearing alarm calls with noise compared to unmodified alarm calls ($p = 0.027$, $d = 0.569$) or calls with silence ($p = 0.024$, $d = 0.633$). No significant difference was found between alarm calls and calls with silence ($p = 0.894$, $d = 0.0340$).

Marmots traded-off foraging with heightened vigilance and sheltering, since marmots significantly increased the proportion of time spent rear-looking or in the burrow (95% confidence intervals: normal calls 0.039–0.343, calls with noise 0.130–0.466, calls with silence 0.041–0.296). Although there was a significant increase in time spent vigilant after playback of the calls containing noise or silence, no significant difference was found after hearing normal alarm calls (95% confidence intervals: normal calls −0.003 to 0.231, calls with noise 0.057–0.372, calls with silence 0.005–0.316).

Our exploration of other factors that could influence playback response suggests that our results were not confounded (i.e., other variables did not provide an alternative explanation of the observed results), and thus we can interpret them with some confidence. We found no significant difference in the proportion of time spent foraging during baseline minutes between the three stimuli ($F_{2,17} = 0.448$, $p = 0.642$, partial $\eta^2 = 0.024$). Likewise, we found no significant difference in the proportion of time spent engaged in total vigilance ($F_{2,17} = 0.207$, $p = 0.814$, partial $\eta^2 = 0.011$) or rear looking plus in burrow ($F_{2,17} = 0.994$, $p = 0.364$, partial $\eta^2 = 0.052$). We found no significant or substantial effects of sex ($F_{2,17} = 0.475$, $p = 0.626$, partial $\eta^2 = 0.027$), age ($F_{2,17} = 0.527$, $p = 0.595$, partial $\eta^2 = 0.030$), or maternity ($F_{2,17} = 0.273$, $p = 0.763$, partial $\eta^2 = 0.016$) on time allocated to foraging after hearing the calls. Using playback order as within-subjects factor instead of stimulus, we found a significant and consistent order effect for time allocated to foraging ($F_{2,17} = 3.425$, $p = 0.043$, partial $\eta^2 = 0.160$). Although pair-wise comparisons showed no significant difference, marmots seemed to spend less time foraging during the minute following the first playback than after the second one, and less time after the second playback than after the third one. However, since playback order was balanced between the three stimuli, with 5–7 playbacks at each order for each stimulus, we could assume that this order effect did not confound our interpretation of stimulus effects. There was a significant positive relationship between the number of playbacks previously heard by an individual, including those specifically directed to it, and the proportion of time spent foraging ($R^2 = 0.494$, $p < 0.0005$). This result is consistent with an order effect, but again, our design allows us to ignore this effect. We found no relationship between the number of adults within 50 m of the subject and the proportion of time spent foraging ($R^2 = 0.024$, $p = 0.431$) or between the maximum number of adults at the bait and the proportion of time spent foraging ($R^2 = 0.151$, $p = 0.130$).

Discussion

While normal adult yellow-bellied marmot alarm calls do not contain noise, marmots hearing calls with noise inserted into them had an enhanced response; marmots spent significantly less time foraging after hearing alarm calls that included a short burst of noise than after hearing their normal alarm calls or calls with a short burst of silence. The change in time allocated to foraging is an appropriate metric of responsiveness in yellow-bellied marmots (e.g., Blumstein & Daniel 2004; Blumstein et al. 2004, 2008) because individual marmots often allocate their time to a variety of other antipredator behaviors (vigilance, escape, hiding) idiosyncratically. Moreover, as activities other than foraging and antipredator behaviors were rare, an analysis where we used total antipredator behavior revealed similar results. The fact that all subjects foraged before playback, and that playback terminated foraging and led to a variety of different antipredator behaviors is compelling. The number of replicates was not sufficient to study each antipredator behavior independently. Thus, marmots perceive the addition of a brief burst of noise, a type of non-linearity, but not a brief burst of silence, which constitutes an abrupt frequency transition, as evocative.

In a perceptual sense, it is possible that such a brief burst of noise was perceived as a super-normal stimulus. Extensive experimentation would be required to map the perceptual landscape of such sounds. It is also possible that natural background noise masked the 5-ms gap. In such a case, this alarm call plus silence may not have been an appropriate control. We cannot formally evaluate this but note that, to us, the stimuli sounded different when broadcast through our speakers in the environment and at the distances the marmots heard them.

A revealing caveat is in order. Yellow-bellied marmot 'chucks' contain noise. Chucks, a low-risk and very quiet call that signals 'concern', comprise <<1% of all alarm calls (Blumstein & Armitage 1997). Yet, even when played back at similar amplitudes as alarm calls, chucks were less evocative than alarm calls, perhaps because they are rare and not associated with predatory attack. We speculate that the transition from harmonic to non-linear attributes was what was specifically evocative. If so, noisy chucks do not have the abrupt transitions that characterize the appearance of non-linearities in tonal calls (e.g., Suthers et al. 2006), and thus the noise alone was not especially evocative. Additionally, previous work (Blumstein et al. 2008) found that yellow-bellied marmot pup screams, which naturally contain a variety of abrupt-onset non-linearities, elicited heightened responses in adults. Because many mammalian vocalizations may contain noise, it remains to be studied whether it is noise, or an abrupt transition to noise (or another non-linear vocal attribute) that is generally evocative.

Collectively, these results suggest that the addition of abrupt-onset non-linearities to tonal calls were especially evocative, and we infer that such evocative calls would be harder to habituate to. In support of this inference, we note that intense and evocative stimuli are easier to learn and more difficult to forget, and thus they should be more difficult to habituate to (Shettleworth 1998; Speed 2000). We believe that this is the first test of the hypothesis that the addition of abruptly occurring non-linear vocal phenomena increase evocativeness. Because more evocative signals should be more difficult to habituate to, this result is an indirect test of the hypothesis that non-linearities function to prevent habituation. This hypothesis should be verified with carefully conducted habituation experiments.

We believe that this result illustrates a general phenomenon and somewhat contradicts Morton's (1977) expectation that vocalizations from alarmed animals will necessarily be tonal, perhaps to make it harder for predators to locate them (Marler 1955). Owren & Rendall (2001) noted that rapidly paced, broad-bandwidth sounds are used by animal handlers to initiate movement. Similarly, alarm calls from some animals are noisy, perhaps because they are intended to attract attention and induce movement.

Alarmed animals may lose control of their vocal apparatus and this loss of control may create the sudden onset of non-linearities. While the presence of non-linearities was not emphasized, alarmed meerkats (*Suricata suricata*) communicate risk in their functionally referential calls by the addition of what appears to be deterministic chaos (Manser 2001). Vervet monkey (*Cercopithicus aethiops*) alarm calls are 'noisy' (Cheney & Seyfarth 1990). Highly aroused chimpanzees (*Pan troglodytes*) add non-linearities to their pant-hoots (Riede et al. 2004), and the calls of highly aroused piglets, Japanese macaques, and domestic dogs all contain non-linearities (Tokuda et al. 2002). We expect arousal levels, and in some cases fear, may be honestly communicated by the addition of non-linearities to tonal calls. Tonal calls with non-linearities sound more 'shrill' to our ears. Thus, it is the abrupt transition to non-linear vocal phenomena that may be the sound of arousal.

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