Published in The Journal of the Acoustical Society of America, Vol. 113, Issue 5, 2003, p. 2919-2926
which should be used for any reference to this work

Pulse register phonation in Diana monkey alarm calls

Tobias Riede[a)]
Department of Psychology, 245 Uris Hall, Cornell University, Ithaca, New York 14853

Klaus Zuberbühler[b)]
School of Psychology, University of St. Andrews, St. Andrews, Fife KY 16 9JU, Scotland, United Kingdom

The adult male Diana monkeys (*Cercopithecus diana*) produce predator-specific alarm calls in response to two of their predators, the crowned eagles and the leopards. The acoustic structure of these alarm calls is remarkable for a number of theoretical and empirical reasons. First, although pulsed phonation has been described in a variety of mammalian vocalizations, very little is known about the underlying production mechanism. Second, Diana monkey alarm calls are based almost exclusively on this vocal production mechanism to an extent that has never been documented in mammalian vocal behavior. Finally, the Diana monkeys' pulsed phonation strongly resembles the pulse register in human speech, where fundamental frequency is mainly controlled by subglottal pressure. Here, we report the results of a detailed acoustic analysis to investigate the production mechanism of Diana monkey alarm calls. Within calls, we found a positive correlation between the fundamental frequency and the pulse amplitude, suggesting that both humans and monkeys control fundamental frequency by subglottal pressure. While in humans pulsed phonation is usually considered pathological or artificial, male Diana monkeys rely exclusively on pulsed phonation, suggesting a functional adaptation. Moreover, we were unable to document any nonlinear phenomena, despite the fact that they occur frequently in the vocal repertoire of humans and nonhumans, further suggesting that the very robust Diana monkey pulse production mechanism has evolved for a particular functional purpose. We discuss the implications of these findings for the structural evolution of Diana monkey alarm calls and suggest that the restricted variability in fundamental frequency and robustness of the source signal gave rise to the formant patterns observed in Diana monkey alarm calls, used to convey predator information.

I. INTRODUCTION

The vocalizations of many mammals are the result of two distinct components: the oscillating vocal folds within the larynx produce a primary acoustic signal, which then undergoes a filtering process within the vocal tract where various frequency bands are dampened to different degrees (van den Berg, 1958; Fant, 1960; Titze, 1994; Owren and Linker, 1995). Basic vocal fold behavior can be described as the following: *Bernoulli* forces cause the vocal folds (if close to each other) to be sucked together, creating a closed airspace below the glottis. Continued subglottal air pressure from the lungs builds up underneath the closed folds. Once this pressure becomes high enough, the folds are blown outward, thus opening the glottis and releasing a single ‘‘puff’’ of air (van den Berg, 1958). As the subglottal pressure increases, two effects can be observed. First, the motion of the vocal folds becomes faster (demonstrated in computer models: Ishizaka and Flanagan, 1972; Steinecke and Herzel, 1995, and *in vitro*: Titze, 1989). Second, the sound pressure level increases (Gramming, 1988; Titze, 1994). The fundamental frequency of the sound produced by the vocal folds is additionally directly related with the tension of the vocal fold tissue (Titze, 1989, 1991).

Adult male Diana monkeys (*Cercopithecus diana*) produce acoustically distinct alarm calls to two of their predators, the crowned eagle and the leopard (Zuberbühler *et al.*, 1997; Zuberbühler, 2000a). Playback experiments have shown that nearby listeners respond to these alarm calls as if the corresponding predator were present, suggesting that these calls inform nearby recipients about important ongoing events in the environment (Zuberbühler *et al.*, 1999; Zuberbühler, 2000b). Acoustically, the Diana monkeys' alarm vocalizations consist of a bout of calls. Bouts vary in the number of calls from one to more than a dozen. Individual calls are characterized by a highly stereotypic pulse pattern and calls are interspersed by short harmonic elements (Fig. 1).

The single pulses within each call resemble a damped oscillation: a rapid, transient change in signal amplitude from a baseline value to a higher or lower value, followed by a rapid return to the baseline value. Elsewhere, we showed that the formant peak frequency and formant transition of the pulse elements is the single most important parameter to differentiate eagle versus leopard alarm calls (Riede and Zuberbühler, in press), suggesting that similar to human speech sounds, some primate vocalizations convey important semantic information by formant structures. Although research

---

[a)] Present address and address for correspondence: Tobias Riede, 315 Jordan Hall, School of Medicine, Indiana University, Bloomington, IN 47405. Electronic mail: tobiasriede@web.de

[b)] Electronic mail: kz3@st-andrews.ac.uk

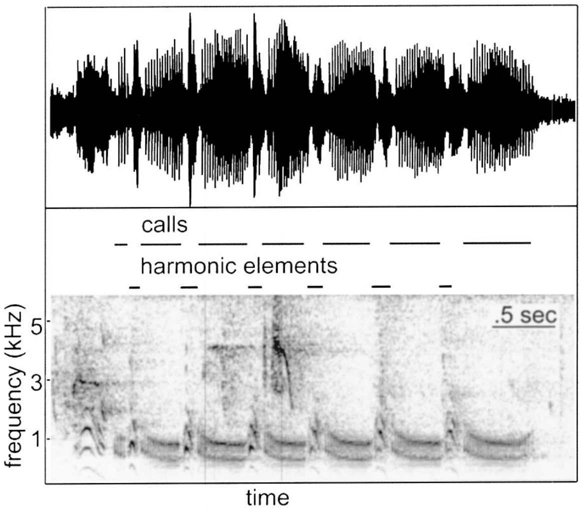

FIG. 1. Time domain and spectrogram of a leopard alarm bout, consisting of seven calls. Basic unit of the call is the pulse as shown in the ''zoom in'' picture of Fig. 2.

on the structural evolution of animal vocalizations is not new (Morton, 1977), comparatively little is still known about how natural and sexual selection affected the acoustic structure of primate alarm calls (Zuberbühler, 2003). Here, we provide a detailed acoustic analysis of the source characteristics of Diana monkey alarm calls to elucidate the adaptive significance and physiological constraints of this remarkable vocalization.

Human speech sounds can be produced using three different registers. A register can be described by the frequency range covered and by the specific mode of vocal fold behavior by which it is produced (e.g., Hollien, 1974; Titze, 1994; Svec *et al.*, 1999). Although each register covers a certain frequency range, neighboring registers overlap significantly. Normal speech is delivered in the so-called modal (or chest) register (fundamental frequency range 100–300 Hz). Humans are also capable to produce speech using either the falsetto (or flagolet) register (fundamental frequency >300 Hz) or the pulse (or vocal fry) register [fundamental frequency <100 Hz (Blomgren *et al.*, 1998)]. Recent studies suggest the existence of a separate fourth register, i.e., the vocal-ventricular phonation mode, like pulse register covering the frequency range below 100 Hz but unlike pulse register involving the ventricular folds (''false folds'') into the mode of production (Fuks *et al.*, 1998; Lindestad *et al.*, 2001). According to this terminology we used the term ''pulse register'' to describe the Diana monkey calls, because these vocalizations strongly resemble the pulse register of humans [see Blomgren *et al.* (1998) for a review].

Pulse register differs in acoustical, physiological, and perceptual characteristics from other phonation types [reviewed in Gerratt and Kreiman (2001)]. Vocal fold vibration during pulse register is characterized by glottal pulses of alternating amplitudes or by irregular trains of pulses (Hollien and Michel, 1968). The vocal fold length is shorter for the pulse register than for even the lowest frequency of phonation in the modal register (Hollien *et al.*, 1969). The vocal fold vibratory pattern of the pulse register in humans exhibits a very short open period (probably less than 25% of the entire cycle) and a very long period where the vocal folds are completely adducted and a small vocal fold excursion (Hollien *et al.*, 1977).

The fundamental frequency is affected by different factors in each of the three registers. In the modal register, the fundamental frequency is mainly determined by changes in vocal fold length and stiffness (Murry and Brown, 1971). Moreover, there is a positive correlation between vocal fold thickness (i.e., mass, length, and stiffness) and fundamental frequency [reviewed in Titze (1994)]. This relationship is absent in the pulse register (Hollien *et al.*, 1969; Allen and Hollien, 1973). Instead, the fundamental frequency of the pulse register appears to be predominantly determined by changes in subglottal air pressure.

To investigate the vocal production mechanism of the Diana monkey, we analyzed the relationship between call amplitude (a reliable estimator of subglottal pressure) and fundamental frequency. We predicted a positive relationship between these two parameters if Diana monkey alarm calls are the product of the same source production mechanism that is responsible for the human pulse register.

A second aim of this study was to investigate the role of nonlinear phenomena in the vocalizations of Diana monkey alarm calls. Nonlinear phenomena are relevant in this context because they can be directly related to events at the laryngeal source. Several lines of research suggest that nonlinear phenomena are common and ubiquitous in mammalian vocalization behavior (Wilden *et al.*, 1998; Mergell *et al.*, 1999; Riede *et al.*, 1997, 2000; Fischer *et al.*, 2000). Phenomena such as frequency jumps, subharmonics, biphonation, and deterministic chaos are commonly observed, usually the result of deviations from the regular harmonic vibration pattern of the vocal folds, such as nonsynchronously oscillating left and right vocal folds or simultaneously oscillating horizontal and vertical components of the vocal folds (e.g., Herzel *et al.*, 1994; Berry, 2001; Berry *et al.*, 1994; Steinecke and Herzel, 1995; Tigges *et al.*, 1997; Neubauer *et al.*, 2001). The two combined approaches are likely to yield important insights into the sound production mechanism underlying male Diana monkey alarm calls.

II. MATERIAL AND METHODS

A. Study site and subjects

Data were collected in an approximately 40-km^2 study-area of primary rain forest surrounding the Centre en Recherche d'Ecologie (University of Cocody, Abidjan) research station (5°50′N, 7°21′W) in the Taï National Park, Côte d'Ivoire, between June 1994 and June 1997. Seven monkey species are regularly observed in the area: the western red colobus (*Colobus badius*), the western black-and-white colobus (*Colobus polykomos*), the olive colobus (*Procolobus verus*); the Diana monkey (*Cercopithecus diana*), the lesser white-nosed monkey (*Cercopithecus petaurista*), the Campbell's monkey (*Cercopithecus campbelli*), and the sooty mangabey (*Cercocebus torquatus*). Diana monkey groups typically consist of about 20–25 individuals with one adult male and several adult females with their offspring. Groups occupy stable home ranges of approximately 60 ha. Diana monkeys eat primarily fruit and insects and they are found at all levels of the forest but prefer the main upper canopy. None of the animals were habituated to human presence. However, all data were so that the animals were unaware of the observer's presence.

B. Recordings and acoustic analysis

We recorded Diana monkey alarm vocalizations given in response to playbacks of African leopard (*Panthera pardus*) and crowned eagle (*Stephanoaetus coronatus*) vocalizations, using a Sony WMD6C tape recorder and a Sennheiser microphone (ME88 head with K3U power module) on 90-min type IV metal tapes. The frequency response of the microphone (40 Hz to 20 kHz; ±2.5 dB) and the tape recorder (40 Hz to 14 kHz, ±3 dB; distortion of 0.1%; signal-to-noise-ratio of 57 dB) are flat and within the frequency range of analysis. Playbacks of predator vocalizations were conducted randomly throughout the day, usually between 08:00 and 17:00 GMT. Daytime therefore cannot explain the differences in the vocal patterns. All recordings were made at distances of about 50 m from the focal animal, i.e., the adult male of a Diana monkey group. Individual distances varied randomly across trials and therefore cannot explain the patterns. Male alarm calls transmit to about 700 m, i.e., sound attenuation at short distances was unlikely to have affected the acoustic variables. The study area contained between 40 and 80 different groups of Diana monkeys with one adult male each. Because we did not know the exact location of these groups' home ranges, we selected ten different groups for experimental playbacks that were located at least 1 km apart from each other, which guaranteed that data came from ten different groups, i.e., were independent. This data set resulted in a set of 25 eagle alarm bouts (5 bouts from 5 different males) and 25 leopard alarm bouts (5 bouts from 5 different males). We digitized all recordings at a 16-bit quantization and a 44-kHz sampling rate using Signalize software. We performed signal analysis on a PC using the signal processing software HYPERSIGNAL-Macro™ using a DSP32C PC System Board. We completed the spectrographic analysis by using 512-point fast Fourier transforms, with 75% frame overlapping, a 44-kHz sampling frequency, and a Hanning window. To avoid aliasing effects we low-passed filtered all calls at 22 kHz.

C. Call parameters

A male Diana monkey alarm vocalization consists of one to many calls per bout (Fig. 1). The basic acoustic unit within a call is the pulse, defined as a rapid, transient change in the amplitude of the signal from a baseline value to a higher or lower value, followed by a rapid return to the baseline value, resembling a damped oscillation (Fig. 2).

Pulse duration is measured as the interval between the onset of a pulse to the onset of the subsequent pulse. Fundamental frequency is defined as the inverse (i.e., 1/pulse duration in Hz; pulse duration measured in seconds). Throughout the paper we use the term "fundamental frequency" to refer to the inverse value of "pulse duration" in the waveform. We quantified the variation of the fundamental frequency within calls by the parameter within-call jitter, defined as cycle-to-cycle variability in the fundamental frequency (Titze, 1994). Fundamental frequency ranges between 8.3 and 24 ms (mean±SD 16.1±2.0) in eagle alarm calls and between 13.3 and 29.9 ms (mean±SD 17.4±2.4) in leopard alarm calls (Riede and Zuberbühler, in press). Call duration and jitter ranges in eagles and leopard alarm calls between 6.4% and 9.2% (Riede and Zuberbühler, in press). In this study we investigate the development of the two parameters maximum amplitude of a pulse and fundamental frequency within a call. Both parameters were normalized within calls. For the correlation between maximum amplitude of a pulse and fundamental frequency we considered the means of the pulses at position 0%, 25%, 50%, 75%, and 100% within the call. Only calls with more than ten pulses and with very low background noise level, i.e., a high signal-to-noise ratio, were considered, resulting in a data set of 10 leopard and 21 eagle alarm calls, respectively.

To test if pulse time series are the result of individual-

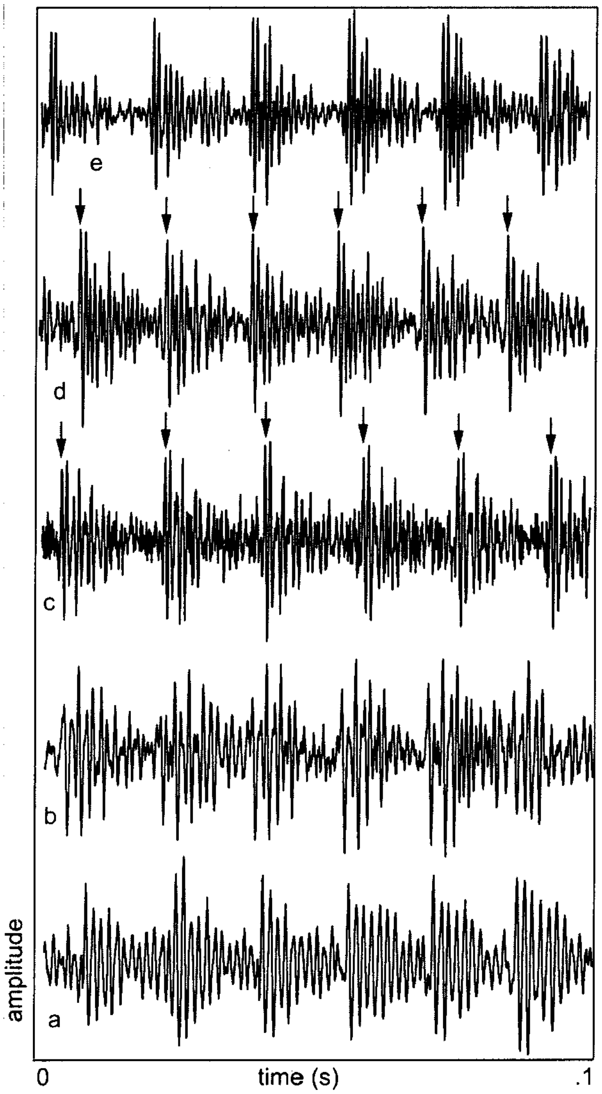

FIG. 2. Time series of pulses of five different individuals. The pulse is the basic acoustic unit in the alarm call; it is defined as a rapid, transient change in the amplitude of the signal from a baseline value to a higher or lower value, followed by a rapid return to the baseline value. Arrows point to the first or second peak in the pulse waveform.

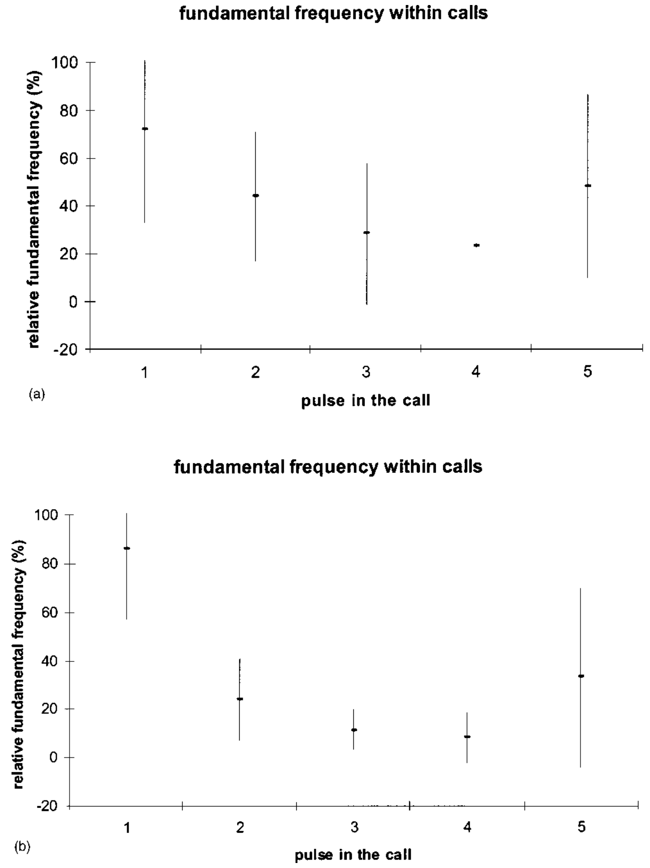

FIG. 3. Fundamental frequency over syllables in (a) leopard alarm calls ($N=10$ syllables) and (b) in eagle alarm calls ($N=21$ syllables). Each data point in the diagram represents the mean ± standard deviation of the relative fundamental frequency within $N=10$ calls (leopard alarm) and $N=21$ calls (eagle alarm). Since calls are of different duration, i.e., they consist of a different number of pulses, call duration was standardized. The five pulses on positions 0%, 25%, 50%, 75%, and 100% of the total number of pulses within a call were considered for the graphs.

specific patterns, cross correlations between pulse time series were undertaken. Five pulses were selected from each of five calls, cut and saved as a text compatible ASCII file. In NCSS 2001 statistical software single cross correlations were run (a) on the within-call level, (b) the between-call and within-individual level, and (c) on the between-individual level. Finally, we were interested in the occurrence of nonlinear phenomena (frequency jumps, subharmonics, biphonation, deterministic chaos) in the alarm calls. For this purpose we inspected the call spectrograms visually for consistency of the pulse pattern, using a data set of 50 calls plus an additional data set of 100 calls from other individuals.

III. RESULTS

A. Fundamental frequency versus maximum amplitude of a pulse

Fundamental frequency depended on the position of the pulse within the call. Fundamental frequency was lower at the beginning and at the end of the call than in the middle of the call. Figure 3 summarizes the development of fundamental frequency over a call of leopard alarm calls ($N=10$ calls) and eagle alarm calls ($N=21$ calls).

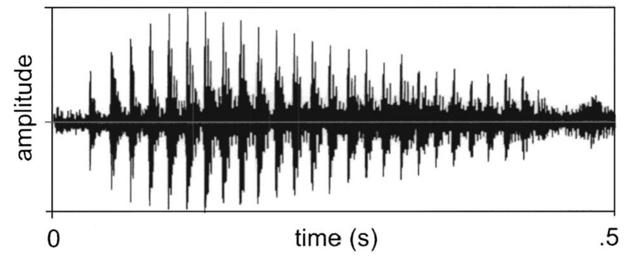

FIG. 4. Time domain of a call. Note the increase in amplitude toward the middle of the call and the amplitude decreases toward the end.

Even maximum amplitude of pulses depended on the position of the pulse within a call. Pulses in the middle of the call were louder than those at the beginning or the end of the call (Fig. 4).

Figure 5 summarizes the development of maximum amplitude of pulses within calls of leopard alarm calls ($N=10$ calls) and eagle alarm calls ($N=21$ calls).

Comparing both parameters, there is a suggestive positive correlation between fundamental frequency and maximum amplitude of pulses within a call in leopard alarm calls (Pearson, $N=5$, $r=0.8$, $P=0.1$) and there is a significant positive correlation between fundamental frequency and maximum amplitude of pulses in eagle alarm calls (Pearson, $N=5$, $r=0.96$, $P=0.0089$). For the correlation the five mean values, as shown in Figs. 3 and 4, have been used.

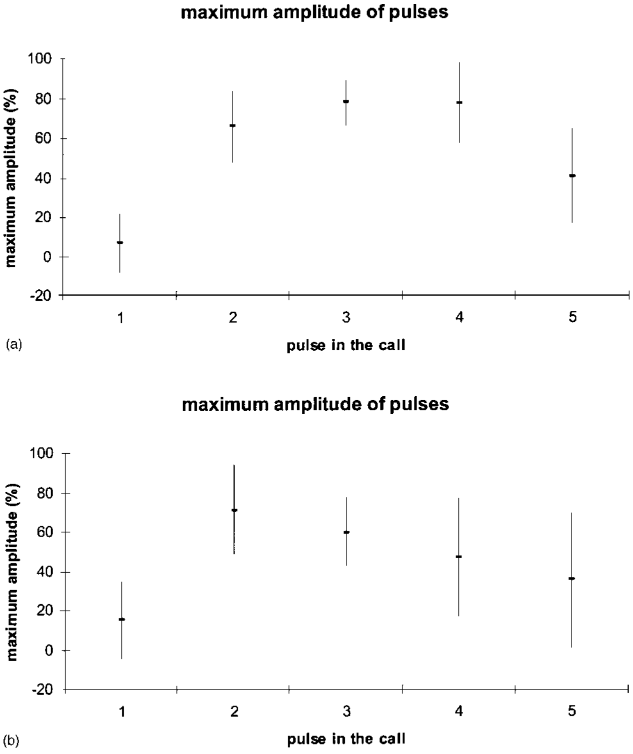

FIG. 5. Maximum amplitude of pulses (a) in leopard alarm calls ($N=10$ calls) and (b) in eagle alarm calls ($N=21$ calls). Each data point within the diagram represents the mean ± standard deviation of the maximum amplitude of pulses of $N=10$ calls (leopard alarm) and $N=21$ calls (eagle alarm). Since calls are of different duration, i.e., they consist of a different number of pulses, call duration was standardized. The five pulses on positions 0%, 25%, 50%, 75%, and 100% of the total number of pulses within a call were considered for the graphs.

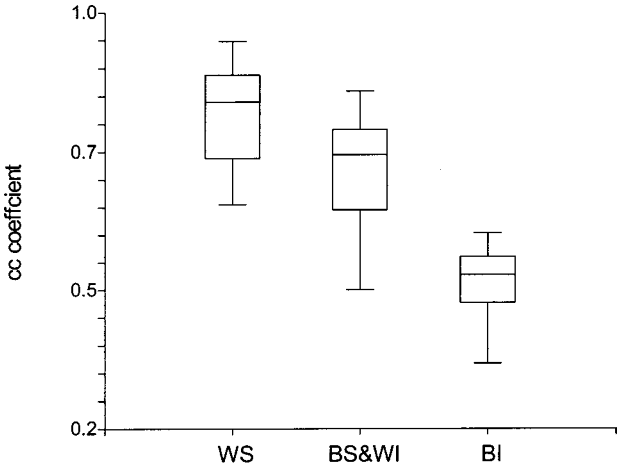

FIG. 6. Cross correlations of pulse time series on three levels. WS—within calls, BS&WI—between calls and within individuals, BI—between individuals. Cross correlation values can be considered as similarity indexes between two time series, saying the higher the cross correlation coefficient the higher the similarity. Within calls the similarity between pulses is highest.

B. Similarity in the pulse waveform

The waveform of a pulse varied within and between individuals. For instance, the maximum amplitude of a pulse can be consistent within the first single cycle of a pulse or alternatively, within one of the later cycles (indicated by arrows in Fig. 2). Cross correlations between single pulses showed an individual specific pattern, delivering highest cross correlation values within calls, being less similar between calls within individuals, and being least between individuals (Fig. 6). The differences between conditions were significant ($N_1=25$, $N_2=25$, $N_3=25$, $F=89.2$, $P<0.001$) with *posthoc* comparisons showing that all means differed from one another. As illustrated in Fig. 6, the means of the two ‘‘within individual’’ conditions (within calls and between calls) were closer to each other than the ‘‘between individual’’ condition to each of the other two conditions (Fig. 6).

C. Nonlinear phenomena

We investigated the calls for the occurrence of nonlinear phenomena. Pulses occurred in a very regular pattern, i.e., visual inspection of the spectrograms delivered no deviations from the pulse pattern, suggesting a rigid and not deviating vibration pattern of the oscillating system (of the sound source). This was true for the whole data set of 50 calls. Even in the additional data set of 100 additional calls no nonlinear phenomena were discovered.

IV. DISCUSSION

The acoustic structure of male Diana monkey alarm calls is remarkable. These vocalizations consist of trains of loud and low-pitched calls that carry over long distances of up to a kilometer through dense tropical forest habitat. A pulse of 8- to 30-ms duration is the basic unit of male Diana monkey alarm vocalizations. Up to 30 pulses are associated to a call. Several calls build a bout. Between two calls there is a short harmonic element, a sound probably uttered during inspiration. The pulse pattern is very robust, being not interrupted by other phonation types (vibration modes of the source). In 150 different calls produced by more than a dozen different males we did not find any other than the pulse pattern. The fundamental frequency of male Diana monkey alarm calls ranges between 33 and 120 Hz (Riede and Zuberbühler, in press) similar to fundamental frequency ranges of pulsed phonation in *Felidae* [$F0$ in purring between 10 and 45 Hz (Peters and Tonkin-Leyhausen, 1999)] and humans [$F0$ in pulse register between 10 and 90 Hz (Henton and Bladon, 1988)]. Although similar patterns were found for instance in felids (Peters and Tonkin-Leyhausen, 1999) or humans (Titze, 1994) unlike to male Diana monkey, cats do produce all kinds of other vocalizations (Peters, 1981) and in humans the occasional occurrence of a subharmonic regime within a pulse register utterance is reported (Titze, 1994).

The aim of the present study was to investigate the acoustic characteristics of pulsed phonation in Diana monkeys. The sound production mechanism in this species is of particular interest since it has been shown that formant characteristics of a single pulse conveys important information to nearby listeners about ongoing predation events (Zuberbühler, 2000b; Riede and Zuberbühler, in press). Our data confirmed the very narrow range in fundamental frequency in the Diana monkey pulse register, suggesting very limited vocal fold adjustments. In a given adjustment of the vocal folds (i.e., a given length and tension), which is not changed during a single utterance, fundamental frequency seems to be exclusively regulated by the one variable—subglottal pressure (Murry and Brown, 1971). This stands in contrast to the modal phonation type, where the fundamental frequency is controlled mainly by vocal fold tension. Subglottal pressure has been found to correlate both with fundamental frequency (Ishizaka and Flanagan, 1972; Steinecke and Herzel, 1995; Titze, 1989) and with signal amplitude (Gramming, 1988; Titze, 1994).

In male Diana monkeys, we found a positive correlation between the fundamental frequency and the maximum amplitude of a pulse. Since signal amplitude is mainly controlled by subglottal pressure (Gramming, 1988; Titze, 1994), we conclude that fundamental frequency in male Diana monkey alarm calls is similarly controlled by subglottal pressure. Male Diana monkeys differ from humans in that they apparently do not switch to a higher register to produce vocalizations with higher fundamental frequencies. Male Diana monkeys, it appears, are constrained by a pulsed phonation mechanism whose fundamental frequencies are entirely regulated by subglottal pressure.

A. The evolution of Diana monkey alarm calls

Previous work has shown that the fundamental frequency of mammalian vocalizations tends to covary with context relevant aspects, like individual identity, sex or degree of arousal [reviewed in Tembrock (1996)]. If, however, the primary signal is rigid, repetitive and broadband and shows little variability in its most important parameter fundamental frequency, as it is the case in the Diana monkey,

TABLE I. Examples of pulsed utterances in other species than Diana monkeys, giving the name of the utterance, the extent of occurrence, and the reference.

Species	Call type	Description	Reference
Primates			
Human, *Homo* sapiens	Creaky voice	Voluntarily, end-of utterance phenomenon or as a pathological voice	Reviewed in Henton and Bladon (1988)
Chacma baboon, *Papio ursinus*	Wahoo	End of call with some few pulses	Fischer *et al.* (2002)
Gelada baboon, *Theropithecus gelada*			Richman (1976)
Pigtailed macaque, *Macaca nemestrina*	Intention notes, inspiratory note, vibrato growl, bark	A group of calls subsummarized as ''harsh sounds''	Grimm (1967)
Squirrel monkey, *Saimirisciureus*	Girren, churr	A separate call within the repertoire	Winter (1969) (Fig. 9); Ploog *et al.* (1975)
Red howling monkey, *Alouatta seniculus*	Roars	In the climax of the roar	Schön Ybarra (1986) (p. 209)
Other mammals			
Several felidae	Purring		Peters (1981)
Koala, *Phascolarctos cinereus*	Bellow	Seemingly the whole utterance is pulsed	Smith (1980) (p. 21, Figs. 9 and 10)
Cetaceans	Clicks	Part of the sonar system or of other repertoire	Au (1993)

then this might provide a reliable and fruitful basis for the evolution of more sophisticated vocal tract performance. Indeed, other work has shown that formant modulation plays the most important role in the acoustic differentiation of eagle and leopard alarm calls in male Diana monkeys (Zuberbühler, 2000b; Riede and Zuberbühler, in press). Diana monkeys manage to filter the primary source signal produced by the vocal folds in their vocal tracts to product acoustically distinct eagle and leopard alarm calls. Because of their broad bandwidth, pulses are particularly well suited to picture the resonance characteristics of the vocal tract and serve as acoustic raw material for filtering effects in the vocal tract.

Interestingly, human singing tutelage is often based on using pulse register phonation as an exercise to ''tune'' the vocal tract (Miller *et al.*, 1997). By singing a particular vowel in pulse register the trainee can examine his or her vocal tract performance. Once successful, the trainee switches back to the actual singing voice while maintaining the vocal tract configuration. This exercise should enable the performer to tune the formants and fundamental frequency optimally.

This example illustrates that the simple and robust pulse signal is physiologically easy to produce, but is insufficient as a source of acoustic variation to be useful to convey contextual information. Instead, phonation based on a pulse signal is likely to favor the evolution of vocal tract characteristics that enable the caller to engage in sophisticated molding of the source, i.e., to engage in articulatory maneuvers. Research focusing on the signal production mechanisms will be necessary to determine the general evolutionary trends that were likely to have affected Diana monkey vocal behavior.

In recent years it became more evident that the mammalian larynx can be considered as a nonlinear system; several studies showed that sudden changes in the vibration mode of the vocal folds are more the normal picture rather than an exception (Wilden *et al.*, 1998; Riede *et al.*, 2000). Those studies are contrasted by the findings presented here, showing that male Diana monkey alarm call pulsed phonation was free of any interruption of the pulse pattern. Anatomical data on the male Diana monkey larynx will be necessary to illuminate the evolution of this special kind of vocalizations. Possibly, anatomical adaptations make the vocal folds ''special'' for this kind of vibration behavior, leading to the observed highly stabilized vibration pattern.

B. Pulse phonation—an exclusive vocal pattern in male Diana monkeys?

Table I reviews studies that mention pulsed phonation as part of a species repertoire or present spectrograms, which suggest the occurrence of pulsed vocal utterances.

In land mammals, the felids seem to be the most intensively studied group that show pulsed phonation (Peters and Tonkin-Leyhausen, 1999). The time series of purring, however, appears different from Diana monkey alarm calls and humans pulse register (Fig. 7). In humans, pulse register

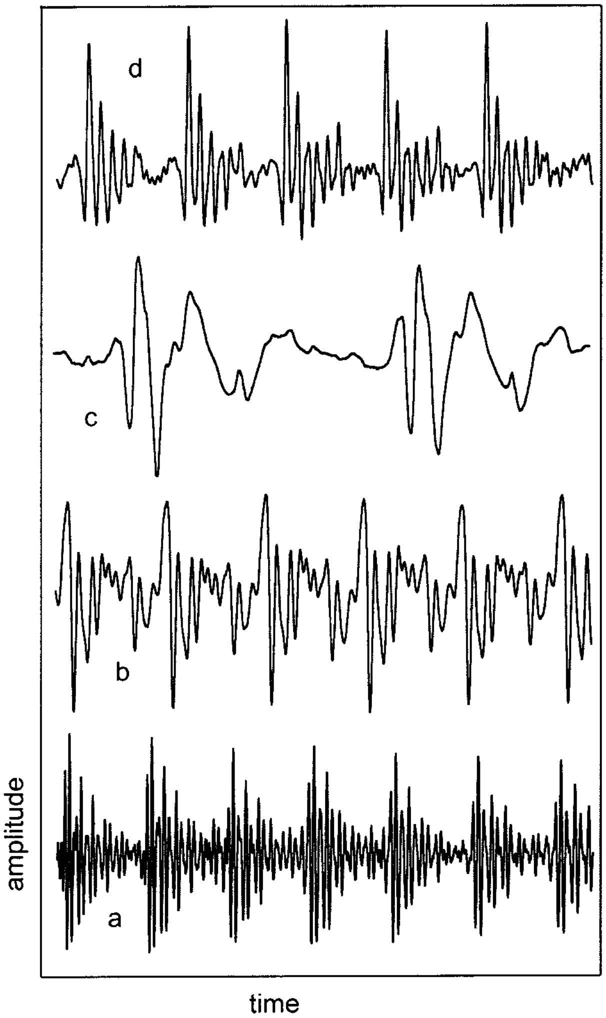

FIG. 7. Time series of pulsed phonation in different land mammals. (d) Domestic cat, (c) leopard, (b) human creaky voice, and (a) Diana monkey.

does not seem to play an important role in everyday speech. Instead it is considered an ‘‘end-of-utterance’’ phenomenon, indicating that pulses often occur at the end of words or sentences, and in men more often than in women (Henton and Bladon, 1988). However, no studies have dealt in any depth with the incidence of vocal fry in natural, unprovoked conditions in humans (Henton and Bladon, 1988). For other species this kind of a ‘‘single mode’’ source signal was apparently not yet described. In contrast to all these findings, our results suggest that in male Diana monkeys pulse register is the main mode at the source.

C. Implications for the receiver

Animal alarm calls have often been shown to be repetitive, i.e., consisting of short and similarly structured segments which are repeated, for instance in the vervet monkey snake alarm calls (Owren, 1990). Studies on the psychological value of visual and acoustic signals have shown that repeating short elements to form a signal are the most effective way to attract attention and alert others [reviewed in Bradbury and Vehrencamp (1998)]. Diana monkey alarm call pulses are short and repetitive. It is interesting to note that silent gaps of about 5 ms can still be detected by humans (e.g., Abel, 1972; Buus and Florentine, 1985). Assuming the gap detection ability of nonhuman primates is comparable to that of humans, the pulse duration of male Diana monkey alarm calls lies comfortably above that threshold, suggesting the pulsed structure of Diana monkey alarm calls is perceived as an attention attracting structure. Psychophysical experiments manipulating the number of pulses might be suitable to determine the minimum amount of information necessary for a Diana monkey to discern eagle from leopard alarm calls or to identify calls as those of a conspecific.

V. CONCLUSION

To investigate the mechanisms of sound production in Diana monkeys, eagle and leopard alarm calls from ten different Diana monkey males were digitized and subjected to spectrographic analysis. Results showed that the fundamental frequency of these calls ranged between 33 and 120 Hz, comparable to the human pulse register, which tends to range between 10 and 90 Hz. Jitter was very small and did not vary significantly between individuals or alarm call type. Nonlinear phenomena were virtually absent in male Diana monkey vocalization and pulses were not interrupted by any other vibration modes of the vocal folds. Over the entire calls, fundamental frequency was low at the beginning and at the end of the syllable and highest in the middle of the call, while the amplitudes of pulses increase towards the middle and then decrease toward the end of the call, indicating that fundamental frequency and maximum amplitude of a pulse were correlated, which suggested that the fundamental frequency in Diana alarm calls is controlled by subglottal pressure rather than vocal fold stiffness changes. The pulsed phonation in male Diana monkey alarm call, therefore, appeared to be a special adaptation delivering a robust source broadband signal for subsequent vocal tract filtering.

ACKNOWLEDGMENTS

We thank Michael Owren and two anonymous reviewers for important comments on an earlier version of the manuscript. This work was supported by a fellowship within the Postdoc Program of the German Academic Exchange Service (DAAD) to TR.

Abel, S. M. (**1972**). ‘‘Discrimination of temporal gaps,’’ J. Acoust. Soc. Am. **52**, 519–524.

Allen, E., and Hollien, H. (**1973**). ‘‘A laminagraphic study of pulse (vocal fry) phonation,’’ Folia Phoniatr. **25**, 241–250.

Au, W. W. L. (**1993**). *The Sonar of the Dolphin* (Springer Verlag, New York).

Berry, D. A. (**2001**). ‘‘Mechanisms of modal and nonmodal phonation,’’ J. Phonetics **29**, 431–450.

Berry, D. A., Herzel, H., Titze, I. R., and Krischer, K. (**1994**). ‘‘Interpretations of biomechanical simulations of normal and chaotic vocal fold oscillations with empirical eigenfunctions,’’ J. Acoust. Soc. Am. **95**, 3595–3604.

Blomgren, M., Chen, Y., Ng, M. L., and Gilbert, H. R. (**1998**). ‘‘Acoustic, aerodynamic, physiologic, and perceptual properties of modal and vocal fry registers,’’ J. Acoust. Soc. Am. **103**, 2649–2658.

Bradbury, J. W., and Vehrencamp, S. L. (**1998**). *Principles of Animal Communication* (Sinauer, Sunderland).

Buus, S., and Florentine, M. (**1985**). ‘‘Gap detection in normal and impaired listeners: The effect of level and frequency,’’ in *Time Resolution in Auditory Systems*, edited by A. Michelsen (Springer, New York).

Fant, G. (**1960**). *Acoustic Theory of Speech Production* (Mouton, The Hague).

Fischer, J., Hammerschmidt, K., Cheney, D. L., and Seyfarth, R. M. (**2002**). “Acoustic features of male baboon loud calls: influences of context, age, and individuality,” J. Acoust. Soc. Am. **111**, 1465–1474.

Fuks, L., Hammarberg, B., and Sundberg, J. (**1998**). “A self-sustained vocal-ventricular phonation mode: acoustical, aerodynamic and glottographic evidences,” TMH-QPRS **3**, 49–59.

Gerratt, B., and Kreiman, J. (**2001**). “Toward a taxonomy of nonmodal phonation,” J. Phonetics **29**, 365–381.

Gramming, P. (**1988**). “The phonetogram: An experimental and clinical study,” Malmoe Sweden, Dept. Otolaryngology, Univ. of Lund.

Grimm, R. J. (**1967**). “Catalogue of sounds of the pigtailed macaque (Macaca nemestrina),” J. Zool. Lond. **152**, 361–373.

Henton, C., and Bladon, A. (**1988**). “Creak as a sociophonetic marker,” in *Language, Speech, and Mind: Studies in Honour of Victoria A. Fromkin*, edited by L. M. Hyman and C. N. Li (Routledge, London), pp. 3–29.

Herzel, H., Berry, D., Titze, I. R., and Saleh, S. (**1994**). “Analysis of vocal disorders with methods from nonlinear dynamics,” J. Speech Hear. Res. **37**, 1008–1019.

Hollien, H. (**1974**). “On vocal registers,” J. Phonetics **2**, 125–143.

Hollien, H., and Michel, J. (**1968**). “Vocal fry as a phonational register,” J. Speech Hear. Res. **11**, 600–604.

Hollien, H., Damsté, H., and Murry, T. (**1969**). “Vocal fold length during vocal fry phonation,” Folia Phoniatr. **21**, 257–265.

Hollien, H., Girard, G. T., and Coleman, R. F. (**1977**). “Vocal fold vibratory patterns of pulse register phonation,” Folia Phoniatr. **29**, 200–205. (**1972**).

Ishizaka, K., and Flanagan, J. L. (**1972**). “Synthesis of voiced sounds from a two-mass model of the vocal cords,” Bell Syst. Tech. J. **51**, 1233–1268.

Lindestad, P., Soedersten, M., Merker, B., and Granqvist, S. (**2001**). “Voice source characteristics in Mongolian ‘throat singing’ studied with high-speed imaging technique, acoustic spectra, and inverse filtering,” J. Voice **15**, 78–85.

Mergell, P., Fitch, W. T., and Herzel, H. (**1999**). “Modeling the role of non-human vocal membranes in phonation,” J. Acoust. Soc. Am. **105**, 2020–2028.

Miller, D. G., Sulter, A. M., Schutte, H. K., and Wolf, R. F. (**1997**). “Comparison of vocal tract formants in singing and nonperiodic phonation,” J. Voice **11**, 1–11.

Morton, E. S. (**1977**). “On the occurrence and significance of motivation—structural rules in some bird and mammal sounds,” Am. Nat. **111**, 855–869.

Murry, T., and Brown, W. S., Jr. (**1971**). “Subglottal air pressure during two types of vocal activity: vocal fry and modal phonation,” Folia Phoniatr. **23**, 440–449.

Neubauer, J., Mergell, P., Eysholdt, U., and Herzel, H. (**2001**). “Spatio-temporal analysis of irregular vocal fold oscillations: biphonation due to desynchronization of spatial modes,” J. Acoust. Soc. Am. **110**, 3179–3192.

Owren, M. J. (**1990**). “Acoustic classification of alarm calls by veret monkeys (*Cercopithecus aethiops)*,” J. Acoust. Soc. Am. **101**, 2951–2963.

Owren, M., and Linker, C. D. (**1995**). “Some analysis techniques that may be useful to acoustic primatologists,” in *Current Topics in Primate Vocal Communication*, edited by E. Zimmermann, J. Newman, and U. Jürgens (Plenum, New York), pp. 1–27.

Peters, G. (**1981**). “Das Schnurren der Katzen,” Säugetierkundl. Mitteilungen **29**, 30–37.

Peters, G., and Tonkin-Leyhausen, B. A. (**1999**). “Evolution of communication signals of mammals: friendly close range vocalizations in felidae (Carnivora),” J. Mammalian Evol. **6**, 129–159.

Ploog, D., Hupfer, K., Jürgens, U., and Newman, J. D. (**1975**). “Neuroethological studies of vocalization in squirrel monkeys with special reference to genetic differences of calling in two subspecies,” in *Growth and Development*, edited by M. A. B. Brazier (Raven, New York).

Richman, B. (**1976**). “Some vocal distinctive features used by gelada monkeys,” J. Acoust. Soc. Am. **60**, 718–724.

Riede, T., and Zuberbühler, K. (in press). “The relationship between acoustic structure and semantic information in Diana monkey alarm calls.” J. Acoust. Soc. Am.

Riede, T., Wilden, I., and Tembrock, G. (**1997**). “Subharmonics, biphonations, and frequency jumps—common components of mammalian vocalization or indicators for disorders,” Z. Säugetierkunde **62**, 198–203.

Riede, T., Herzel, H., Mehwald, D., Seidner, W., Trumler, E., Böhme, G., and Tembrock, G. (**2000**). “Nonlinear phenomena in the natural howling of a dog-wolf mix,” J. Acoust. Soc. Am. **108**, 1435–1442.

Schoen Ybarra, M. A. (**1986**). “Loud calls of adult male red howling monkeys (*Alouatta seniculus*),” Folia Primatol (Basel) **47**, 204–216.

Smith, M. (**1980**). “Behavior of the Koala, Phascolarctos cinereus (Goldfuss), in captivity, III. Vocalizations,” Aust. Wildl. Res. **7**, 13–34.

Steinecke, I., and Herzel, H. (**1995**). “Bifurcations in an asymmetric vocal fold model,” J. Acoust. Soc. Am. **97**, 1874–1884.

Svec, J. G., Schutte, H. K., and Miller, D. G. (**1999**). “On pitch jumps between chest and falsetto registers in voice: Data from living and excised human larynges,” J. Acoust. Soc. Am. **106**, 1523–1531.

Tembrock, G. (**1996**). *Akustische Kommunikation der Säugetiere. Wissenschaftl* (Buchgesell, Darmstadt).

Tigges, M., Mergell, P., Herzel, H., Wittenberg, T., and Eysholdt, U. (**1997**). “Observation and modeling of glottal biphonation,” Acustica **83**, 707–714.

Titze, I. R. (**1989**). “On relation between subglottal pressure and fundamental frequency in phonation,” J. Acoust. Soc. Am. **85**, 901–906.

Titze, I. R. (**1991**). “Mechanisms underlying the control of fundamental frequency,” in *Vocal Fold Physiology: Acoustic, Perceptual and Physiological Aspects of Voice Mechanisms*, edited by J. Gauffin and B. Hammarberg (Singular, San Diego), pp. 129–138.

Titze, I. R. (**1994**). *Principles of Voice Production* (Prentice Hall, Englewood Cliffs, NJ).

van den Berg, J. (**1958**). “Myoelastic-aerodynamic theory of voice production,” J. Speech Hear. Res. **1**, 227–244.

Wilden, I., Herzel, H., Peters, G., and Tembrock, G. (**1998**). “Subharmonics, biphonation, and deterministic chaos in mammal vocalization,” Bioacoustics **9**, 171–196.

Winter, P. (**1969**). “Dialects in squirrel monkeys: vocalization of the roman arch type,” Folia Primatol (Basel) **10**, 216–229.

Zuberbühler, K. (**2000a**). “Causal knowledge of predators’ behavior in wild Diana monkeys,” Anim. Behav. **59**, 209–220.

Zuberbühler, K. (**2000b**). “Referential labeling in Diana monkeys,” Anim. Behav. **59**, 917–927.

Zuberbühler, K. (**2003**). “The effects of natural and sexual selection on the evolution of guenon loud calls,” in *The Guenons*, edited by M. Glenn and M. Cords (Plenum, New York).

Zuberbühler, K., Cheney, D. L., and Seyfarth, R. M. (**1999**). “Conceptual semantics in a non-human primate,” J. Comp. Psychol. **113**, 33–42.

Zuberbühler, K., Noe, R., and Seyfarth, R. M. (**1997**). “Diana monkey long-distance calls: messages for conspecifics and predators,” Anim. Behav. **53**, 589–604.