

Acoustical expression of arousal in conflict situations in tree shrews (*Tupaia belangeri*)

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Abstract Empirical research on human and non-human primates suggests that communication sounds express the intensity of an emotional state of a signaller. In the present study, we have examined communication sounds during induced social interactions of a monogamous mammal, the tree shrew. To signal their unwillingness to mate, female tree shrews show defensive threat displays towards unfamiliar males paralleled by acoustically variable squeaks. We assumed that the distance between interacting partners as well as the behavior of the male towards the female indicates the intensity of perceived social threat and thereby the arousal state of a female. To explore this hypothesis we analyzed dynamic changes in communication sounds uttered during induced social interactions between a female and an unfamiliar male. Detailed videographic and sound analyzes revealed that the arousal state predicted variations in communication sound structure reliably. Both, a decrease of distance and a male approaching the female led to an increase in fundamental frequency and repetition rate of syllables. These findings support comparable results in human and non-human primates and suggest that common coding rules in communication sounds govern acoustic conflict regulation in mammals.

Keywords Communication · Emotion · Defensive threat · Conflict · Sounds

Abbreviations

AFRMB	Analysis of female response to male behavior
AFRMP	Analysis of female response to male proximity
F_0	Fundamental frequency
IR	Interquartile range
ISI	Intersyllable interval
PF	Peak frequency

Introduction

Communication sounds are an integral part of conflict resolution in mammals. In order to avoid costly physical aggressive confrontations, communication partners should reliably express their emotional states during social interactions (e.g. Aureli and Smucny 2000). Since Darwin (1872), it is assumed that communication sounds in animals and man convey the emotional state of a sender. Morton's (1977) motivation-structural rules, based on qualitative comparisons of sonagrams of 28 species of birds and mammals, predicted a relationship between the acoustic structure of communication sounds and the social contexts of sound production. Experimental studies on nonhuman primates support the view that different types of communication sounds are associated with different context-specific emotional states of the sender (e.g., Jürgens 1979; Kalin et al. 1992; Scheumann and Zimmermann 2007). Furthermore Ehret (2006), based on a literature review of communication sounds in nonhuman mammals, hypothesized that the arousal dimension of an emotion—the so-called affective intensity (e.g. Rendall 2003)—influences the acoustic parameters of context-specific communication sounds predictably.

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Empirical studies on nonhuman primates suggested arousal-related differences within the same sound type during social interactions [e.g. grunts uttered during group movements and mother–infant interactions in baboons (Rendall 2003), food-associated calls in rhesus macaques (Hauser and Marler 1993)]. Likewise, studies on the expression of emotions in man suggested that physiological arousal influenced the acoustic structure of a vocal expression reliably (Bachorowski 1999; Bänziger and Scherer 2005). Across studies of human and non-human primates, arousal was found to be expressed by a set of distinct acoustic parameters in the frequency and time domain (F_0 , F_0 range and F_0 contour, sound intensity, tempo), most probably related to arousal-based physiological activation of the nervous system.

To date, however, there is a lack of information concerning the effect of arousal on communication sound production during social interactions in non-primate mammals. Hence it is unclear to what extent findings in primates can be generalized across further mammalian lineages. Tree shrews are suitable model to gain first insight into the situation for a mammalian radiation, genetically closely related to primates (Sargis 2004). To study the effect of arousal on communication sound production we analyzed dynamic changes in the acoustic structure during induced social interactions.

Tree shrews are highly vocal and live as monogamous pairs in dense vegetation of tropical forest areas of Southeast Asia (Emmons 2000). Breeding of tree shrews is often difficult (von Holst 1986). In about 80% of all arbitrarily formed pairs, the female aggressively rejects approaches of the male (von Holst 1986) by displaying a male-directed defensive threat display (Binz and Zimmermann 1988), i.d. an open-mouth bared-teeth stare combined with loud and acoustically highly variable communication sounds, termed squeaks. The male usually responds by withdrawal from the female.

In the present study we used a standardized social encounter paradigm, in which pair-bonded females, unwilling to mate, were exposed to unfamiliar, sexually interested males. We thus experimentally induced communication sounds within a standardized behavioral context. We supposed that variations in the acoustic expression of squeaks given during defensive threat displays of females could be predicted by changes in the perceived degree of social threat or aversiveness of the sender. Following McNaughton and Corr (2004) we assumed that the perceived degree of social threat, and thereby the male-induced arousal state of a female, can be operationalized either by the distance between male and female or by the approach-withdrawal behavior of the male towards the female. If the perceived degree of social threat induces variations in the arousal state of a female which are

expressed by corresponding changes in the acoustic expression of squeaks, we would expect predictable and comparable acoustic variations related to both, the distance between male and female and the type of behavior the male directed towards the female.

We examined the variation in the acoustic design of these spontaneously uttered communication sounds in relation to the perceived degree of social threat and thereby the arousal state of the sender by applying a multiparametric sound analysis as well as a frame-by-frame video analysis. Our results will be compared to data on other mammals.

Methods

Subjects

Tree shrews (*Tupaia belangeri*) were housed in wire mesh cages (size 150 cm × 150 cm × 80 cm) from EB-ECO, Castrop-Rauxel, Germany, each provided with at least two nest boxes, a variety of branches, and several wooden resting shelves. Diet consisted of *Tupaia* pellets from Altromin, Lage, Germany, fresh fruits and as rewards some mealworms or locusts. Animals were fed once a day early in the morning. They had ad libitum access to water. For further details on animal maintenance see Hertenstein et al. (1987). Experimental subjects were six captive-born females aged 1–7 years, which had already formed a harmonic pair bond (von Holst 1986) with their mate. In addition, six males, unfamiliar to the females, aged 1–6 years were involved in the experiments.

Data collection

Design of the social encounter experiment and experimental set-up

To induce a comparable emotional state in all of the six females, we performed one social encounter experiment between each of the pair-bonded females and a sexually interested unfamiliar male.

Social encounter experiments were conducted in a wire-mesh encounter cage (size 100 cm × 100 cm × 75 cm) from EBECO in a sound-attenuating room. The cage consists of two compartments linked through a connecting door. Tree shrews were individually habituated to this new environment prior to testing.

For an encounter experiment, each interaction partner was removed from its respective home cage in its nest box and put into one compartment of the encounter cage. As soon as both animals left their nest boxes, we opened the

connecting door and the encounter experiment started. One encounter experiment lasted 15–30 min.

During an encounter experiment communication sounds were recorded by two microphones (Sennheiser, Wedemark, Germany, K6/ME62 and ME64), fed into a pre-amplifier (Avid Technology, Öhringen, Germany, M-Audio DMP3), digitized at a sampling frequency of 100 kHz (A/D converter: National Instruments, Austin, TX, USA, DAQCard-6062E; software: Engineering Design, Belmont, MA, USA, NIDisk), and stored as uncompressed audio files on a laptop (Toshiba, Irvine, CA, USA, Satellite A10-s100). The behavior of the interaction partners was synchronously videotaped by two video cameras (Sony, Tokyo, Japan, DCR-HC 30 E and HC 85 E). One was arranged in front of, the other on top of the encounter cage. To determine the shortest distance ($|\vec{x}|$) between male and female in each sound-correlated defensive threat display during an encounter experiment, we measured the distance between the animals in three dimensions. Therefore we attached 2 dm scales to the front of the encounter cage to measure the distance between the animals in the width (x_1) and the height (x_2) and 1 dm scale to the top to measure the distance in the depth (x_3). We used these values (x_1, x_2, x_3) to calculate the length of the vector ($|\vec{x}| = \sqrt{x_1^2 + x_2^2 + x_3^2}$), corresponding to the absolute distance between the animals. The distortion error of the absolute distance between the two animals, determined by video analysis, can be calculated by using the Gaussian error propagation (Eq. 1) of the error of each dimension (width x_1 , height x_2 and depth x_3). The distortion error in each dimension is dependent on the distance between the animal and the different scales. Since the decimeter scales were attached on top and at the front of the encounter cage and the cameras were located relatively close to the cage, the measure is further biased if the animal (of interest) is far away from the scales. This distortion affects the measurement error of each dimension, which we estimated to be on average $\sigma = 0.5$ cm, by a factor of <1.3 (height), <1.4 (width) and <1.67 (depth). Therefore, the deviation of the absolute distance measure averages by

$$\sigma_{\text{tot}} = 2 \times \sqrt{(\sigma_h^2 + \sigma_w^2 + \sigma_d^2)} = 2.55 \text{ cm}, \quad (1)$$

with $\sigma_h = 0.5 \text{ cm} \times 1.3$, $\sigma_w = 0.5 \text{ cm} \times 1.4$ and $\sigma_d = 0.5 \text{ cm} \times 1.67$.

For one part of further analysis we were interested in the two defensive threat displays during an encounter experiment in which (1) the shortest distance between the respective interacting pair was at its maximum value (called maximum distance) and (2) in which the shortest distance was at its minimum value (called minimum distance).

Experimental paradigm to define the arousal state of a female during a social encounter experiment

Most of the social interactions between a male and male-bonded female could be described as follows: The sexually interested male tried to approach the female. The female rejected this contact approach by turning to the male and displaying a defensive threat display towards him, e.g. open-mouth bared-teeth display (=aggressive stare, Binz and Zimmermann 1988) paralleled by squeaks. During such a display the female remained at a given site. In most cases, the male then responded by withdrawal from the female. Soon afterwards he tried to contact her again. We assumed that both a withdrawal of the male and a maximum distance between male and female operationalize a low social threat for the female and induce a low-arousal state. Accordingly, an approach of the male towards the female as well as a minimum distance between male and female operationalizes a high social threat for the female and evokes a high-arousal state. By these inferred low- and high-arousal conditions we could explore arousal-related variations of communication sounds during a partner evoked emotional response, the defensive threat display.

Videographic analysis of sound-correlated behavior

From the videotaped social encounter experiments we selected sound-correlated defensive threat responses of the female towards the male. Using the software Interact 7.2.5 (Mangold, Arnstorf, Germany), these selected interactions were analyzed frame-by-frame. Two different analyses were performed to explore arousal-related variations of communication sounds recorded during the defensive threat display of a female: (1) An analysis of female response to male behavior (AFRMB). Here, those sound-correlated defensive threat displays of the female were selected, in which an approach of the male was followed by a withdrawal. (2) An analysis of female response to male proximity (AFRMP). Here, two sound-correlated defensive threat displays per pair were selected, i.e. the interaction in which the distance between the interacting male and female was maximum and the one in which the distance was minimum. In all respective interactions, no body contact occurred between the animals.

Female communication sounds were analyzed in the following way: (1) In the AFRMB, we divided each male-induced sound-correlated behavioral response of a female into two parts, the approach and the withdrawal phase of the male. In subsequent acoustical analyses we compared syllables from the approach phase with syllables from the withdrawal phase (Fig. 1a). Altogether, we considered 16 male-induced sound-correlated behavioral responses of females (mean per animal 2.7, range 1–4) and analyzed 151

syllables. The variable number of analyzed responses of each female depends on the occurrence of defensive threat displays, in which an approach of the male was followed by a withdrawal. (2) In the AFRMP, we focussed on two points in time during each encounter experiment: (1) the sound-correlated defensive threat display at which the maximum distance between the interacting male and female occurred and (2) the sound-correlated defensive threat display at which the shortest distance during an encounter experiment occurred. Two syllables associated with these two time points were then used for further acoustic analysis (Fig. 1a, b). We therefore considered 12 male-induced sound-correlated defensive threat displays of females and analyzed 24 syllables.

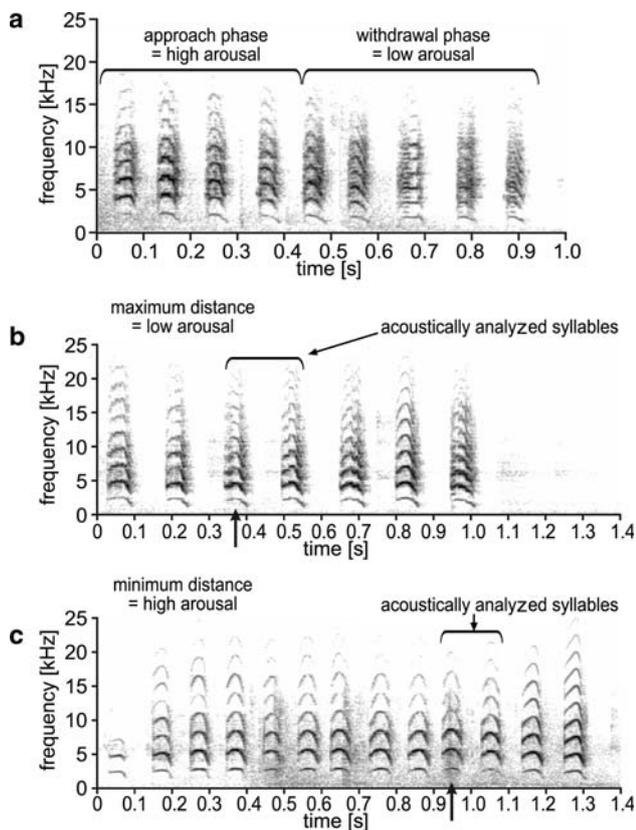


Fig. 1 **a** Sonogram of a female squeak recorded during a male-induced defensive threat display. The sound was divided into two parts, syllables uttered during the approach phase and those uttered during withdrawal. Syllables from both phases were analyzed and compared. **b** Sonogram of a female squeak uttered during a male-induced defensive threat display when the shortest distance between the interaction partners was at its maximum. The arrow indicates the point in time of maximum distance between male and female during this threat display. Two syllables associated with that point in time were analyzed. **c** Sonogram of female squeak obtained during a male-induced defensive threat display when the shortest distance between the interaction partners was at its minimum. The arrow indicates the point in time of minimum distance between male and female during this threat display. Two syllables associated with that point in time were analyzed

Acoustic analysis

Multiparametric analyses of communication sounds were carried out with SIGNALTM software (Engineering Design, version 4.02.04) by conducting a 1,024-point Fast Fourier Transformation (FFT) with a time resolution of 10.2 ms and a frequency resolution of 97.7 Hz. The temporal measurements were done in oscillograms using BatSound Pro software (Pettersson Elektronik AB, Uppsala, Sweden, version 3.31).

A squeak (Fig. 1a) consisted of a sequence of short, broadband frequency-modulated, harmonic units, called syllables. Whereas the general frequency contour of these syllables remained relatively stable throughout the whole sound, repetition rate and F_0 varied considerably. To explore whether this acoustic variation may be predicted either by the behavior of the male or the proximity of the male to the female, we characterized squeaks and squeak syllables by nine different acoustic variables, three in the temporal and six in the spectral domain (Fig. 2a, b; Table 1).

Statistical analyses

Using univariate statistics we calculated the median for each measured acoustic variable per subject. In total we

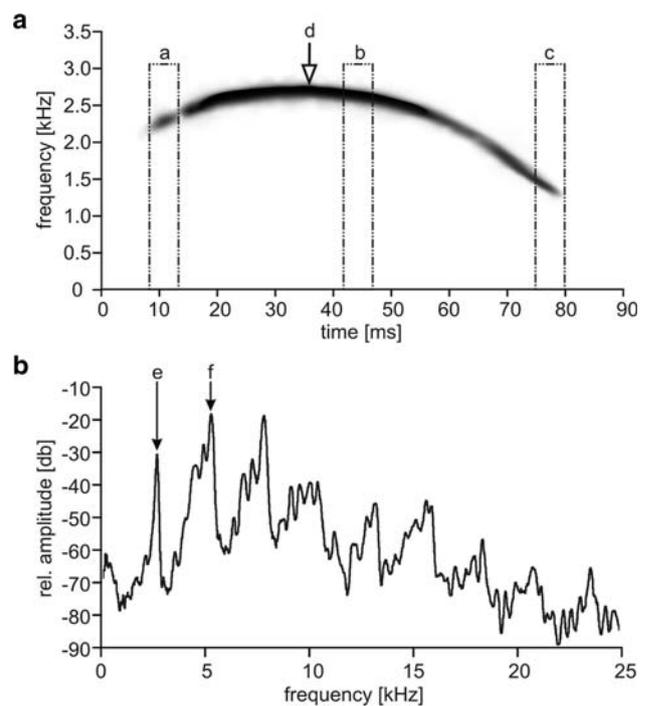


Fig. 2 **a** Sonogram of the F_0 of a squeak syllable and description of the measured spectral parameters. **a** time slice for measuring the F_0 -peak-onset; **b** time slice for measuring the F_0 -peak-middle; **c** time slice for measuring the F_0 -peak-end; **d** F_0 -maximum. **b** Power spectrum of the time slice **b**; **e** F_0 -peak; **f** peak frequency

Table 1 Definition of sound parameters

Sound parameter	Definition
Number of syllables per sound ^b	
Duration (ms) of a syllable ^c	Time between onset and offset of a syllable
Intersyllable interval (ms) ^b	Time between two successive syllables
Peak frequency (kHz) ^a	Maximum acoustic energy of a whole syllable
F_0 -peak (kHz) ^a	Maximum acoustic energy of the F_0 of a whole syllable
F_0 -peak-onset (kHz) ^a	Maximum acoustic energy of the F_0 at the start (first 5 ms) of a syllable
F_0 -peak-middle (kHz) ^a	Maximum acoustic energy of the F_0 in the middle (5 ms) of a syllable
F_0 -peak-end (kHz) ^a	Maximum acoustic energy of the F_0 at the end (last 5 ms) of a syllable
F_0 -maximum (kHz) ^b	Highest frequency of the F_0 of a syllable

F_0 fundamental frequency

^a Measurements were made in power spectra

^b Measurements were made in sonagrams

^c Measurements were made in oscillograms

analyzed 151 syllables in the AFRMB and 24 syllables in the AFRMP condition. To examine to what extent arousal will affect communication sounds in tree shrews, we compared acoustic variables of squeak sounds between the low- and high-arousal condition in the AFRMB and in the AFRMP by a nonparametric test for dependent data, the Wilcoxon Signed Rank Test (Bortz 1993). To bring about a global decision about the null hypothesis (the proximity of the interaction partners/the behavior of the male related to the female has no predictable influence on the acoustic structure of the syllables of squeaks), we used the Fisher's Omnibus Test (Haccou and Meelis 1994). This test considered the multiple P values of the single Wilcoxon Signed Rank tests to create an overall P value. This overall P value resulted in an acceptance or refusal of the null hypothesis and hence put aside α -adjustments for each variable which were necessary when testing the same null hypothesis several times. All statistical tests were conducted with α set at 0.05. Fisher's Omnibus Tests were done manually. All other calculations were conducted with SPSS software (SPSS, Chicago, IL, version 13.0).

Results

Concerning the behavior of the male towards the female we found a predictable influence on the acoustic structure of squeak syllables (Fisher's Omnibus Test: $\text{Chi} = 33.30$, $\text{DF} = 16$, $P < 0.05$). Syllables uttered by the female during the male-approach phase showed a significantly higher F_0 -peak, F_0 -peak-onset, F_0 -maximum and significantly shorter intersyllable intervals than syllables uttered during a withdrawal of the male (Table 2).

Furthermore the proximity of the interaction partners had a predictable influence on the acoustic structure of

squeak syllables (Fisher's Omnibus Test: $\text{Chi} = 33.93$, $\text{DF} = 18$, $P < 0.05$). At the minimum distance between male and female [mean 8.5 (± 3.5) cm], syllables showed a significantly higher F_0 -peak-onset and significantly shorter intersyllable intervals than at the maximum distance [mean 25.0 (± 9.5) cm]. Likewise, F_0 -peak and the F_0 -maximum showed a clear tendency to be higher (Table 3).

A variation of the behavior of the male towards the female and a variation of proximity of male and female induced comparable changes in the acoustic structure of female communication sounds within a defensive threat display. Thus, increasing arousal evoked by increasing social threat is expressed in squeak syllables by an upward shift in F_0 -peak-onset and shorter intersyllable intervals (Fig. 3a, b).

Discussion

The acoustic structure of squeaks of female tree shrews varied predictably related to the behavior of the male and the proximity between both animals. This confirms our hypothesis that the perceived social threat and thereby the arousal state is expressed acoustically during dynamic social interactions.

Squeaks given during high-arousal situations were characterized by a higher syllable repetition rate, indicated by shorter intersyllable intervals, as well as by an upward shift in the F_0 -peak-onset. Frequency shifts thereby ranged between 155 and 275 Hz. Heffner et al. (1969), using a conditioned suppression paradigm, showed that tree shrews were able to discriminate frequency differences of 42 Hz at 2 kHz. Hence, the frequency changes observed in the present study are perceivable for the animals and of potential behavioral relevance. The duration of intersyllable

Table 2 Acoustic differences in squeak sounds of females related to the approach-withdrawal behavior of the male towards the female ($N = 6$, Wilcoxon Signed Rank Test); all spectral measurements refer to syllables

Parameter	Behavior	Median	IR	<i>P</i> value
Duration (ms)	Withdrawal	63.50	11.38	1.00
	Approach	60.50	14.63	
ISI (ms)	Withdrawal	77.25	36.56	0.03
	Approach	54.50	10.13	
PF (kHz)	Withdrawal	5.200	0.987	0.44
	Approach	5.493	1.657	
F_0 -peak (kHz)	Withdrawal	2.277	0.604	0.03
	Approach	2.512	0.548	
F_0 -peak-onset (kHz)	Withdrawal	1.856	0.610	0.03
	Approach	2.295	0.586	
F_0 -peak-middle (kHz)	Withdrawal	2.393	0.635	0.75
	Approach	2.442	0.562	
F_0 -peak-end (kHz)	Withdrawal	1.758	0.537	0.22
	Approach	2.002	0.610	
F_0 -maximum (kHz)	Withdrawal	2.313	0.613	0.03
	Approach	2.413	0.538	

F_0 fundamental frequency, *ISI* intersyllable interval, *PF* peak frequency, *IR* inter-quartile range

Table 3 Acoustic differences in squeak sounds of females related to the distance between male and female ($N = 6$, Wilcoxon Signed Rank Test); all spectral measurements refer to syllables

Parameter	Distance	Median	IR	<i>P</i> value
Number of syllables per sound	Maximum	9.00	4.75	0.91
	Minimum	7.50	10.25	
Duration (ms)	Maximum	58.75	17.38	1.00
	Minimum	62.50	11.38	
ISI (ms)	Maximum	67.75	44.00	0.03
	Minimum	48.00	13.38	
PF (kHz)	Maximum	6.055	1.395	0.16
	Minimum	4.959	1.660	
F_0 -peak (kHz)	Maximum	2.295	0.603	0.09
	Minimum	2.633	0.524	
F_0 -peak-onset (kHz)	Maximum	2.002	0.610	0.03
	Minimum	2.197	0.693	
F_0 -peak-middle (kHz)	Maximum	2.246	0.781	0.13
	Minimum	2.637	0.586	
F_0 -peak-end (kHz)	Maximum	1.709	1.123	0.31
	Minimum	2.197	0.732	
F_0 -maximum (kHz)	Maximum	2.153	0.564	0.09
	Minimum	2.522	0.459	

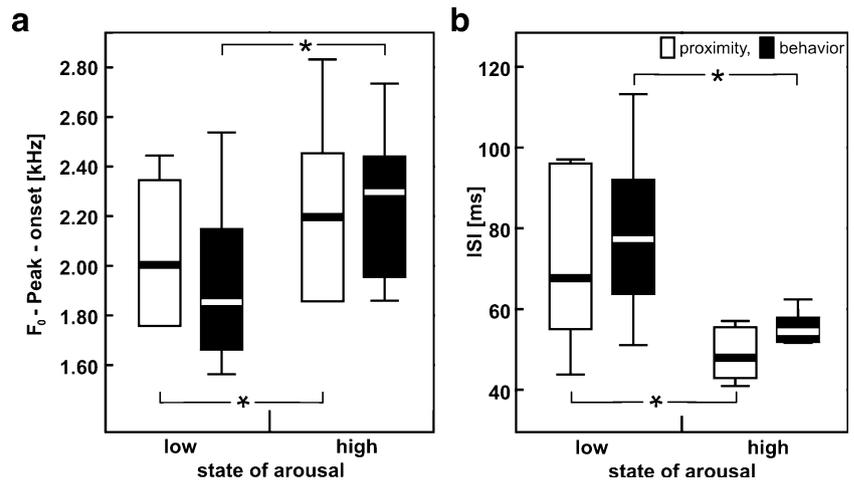
F_0 fundamental frequency, *ISI* intersyllable interval, *PF* peak frequency, *IR* inter-quartile range

intervals ranged between 51 and 75 ms. Studies concerning repetition rate discrimination in tree shrews has not been done yet. However, as already postulated by Ehret (2006), the repetition rate of syllables in sounds may be of potential importance for the perception of the urgency of a response. Ongoing playback experiments will explore to what extent tree shrews perceive these spectral or temporal changes as meaningful.

All analyzed squeaks of female tree shrews were expressed during defensive threat displays, an aversive

behavior of the female toward the male. Female tree shrews are usually lighter than males and thus physically in an inferior position (Fuchs 1999). We therefore assume that the defensive threat display of females reflects anxiety or fear (compare LeDoux 2000; Kalin et al. 1998). Morton (1977) examined sounds of 28 species of birds and mammals respectively and could demonstrate that vocalizations during friendly, appeasing or fearful situations have a high F_0 and a harmonic composition. Compared to other communication sounds of tree shrews, squeaks are high-fre-

Fig. 3 F_0 -peak-onset (a) and ISI duration (b) of squeak syllables varying between high- and low-arousal states of the females in relation to the behavior of the male and the proximity of male and female. The stars and brackets indicate significant differences ($P < 0.05$) between the respective acoustic parameters



quency (Binz and Zimmermann 1988) and therefore coincide with this part of Morton's motivation-structure rules.

Ehret (2006) hypothesized that sounds which evoke aversion in conspecifics, lie in the best hearing range of the respective species. Tree shrews showed lowest auditory thresholds in the range between 1.3 and 10 kHz, as measured by unconditioned behavioral responses (Zimmermann 1993). Therefore, squeak syllables with a mean PF of $5.3 (\pm 1.1)$ kHz corroborate this hypothesis.

Ehret (2006) furthermore stated that a changing arousal state of a sender should be encoded acoustically. This assumption gained support by our results in tree shrews. Squeaks given during social interactions in a high arousal situation showed shorter intersyllable intervals and an upward shift in the F_0 -peak-onset. Similar results were yielded for rhesus macaques (Hauser and Marler 1993) and baboons (Rendall 2003). An increase of arousal during social interactions was associated with shorter intersyllable intervals or higher syllable repetition rates. In baboons even an increase of F_0 was found. Corresponding changes in articulation rate and F_0 were also detected in humans (Bänziger and Scherer 2005). In a non-primate mammal, the African elephant, fundamental frequency was not related to arousal. Here subordinate females produced social sounds (rumbles) with lower cepstral coefficients, suggesting low tonality and unstable pitch in the voice, in the presence of dominant females, compared to rumbles produced in the absence of them (Soltis et al. 2005). Studies on communication sounds which were uttered in alarm or isolation situations corroborated the previously mentioned findings of primates. In barbary-macaques sounds given during a nocturnal disturbance of an observer showed shorter durations, longer intersyllable intervals and a shift to lower frequencies with increasing habituation to the situation (Fischer et al. 1995). A shift to higher frequencies suggested to be related to an increase in arousal was also

noted for electrically induced aversive sounds in squirrel monkeys (Fichtel et al. 2001). Furthermore alarm sounds uttered during changing predation risks within the same situation showed comparable results for non-primate mammals. Suricates (Manser 2001) as well as yellow-bellied marmots (Blumstein and Armitage 1997) decreased intersyllable intervals of sounds with increasing predation risk. Moreover distress sounds of isolated guinea pig pups (Monticelli et al. 2004) showed a decrease in duration and an increase in mean frequency with an increasing time of separation.

Altogether these findings support the view that universal coding rules in sound communication regulate conflict situations across mammals. Thus, an upward shift in frequency as well as an increase in syllable repetition rate seems to reflect changes in arousal across quite different mammalian lineages (Carnivora, Rodentia, Scandentia, and Primates). These changes in acoustic structure may be related to physiological constraints associated with a generalized activation of the nervous system. The rate at which the vocal cords open and close during vocal production determines the period and, hence, the F_0 of the glottal air flow (e.g. Scherer 1979; Lieberman and Blumstein 1988). The rate in turn is determined by the tension of the extrinsic and intrinsic laryngeal muscles, the mass and shape of the moving vocal cords and by the subglottal air pressure generated by the lungs. An upward shift in F_0 can be explained by an increasing subglottal air pressure as well as by an increase in general muscle tone of the vocal cords, both effects of sympathetic arousal. A faster breathing rate, which is also an effect of sympathetic arousal, leads to higher repetition rates of speech syllables (Scherer 1979; MacLarnon and Hewitt 2004). These physiological effects on the source of sound production, the larynx, which displays gross similarities in anatomy across different mammalian taxa (Tembrock 1977), represent

comparable constraints across mammals and may explain common coding rules in communication sound production during conflict regulation in mammals.

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