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Effects of Early Traumatic Experience on Vocal Expression of Emotion in Young Female Rhesus Macaques

Tanja Jovanovic[1] and **Dario Maestripieri**[1,2]

[1]Yerkes National Primate Research Center, Emory University, Atlanta, GA 30329

[2]Department of Comparative Human Development, The University of Chicago, 5730 S. Woodlawn Avenue, Chicago, IL 60637. dario@uchicago.edu

Abstract

The present study used a cross-fostering procedure to investigate the effects of early traumatic experience on vocal expressions of emotions in rhesus macaques (*Macaca mulatta*). The subjects of the study were 12 juvenile females: six were born to abusive mothers and reared by nonabusive controls, and six were born to controls and reared by abusive mothers. The cross-fostering took place within 24–48 hours after birth. Vocalizations were recorded from the subjects in their social groups during their first two years of life. Abusive mothers maltreated their adopted daughters in the first 2–3 months after birth with patterns similar to those previously shown with their biological offspring. Abused females produced proportionally more noisy screams compared to controls. While controls used noisy screams during contact aggression and tonal screams during non-contact aggression, the screams from the abused animals appeared to be distributed equally across contexts. Acoustical analyses revealed that the screams of the abused females were less modulated and had lower fundamental frequencies compared to the screams of controls. Taken together, these results suggest that traumatic experiencee in the first few months of life can have long-term effects on vocal emotional expression in rhesus macaques.

Keywords

rhesus macaque; maternal abuse; vocalizations; acoustical analysis; emotional expression

INTRODUCTION

In humans, traumatic experiences can permanently alter the expression of emotions and the perception and processing of emotional expressions. For example, abused children exhibit impaired ability to process and appropriately categorize facial expressions of emotions (Pollak, Cicchetti, Klorman, & Brumaghim, 1997; Pollak & Kistler, 2002). Furthermore, the phenomenon of ‘alexithymia’, or inability to verbally describe emotion, has been well documented in survivors of traumatic events (Berenbaum, 1996; Clayton, 1997). Research on human speech patterns has found that specific acoustic variables, such as fundamental frequency range and modulation, are associated with a number of diverse emotions, such as joy, disgust, sadness, fear, and anger (Banse & Scherer, 1996; Protopapas & Lieberman, 1997). However, the extent to which the development of vocal expression of emotion is affected by experience, and in particular, by early traumatic events, is largely unknown in human and non-human primates.

Correspondence to: D. Maestripieri.

Maternal abuse of infant offspring is an example of a naturally occurring early traumatic experience in non-human primates. Infant abuse in group-living rhesus macaques shares a number of similarities with human child abuse including the percentage of abusive parents in the population, the transmission of abuse across generations, some psychological characteristics of abusive parents, the role of stress in triggering abuse, and the higher vulnerability of young infants to abuse (Maestripieri & Carroll, 1998). In rhesus macaques, abusive mothers drag their infants by their tails, arms, or legs, push and shove them to the ground, throw them, and step or sit on them. The immediate consequences of abuse may vary from infant distress without any observable injury to infant death (Maestripieri, 1998). Abuse also has long-term consequences for behavioral and neuroendocrine development (e.g., Maestripieri, 2005; Sanchez, McCormack, Grand, Fulks, Graff, & Maestripieri, 2010). Yet, the effects of this early traumatic experience on vocal expression of emotion remain generally uninvestigated.

Non-human primate vocalizations may convey information about internal states such as emotions and motivation as well as about external events, such as the context in which the calls occur (Rendall, Owren, & Ryan, 2009; Seyfarth & Cheney, 2003). Darwin (1872) was the first to describe the emotional aspects of animal vocalizations, whereas recent studies have focused on the acoustic variables that express emotions such as fear, aversion, and arousal (e.g., Fichtel & Hammerschmidt, 2002; Fichtel, Hammerschmidt, & Jürgens, 2001). Interestingly, the same variables have been associated with emotional expression in animals and humans, i.e., frequency range and modulation. Furthermore, primate vocalizations appear to be modulated by brain circuits that regulate emotion. For example, Newman and Bachevalier (1997) reported that lesions to the amygdala affected the frequency contour, i.e., mid-slope, of the infant isolation calls in rhesus macaques.

Studies of human and non-human primates have found that motivation or affect tend to be encoded in the amplitude and duration of the vocalization (rhesus macaques: Gouzoules, Gouzoules, & Marler, 1984; humans: Scherer, 1992), in the frequency range or bandwidth (squirrel monkeys: Fichtel et al., 2001; lemurs: Fichtel & Hammerschmidt, 2002; humans: Scherer, 1992), and frequency modulation and/or “jitter factor” (cotton-top tamarins: Goedeking, 1988; squirrel monkeys: Fichtel et al., 2001; humans: Scherer, 1992). Referential information may be communicated by use of structurally different call types in different contexts, as may be the case with macaque agonistic screams and vervet monkey predator alarm calls (Seyfarth & Cheney, 2003). Early experience could influence the acoustic structure of vocalizations, particularly their affective component, or their contextual usage, or both. We hypothesized that early infant abuse may alter emotional vocal expression and predicted, on the basis of previous research, that the calls of abused infants may be characterized by low affective content.

Some human studies have reported that the cries of "atypical" infants (e.g., premature, with Down syndrome, or with brain damage) are higher-pitched than normal, and that high-pitch and long cries are generally less effective in eliciting caregiving responses from listeners (e.g. Frodi, 1985). In a previous study we compared the vocalizations of abused and non-abused rhesus macaque infants and reported some differences in the structure of their isolation calls (Maestripieri, Jovanovic, & Gouzoules, 2000). Because in this study both abuse and infant vocalizations were recorded during the first three months of life and the infants had been reared by their biological mothers, it was difficult to assess whether the acoustic characteristics of the abused infants’ calls were a consequence of their experience or were genetically inherited from their mothers. In the present study, we investigated the vocal development of abused and non-abused rhesus macaque females during their first two years of life. To disentangle genetic and experiential contributions to vocal development, all infants were cross-fostered at birth and reared by unrelated mothers.

METHODS

Subjects and Housing

This study was conducted with young female rhesus macaques living in 5 social groups at the Field Station of the Yerkes National Primate Research Center in Lawrenceville, GA (U.S.A.). The groups were housed in 38 × 38 m outdoor compounds with attached indoor areas and consisted of 2–5 adult males and 30–35 adult females with their immature offspring. All groups had a stable matrilineal structure and a linear dominance hierarchy. The adult males were unrelated to the adult females within their groups and replaced by other males every 4–5 years. The groups were fed Purina brand monkey chow twice daily and water was always available. All research followed the guidelines in the *NIH Guide for the Care and Use of Laboratory Animals* and was approved by the Emory University Institutional Animal Care and Use Committee.

Cross-Fostering Procedure

Twelve female infants born in 1999 were cross-fostered shortly after birth and reared by unrelated foster mothers living in a different group. The biological and foster mothers were selected during pregnancy, according to their history of abusive behavior. Only mothers who previously exhibited mild rates of abuse (i.e. mothers whose infants survived without serious injury) were used for this study. Six infants were born to abusive mothers and adopted by nonabusive control mothers. Six infants were born to control mothers and adopted by abusive mothers (for a detailed description of the cross-fostering procedure see Maestripieri, Megna, & Jovanovic, 2000). These subjects were part of a larger cross-fostering study involving 13 abusive and 13 control mothers; the adoption success rate was 61.54% for abusive mothers and 100% for controls (Maestripieri, Megna, & Jovanovic, 2000). Precise information on the ages of all infants when the cross-fostering procedure was performed is provided by Maestripieri (2001).

The mother-infant dyads were observed once a week for 1 hour during the first three months of life. Observations were made by three observers, after Cohen's Kappa for inter-observer reliability exceeded 0.80. The mother's behavior was considered abusive if it involved one or all of the following: dragging the infant on the ground, crushing, stepping, or sitting on the infant, throwing, hitting, biting, stretching, or dangling the infant. All of the abusive mothers exhibited several or all of these behaviors towards their infants, while none of the control foster mothers did. The average rate of abuse for the abused infants was 0.61±0.17 episodes per hour in the first month of life. We previously showed that abusive mothers exhibited rates and patterns of abuse that were very similar to those exhibited with their biological offspring the previous year (Maestripieri et al., 2000). Thus, this study examined naturally occurring abuse and the cross-fostering procedure did not alter the likelihood of abuse. The rates of infant abuse in this rhesus macaque population are comparable to those of pigtail macaques and sooty mangabeys in the same research facility (Maestripieri & Carroll, 1998) but higher than those occurring in the free-ranging rhesus macaque population on Cayo Santiago, Puerto Rico (D. Maestripieri, personal observation). None of the infants reared by control mothers experienced any abuse. There were no differences in dominance ranks or aggression received by other individuals between abused and control subjects.

Vocal Recording and Analysis

The infant vocalizations were recorded using a Sony TCM-5000EV Version II portable cassette recorder, a Sennheiser directional microphone (model ME66) and a microphone amplifier (model SME-BA3, Mineroff, Inc.). Vocalizations were recorded while the subjects lived in their large social groups; recordings were made for an hour from each group, three days a week for six months after the first year of life, and again for six months after the second year of life. The calls were recorded using an all-occurrences sampling method (Altmann, 1974). Immediately following the recording of a vocalization, the concurrent social context was described on the audiotape. The social context was defined by the levels of aggression towards the caller: in contact aggression the aggressor grabbed, pushed, or bit the victim, and in non-contact aggression the aggressor threatened, chased, or charged the victim. The tapes were digitized on an IBM-compatible computer using Cool Edit Pro 1.2 signal software (Syntrillium, Inc.). In addition, Cool Edit Pro was used for noise reduction and signal amplification. Spectral signals were transformed for analysis with a resolution of 4096 FFT (Fast Fourier Transform) filter size and the Blackmann-Harris windowing function. The calls were analyzed using software developed by Dr. Brenda McCowan (McCowan, 1995; McCowan & Reiss, 1995; 2001), which measured 60 equally distributed time and frequency points in a signal. The acoustical parameters were derived from these 60 points.

Data Analysis

Because of the large intra-individual variability, the calls were not averaged for each subject; under these conditions, data pooling allows for more conservative analyses (Leger & Didrichsons, 1994; McCowan & Reiss, 2001). Some individuals produced more screams than others, so prior to any data analyses the contributions from these subjects were randomly reduced so that no particular individual contributed disproportionally to the dataset. Consequent to data pooling the sample sizes were very large; thus the effect size (η^2) was reported for each analysis.

The calls were measured with 17 different acoustic variables (see Table I). Because of possible inter-correlations between many of these variables, principal components analyses (PCA) were performed in order to extract orthogonal components from the data set of acoustic parameters. The varimax rotation was used in order to enhance the interpretability of the components (Tabachnick & Fidell, 1983). This procedure has been used in analyses of the acoustic variables in human speech patterns (Owren & Bachorowski, 1999). 3.0 was used as the cutoff for the Eigenvalue.

Noisy screams were defined as atonal vocalizations with broad bandwidth and durations of around 500 ms. Tonal screams were defined as calls with a narrow frequency range and durations of 500 ms to 1000 ms. Depending on the call type, the number of variables included in the PCA differed; for instance, noisy screams included fewer variables since many parameters appropriate for narrow frequency band calls were inappropriate for this scream category. The scores of the extracted PCA factors were then analyzed in a multivariate analysis of variance (MANOVA) with abuse group and social context as independent variables; if the analysis resulted in a significant Wilks' λ, then the between-subjects F-tests for the PCA components were considered. The differential use of call types across groups and social contexts was compared using Log-likelihood ratio *G* tests.

RESULTS

We analyzed 342 noisy and tonal screams recorded from the 12 cross-fostered subjects at one and two years of age (every subject had at least one call of each type analyzed sonographically). Of these, 35.1% (122 screams) were produced by five of the six abused cross-fostered subjects (no screams were recorded from one abused subject), and 64.9% (220 screams) were produced by the six control subjects. In general, abused animals produced proportionally more noisy screams (56% of all screams) compared to control animals (34% of all screams) ($G(1) = 14.06$, $p<0.001$). When the analysis compared the abused and control subjects' scream production separately across different contexts, the

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results showed that the two groups did not use calls in the same way. Control animals were likely to use noisy screams when they were victims of contact aggression and tonal screams during non-contact aggression ($G(1)=13.19$, $p<0.01$; see Figure 1). In contrast, abused animals showed no context-specific scream distribution ($G(1)=0.12$, ns; see Figure 1).

Effects of Abuse on Acoustical Structure of Screams

Noisy screams—Nine acoustic variables were included in the PCA for noisy screams, which yielded three components cumulatively accounting for 82.87% of the variance in 133 screams (see Table II for the description of the PCA components). These three factors were described as "Fundamental Frequency", "Frequency Range", and "Duration and Variability". As opposed to tonal screams, noisy screams are by definition broad-banded and do not have a clearly defined fundamental frequency; however, most screams have concentrations of energy within this broad band, where the amplitude of the scream is the greatest. In the present study, this area of energy was referred to as the fundamental frequency of the scream and was represented by the first factor of the PCA. Likewise, the third factor, which included frequency variability, was measuring the point-by-point changes in the frequency of the maximum amplitude throughout the call, rather than the perturbations of a frequency band, as would be the case for tonal screams.

A group by context MANOVA of the PCA factor scores resulted in a significant interaction effect (Wilks' $\lambda=0.93$, $F3, 127 =3.04$, $p<0.05$). When attacked by another individual, the abused subjects produced noisy screams (N=34 screams by five subjects) that were acoustically different from those of the five control subjects (N=48 screams by five subjects; Wilks' $\lambda=0.86$, $F3, 78 =4.13$, $p<0.01$). The screams of abused subjects were significantly lower on the "Fundamental Frequency" ($F1, 80 =7.45$, $p<0.01$, $\eta^2=0.08$) and "Duration and Variability" PCA factors ($F1, 80 =4.43$, $p<0.05$, $\eta^2=0.05$). Figure 2 shows representative spectograms of contact aggression noisy screams from one abused and one control subject. However, when the subjects were compared in the context of non-contact aggression, the screams of abused subjects (N=30 screams) and control subjects (N=21 screams) did not differ significantly (Wilks' $\lambda= 0.87$, $F3, 47 =2.29$, ns.)

Tonal screams—For tonal screams, all 17 acoustic variables were included in a PCA that extracted six factors accounting for 84.21% of the variance in 180 screams. These six components were described as "Frequency Range", "Fundamental Frequency", "Duration and Variability", "Start Slope", "Peak Frequency Location", and "Final Slope". The acoustic variables with high loadings for each component are listed in Table III.

Unlike noisy screams, there was no interaction effect of group and context on tonal screams (Wilks' $\lambda=0.95$, $F6, 171 =1.53$, ns). Across both contexts, the screams of abused and control subjects were significantly different (N=43 screams by five abused subjects, and N=137 screams by five control subjects; Wilks' $\lambda=0.83$, $F6, 171 =5.73$, $p<0.01$). Abuse significantly affected screams on two factors: the screams of abused subjects had lower values for the components of "Fundamental Frequency" ($F1, 176 =17.42$, $p<0.01$, $\eta^2=0.09$) and "Duration and Variability" ($F1, 176 =9.01$, $p<0.01$, $\eta^2=0.05$) when compared to the screams of control subjects (see Figure 3 for representative spectrograms).

DISCUSSION

In the present study we found that early maternal abuse altered the pattern of scream usage and the acoustical structure of screams in rhesus macaque females during their first 2 years of life. The nonabused controls produced relatively more noisy than tonal screams in the context of contact aggression, and more tonal screams in non-aggressive contexts. In contrast, the abused animals produced more noisy than tonal screams in both aggressive and non-aggressive contexts. Previous research has shown that adult rhesus macaque females use noisy screams during severe contact aggression and tonal screams during non-contact aggression (Gouzoules et al., 1984). Thus, the abused females in this study did not appear to use calls appropriately.

The acoustical properties of screams varied in relation to the context in which they were produced and, again, there were significant differences between abused and nonabused females. When attacked by another animal, abused females produced noisy screams of lower peak amplitude frequencies and less frequency modulation than did the control subjects. We found similar results in the acoustical analysis of tonal screams across both social contexts. Given that frequency modulation has been associated with emotional expression in animal vocalizations as well as in human speech (see above), these findings suggest that abused animals evidenced deficits in emotional expression even two years after the traumatic experience.

Taken together, the results of the present study indicate that early maternal abuse was associated with long-term alterations in both the context of usage and the acoustic structure of vocalizations with a strong affective component such as screams. The use of cross-fostered subjects for this study allow us to conclude with a certain confidence that the vocal communication patterns of abused females are the result of their early traumatic experience and exclude the possibility that they are genetically inherited from abusive mothers. Other studies of early stress and developent in rhesus macaques, some of which included the subjects of this study, have shown that maternal rejection and abuse early in life can result in long-term alterations in neural and neuroendocrine mechanisms underlying emotion regulation such as the brain serotonergic system and the hypothalamic-pituitary-adrenal axis (Maestripieri, Higley, Lindell, Newman, McCormack, & Sanchez, 2006; McCormack, Newman, Higley, Maestripieri, & Sanchez, 2009; Sanchez et al., 2010). The present study contributes to this body of work by showing that early traumatic experience can affect not only the physiological substrates of emotional responses to stressful situation, but also how emotional responses are communicated to other individuals through species-typical vocal signals. Although it is possible that the experience of abuse in itself may have altered the production of infant distress vocalizations, it cannot be ruled out that the abusive mothers' lower responsiveness to their infants' distress (Maestripieri, Jovanovic, & Gouzoules, 2000) may also have contributed to altering some acoustic characteristic of their vocalizations. Further research is needed to elucidate the mechanisms through which early stressful experience may alter vocal production in monkeys and assess the relative contributions of different aspects of the caregiver's behavior.

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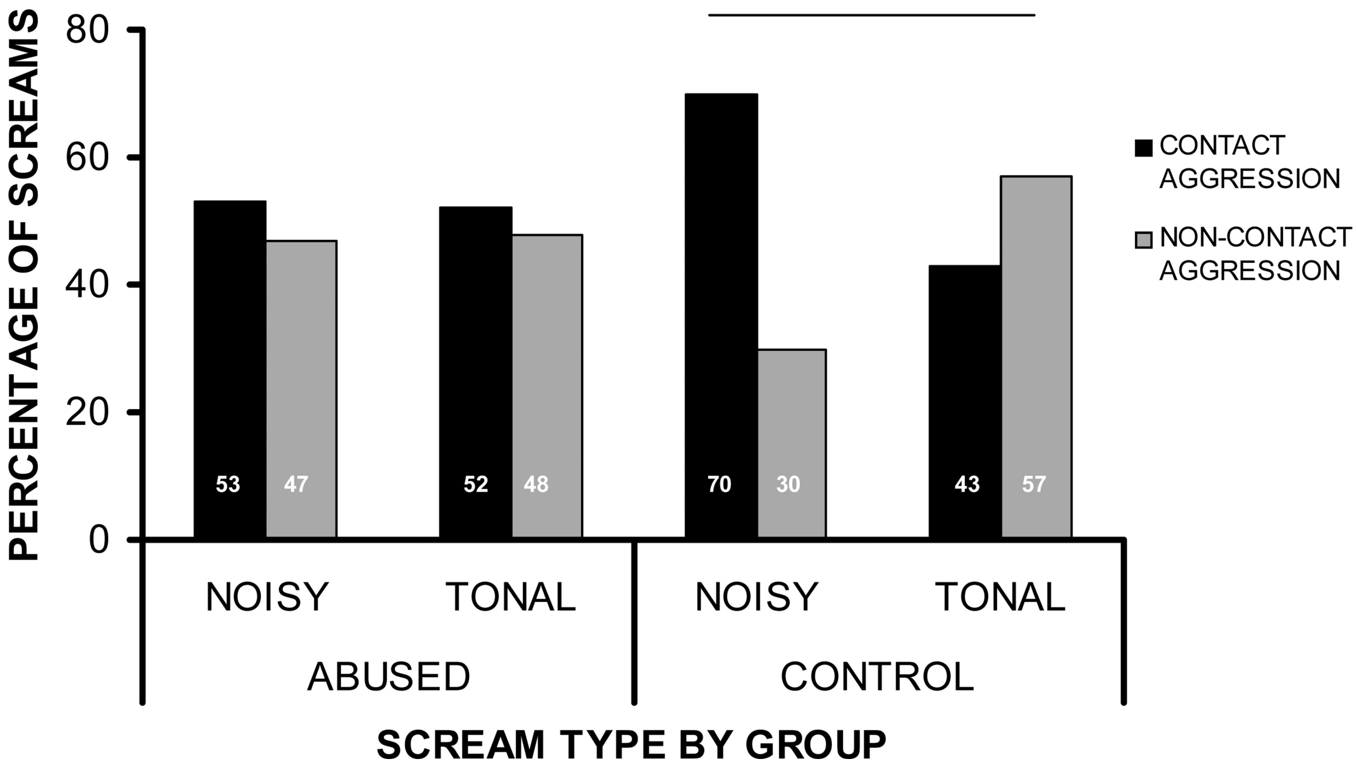

FIGURE 1.
Percentage of screams by context and abuse in juvenile screams.
Only control infants show contextually discriminant use of calls. The number of screams is shown on the bar; the number of subjects in each group is six.
** $p<0.01$

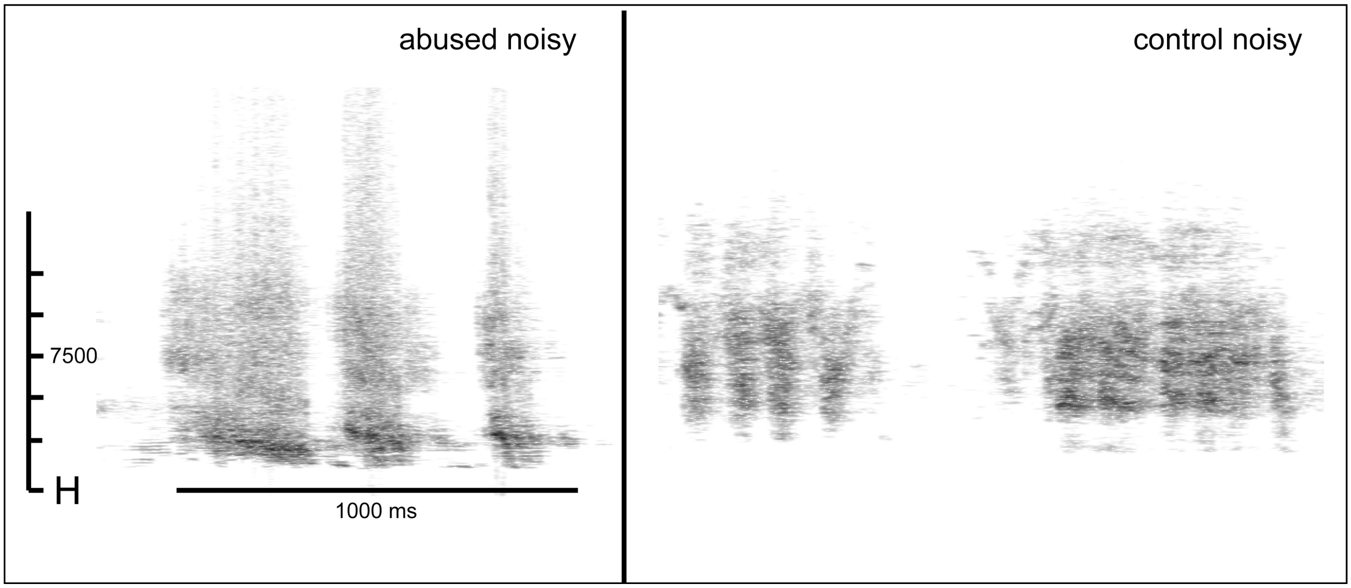

FIGURE 2.
Spectrograms of representative noisy screams produced during contact aggression by an abused subject and a control subject. The frequency is measured in Hz, the call duration in ms. Amplitude is depicted by intensity, i.e., the darkest areas of the spectogram are where the energy of the call is the greatest.

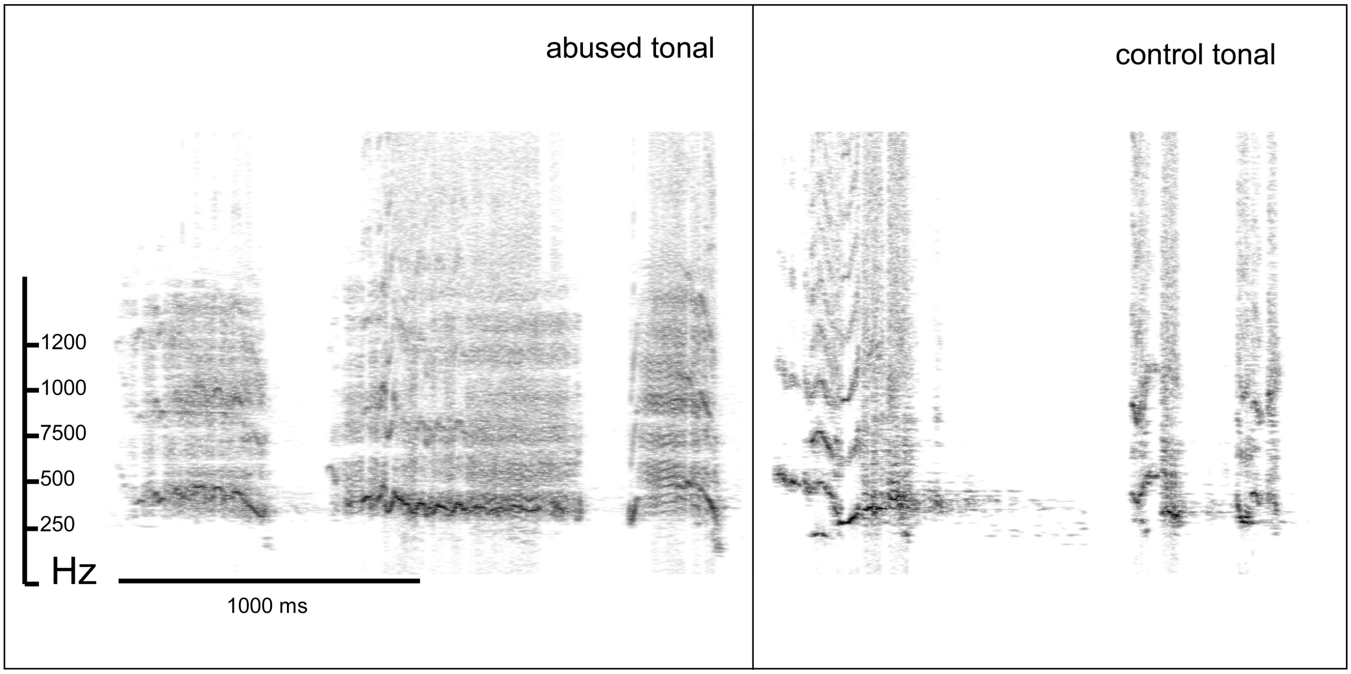

FIGURE 3.
Spectrograms of representative tonal screams produced by an abused subject and a control subject. The frequency is measured in Hz, the call duration in ms. Amplitude is depicted by intensity, i.e., the darkest areas of the spectogram are where the energy of the call is the greatest.

TABLE I

List of acoustic variables used in present study.

ACOUSTIC VARIABLE	DESCRIPTION
Start Frequency	frequency at start of call (Hz)
End Frequency	frequency at end of call (Hz)
Mean Frequency	average frequency (Hz)
Minimum Frequency	minimum frequency in the call (Hz)
Maximum Frequency	maximum frequency in the call (Hz)
Peak Amplitude Frequency	frequency with maximum amplitude (Hz)
Maximum / Mean	maximum to mean frequency ratio
Mean / Minimum	mean to minimum frequency ratio
Frequency Range	difference between max and min frequency (Hz)
Jitter Factor	number of perturbation in the call
Coefficient Modularity	number and magnitude of perturbations in the call
Maximum Freq. Location	percent of call where the maximum freq. is located
Minimum Freq. Location	percent of call where the minimum freq. is located
Start Slope	initial frequency slope (first 1/3 of call)
Mid Slope	middle frequency slope
Final Slope	final frequency slope (last 1/3 of call)
Duration	duration of call (ms)

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TABLE II

Acoustic variable loadings for PCA components of noisy screams.

	COMPONENTS (Cum. VAF = 82.87%)		
ACOUSTIC VARIABLES	**1 = Peak Amplitude Freq. Eigenvalue = 4.01 VAF = 44.59%**	**2 = Frequency Range Eigenvalue = 2.32 VAF = 25.83%**	**3 = Duration & Variablilty Eigenvalue = 1.12 VAF = 12.44%**
Mean Frequency	**0.95**	0.15	0.11
Peak Amplitude Freq.	**0.85**	0.08	0.11
Minimum Frequency	**0.79**	−0.11	−0.53
Maximum / Mean	−0.16	**0.96**	0.00
Frequency Range	0.27	**0.85**	0.42
Maximum Frequency	0.65	**0.74**	0.12
Mean / Minimum	−0.09	0.20	**0.79**
Duration	0.08	0.02	**0.71**
Coefficient Modularity	0.45	0.51	**0.56**

Abbreviations: VAF= variance accounted for. Significant loadings (>0.55) are printed in bold type.

TABLE III

Acoustic variable loadings for PCA components of tonal screams.

	COMPONENTS (Cum. VAF = 84.21%)					
ACOUSTIC VARIABLES	**1 = Freq. Range Eigenvalue = 5.16 VAF = 28.66%**	**2 = Fundamental Freq. Eigenvalue = 3.57 VAF = 19.85%**	**3 = Dur. & Modularity Eigenvalue = 2.23 VAF = 12.36%**	**4 = Start Slope Eigenvalue = 1.84 VAF = 10.21%**	**5 = Peak Location Eigenvalue = 1.31 VAF = 7.26%**	**6 = Final Slope Eigenvalue = 1.06 VAF = 5.87%**
Frequency Range	**0.88**	0.21	0.30	0.20	−0.06	−0.04
Maximum / Mean	**0.87**	−0.13	0.19	−0.25	0.02	0.07
Maximum Frequency	**0.69**	**0.64**	0.25	−0.03	−0.07	−0.05
Mean Frequency	0.12	**0.94**	0.07	0.14	−0.11	−0.10
Peak Amplitude Freq.	0.04	**0.85**	0.11	0.30	−0.11	−0.15
End Frequency	−0.10	**0.82**	0.07	−0.11	0.29	0.22
Minimum Frequency	−0.33	**0.79**	−0.09	−0.41	−0.02	−0.03
Start Frequency	0.30	**0.56**	−0.10	−0.53	−0.38	0.02
Duration	0.02	0.01	**0.92**	0.01	−0.02	0.01
Jitter Factor	0.58	0.04	**0.75**	0.07	0.12	0.03
Coefficient Modularity	0.53	0.36	**0.67**	0.16	0.03	0.02
Start Slope	−0.16	0.16	0.03	**0.84**	0.19	0.07
Mean / Minimum	0.46	−0.10	0.08	**0.71**	−0.03	0.00
Location of Min. Freq.	−0.07	0.00	−0.02	−0.05	**−0.80**	0.17
Location of Max. Freq.	−0.13	−0.03	0.00	0.12	**0.70**	0.12
Mid Slope	−0.07	0.05	0.10	−0.26	0.26	**−0.84**
Final Slope	−0.16	−0.03	0.23	−0.32	0.39	**0.72**

Abbreviations: VAF= variance accounted for. Significant loadings (>0.55) are printed in bold type.