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Elasticity and stress relaxation of a very small vocal fold

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Abstract

Across mammals many vocal sounds are produced by airflow induced vocal fold oscillation. We tested the hypothesis that stress-strain and stress-relaxation behavior of rat vocal folds can be used to predict the fundamental frequency range of the species' vocal repertoire. In a first approximation vocal fold oscillation has been modeled by the string model but it is not known whether this concept equally applies to large and small species. The shorter the vocal fold, the more the ideal string law may underestimate normal mode frequencies. To accommodate the very small size of the tissue specimen, a custom-built miniaturized tensile test apparatus was developed. Tissue properties of 6 male rat vocal folds were measured. Rat vocal folds demonstrated the typical linear stress-strain behavior in the low strain region and an exponential stress response at strains larger than about 40%. Approximating the rat's vocal fold oscillation with the string model suggests that fundamental frequencies up to about 6 kHz can be produced, which agrees with frequencies reported for audible rat vocalization. Individual differences and time-dependent changes in the tissue properties parallel findings in other species, and are interpreted as universal features of the laryngeal sound source.

Keywords

larynx; viscoelastic properties; bioacoustics; anisotropy

Introduction

The voice of most terrestrial mammals is produced in the larynx by flow-induced vibrations of the vocal folds. The vibrations modulate the glottal air flow, thus creating pressure fluctuations which can be perceived as sound. The basic rate of vibrations is determining the fundamental frequency (F0) of the perceived sound. F0 depends on the driving lung pressure (Titze 1989), the size/length of the vocal folds and, most importantly, on the tension of the vocal folds (Titze, 1989). Length changes of a vocal fold lead to dramatic changes in tension which is the main mechanism to regulate F0 in humans (Hollien, 1960; Hirano et al., 1969) and in non-human mammals (e.g. Brown et al., 2003). Vocal fold tissue responds differently

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Conflict of interest statement

None declared.

to dorso-ventral elongation between individuals, sexes, as well as species (Haji, 1990; Min et al., 1995; Chan et al., 2007; Hunter and Titze, 2007; Zhang et al., 2009; Riede et al., 2010; Alipour et al. 2011) contributing to vocal differences at all three levels. Tensile data exist for a range of large and medium sized vocal folds (Min et al., 1995; Chan et al., 2007; Riede and Titze, 2008; Riede et al., 2010; Riede, 2010) but not for very small species. There are at least two reasons why elastic moduli of vocal fold tissue in small mammals could be very different from those found in larger mammals. First, boundary effects may affect bending properties in small vocal folds more than in large vocal folds (Titze and Hunter, 2007). The greater stiffness at the dorsal and ventral anchor point of a vocal fold may reduce effective length more dramatically if overall length is small. Second, a number of small mammals (rodents, primates, microchiropteran bats) produce sound in the ultrasonic range. If the string model would be applicable in the same way as suggested for the human vocal fold (Titze, 1989), huge elastic moduli would be necessary to achieve those large oscillation rates, and those moduli would have to be accommodated by specialized tissue designs. This study investigated the tensile properties in a very small vocal fold using a custom-built tensile testing apparatus. Data allow a direct comparison with studies in large mammals, in order to assist in the understanding of the functional morphology of laryngeal sound production across the wide range of more than 5000 mammal species, most of which use their vocal folds to produce acoustic signals relevant in communication.

The challenge for collecting stress data from very small samples is to control and quantify the force transmission from the mounting apparatus to the tissue as well as the determination of the changing tissue geometry (Sharpe, 2003). Some tests have been suggested to measure stress in small samples (e.g. Daley et al., 2007; Hertegard et al., 2009; Zörner et al., 2010). However, these techniques are not designed to measure tensile strain and results are therefore not directly comparable to data collected in other species. In the current study, we use a miniaturized tensile test apparatus to investigate the stress-strain behavior of rat vocal folds. A dual-camera system is used to acquire images of the tissue during stretching allowing for cross sectional estimations. An image processing procedure was exploited to determine the critical cross sectional area.

We have tested adult male rat (*Rattus norvegicus*) vocal folds which measure 1 to 2 mm in dorso-ventral length. The fundamental frequency of rat vocalizations ranges between 2 kHz and 75 kHz (Brudzinski and Fletcher, 2010). Sounds below 20 kHz are presumably produced by airflow induced vocal fold oscillations during expiration, while ultrasound (> 20 kHz) is produced by a whistle-like mechanism (Roberts, 1975a,b,c; Roberts, 1973). However, much detail of a rat's vocal production mechanism is still unknown (Brudzinski and Fletcher, 2010) although the rat is one of the most frequently used models in biomedical research including voice physiology. We have applied the string model to make predictions about the expected fundamental frequency range that can be produced by a rat vocal fold.

Methods

Larynges were collected from six 3-months old male Sprague-Dawley rats. Tissue was collected immediately after the animal was sacrificed. The tissue was quickly frozen in Ringer solution in liquid nitrogen and kept at -80°C until the experiment. The tensile test apparatus is explained in detail in the Supplemental information S1.

Tensile tests

Experiments were conducted with a system under displacement control, recording displacement (resolution of 1 μm) and force (resolution of 0.1 mN). Displacement was applied in the dorso-ventral direction. A dual-camera system acquired images (300×300 pixels, resolution 0.0345 mm/pixel) of the tissue during stretching allowing for cross

sectional area estimations, stress calculation and determination of the Poisson's ratio (further details in Supplemental information S2).

An adult male rat vocal fold measures in vivo ca. 1.5 to 2 mm. The bracket (Supplemental Figure SF2) held the clamp distance constant at 1mm during the mounting of the tissue between the clamps. After the clamps were fixed between the load cell and a mounting rack on the other side, the bracket was removed. The tissue was pre-conditioned by straining it by 0.2 mm in 3 cycles at a rate of 1 Hz. We then waited for 3 minutes. If the tissue showed a zero or negative stress after 3 minutes, a pre-strain of 0.1 mm was added. This was repeated until the tissue showed a small positive stress after preconditioning and the 3 minute wait. All 0.1 mm increments were added to the initial 1mm length adding up to the gauge length before the following tests were conducted. In five specimen 0.1 mm, in one 0.2 mm were added to the initial 1 mm length.

Force-elongation data were obtained by three loading regiments, a) sinusoidal cyclic loading and unloading, b) a stepwise loading to measure stress relaxation, and c) a singular loading beyond ultimate stress. The cyclic loading and unloading was performed at 1 Hz for 15 times by displacements of 0.2 mm, 0.4 and 0.6 mm. The tissue was rested for 20 seconds between tests.

Stress relaxation was measured under fixed strains of 0.2, 0.4 and 0.6 mm using a 500 ms ramp time and a 20 s holding period followed by an unloading to the original length.

After two minutes of rest, the tissue was strained to 5 mm at a rate of 1mm/s in order to measure ultimate stress. On average the tissue tore apart at about 1 to 1.5 mm of displacement.

Modeling the stress-strain response

The stress-strain response of large vocal fold tissue for cyclic loading-unloading has previously been modeled by a linear model in the low-strain region and a nonlinear model in the high-strain region (Min et al., 1995; Chan et al., 2007; Riede and Titze, 2008; Riede et al., 2010; Riede 2010). The same models have been applied here. Details are given in the Supplemental Information S3.

The stress relaxation curves at fixed strain were modeled with exponential 2-phase-decay functions between the time point when the maximum stress was achieved and ten seconds thereafter (Eq. 1):

$$\sigma(t) = P + (\sigma_0 - P) \left[\frac{\text{PercentFast}}{100} * e^{(-K_{\text{Fast}} * t)} + \left(1 - \frac{\text{PercentFast}}{100}\right) * e^{(-K_{\text{Slow}} * t)} \right], \quad \text{Eq. 1}$$

where P is the estimated plateau, K are the rate constants for the fast and the slow relaxation, respectively, and σ_0 is the peak stress at time point zero (t_0). Half-life (HT) is computed as $\ln(2)/K$.

Estimation of fundamental frequency (F_0)

According to the string model, F_0 is determined by:

$$F_0 = \frac{1}{2L} \sqrt{\frac{\sigma}{\rho}}, \quad \text{Eq. 2}$$

where L is the string (or vocal fold) length, σ is the tissue stress, and ρ is the tissue density (1.02 g/cm^3).

The cyclic loading data were used to estimate a rat's F_0 range. The peak stress data from each of the 15 cycles in the cyclic loading experiment were used to estimate F_0 relaxation due to repeated straining.

Results

1) Tensile tests

Linear and nonlinear models (Figure 1) reached regression coefficients of 0.97 and higher (Table 1). The average linear strain limit was 45% (Table 1). Hysteresis between the loading and unloading curve ranged between 29 and 38% (Table 1).

Beyond (non-physiological) strain of 150% (150 to 400%) the exponential growth of the stress-strain curve slowed a little suggesting some degree of yielding in the molecular bonds of the connective tissue. The tissue could be stretched by 210–600% of its original length before rupture occurred, at which point stresses between 70 to 340 kPa were reached. Unlike in large mammal vocal folds, rupture occurred not at the insertion points at thyroid or arytenoid cartilage but in mid-membraneous portion of the vocal fold tissue.

The average Poisson's ratio was 0.199 in six vocal folds (Table 1), and ranged between 0.14 and 0.28.

2) Stress relaxation

Strained rat vocal folds relax by 23 to 43% within 10 seconds (Figure 2 and Table 2). Most of this relaxation happens very fast (Table 2), almost independent of the magnitude of the displacement (ANOVA, $N_{1,2,3}=6$; fast phase: $F=3.3$, $P=0.06$; slow phase: $F=1.4$, $P=0.24$) (Table 2, Figure 3).

3) Inter-individual variability and predicting fundamental frequency

Differences in viscoelastic properties contribute to individual differences in vocal behavior. Elastic moduli and relaxation parameters show large coefficients of variations (up to 30%, Table 2). The decay rate in the fast and slow phase showed also large variability between individuals (coefficient of variation averaged over all three displacements and all six individuals, $CV_{\text{fast}}=25\%$; $CV_{\text{slow}}=13\%$).

Fundamental frequency of a 1-mm long male vocal fold ranges between 100 Hz and 3.3 kHz for strains between 0 and 100%, but can reach a maximum of 4 or 6 kHz in some individuals (Figure 4).

Discussion

Stress-strain data suggest that a rat's vocal fold tissue can oscillate at rates of up to about 6 kHz. This overlaps with frequencies of audible vocalizations which are produced by a mechanism involving airflow induced vocal fold oscillation. Audible rat vocalizations include 'screams', 'chatters' and low-frequency 'whistles' (Nitschke, 1982; Ewer, 1971; Roberts, 1975b; Kaltenwasser, 1990; Jourdan et al., 1995). The fundamental frequency of these call types ranges between 1 and 6 kHz. Some authors provide a smaller frequency range of 2 to 4 kHz (Brudzinski and Fletcher, 2010). There are, to our knowledge, no vocalizations reported with fundamental frequencies between 10 and 20 kHz in adult rats. Vocalizations above 20 kHz are produced by a different mechanism, presumably resembling a whistle (Roberts 1975b; Brudzinski and Fletcher, 2010).

Rat vocal folds can be operated below longitudinal strains of about 100%. Our data suggest a combination of lamina propria and epithelium starts to suffer permanent damage at strains larger than 100%. The moduli at those strain are not exceptionally large and are unlikely to support oscillations rate larger than 6 to 8 kHz. This is in line with the notion that the rat larynx shows no adaptations for producing and sustaining large forces (Roberts, 1975a; Inagi et al., 1998).

The differentiation of a stress-strain response into a linear and nonlinear phase, the existence of hysteresis, the magnitude of stress relaxation under fixed strain (Figure 3) or during repeated loading-unloading cycles (Figure 4) liken the rat vocal fold to that of larger mammals. Data indicate that short-term mechanical responses of the lamina propria are relevant and of similar quality across mammals. Such features are most likely critical for acoustic characteristics, such as the fundamental frequency contour within single vocal utterances as well as within longer bouts (Chan et al., 2009; Riede, 2010). For example, F₀ declination refers to a long-term F₀ decrease in human speech which is found in many languages (e.g. Swerts et al. 1996). The cycle-to-cycle relaxation is likely to play an important part in this phenomenon in human speech as well as in nonhuman vocalization. Furthermore variability in vocal fold viscoelastic properties are an important component contributing to the individual specificity of a voice, just like in other species (e.g. Chan et al., 2007; Riede and Titze, 2008; Riede, 2010).

The current approach provides comparative data for small vocal folds. Furthermore, the optical approach allowed to more precisely determine Poisson's ratio for which only few empirical data on vocal folds exist (Titze 2006). Incompressibility implies a Poisson's ratio of 0.5. The high water content in many biological tissues justifies this assumption (water being nearly incompressible). Values in rat vocal folds were relatively low $\nu=0.2$, possibly owing to fibrillar proteins being highly dis-organized in a rat's lamina propria (Ling et al. 2010; Reese et al. 2008). Possibly the integrity of the lamina propria is affected if the thyroarytenoid muscle is removed. The muscle provides normally a natural lateral boundary to the lamina propria. The exact reasons remain to be further investigated. Recent studies using vocal fold physical models have assumed similar ranges for Poisson's ratio (0.2 to 0.45) in designing the vocal fold lamina propria (Drechsel 2007). However, data presented here can be improved in at least two ways. First, the ideal string model demonstrated limitations in predicting F₀. Alternative models, such as the beam model, or composite models lead to 30 to 25% higher F₀ predictions in humans, which were actually closer to the naturally observed frequency range (Zhang et al. 2007). Second, current stretch-release setups, including the one described here, require a destruction of the material and therefore do not allow a repeated measurement. By collecting as much as possible information about a single model system (such as for example the rat), the combination of destructive techniques which provide more direct measures and non-destructive techniques (e.g. Daley et al., 2007; Hertegard et al., 2009, Zörner et al., 2010) which require separate methods to determined important variables, for example Poisson's ratio, might eventually allow to establish reliable and robust correlations which require no or little assumptions.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Stress-Strain response in time from a 1 Hz sinusoidal loading and unloading of epithelium and *lamina propria* to a strain of 0.6 mm. (A) Note that the amplitude of strain remains constant while stress decreases over time. The decrease in peak stress is a result of stress relaxation. Stress-strain relationship for a single cycle from the same data set is shown in (B) and Young's modulus in (C). The upper part of the “banana-shaped” curve is the loading phase. The lower part is the unloading phase. The difference between both curves is due to hysteresis of the tissue, i.e. lower stress in the tissue during the unloading phase. The low strain region was fitted with a linear regression line (thick dotted line), while the high-strain region was modeled with exponential functions (thick dashed line). The limit between the linear and the nonlinear region is the ‘Linear strain limit’, (ϵ_1) here approx. 0.4.

Figure 2. Load-strain and stress relaxation curve. The vocal fold tissue is stretched at a predetermined rate (here by 0.6 mm within 500 ms) to the desired strain at which it is held for 10 seconds.

Figure 3.
Average rate constants (mean and standard deviation) for the fast and the slow relaxation at 0.2, 0.4 and 0.6 mm displacement.

Figure 4.

Average peak stresses (mean and standard deviation) in 15 subsequent loading cycles. The cycle-to-cycle relaxation may play an important role in the drop of the fundamental frequency in a string of vocal utterances, a phenomenon known as ‘fundamental frequency declination’ in human speech. The same relaxation behavior has been observed in vocal fold tissue of other species.

Figure 5. Fundamental frequency (F0) predicted by the string model (equation 2). The linear and nonlinear stress response was implemented in equation 2 for strains between 0 and about 100%. The red line indicates the average model for the relationship between vocal fold length and F0 for six male vocal folds.

Table 1

Average parameters of the linear (S3-Eq. 2: $\sigma = a\varepsilon + b$) and the exponential (S3-Eq. 3: $\sigma = Ae^{B\varepsilon}$) model for curve-fitting the empirical stress–strain response of the vocal fold: regression coefficient, r^2 ; linear strain limit, ε_1 (in %); Hysteresis, H (in %); Poisson's ratio, ν . All means and standard deviations are based on 6 measurements.

	mean $\pm$ stdev	CV (%)
A	7.8 $\pm$ 2.1	26.9
B	0.02 $\pm$ 0.3	1500
r^2	0.97 $\pm$ 0.01	
ε_1	45.8 $\pm$ 3.8	25.9
a	0.5 $\pm$ 0.1	20.0
b	4.4 $\pm$ 1.2	27.3
r^2	0.99 $\pm$ 0.003	
H	32.0 $\pm$ 4.0	12.5
ν	0.199 $\pm$ 0.054	27.1

Table 2

Average parameters (means and standard deviations based on 6 male vocal fold samples) of the exponential 2-phase decay model (Eq. 1) for curve-fitting the stress relaxation curve of the vocal fold at fixed strains (0.2, 0.4 and 0.6 mm): peak stress σ_0 (in kPa); Plateau stress, P (in kPa); a rate constant K for fast and slow phase (in s^{-1}), stress half life HT (in s) for fast and slow phase; %fast the fraction of the span (from Y0 to Plateau) accounted for by the faster of the two components; regression coefficient r^2 .

displacement (mm)	0.2	0.4	0.6
drop from peak stress in 10 sec	23.6±3.9	35.4±7.2	42.7±5.0
σ_0	5.7±3.9	26.9±20.4	65.3±48.9
P	4.3±2.7	16.2±11.4	36.5±20.9
K_{fast} (s^{-1})	4.8±1.7	6.7±1.0	5.8±1.1
K_{slow} (s^{-1})	0.29±0.05	0.33±0.04	0.31±0.03
HT _{fast} (sec)	0.16±0.07	0.10±0.02	0.13±0.03
HT _{slow} (sec)	2.4±0.4	2.1±0.2	2.2±0.2
% fast	53.7±3.2	51.8±3.9	51.5±3.5
r^2	0.9676	0.9911	0.9947