Frazer Sissom DE, Rice DA, Peters G. 1991. How cats purr. J Zool , Lond 223:67-78.

Keywords: Acinonyx jubatus/cheetah/domestic cat/Felis silvestris/Felis silvestris catus/frequency/
larynx/morphology/Puma/Puma concolor/purring/research/vibration

Abstract: We measured purring in unrestrained intact pumas, cheetahs and domestic cats. Domestic cats, *Felis silvestris* f. *catus*, purr at a frequency of 26.3 ± 1.95 (S.D.) Hz. The frequency at midexpiration exceeds that at mid-inspiration by 2.4 ± 1.3 Hz. Purring frequency for individuals does not change with age. Purring can occur simultaneously with other vocalization. Two-channel acoustic measurements confirm that the primary mechanism for sound and vibration production is a centrally driven laryngeal modulation of respiratory flow. The diaphragm and other muscles appear to be unnecessary for purring other than to drive respiration.

J. Zool., Lond. (1991) **223**, 67–78

How cats purr

DAWN E. FRAZER SISSOM, D. A. RICE*
Department of Biomedical Engineering, Tulane University, New Orleans, LA 70118, USA
AND G. PETERS
Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 150-164, D-5300 Bonn 1, West Germany

(*Accepted 16 November 1989*)

(With 4 figures in the text)

We measured purring in unrestrained intact pumas, cheetahs and domestic cats. Domestic cats, *Felis silvestris* f. *catus*, purr at a frequency of 26·3 ± 1·95 (S.D.) Hz. The frequency at mid-expiration exceeds that at mid-inspiration by 2·4 ± 1·3 Hz. Purring frequency for individuals does not change with age. Purring can occur simultaneously with other vocalization. Two-channel acoustic measurements confirm that the primary mechanism for sound and vibration production is a centrally driven laryngeal modulation of respiratory flow. The diaphragm and other muscles appear to be unnecessary for purring other than to drive respiration.

Contents

Introduction

Many species of cats (Felidae) and some civets and genets (Viverridae, *sensu stricto*) are known to purr (Wemmer, 1977; Peters, 1981). Purring is heard as a soft buzzing sound, like a rolled 'r', that has a fundamental frequency of approximately 25 Hz. This sound is accompanied by a

* To whom correspondence should be addressed

0952-8369/91/001067 + 12 $03·00

palpable vibration on some regions of the body surface. The sound varies rhythmically with breathing and is continuous during both inspiration and expiration, varying in intensity and in duration according to the cat's state of arousal (Moelk, 1944). Despite many years of observation, our understanding of the mechanism of cats' purr is still incomplete. Questions remain concerning which organs are involved and what processes produce the sound and vibration.

A number of different mechanisms of purr production have been proposed including aerodynamic and hemodynamic vibration of the true and false vocal chords, the soft palate, and the arterial system (e.g. Mellen, 1940; Burger, 1966; McCuistion, 1966; Mery, 1969; Beadle, 1977). A consensus for a mechanism is emerging, however, (Beaver, 1983; Stogdale & Delack, 1985). Stimulation of various regions in the brain can elicit purring (Gibbs & Gibbs, 1936; de Lanerolle & Lang, 1988), demonstrating that it is centrally controlled. In chronically instrumented cats Remmers & Gautier (1972) showed that muscles of the larynx and diaphragm have an electromyographic (EMG) response synchronous with purring, suggesting that these muscles are active at the fundamental frequency of purring. Cutting laryngeal and thoracic (rhizotomy) sensory nerves did not change the purring. This suggests that purring is driven by an oscillator located in the central nervous system rather than by a myoneural reflex. They found that sound and tracheal pressure varied synchronously with the EMGs and concluded that purring results from muscular vibrations of the diaphragm and a repetitive closing of the glottis. Kirkwood *et al.* (1987) show that the intercostal muscles are involved.

We present acoustic measurements that quantify some aspects of the purr sound and vibration. These support the laryngeal mechanism but argue against the mechanical involvement of the diaphragm and intercostal muscles.

Methods

A strip chart recorder with a frequency response extending from 0–60 Hz recorded 10 domestic cats that would purr when petted at an animal shelter. These cats ranged in age between an estimated 10 weeks and more than 8 years and in weight from 0·7–6·6 kg. Microphones (B&K #4165) with a lower limiting frequency of less than 3 Hz registered the purring. They were held by hand and moved around the body at distances less than 1 m. Shaving or wetting the fur permitted contact measurements using a latex coupler.

In the laboratory a digital oscilloscope permitted wideband 2 channel measurements to determine the relative phase of the sound and vibration at pairs of surface locations. The primary sites for measurement were: (a) acoustic, near the mouth; (b) immediately over the larynx; (c) on the chest cephalad of the diaphragm, right and left sides at the level of the first pair of nipples; (d) on the abdomen, caudad of the diaphragm, right and left sides at the level of the third pair of nipples.

The same observer estimated for each of the domestic cats the magnitude of the thoracic surface vibration and the loudness of the purr on a scale of 0–5, where 0 represented undetectable and 5 was the greatest expected.

We also made single channel acoustic recordings of purr in puma (*Puma concolor*), cheetah (*Acinonyx jubatus*) and domestic cats using a Sennheiser MD 421-2 or a Knight KN4550, microphones with a lower limiting frequency of about 40 Hz. These recordings were made at distances from the mouth between 0·5 and 1 m in the former 2 species and less than 0·2 m in the latter.

Results

Purring sound and vibration continued steadily during both inspiration and expiration but varied with respiration. During inspiration the sound quality differed slightly from that during

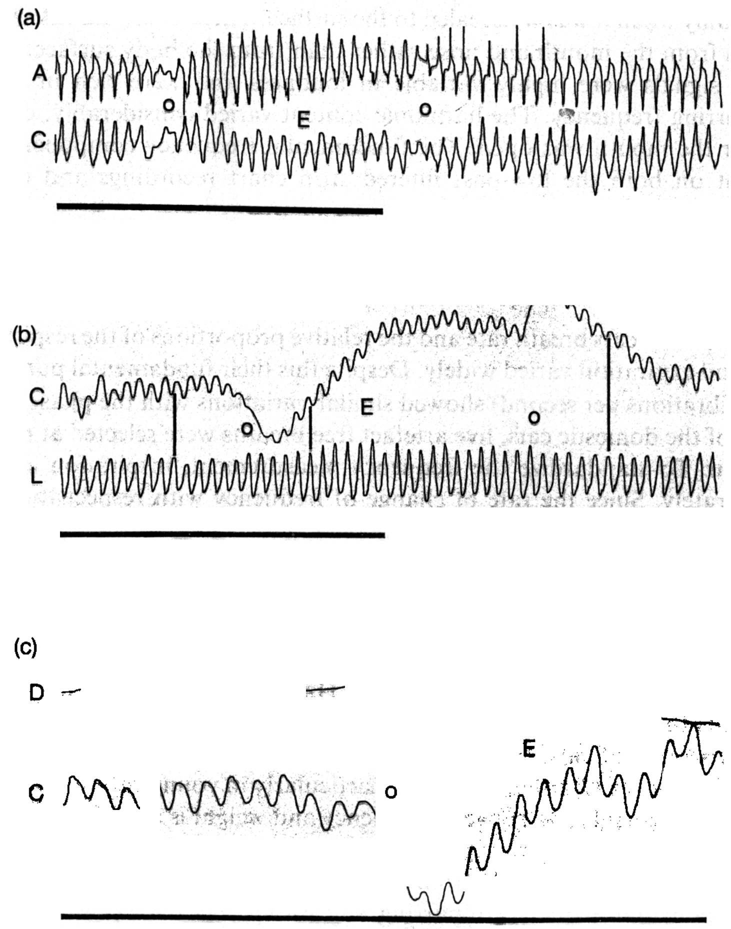

FIG. 1. Simultaneous recordings of sound and vibration. (a) Purr at the mouth (A) and the chest (C). The phase of the fundamental frequency is always opposite, and amplitude minimum occurs at times of flow reversal (O). The expiratory phase (E) is marked on each recording. (b) Purr on the chest (C) and larynx (L). The laryngeal waveform is continuous and little affected by respiratory flow. The phase of the chest signal changes 180° when respiratory flow reverses. (c) Chest and subdiaphragmatic signal (D) showing phase opposition of respiratory movement and minimal purr signal on the abdomen. A pressure increase causes downward deflection. Horizontal bars indicate 1·0 sec.

expiration, and there seemed to be a slight pause between each phase of respiration. The microphone measurements confirmed these subjective observations and displayed the pause as a distinct amplitude minimum for both the sound and the vibration. Wide-band recordings of both the acoustic waveforms (top trace) and the surface vibration during a respiratory cycle are shown in Fig. 1.

Purring was never very loud and the measurements showed a typical amplitude to be 84 dB SPL 3 cm from the mouth. Moving the microphone around the cat at a constant distance from the surface shows that the maximum amplitude, by far, occurs near the mouth and nose. Surface vibrations registered by the microphone could be of large amplitude (over 110 dB) but only within the coupler and only when it was well sealed to the surface. These observations show that the purr sound emanates from the mouth and nose rather than from the body surface.

The acoustic signals were highly variable in loudness and were rich in harmonics of the fundamental purring frequency. The harmonic content varied considerably, depending in large part on whether the mouth was open. The fundamental frequency component was strong and readily apparent on both the low-pass filtered strip chart recordings and on the wide-band displays.

Fundamental purring frequency

In all of our domestic cats breath rate and the relative proportions of the respiratory cycle taken by inspiration and expiration varied widely. Despite this their fundamental purring frequency (f_0, the number of vibrations per second) showed similar variations with the phase of the respiratory cycle. For each of the domestic cats, five artefact free breaths were selected at random from each recording session. To standardize the frequency measurement, inspiration and expiration are considered separately. Since the rate of change of frequency with respect to time was greatest during the beginning and end of each respiratory phase, we eliminated these periods and measured the time it took an integral number of vibration cycles to occur. For each cat we found the fundamental frequency of purring from $f_0 = 1/T$, where T is the period of one cycle, and averaged the frequencies within each phase over the five breaths.

The fundamental frequency of purring averaged over inspiration and expiration equals $26{\cdot}3 \pm 1{\cdot}95$ (S.D.) Hz and ranges between 23 and 31 Hz. Fundamental frequency of purring at mid-expiration exceeds that at mid-inspiration by $2{\cdot}4 \pm 1{\cdot}3$ Hz ($P < 0{\cdot}001$).

For this small sample of cats, frequency does not correlate with chest circumference, nose to rump length, weight or sex ($P > 0{\cdot}05$). Weight, particularly in young cats, can serve as a proxy for age. Thus, the lack of correlation between frequency and weight is an indication that frequency is not correlated with age.

We recorded one cat intermittently from age 12 weeks to an age of three years and found no change in its fundamental frequency of purring, suggesting that it is stable over time for a specific individual.

To study fundamental frequency variation with phase of respiration, we observed this cat in detail. Figure 2 shows that the purr vibration period ($T = 1/f_0$) varies consistently with respect to the respiratory cycle, and varies least during inspiration.

Surface vibration

In contrast with the acoustic signal contact measurements, using a coupler produced waveforms that had large amplitudes at the fundamental purring frequency and much smaller harmonic content than the acoustic waveforms. This can be seen by the relative smoothness of the vibrations in the centre and bottom of Fig. 1. The purr vibrations are superimposed on the respiratory movements that appear as variations in the baseline in Fig. 1b and c. When the coupler is not well sealed to the surface (as in the second trace, Fig. 1a), the low frequency response is attenuated so that the apparent harmonic content is increased and the very low frequency respiratory fluctuations are diminished. The lack of harmonic content of the surface vibration, compared to that of the acoustic signal, is a further indication that the purr sound radiates largely from the mouth rather than from the body surface.

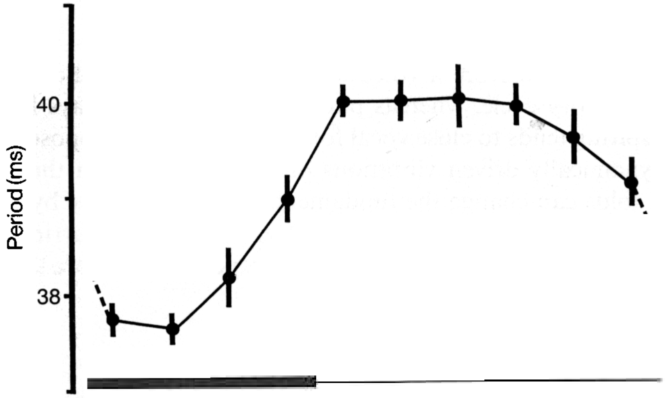

FIG. 2. Purr vibration period over the respiratory cycle. Measurements were made on six breaths recorded over two days from one domestic cat. Since the respiratory period varied, but expiration consumed about 40% of the time, each breath was divided into 10 equal epochs with four allotted to expiration. Heavy horizontal bar: expiration; vertical error bars: standard error of the estimate (S.E.E.).

The amplitude of the purr vibration measured with microphones coupled to the body surface is greatest over the lungs and immediately over the larynx and is dramatically diminished or absent elsewhere. This corresponds to the distribution of palpable vibration. Thoracic vibratory amplitude is not correlated with purr loudness or sex ($P > 0{\cdot}1$), but it does decrease as chest circumference and weight increase.

Synchrony and phase of purr signals

Two microphones measured the purring. They were either air coupled, coupled to the body surface, or both. The recordings showed that all purr sounds and vibrations (within a single phase of respiration) occurred synchronously, i.e. they had the same fundamental frequency and the relative phase between any two signals remain constant. The signals could be in phase, antiphasic (phase angle equals 180°), or anywhere in between. This synchrony indicates that purring is driven by either a single source or a well coordinated set of sources. A consequence of this synchrony is that either acoustic or contact measurements can provide signals useful for frequency determination.

Signals from any pair of contralateral sites are always in phase. Signals from any pair of ipsilateral points over the lungs are always in phase. Simultaneous recordings from the mouth and chest are always 180° out of phase regardless of the direction of respiratory flow (Fig. 1a). The phase of the fundamental frequency changes by 180°, and the amplitude of both the acoustic and surface signals diminishes when respiratory flow reverses except when measured on the larynx (Fig. 1a, b).

Figure 1b (L) shows that the laryngeal surface vibrations are continuous and undiminished during flow reversal. Measurements on the neck over the trachea and throat 2 cm above and 2 cm below the larynx showed weak surface vibrations that were always antiphasic.

The abdominal recordings often failed to show visible response at the purring frequency, but when they did, the signal was in phase with the signals measured on the thorax anterior to the diaphragm.

Discussion

Purring is distinctly different from a voice which is produced by phonation. Purring occurs during the entire respiratory cycle, whereas phonation is almost always limited to expiration, probably because inspiring tends to close vocal folds that are closely apposed. The voice sound is generated by aerodynamically driven vibrations of the vocal folds in the larynx. Varying the tension of the vocal folds can change the fundamental voice frequency by several octaves. The fundamental voice frequency usually exceeds 100 Hz. In contrast, purring is a low frequency phenomenon with a frequency that varies relatively little, perhaps no more than 20%, in any given individual.

Purr audibility

Our observations confirm that the amplitude and loudness of the purr sound can vary over a large range for different individuals and for a single individual at different times (Moelk, 1944). To assess the audibility of purring one must consider both the sound amplitude and the auditory capability of the listener. Below 2000 Hz the auditory threshold of adult cats is similar to that of humans (Neff & Hind, 1955; Heffner & Heffner, 1985) but much greater for kittens (Romand & Ehret, 1984). There is very little sound in the purr at frequencies above 2 kHz (Peters, 1981). Based on the similarity of the audiograms below 2 kHz, it appears that the auditory sensitivity of adult cats is very nearly equal to that of adult humans when listening to purring.

At 25 Hz the threshold of hearing is about 65 dB, decreasing to about 0 dB at 1000 Hz. A purr of medium loudness from one domestic cat was measured at 84 dB SPL 3 cm from the mouth. Assuming that the sound spreading is uniform, the amplitude is 64 dB at 30 cm. This implies that the purring fundamental frequency itself will not be heard at distances greater than about half a metre. Figure 3 shows that the signal contains a number of harmonics which approach the background level at approximately 250 Hz. At frequencies below 1 kHz the threshold of audibility decreases with increasing frequency at a rate greater than the amplitude of these harmonics decreases. This suggests that it is the harmonics of the fundamental purring frequency that contribute most to audibility of the purr sound. Analysis of this signal indicates that the purr will be barely audible at distances greater than 3 metres. This agrees with our informal observations in the laboratory. The greater amplitude and relative harmonic content of the purr signal during inspiration makes it both louder and rougher than the sound during expiration, as is reported by Moelk (1944). Since purring is a typical sound made by both mother and kittens during nursing, its low audibility likely serves to reduce the risk of detection during this activity.

Frequency variation

We found that the fundamental purring frequency increased during expiration. Other investigators report little change in fundamental frequency during respiration (Remmers & Gautier, 1972), a frequency increase during inspiration (Denis, 1969) (opposite of our observations), or a 2–3 Hz variation over the respiratory cycle (Kirkwood *et al.*, 1987) (in agreement). Differences in stress levels, experimental conditions, or variations in the state of arousal of the subjects may account for differences in the observations.

It is not clear why the fundamental purring frequency should vary during the respiratory cycle. One possibility is that the cat is exciting a mechanical resonator at the purring frequency. A

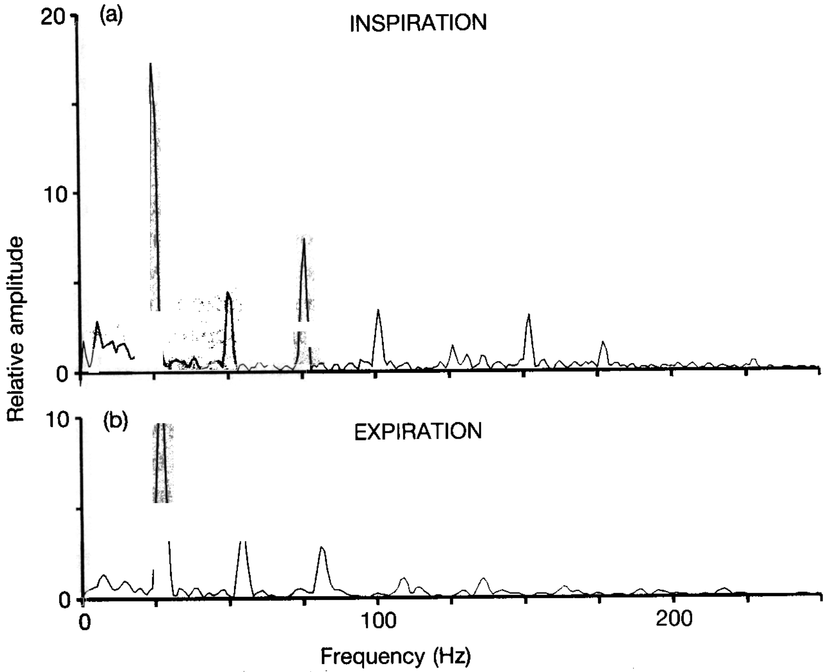

FIG. 3. Spectra of purr recorded at the mouth of a domestic cat. The fundamental frequency component has the greatest amplitude, and the harmonics generally diminish as frequency increases. (a) Inspiration has a lower fundamental frequency, greater amplitude, and greater harmonic content than (b) expiration.

resonator can provide large amplitude vibrations with a small energy input. Two reasons oppose this: 1. The frequency pattern does not follow the mechanical variables associated with respiration. A frequency change results from changing the volume or mass of a resonator. For ratio of tidal volume to functional residual capacity of 0·2, the resonant frequency should vary about 10%, approximately the observed variation. However, Fig. 2 shows that the frequency is nearly constant during inspiration when lung volume is steadily increasing and other variables associated with the respiratory cycle are changing; 2. The frequency varies little with body size. The frequency of a resonator is inversely proportional to the square root of its mass (Böhme, 1974). Our cats covered a mass range of 9:1 suggesting a frequency range of 1:3, an easily observable amount. These observations suggest that the purr frequency is not determined by a mechanical resonator, nor do cats track a mechanical resonance as they grow.

Mechanism

The continuing surface vibration measured over the larynx confirms the mechanical activation of the laryngeal muscles at the purr frequency reported by Remmers & Gautier (1972) from EMG data. Activation of these muscles is necessary to appose the vocal folds within the larynx.

Hardie *et al.* (1981) report an absence of purring in cats with laryngeal paralysis, and its return along with the return of the voice after recovery from partial laryngectomy. This observation indicates that a functional larynx may be necessary for purring to occur.

This evidence indicates that purring arises from the gating of respiratory flow by the larynx. Increasing laryngeal resistance to respiratory flow by apposition of the vocal folds will cause a relative pressure increase at the upstream side and a pressure decrease downstream of the larynx. This causes the phase differences observed across the larynx. Further, a point upstream of the larynx during inspiration will be downstream during expiration. This explains the phase reversal observed in the recordings.

During flow reversal when the respiratory flow stops, the amplitude of both the sound and vibration diminishes, suggesting that laryngeal interaction with respiratory flow provides the dominant source of both. A simple experiment demonstrates the effectiveness of this mechanism for sound production: whisper the word 'tee' during both inspiration and expiration. Note that significant sound is generated at ordinary flows when the tongue separates from the palate. When the respiratory flow is exactly zero, the sound becomes inaudible or is limited to the sound of the articulation itself, a distinctly different type of sound.

The source of the sound appears to be the sudden opening of the vocal folds (Remmers & Gautier, 1972) that produces a sound very rich in harmonics. The vocal tract filters this sound and conducts it to be radiated from the mouth and nose. Variable filtering in the vocal tract can produce the variations in quality and loudness that is observed. We note that periodic incomplete apposition avoids a sudden opening and will result in a signal that has a strong fundamental frequency and weak harmonics. Under these circumstances purring could continue inaudibly.

Inspiration tends to close the glottis, and therefore the vocal folds will tend to snap open and closed as they are approximated. This action will gate the flow more sharply and tend to increase the harmonic content of the sound produced. This effect may explain the observation of Moelk (1944) that inspiration produces purr sounds that are louder and harsher than those of expiration.

Role of the diaphragm

Remmers & Gautier (1972) found that diaphragmatic EMGs were alternating or antiphasic with laryngeal EMGs during inspiration and were absent during expiration. They suggest that this may improve ventilatory efficiency during purring by not tensing the diaphragm during laryngeal closure. Their data show a sublaryngeal tracheal pressure drop during laryngeal closure (Remmers & Gautier, (1972): Fig. 7). This pressure drop demonstrates, however, that ventilatory efficiency is decreased, but is in accordance with the model that laryngeal resistance causes a downstream pressure drop.

Our data show very little vibration amplitude on the abdomen below the diaphragm and no great differences between thoracic and abdominal vibration amplitude between inspiration and expiration. Further, the phase of the subdiaphragmatic signal is the same as that of the thoracic signal. If the diaphragm were active, the signals on opposite sides of the diaphragm would be 180° out of phase. These observations suggest that the diaphragm is not responding mechanically at the fundamental frequency of purring.

Measurements of diaphragmatic response to phrenic nerve stimulation indicate that the mechanical fusion frequency (the frequency at which the muscle produces a constant or tonic contraction rather than a phasic or vibratory response) is reached at the purring frequency (Evanich, Franco & Lourenco, 1973; Evanich & Lourenco, 1976). Muscle EMGs show a response at the stimulation frequency to stimulation above the mechanical fusion frequency. Therefore an EMG response does not necessarily indicate that the muscle is responding with a force that varies at the stimulation frequency. The reason for the observed diaphragmatic EMG activity at the purring frequency is unclear. The alternation of the laryngeal and diaphragmatic EMG bursts may result from the additional travel time it takes simultaneously generated neural signals to reach the more distant diaphragm. The fact that the bursts in one signal occur in the silent period of the other signal may be coincidental. In any case, since the diaphragm is the primary muscle of respiration and is normally active only during inspiration, the absence of diaphragmatic EMG activity during expiration is physiologically appropriate.

Role of the intercostal muscles

Remmers & Gautier (1972) measured from intercostal muscle but reported no purring activity. Kirkwood *et al.* (1987) found intercostal EMG purring activity that occurred as periodic bursts at the purring frequency during both inspiration and expiration. An asymmetric posture or unilateral cutting of sensory nerves caused bilateral asymmetry in the EMG. This indicates that the response originates from a reflex mechanism rather than from central stimulation. No mechanical response from these muscles is apparent from our acoustic or vibration recordings, but our measurements were not designed to study this question. On the other hand, the presence of a reflex response could add to the surface vibration. This reflex vibration should be proportional to the stimulus vibration and should undergo a constant delay. The stimulus and reflex vibrations would add together to a composite vibration that has a phase that is strictly dependent upon the phase of the stimulus vibration. Thus, even if intercostal muscle reflex activity were present, it would not invalidate our observations on the phase changes of the thoracic vibrations.

Source of thoracic vibrations

As respiratory flow reverses, thoracic vibratory amplitude and purr sound decrease in amplitude and reverse in phase. This indicates that the surface vibrations are caused by the same pressure difference across the larynx as is the sound. Pressure changes propagate as sound waves from the trachea to the surface of the lung at speeds approaching 300 m/s (Rice & Rice, 1987). In animals the size of domestic cats the time it takes for the tracheal sound to reach the pleura is under 1 ms. This approaches the resolution of our measurements, so it is not surprising that all the thoracic surface recordings are in phase with each other.

The distribution over the surface of the thorax is the same as that for lung sounds: strongest over the lung fields, and falling off rapidly away from the lung. The low-pass filtering by the chest of sounds travelling from the lung to the thoracic surface (Böhme & Böhme, 1972) is in accordance with our observations of relative lack of harmonics to be found in the purring surface vibration. Further, if the chest wall is passive the surface vibration amplitude should decrease as the chest wall becomes more massive. The observed decrease of surface vibration amplitude as chest size and body weight increase supports this.

Phonation during purring

In three species, puma, cheetah and domestic cat, we have recorded the effect of voicing—other than the purring sound—attempted during purring. This appears to occur mainly during expiration. An example from a cheetah is shown by Fig. 4. The modulating frequency is equal to the unvoiced purring frequency during expiration. A major determinant of f_0, the fundamental

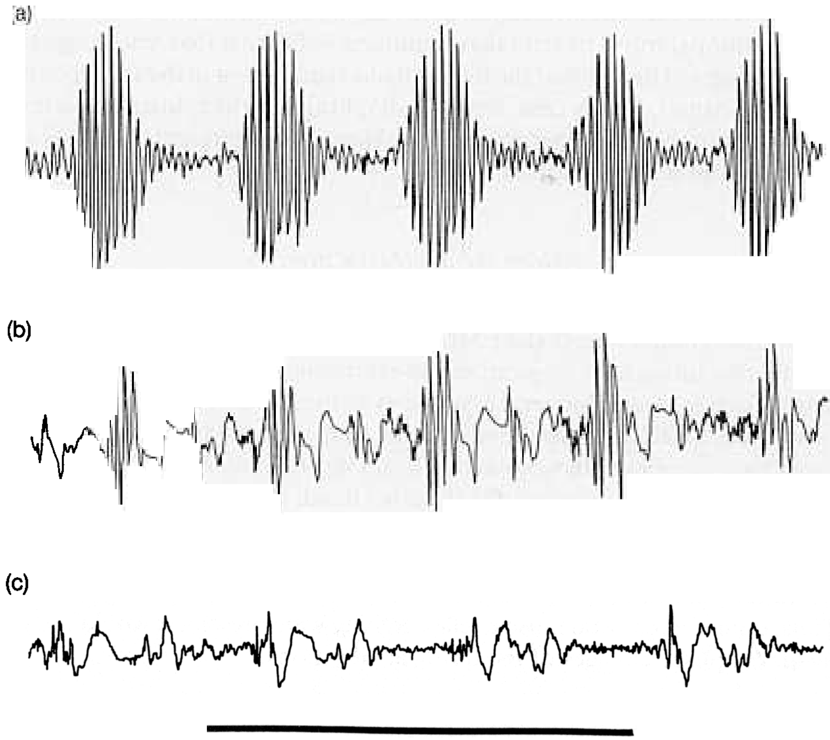

FIG. 4. Cheetah purring. (a) Mixed voice and purr. (b) Less voice. (c) Purr only. (a) Traces were taken during expiration and show a purr frequency of 26 Hz. (c) Trace is amplified and taken during inspiration. Purr frequency is 21 Hz. Recording system has lower limiting frequency of 40 Hz. Bar indicates 0·1 sec.

voice frequency, is vocal fold tension (Titze & Durham, 1987). Since the separation of the vocal folds can be controlled independently of their length, it appears to be possible to have the aerodynamic mechanisms of phonation occurring simultaneously with the periodic apposition that occurs during purring.

The amplitude of the voice depends upon the amplitude of the vocal fold vibration. This in turn depends on the aerodynamic driving force that is related to the degree of apposition of the vocal folds. It follows that variation in vocal fold separation with purring will cause the voice to vary in amplitude at a rate equal to the fundamental purring frequency. This appears to be occurring in Fig. 4a and b. Figure 4a shows a 200 Hz signal with an amplitude that varies at a rate of 26 Hz. Figure 4b shows a 200 Hz signal that occurs in periodic bursts recurring at 26 Hz along with portions of a purr-like waveform. Purring alone is shown in Fig. 4c. This suggests that the amplitude or proportion of time spent voicing is variable over a large range, as is purring itself. The voice frequency for this cat is approximately 200 Hz during purring for all degrees of voice inclusion in the purring process that we observed. This suggests that the vocal folds were kept at a constant tension during purring as their degree of apposition varied.

The purpose of this discussion is not to define a particular, detailed mechanism for simultaneous purr and voice production, but to show how it is physiologically possible, that it is consistent with our model of purring, and that it does occur.

Limitations

It is difficult to control or measure simultaneously all the activities and effects observed during purring. Since the observations are all highly correlated, it is possible that confounding has occurred. The mechanism for sound and vibration production that we propose is the simplest that explains the plethora of observations. A definitive experiment would be to insert an endotracheal tube and induce a cat to purr. This tube would prevent laryngeal interaction with the respiratory flow. If vibration is limited to the larynx, and no sound or vibration occurs elsewhere, this would confirm that nonlaryngeal mechanisms contribute little to purring. Variations on this include using tracheotomized or laryngectomized animals.

Conclusion

We conclude that the primary mechanism for both the sound and the vibration of purring is a centrally driven periodic laryngeal modulation of respiratory flow. Mechanical input from other muscles is neither necessary nor observed except for that which is required to drive respiration. Voice production proper during purring is possible and does occur.

We thank the Louisiana SPCA, New Orleans, and B. Fleury for providing subjects and facilities.

REFERENCES

Beadle, M. (1977). *The cat: history, biology, and behavior.* New York: Simon & Schuster.

Beaver, B. V. (1983). Purr-fect communication. *Vet. Med./Small Anim. Clin.* **78:** 41.

Böhme, H-R. (1974). Versuch einer physikalischen Charakterisierung des passiven Schallverhaltens der Lunge am Modell. *Zschr. inn. Med.* **29:** 401–406.

Böhme, H-R. & Böhme, H. (1972). Unterschiedliches Durchlaßverhalten der Lunge auf niederfrequenten Schall bei Lungenemphysem. *Zschr. inn. Med.* **27:** 765–770.

Burger, C. (1966). *All about cats.* New York: Random House.

Denis, B. (1969). *Contribution a l'etude du ronronnement chez le chat domestique (**Felis catus** L.) chez le chat sauvage (**Felis silvestris** S.). Aspects morpho-fonctionnels, acoustiques et ethologiques.* DVM thesis, Nancy University.

de Lanerolle, N. C. & Lang, F. F. (1988). Functional neural pathways for vocalization in the domestic cat. In *Physiological control of mammalian vocalization* Ch. 3. Newman, J. D. (Ed.). New York: Plenum Press.

Evanich, M. J., Franco, M. J. & Lourenco, R. V. (1973). Force output of the diaphragm as a function of phrenic nerve firing rate and lung volume. *J. appl. Physiol.* **35:** 208–212.

Evanich, M. J. & Lourenco, R. V. (1976). Frequency response analysis of the diaphragm *in vivo. J. appl. Physiol.* **40:** 279–735.

Gibbs, E. L. & Gibbs, J. (1936). A purring center in the cat's brain. *Comp. Neurol.* **64:** 209–211.

Hardie, E. M., Kolata, R. J., Stone, E. A. & Steiss, T. E. (1981). Laryngeal paralysis in three cats. *J. Am. vet. med. Ass.* **179:** 879–882.

Heffner, R. S. & Heffner, H. E. (1985). Hearing range of the domestic cat. *Hearing Res.* **19:** 85–88.

Kirkwood, P. A., Sears, T. A., Stagg, D. & Westgaard, R. H. (1987). Intercostal muscles and purring in the cat: the influence of afferent inputs. *Brain Res.* **405:** 187–191.

McCuistion, W. R. (1966). Feline purring and its dynamics. *Vet. Med./Small Anim. Clin.* **61:** 562–566.

Mellen, I. M. (1940). *The science and mystery of the cat*: 54–57. New York: Chas. Scribner's Sons.

Mery, F. (1969). *The life, history and magic of the cat.* [Street, E. (transl.)] New York: Grosset & Dunlap.

Moelk, M. (1944). Vocalizing in the house cat: A phonetic and functional study. *Am. J. Psychol.* **57:** 184–205.

Neff, W. D. & Hind, J. E. (1955). Auditory thresholds of the cat. *J. acoust. Soc. Am.* **27:** 480–483.

Peters, G. (1981). Das schnurren der Katzen (Felidae). *Säugetierk. Mitt.* **29:** 30–37.

Remmers, J. E. & Gautier, H. (1972). Neural and mechanical mechanisms of feline purring. *Resp. Physiol.* **16:** 351–361.

Rice, D. A. & Rice, J. C. (1987). Central to peripheral sound propagation in excised lung. *J. Acoust. Soc. Am.* **82** (4): 1139–1144.

Romand, R. & Ehret, G. (1984). Development of sound production in normal, isolated, and deafened kittens during the first postnatal months. *Devl Psychobiol.* **17:** 629–649.

Stogdale, L. & Delack, J. B. (1985). Feline purring. *J. Am. vet. med. Ass.* 7(7): 551–552.

Titze, I. R. & Durham, P. L. (1987). Passive mechanisms influencing fundamental frequency control. In *Laryngeal function in phonation and respiration* Ch. 22. Baer, T., Sasaki, C. & Harris, K. S. (Eds). Boston: Little, Brown & Co.

Wemmer, C. M. (1977). Comparative ethology of the large-spotted genet (*Genetta tigrina*) and some related viverrids. *Smithson. Contr. Zool.* No. 239: 1–93.

Note added in proof: It was brought to our attention by J. Jiang, Speech Pathology and Audiology, University of Iowa, that the mechanical fusion frequency for some laryngeal muscles of the cat is above 40 Hz. Experimental data supporting this is found in Hirose, H., Ushijima, T., Kobayashi, T. & Sawashima, M. (1969). *Ann. Otol.* **78:** 297–306.