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Cat purring: all muscle, all air, or a bit of both?

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Cat purring, this unusual pulsed vibration that epitomizes comfort, enjoys a special status in the world of vocal communication research. Indeed, it has long been flagged as a rare exception to the dominant theory of voice production in mammals. A new study presents histological and biomechanical evidence that purring can occur passively, without needing muscle vibration in the larynx controlled by an independent neural oscillator.

In mammals, including humans, vocal signals are produced by gestures that are mostly internal, which makes voice production a bit of a mystery and its investigation particularly difficult. Perhaps as a consequence, it was not until Ferrein's[1] experiments with cadavers published in 1741 that scientists began to understand the nature of voice production: phonation results from the vibration inside the larynx of vocal "ribbons", under the effect of the airflow coming from the lungs. And it took a couple more centuries of investigations for scientists to arrive at the now-dominant *source-filter* theory of voice production[2,3], which states that vocal signals are generated through the combination of the vibration of vocal folds (which are more like lips than strings!) and subsequent filtering by the vocal tract (the throat, the mouth and the nasal cavity). Crucially, the vibration of the vocal folds occurs as the air is forced out of the lungs (or, as we will see, also sometimes *into* the lungs), without neurally-induced muscle contraction at these frequencies.

Yet, seeds of doubt sprouted again in the 1950s and 60s, when a new battle raged in the voice science about the forces that drive human phonation. Phonation involves lateral, oscillatory movements of the two vocal folds within the larynx[4]. As the two vocal folds repeatedly open and close the respiratory airway, this creates a series of regular air "puffs", whose rate of repetition corresponds to the fundamental frequency or f_o of the produced sound, and determines its pitch. But why do the vocal folds oscillate? As we have seen, these vocal fold movements were traditionally thought to be driven aerodynamically by the flow of air from the lungs (reminiscent of a flag flapping in the wind), but the new theory introduced by Husson[5] argued that they were driven actively, by very rapid nerve impulses and muscle contractions that matched the rate of vocal fold oscillations. Husson's theory was disproved for the human voice, since the f_os of human speech (about 100-300 oscillations per second in adults[4]), and especially of singing (over 1000 oscillation per second in sopranos[6]), greatly exceed the possible rate of motor nerve firing or muscle contraction, and because ex-vivo experiments have confirmed that excised human larynges can still phonate normally when air is blown through them.

Thus, the myo-elastic aerodynamic (MEAD) theory triumphed for the human voice[7], and it has since been extended to most vertebrate vocalizations, whose f_o ranges from 10 Hz in infrasonic elephant rumbles[8] to well over 100 kHz in ultrasonic echolocation calls of bats[9]. Yet, one intriguing exception remained: cat purring. Because f_o in purring is so low (20-30 Hz), despite the relatively small size of cats and their larynges, purrs were widely thought to be driven by active muscle contraction[10,11]. Could this exception finally fall, too? In the article titled "Domestic cat larynges can produce purring frequencies without neural input", Herbst et al.[12] show that the vocal folds in excised cat larynges can vibrate at the frequencies characteristic of purring when they are driven solely by air flow, and all nerve firing or muscle contraction is rendered impossible experimentally. *Ex vivo* "excised larynges" experiments work as follows: larynges from animals who die of natural causes are excised and mounted on an experimental set-up that allows the experimenters to control the air pressure below the glottis and to monitor its effect on the onset and periodicity of phonation[13]. In this case, authors show that the vocal folds in cat larynges can vibrate in the absence of muscle activity at frequencies ranging from 15 Hz to 200 Hz, which encompasses the frequencies of purring. At these frequencies the vocal fold behaves in a way reminiscent of what happens in human vocal fry – a pulse-like vocal register also known as strohbass[14], in which the glottis remains closed for the majority of the oscillatory cycle.

The authors also conduct anatomical investigations that confirm the presence of thick *pads* in the vocal folds. Such adaptations can have the effect of slowing down the rate of oscillation of vocal folds by increasing the effective mass in vibration[15]. Similar adaptations have previously been identified in other studies of felids, namely lions and tigers[16], where they are also believed to support the efficient production of high amplitude calls with low f_os.

To conclude, this study shows that the cat's vocal folds, despite their small size, are indeed capable of vibrating solely under the effect of the airflow from the lungs, at a rate that corresponds to that observed in purrs, suggesting that active muscle vibration may not be necessary, after all. However, the authors acknowledge that the anatomical adaptation that enables passive vocal fold vibration at low frequencies might also have evolved to enhance the effects of active muscular vibration. It is indeed much more energy efficient to make an oscillator vibrate at its natural frequency – a phenomenon known as resonance, which makes it possible to achieve very high amplitude oscillations with minimal energy[17]. Thus, Remmers and Gautier[10] may still have been correct about cats generating each pulse of purring with an active muscular contraction, but at a very specific, anatomically optimal frequency close to the natural oscillatory frequency of the vocal folds.

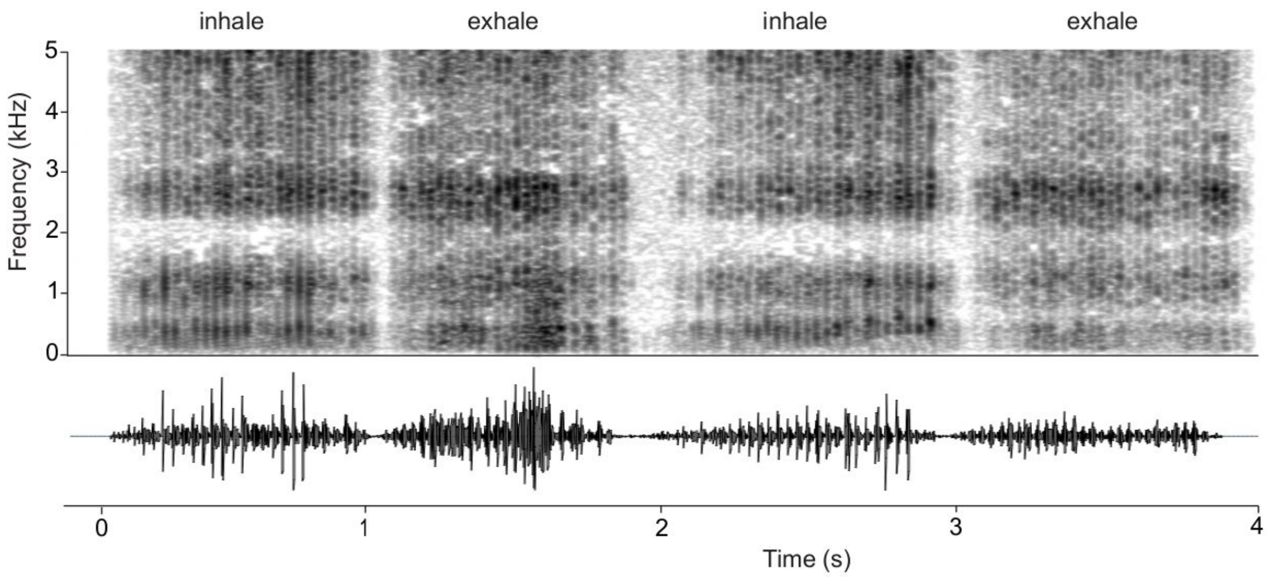

Figure 1. Waveform and spectrogram of a bout of four purrs extracted from a long purring sequence recorded at the cat's nostrils. Purring sequences consist of alternating calls produced during exhalation and inhalation. The fundamental frequency (f_0) of the purr is very low (here 30 Hz) and remains highly regular throughout the sequence, which has led to a debate on whether it is produced by neurally-induced muscular vibration or by passive vibration as a consequence of the airflow. The study by Herbst et al. shows that vibration at these low frequencies does not require muscular activity.

Future work should investigate what happens during the inhalation phase as cat purrs are continuous vocalisations that take place on both inhalation and exhalation[10,11]. In particular, it would be interesting to investigate why the transition between exhalation and inhalation appears to have so little effect on the rate and amplitude of oscillations in the larynx (Fig. 1). Finally, *in vivo* investigations should revisit the presence or absence of neural firing and muscle activity, and test for a possible coupling between muscle- and airflow-induced oscillations documented here.

This paper has the merit of challenging a theory that may have been accepted too hastily, perhaps because we love the "exception that confirms the rule". It calls for more investigations of this intriguing phenomena using the modern tools at our disposal. Science at its best!

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