

# Investigation of the Rat Phonatory System

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## Introduction

The study of animal communication is of interest for a variety of reasons. It helps to elucidate the study of animal emotion, learning, sexual conduct, society, and psychology in general. The study of animal vocalizations is of special interest because of their possible relation to human vocalizations. Research indicates that the neuroanatomical and musculoskeletal structures involved in vocalizations are conserved throughout evolution. Because of their relatively simple neuroanatomy, stereotyped yet interesting call structure, and ease of handling, songbirds have shown to be an excellent laboratory organism to study animal vocalizations. However, an equivalent mammalian organism has yet to be identified. Some work has been done with primates, but practical and ethical considerations have limited research in this field. The potential of one of the most common laboratory organisms for the study of mammalian vocalizations has been overlooked arguably because we can not hear them. Rats have a varied and possibly interesting, although ultrasonic, call repertoire that is used for social interaction. The study of their vocalizations can provide valuable contributions to the field of ethology. In addition, since their phonatory system shares many similarities with those of other mammals, including humans, they can provide insight into how social vocalization behaviors evolve and serve as a model organism for human vocalizations, opening up the possibility to use them for studying human phonatory disorders. Furthermore, unlike most animals, the rat vocal production mechanism is generated by a whistle rather than the vibration of vocal folds. The description of this peculiar mechanism is an interesting fluid dynamics problem in its own right and the investigation of how rats use it to communicate can help us understand how biological systems use principles of physics to accomplish their task. A worthy long term goal in the study of rat communication is to replicate much of the research that has been done in birds. However, since the physical vocal production mechanism between these species is different, a physical model describing the rat whistle production mechanism is a reasonable place to start. A model describing the whistle mechanism can help to classify rat calls as well as elucidate the upstream neural correlates involved in their generation.

## Background on Rat Ultrasonic Vocalizations

Rats are known to produce calls in both the sonic and ultrasonic range. The sonic calls are generally induced by the presence of a predator and are directed at the predator to indicate the targeted rat is ready for a defensive attack. These calls are produced by a mechanism similar to that by which human speech and bird songs are produced. Expiration of air from the lungs causes an increase in subglottal air pressure. Due to the geometry of the vocal folds, this increase in air pressure causes them to vibrate together. This results in a pulsating airflow into the upper vocal tract. The frequency components of the resulting pressure wave are determined by rate at which air pulses through the vocal folds. One model for the dynamics of the vocal folds of song birds was proposed by Laje, Gardner, and Mindlin. In the model, when the vocal folds are stretched apart, air is allowed to flow through them. The vocal folds move like a relaxation oscillator. There is a slow build up in which energy is stored elastically in the tissue as the vocal folds are stretched apart. There is then a rapid discharge of energy as the vocal folds relax back towards each other, until they touch, and air is no longer allowed to flow into the upper tract. The spectral components of the pressure wave are the same as those of the relaxation oscillator motion of the vocal folds[7]. The acoustic properties of this wave are then modified by the resonance properties of the upper vocal tract [3].

Although the mechanism for sonic vocalizations is well understood and seems to be well conserved across species, there is much more uncertainty concerning the mechanism behind ultrasonic vocalizations. There are two basic patterns of rat ultrasonic vocalizations: the 22-kHz call and a variety of 50-kHz calls. The 22-kHz call consists of an approximately pure tone, which in actuality is between 20 and 30-kHz. It is usually induced by the presence of predators and is directed at conspecifics. Calls of this type are associated with a negative emotional state. This is evidenced by a study in which carbachol was injected directly into the basal forebrain, septum, and diencephalic areas of rat brains to stimulate the cholinergic neurotransmitter system. Carbachol injection induced 22-kHz calls as well as behavioral correlates of negative emotional states, such as widely opened eyes, lowered head, crouched body posture, decrease in motor activity, and an increased frequency of prolonged freezing episodes.

The 50-kHz call types are much more varied than the 22-kHz call types. By visual inspection of spectrograms, Wright et al. have identified 14 different call types with frequencies ranging from 30-kHz to 80-kHz. They are generally found in social situations with conspecifics or in appetitive situations (e.g. entering familiar places, meeting familiar members of the social group, reuniting after a period of separation, rough and tumble play of juvenile rats, anticipating a rewarding pharmacological agent, and in males the anticipation of contact with a female rat). Calls of this type are generally associated with positive mental states. This is evidenced by a study in which 50-kHz calls were elicited by direct dopaminergic activation of an area in and around the nucleus accumbens by amphetamine injection. An increase of dopamine in the nucleus accumbens is known to induce increased locomotor activity, exploratory behavior, approach, and investigatory sniffing[2].

While sonic vocalizations are known to be produced by oscillating vocal folds, there is some evidence that the mechanism behind ultrasonic vocalizations is fundamentally different. By measuring the stress-strain relationship of the rat vocal fold, Riede et al. determined the tissue can oscillate at rates up to 6-Hz; this is far too low to account for the production of ultrasonic vocalizations [9]. Furthermore, Roberts performed a study in which both sonic and ultrasonic calls of rodents were recorded after

they were placed in a polythene bag filled with heliox gas. For the sonic calls, it was found that the fundamental frequency was left unchanged. However, the intensity of higher harmonics was found to increase. This is consistent with the vibrating vocal fold model. The fundamental frequency is determined by the oscillation frequency of the tissue, which is not affected by the medium of sound propagation. However, replacing air with heliox gas increases the speed of sound in the vocal tract. Thus, it is expected to see an upward frequency shift in the formant structure of the call. In contrast, for ultrasonic calls it was found that the presence of heliox gas increased the fundamental frequency of the call. This is inconsistent with the vibrating vocal fold model. Riede verified these results by injecting heliox gas into a rat's trachea as it was making a 22-kHz call. He found that the fundamental frequency of the call was increased by up to 17-kHz [8].

## Modeling of the Whistle Mechanism

The observations discussed in the previous section indicate that the calls are produced by some sort of whistle mechanism in the vocal tract, rather than vibrating vocal folds. Roberts has provided some support for this by simulating rat calls with an artificially constructed whistle. The whistle consisted of two aligned circular holes in parallel plates, separated by 1.5 mm. By applying a blowing pressure within the physiological range, he was able to produce sounds in the frequency range 20 to 80-kHz that closely resemble rat calls in frequency and temporal pattern. This type of whistle is known as a hole tone. A jet of air is directed at the posterior aperture. The posterior aperture focuses the jet into a circular shape. The system is aligned so that the circular jet then passes through the anterior aperture, causing the air in the anterior aperture to vibrate like a diaphragm. Part of the sound energy generated by the vibration travels outward. The rest travels backward to the aperture from which the jet emerges. Using biologically realistic values for the rat vocal tract, taking the velocity of the jet to be  $30\frac{m}{s}$ , the length of the vocal tract to be 1.5mm, and using the kinematic viscosity of air, the Reynolds number of the system is calculated to be  $Re = \frac{V*l}{\nu} = 3000$ , where  $V$  is the velocity of the jet, and  $\nu$  is the kinematic viscosity of air. This value for the Reynolds number, along with the back propagating sound energy, makes it likely that disturbances in the flow will occur. The disturbances in the flow will cause more sound energy to back propagate to the first aperture, which will cause greater disturbances in the flow, which in turn will cause more sound energy to propagate backwards. This forms a positive feedback loop. Eventually the disturbances in the flow become so great that vortices, which circulate along the longitudinal axis of the system, are formed and propagate towards the second aperture. These vortices cause the air in the second aperture to vibrate like a monopole sound source. These vibrations produce the sound observed in the far field(see Figure 1) [4].

The whistle constructed by Roberts possesses structural homologies to the anatomy of the rat vocal tract. The vocal tract consists of an approximately cylindrical resonance cavity surrounded on both sides by apertures. Denervation studies of the rat larynx show that the laryngeal muscles that control the vocal folds are essential for the production of ultrasonic vocalizations. Furthermore, by stimulating the brainstem of anesthetized rats to evoke vocalizations and inserting a camera into the vocal tracts of rats, Sanders observed that the vocal folds remained tightly opposed. An opening approximately 1-2 mm apart was observed in the dorsal section of the vocal folds, and the tissue did not oscillate throughout the time course of a call. These observations indicate that the posterior aperture is

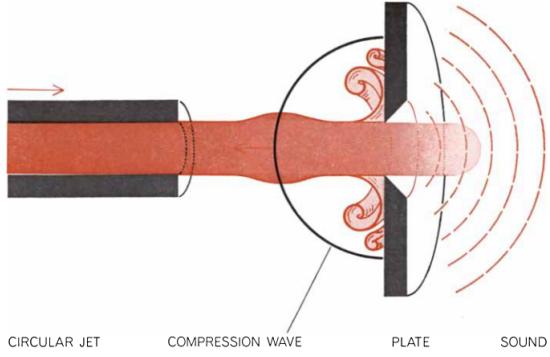


Figure 1: The jet of air emerges from the left aperture and impinges on the right aperture. Sound energy travels back from the right aperture and causes instabilities in the jet. Instabilities in the jet then affect the acoustic field generated at the right aperture, creating a positive feedback mechanism. The jet instabilities also cause the air in the right aperture to vibrate, generating sound that travels away from the system.

formed by the vocal folds themselves. There is some uncertainty as to what structure forms the second aperture. Blocking the nose has little effect on the intensity of sound produced. However, blocking the mouth decreases the intensity but does not eliminate the sound. This indicates the ultrasonic calls are normally emitted from the mouth. However, if the mouth is blocked, some of that energy can be redirected through the nose. This indicates the source of sound is posterior to the junction of the nasal and buccal cavity. There are two structures that could possibly form the second aperture, both located in the oropharynx. The base of the rat tongue can push up against the tip of the soft palate to create a small opening. This second opening would lead predominately in to the mouth, which would agree with Roberts observation that most of the sound energy is emitted through the mouth. The other possibility is that the epiglottis could be stabilized in a semi-closed position. The rodent epiglottis is reinforced by epiglottic cartilage joined with thyroid cartilage and could possibly be rigidly stabilized. If this structure forms the second the aperture, the distance between the anterior and posterior apertures would then be approximately 1-1.5 mm. In addition, the anterior aperture would be aligned to the posterior aperture, formed by the dorsal section of the vocal folds. These dimensions would correspond well to those used by Roberts in the whistle he constructed. These structures are shown in Figure 2 [3, 10].

A quantitative description of the hole tone can be formulated by considering its fluid dynamical and resonant properties. Assuming the jet evolves into a succession of circular vortices symmetric about the longitudinal axis of the whistle. The pressure in the far field can be expressed as

$$p(\mathbf{x}, t) \approx \mp \frac{2\rho_0 f \Gamma R_0}{|\mathbf{x}|} I_1(\kappa R_0) e^{-\kappa R} \sin(2\pi f[t - \frac{L}{U_c}]),$$

where  $f$  is the frequency of the fundamental component,  $\Gamma$  is the circulation of the vortex rings,  $R_0$  is the radius of the first aperture,  $R$  is the radius of the second aperture,  $L$  is the length between

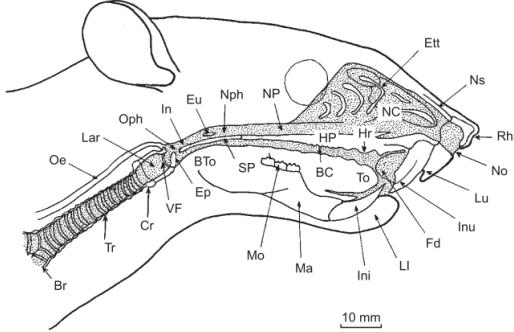


Figure 2: The cross section of the upper respiratory tract of an adult male Wistar rat. Abbreviations: Bc: buccal (oral) cavity; Br: bronchus; BTo: base of the tongue; Cr: cricoid cartilage of the larynx; Ep: epiglottis; Ett: ethmoid bones and nasal turbinates; Eu: opening into eustachian tube; Fd: fold of skin covering diastema; HP: hard palate; Hr: hard palate rugae; In: opening of internal nostrils (choana); Ini: lower jaw incisor; Inu: upper jaw incisor; Lar: larynx; Ll: lower lip; Lu: upper lip; Ma: lower fragment of the mandible; Mo: three molar teeth in the lower jaw (the upper ones are omitted); NC: nasal cavity; No: external nostrils; NP: nasal passage; Nph: nasopharynx (above soft plate); Ns: nasal bones of the skull (fragment); Oe: esophagus; Oph: oropharynx (behind the soft palate); Rhi: rhinarium; SP: soft palate; To: rostral part of the tongue; Tr: trachea; VF: vocal folds.

apertures,  $U_c$  is the convection velocity of the disturbances,  $\kappa = \frac{2\pi f}{U_c}$  is the hydrodynamic wave number, the brackets indicate the quantity  $[t - \frac{L}{U_c}]$  is evaluated at the retarded time  $t - \frac{|\mathbf{x}|}{c_0}$ , and  $I_1$  is a modified Bessel function of the first kind. The operating frequencies of the whistle are known to obey the relation

$$f \frac{L}{U_c} = n - \frac{1}{4},$$

where  $n$  is the mode number. The excited tone depends on the eigenvalues of the equation of motion for the jet. The eigenvalues lie in continuous bands but have discontinuous jumps in between the bands. Within the band, the excited tone is a continuous function of the parameters of the system (velocity for example). When the eigenvalue reaches an edge of the band a discontinuous jump occurs. Furthermore, the eigenvalues can exhibit hysteresis as a function of the parameters. This is a general explanation and more work needs to be done in this area, but this mechanism could explain the frequency jumps observed in recorded rat calls [6].

We have done some analysis of recorded calls demonstrating that observed frequency jumps can be explained by this model. To achieve this we began with the reassigned spectrogram of a call (Figure 3). We then fitted a curve to the continuous path of lowest entropy (red curve) and calculated the time points with sufficiently low entropy (yellow curve). Times with sufficiently low entropy indicate there is a signal stronger than white noise and is a valid point for the fitted curve. We then extracted the points where the fitted curve makes a discontinuous jump (green circles). Figure 4 shows the after jump frequency plotted against the before jump frequency for many recorded calls. It is easily seen

that this data clusters itself into four distinct regions. We then performed a linear regression on each of these clusters. The slopes of these regressions are given in the caption of the figure. From the above equation, assuming the frequency jumps are caused by transitions between different modes, the ratio of the after jump frequency to the before jump frequency is  $\frac{f_2}{f_1} = \frac{n_2 - \frac{1}{4}}{n_1 - \frac{1}{4}}$ . By fitting the calculated slopes to this equation, we found the frequency jumps most closely correspond to jumps between the modes shown in the figure. Furthermore, the  $m_{3 \rightarrow 4}$  and  $m_{4 \rightarrow 3}$  are approximately reciprocals of each other. The same is true for  $m_{4 \rightarrow 5}$  and  $m_{5 \rightarrow 4}$ . This strongly suggests that the transitions correspond to jumps back and forth between the same four modes. Inserting the length of the vocal tract (1.5 mm) into the frequency mode relation above, we found a representative velocity for the convection of disturbances is  $20\frac{m}{s}$ . Using this value for the velocity in the far field pressure equation, we artificially reproduced some of the qualitative features of the calls (Figure 5). The two regions of constant frequency correspond well to 40 kHz,  $n = 3$ , flat calls. The region of varying frequency was obtained by superimposing a 50 Hz and a 30 Hz sinusoidally varying velocity that oscillated around  $20\frac{m}{s}$ . This roughly corresponds to  $n = 4$  frequency modulated calls. More work can be done with this model by fitting its parameters to data and by developing theoretical predictions of when the frequency jumps will occur. With that information we would be able to accurately reproduce calls.

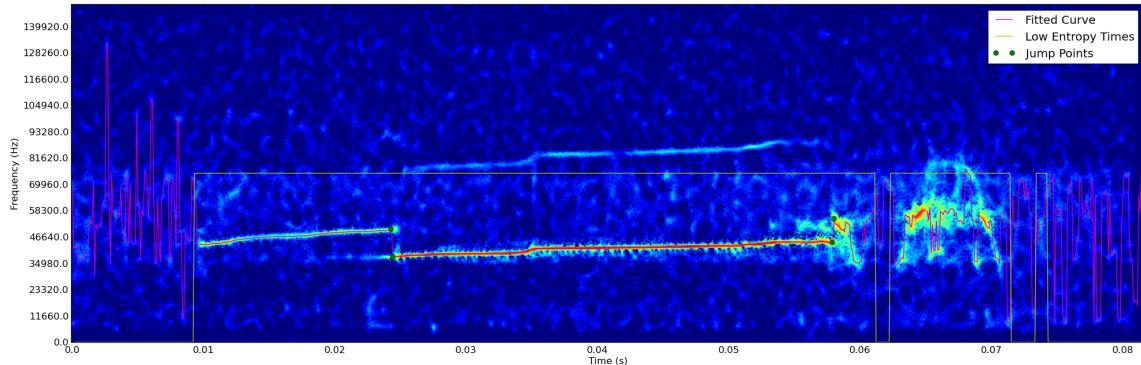


Figure 3: Reassigned spectrogram of rat call

While this model is attractive, since it depends on a low number of parameters, its derivation does not come entirely from first principles. It relies on an ansatz about the form of the vorticity. While I believe we can capture most of the necessary features of the calls with this phenomenological approach, it will be necessary to compare it to a more rigorous approach. This can be obtained by numerically solving the Navier-Stokes equation. This way we can see how accurate the phenomenological model is. To further this work I will need to continue my study of aeroacoustics as well as theoretical and computational fluid dynamics.

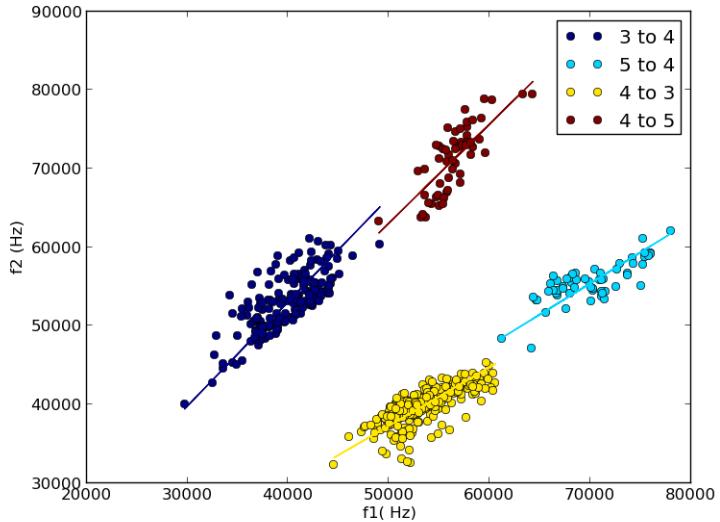


Figure 4: After jump frequency plotted against before jump frequency. The data is divided into four clusters and a linear regression is performed on each cluster. The slopes of the regression lines are  $m_{3 \rightarrow 4} = 1.33$ ,  $m_{4 \rightarrow 3} = 0.75$ ,  $m_{4 \rightarrow 5} = 1.26$ , and  $m_{5 \rightarrow 4} = 0.79$ . The modes that these slopes best correspond to are marked in the figure.

## Dynamical Systems, Neural Correlates, and Classification of Calls

One of the striking features of any neural network is a robust oscillatory signal can often be the output of the complex interactions of a large number of neurons. This can be observed in the forced Kuramoto model in which many different oscillators sync together and move at the same frequency [5]. That the signal is oscillatory is especially remarkable since the number of degrees of freedom of the network scales with the number of neurons. This is a result of dynamical synchronization of the neurons via coupling between them. In essence, a large number of random variables become enslaved to an underlying signal of the system. This greatly reduces the dimensionality of the system and allows the output (in our case the action of the phonatory muscles) to be described by a handful of parameters. This type of approach was taken in describing the oscillatory behavior of the vocal folds in bird syrinxes. In the model, the center of mass position of the vocal folds  $x$  is described by the equations

$$\begin{aligned}\dot{x} &= y \\ \dot{y} &= -kx - cx^2y + by - f_0.\end{aligned}$$

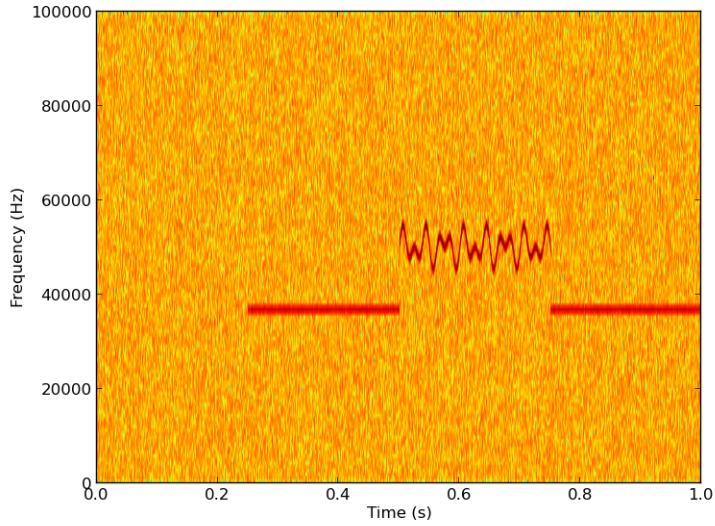


Figure 5: Spectrogram generated using far field equation for hole tone that has some of the qualitative features of rat calls. Biologically realistic parameters were used.

Here  $k$  describes the elasticity of the vocal folds and is a function of activity of the syringeal ventralis muscle. The parameter  $b$  describes the subsyrengeal pressure coming from the lungs and is determined by the chest and air sac muscles. The parameter  $f_0$  describes the adduction and abduction of the vocal folds and is a function of the activity of the m. syringeal dorsalis and tracheobronchialis ventralis muscles. The parameter  $c$  is a term kept constant that describes the nonlinear dissipation of energy when the vocal folds collide. To simulate a call the parameter  $k$ ,  $b$ , and  $f_0$  are varied throughout its time course (see Figure 6). Initially, the cycle begins with a breath. The pressure  $b$  is slightly negative, and the vocal folds are relaxed ( $k$  and  $f_0$  are zero). The parameters are then varied. As  $b$  is built up to positive values  $f_0$  is increased to at least  $k\sqrt{\frac{b}{c}}$  to prevent phonation. When  $b$  is built up to a certain value,  $f_0$  is decreased to zero. This creates a limit cycle in a Hopf bifurcation. The vocal folds then behave as a relaxation oscillator with frequency determined by the evolution of  $k$ . Pulses of pressure enter the vocal tract when the folds are apart. The frequency components of the sound produced are thus equal to the frequency components of the oscillation. To end the vocalization the parameter  $f_0$  is increased for a short time, destroying the limit cycle. The vocal folds remain adducted until the subsyrengeal pressure becomes negative again to allow for the next mini breath. Using this method, calls can be produced that accurately resemble those of birds. Thus, the output of the complex phonatory nervous system of birds can be accurately described by three parameters [7].

Developing a model for the rat phonatory system would benefit from this perspective. This can be compared to the high dimensional description obtained by computationally solving the Navier-Stokes

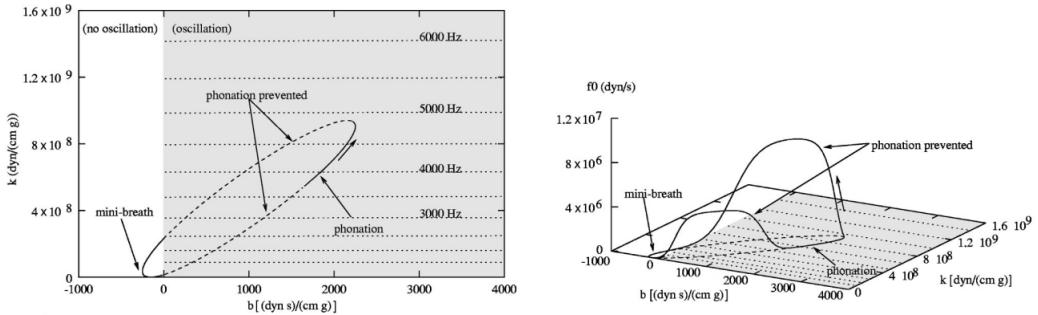


Figure 6: (Left) Time course of the parameters  $k$  and  $b$ . When the line is dotted  $f_0$  is positive, preventing phonation. When the line is solid  $f_0 = 0$ , allowing oscillations. (Right) Same diagram except with  $f_0$  shown on the third axis.

equation, but it will be more elucidating of the structure and function of the phonatory organs and nervous system to have a parsimonious parameter description. It is likely the parameters describe the time course of a rat call are similar to the ones for birds. It has been observed experimentally that subglottal pressure influences call frequency. Although Sanders observed that vocal folds do not move throughout a call, this was done in anesthetized rats, and he did not give details about the calls that were produced. It is possible rats adjust the diameter of the vocal fold aperture throughout a call to modulate the frequency. It is also possible rats adjust the length of the vocal tract by using different structures for the anterior aperture or by changing the position of these structures. This is another possible parameter and could be the cause of observed frequency jumps. Furthermore, it may be beneficial to consider a model that uses a point of a dynamic criticality similar to that of the bird syrinx. This could be desirable as a point of dynamic criticality can reflect a transition between regions of qualitatively different behavior. For example, in the bird model a Hopf bifurcation describes the transition from stationary to oscillating behavior. Furthermore, this type of analysis can aid in the classification of calls based on intrinsic parameters of the phonatory system. In Figure 6, the intrinsic parameters of the bird phonatory system determine the geometric properties of the calls in parameter space. A classification scheme could be proposed based on the intrinsic or geometric parameters.

Some work has been done in describing the oscillatory nature of the pressure pattern in birds. If  $x$  is the subsyrengeal pressure, its dynamics can be accurately described by the two dimensional dynamical system

$$\begin{aligned}\dot{x} &= y \\ \dot{y} &= \alpha(t) + \beta(t)x + x^2 + -xy + -x^3 - x^2y.\end{aligned}$$

By varying the parameter  $\alpha$  and  $\beta$  throughout the time course of a pressure signal, measured pressure patterns in birds can be approximately reproduced. In Figure 7, a limit cycle is created then destroyed as the parameters are varied in and out of the region demarcated by the dotted lines. This reflects

that the pressure signal can transition between oscillatory and monotonic behavior throughout its time course. That this low dimensional description can account for the average activity of thousands of neurons indicates the degrees of freedom of the upstream neural nuclei are collapsed down into a low dimensional output. This process is of interest because understanding this can help researchers understand how these nuclei perform there functions. The pressure pathway in the bird phonatory system consists of the HVC, which projects to the robust nucleus of archistriatum (RA), which then projects to the motor nuclei. The neurons of the HVC and the RA can be modeled as a set of coupled nonlinear oscillators with the Kuramoto model

$$\dot{\theta}_i^\sigma = \omega_i^\sigma - \gamma_i^\sigma \sin(\theta_i^\sigma) + \sum_{\sigma'=1}^2 \frac{K_{\sigma\sigma'}}{N^{\sigma'}} \sum_{j=1}^{N^{\sigma'}} \sin(\theta_j^{\sigma'} - \theta_i^\sigma).$$

In the model,  $\sigma = 1$  refers to HVC population and  $\sigma = 2$  refers to the RA population, and the subscript  $i$  refers to neuron number within the population.  $N$  is the total number of neurons within a population. The phase of a neuron is denoted by  $\theta$ , its natural frequency by  $\omega$ , and the strength of the nonlinearity by  $\gamma$ . The coupling between neurons within and in between groups is denoted by  $K$ , with  $K_{21} = 0$  to indicate RA does not project to HVC. Under certain conditions, the oscillators of this system will synchronize with each other. The system will then be restricted to a submanifold and will exhibit low dimensional dynamics. The bifurcation diagram of the restricted system is shown in Figure 8 (left). Remarkably, the bifurcation diagrams in Figures 7 and 8 are the same (i.e. they are both described by Bogdanov-Takens normal forms). That these bifurcation diagrams are the same indicates the observed pressure patterns can be explained by synchrony of neurons in the upstream nuclei. The vocal pattern generating and respiratory modulation pathways in mammals have been proposed to have the wiring diagram in Figure 8 (right). Pressure patterns in rats exhibit similar transitions from oscillatory to monotonic behavior and could be explained by a similar synchrony model by considering the periaqueductal gray and nucleus retroambigus as the neuronal populations [5, 1].

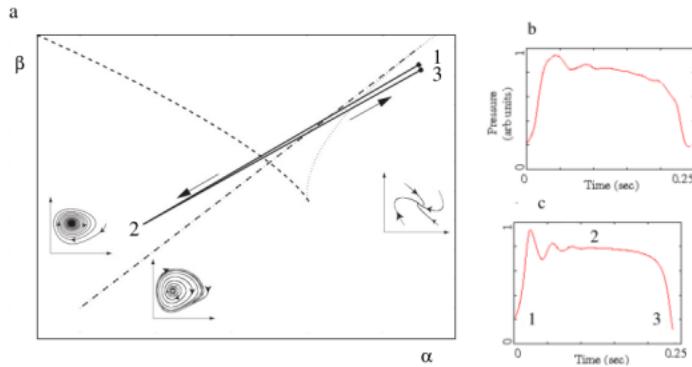


Figure 7: (a) Bifurcation pattern given by dynamical system governing pressure behavior. (b) Measured pressure pattern in bird. (c) Theoretical pressure pattern that approximates measured pressure pattern.

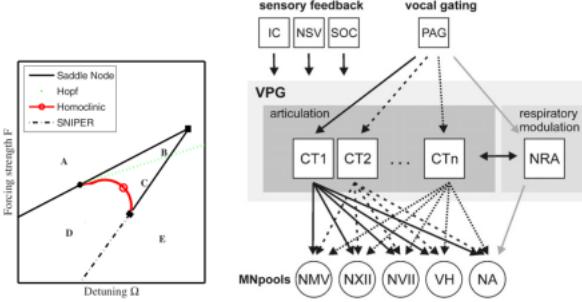


Figure 8: (Left) Bifurcation given Kuramoto model. (Right) Proposed diagram for phonatory neural circuitry. IC: inferior colliculus; NSV: sensory trigeminal nucleus; SOC: superior olfactory complex; PAG: periaqueductal gray; VPG: vocal pattern generator; CT1 CT2 CTn: call type 1 2 n; NRA: nucleus retroambiguus; NMV: motor trigeminal nucleus; NVII: facial nucleus; NXII: hypoglossal nucleus; VH: ventral horn of the spinal cord; NA: nucleus ambiguus;

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