REVIEW

Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production

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Recent work on human vocal production demonstrates that certain irregular phenomena seen in human pathological voices and baby crying result from nonlinearities in the vocal production system. Equivalent phenomena are quite common in nonhuman mammal vocal repertoires. In particular, bifurcations and chaos are ubiquitous aspects of the normal adult repertoire in many primate species. Here we argue that these phenomena result from properties inherent in the peripheral production mechanism, which allows individuals to generate highly complex and unpredictable vocalizations without requiring equivalently complex neural control mechanisms. We provide examples from the vocal repertoire of rhesus macaques, *Macaca mulatta*, and other species illustrating the different classes of nonlinear phenomena, and review the concepts from nonlinear dynamics that explicate these calls. Finally, we discuss the evolutionary significance of nonlinear vocal phenomena. We suggest that nonlinear phenomena may subserve individual recognition and the estimation of size or fluctuating asymmetry from vocalizations. Furthermore, neurally 'cheap' unpredictability may serve the valuable adaptive function of making chaotic calls difficult to predict and ignore. While noting that nonlinear phenomena are in some cases probably nonadaptive by-products of the physics of the sound-generating mechanism, we suggest that these functional hypotheses provide at least a partial explanation for the ubiquity of nonlinear calls in nonhuman vocal repertoires.

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Biological phenomena are noted for their complexity, and animal acoustic behaviour is no exception. Field biologists who have recorded large collections of animal vocalizations, faced with the task of cataloguing and categorizing thousands of exemplars from a species' vocal repertoire, often find themselves drowning in a sea of variability. With no clear dividing lines between call types or the contexts in which calls typically occur, simplifying assumptions must be made. A typical approach is to focus on 'normal' call exemplars that cluster together (subjectively or statistically), disregarding irregular variants that seem to combine elements of two different calls or contexts, or are otherwise difficult to quantify and analyse. The validity of this approach for a

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particular species depends on the proportion of calls thus excluded, and the degree to which such calls play a role in listener perception and hence in social communication. However, it is clear that such a strategy inevitably risks oversimplification.

An alternative approach to understanding complex vocal repertoires takes as its starting point the physics and physiology of the vocal production mechanism itself. From this perspective, the acoustic signal is the result of an interaction between nervous control signals and the mammalian vocal system (respiratory system, larynx and vocal tract), a system in which both physical and physiological constraints play important roles. Significant progress in understanding animal vocal production in the last decade now makes it possible to explore some of the phylogenetic and functional consequences of such constraints, and to develop explicit, testable hypotheses about the role of vocal production mechanisms in structuring animal vocal repertoires. In this paper we will
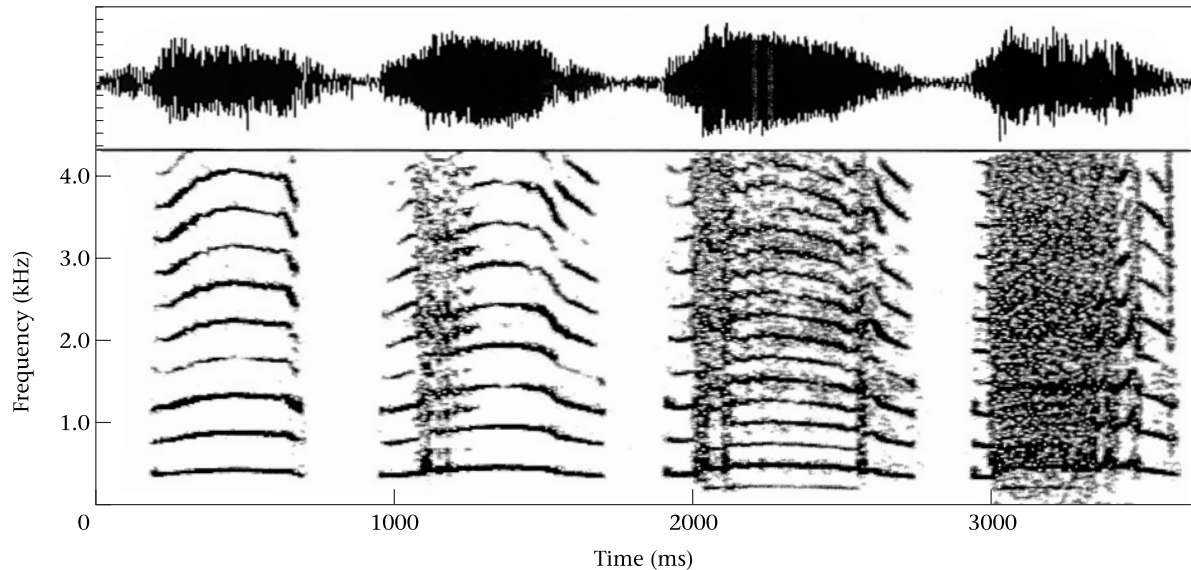
Figure 1. Spectrogram of a series of four consecutive calls by a normal adult rhesus macaque male. The first call is a prototypical 'coo' call, while each of the subsequent calls shows intrusions of nonlinear phenomena including additional spectral bands or 'subharmonics' (calls 2 and 3) and deterministic chaos (final call).

pursue such an approach, exploring the role of the production mechanism in the generation of complex calls, and complex vocal repertoires.

One of the central insights in both physics and theoretical biology in the last decades is that simple mathematical systems can exhibit very complex behaviour if they include nonlinearities. For example, even very simple deterministic equations describing population ecology or the evolution of disease resistance can lead to extremely complex dynamics (May 1974, 1976). Because many of the basic phenomena of physics and physiology are basically nonlinear (meaning that the equations that govern them include squared, cubed or higher-order terms), this insight has played a critical role in physiology (e.g. Mackey & Glass 1977; Glass & Mackey 1988) as well as basic physics (e.g. Lorenz 1963), leading to the development of a powerful suite of conceptual and mathematical tools for analysing such nonlinear systems. However, despite the essential nonlinearity of vocal production mechanisms in animals, there has been little exploration of nonlinear dynamics, or application of these new analytic tools, in the domains of ethology and bioacoustics.

In the current paper we argue that much of the complexity evident in animal vocal repertoires results from nonlinearities in the production system, meaning that rather simple neural commands to the vocal tract can lead to highly complex and individually variable acoustic output. Such nonlinear phenomena have typically been ignored in traditional ethological analyses, due to the lack of an adequate conceptual framework and appropriate analysis tools. However, our data suggest that such phenomena are not rare in nonhuman vocal repertoires, but play a crucial communicative role, in fact forming the bulk of the acoustic output from certain individuals and certain age classes. As an example, we explore the vocal

repertoire of the rhesus macaque, *Macaca mulatta*, showing that even for this intensively studied primate (e.g. Rowell & Hinde 1962; Gouzoules et al. 1984; Hauser 1991, 1993a; Owren et al. 1992; Hauser et al. 1993; Rendall et al. 1996; Fitch 1997), nonlinear phenomena are common but typically ignored (see Hauser 1992 for an exception). We will show how a variety of harsh-sounding, irregular or rapidly changing calls result from nonlinearities in the vocal production apparatus, and provide examples of different classes of nonlinear phenomena from the macaque vocal repertoire. However, our conclusions are by no means limited to macaques or even primates, but probably apply to a wide variety of mammals and birds (see Fee et al. 1998 for consideration of nonlinear phenomena in songbird vocalization). Finally, we will explore some of the functional implications of these findings, arguing that the possibility of nonlinear phenomena has both constrained the evolution of vocal repertoires, and provided adaptive opportunities that have been exploited by many species. Thus, we conclude that an understanding of nonlinear phenomena in vocal production can provide important insights for scientists interested in the evolution of vocal communication.

NONLINEAR PHENOMENA IN VOCAL PRODUCTION

Figure 1 is a spectrogram of four consecutive calls produced in rapid succession by a single normal adult rhesus macaque, recorded under field conditions by Marc Hauser in Cayo Santiago, Puerto Rico. The first call is a prototypical example of a 'coo' (Hauser 1991; Hauser et al. 1993), also termed a 'clear call' (Rowell & Hinde 1962). Perceptually, the next three calls also sound like coos, but each sounds increasingly rough, harsh and

irregular (the behavioural context was one of increasing arousal while approaching food). Acoustically, however, the subsequent calls appear increasingly unlike a prototypical coo. While the brief burst of what looks like broadband noise in the second call might be disregarded, the extra harmonics that appear in the third call occupy the bulk of the vocalization and can hardly be ignored. The last call has a wide region of broadband energy throughout most of the call, although its on- and offset still clearly resemble the first coo in the series. While this 'noisy' region superficially resembles turbulent noise, a closer examination reveals considerable remaining spectral structure, including some traces of harmonics, that would not be present in true 'white noise' (which has equal energy at all frequencies). This call series thus presents us with a continuum from prototypical 'coo' to something that would be quite difficult to classify using standard terminology for macaques, but seems spectrographically (although not perceptually) closer to a scream. A field ethologist attempting to classify these calls is faced with a quandary: based on the identical context, it is tempting to call all four coos, but based on the qualitative differences visible in the spectrogram, a different call category seems warranted for each call. Perhaps we should label them 'clear coo', 'noisy coo', 'extraharmonics coo' and 'coo scream'? Unfortunately the latter approach would lead to a rapid explosion in the number of call categories.

Perhaps because such questions are quite difficult to resolve, irregular vocal phenomena such as those illustrated in Fig. 1 have typically, and understandably, been ignored (Rowell & Hinde 1962; Gouzoules et al. 1984; Hauser 1991; Rendall et al. 1996). However, they are not particularly rare, and in some call categories (e.g. screams) they appear to be quite common. One crucial feature that seems to unite such irregular calls is rapid qualitative acoustic transitions, either within a single call or between calls in a bout. The nature of these transitions can vary, but the most common types are both seen in Fig. 1. The first type, seen in the third call, is the sudden appearance of a second set of harmonics, which corresponds to an abrupt halving of fundamental frequency or 'pitch'. The second type, seen in the fourth call, is an abrupt transition to an extremely broadband 'noisy' spectrum, which none the less has some spectral structure and is quite different both acoustically and perceptually from turbulent noise. For reasons that will become clear in the next section, we will adopt the term 'nonlinear phenomena' to refer to such abrupt transitions, and to vocalizations containing such transitions.

Equivalent nonlinear phenomena can be observed in the human voice, particularly in infant cries (Truby & Lind 1965; Sirviö & Michelsson 1976; Robb & Saxman 1988), and attempting to understand them has been an active and fertile area of speech research in the last decade. The resulting advances in understanding the physics of phonation have provided a compelling and now widely accepted explanation for such phenomena in the human voice (Herzel et al. 1994, 1995). Abrupt transitions between qualitatively different acoustic regimes result from nonlinearities intrinsic to the voice production apparatus itself (Mende et al. 1990). Normally, adult humans tend to avoid these irregular phonatory regimes, and nonlinear phenomena are typical only of infants or adult patients with voice disorders (e.g. vocal fold paralysis, asymmetries or growths). Thus, for understanding normal speech or singing in adult humans, nonlinear phenomena are of peripheral importance outside of the clinical and infant literature.

A central point of the current paper is that this is not the case in nonhuman mammals. Many mammalian vocalizations show nonlinear phenomena, and they appear to play a central role in the repertoire of at least some species. Indeed for certain individuals in subordinate social contexts, or at certain periods of life, nonlinear vocalizations may be the dominant component of an individual's vocal output. To quantify this, we provide some statistics on the vocal output of rhesus macaques from the island of Cayo Santiago, one of the best-studied macaque populations. However, we stress that nonlinear phenomena are by no means limited to macaques (other examples include chacma baboons, *Papio cyncephalus ursinus*: Fischer et al. 1999; African hunting dogs, *Lycaon pictus*: Wilden et al. 1998; zebra finches, *Taeniopygia guttata*: Fee at al. 1998).

We examined spectrograms of 467 calls from 45 rhesus macaques, recorded by the first author on Cayo Santiago, Puerto Rico in July 1996 (Tascam DA-P1 DAT recorder with Sennheiser MKH-60 P48 microphone, sampled at 48 kHz, 16-bit quantization using Audiomedia III software; spectrogram window size 256–1024 points). These recording were made during focal animal follows of individuals belonging to each sex and age class, for purposes of surveying the macaque repertoire, and were not preselected for (or against) nonlinear phenomena. All calls with a sufficient signal-to-noise ratio to distinguish harmonics above background noise, or for nontonal calls, pulses above noise, were included in the analysis. Thus we consider this sample to be fairly representative of this macaque population at this time of year. We recorded the number of calls possessing nonlinear phenomena including abrupt transitions and nonlinear phonatory regimes (see below), along with the identity of the individual calling, its sex and approximate age, and the basic call category (following Rowell & Hinde 1962; Hauser 1991, 1992; Hauser et al. 1993).

We found that a significant proportion of calls posessed strong nonlinearities; overall they composed 30% of the average individual's sample. However, nonlinearities were much more typical of subadult animals (59 of 149 total, or 40%) and females (161 of 269 calls, 60%) and were quite rare in adult males (only 4 of 49 calls). Even among females, the proportion varied from 0 to 100%. Most of the nonlinearities were seen in calls that would traditionally be classified as screams (91%), and the bulk of the remainder were observed in coo vocalizations, with a number of the calls being unclassifiable by the available published descriptions (e.g. 'grunt/screams'). Clear nonlinearities were also occasionally observed in copulation calls, which are produced only by adult males (Hauser 1993a). The high proportion of screams suggests that nonlinearities should be more typical of subordinate

individuals (who are attacked and thus scream often) than of dominants, but we have no quantitative data on dominance rank for this sample.

Thus, nonlinear phenomena were neither rare nor peripheral in this sample, but appear to represent a normal feature of young macaque vocalizations, of screams in all age classes, and of copulation calls (produced only by adult males). Differing phonation qualities could be observed in many distinct call types. These data indicate that nonlinearities are not atypical or abberant, but form a core portion of the rhesus repertoire. We now turn to the explanation of such phenomena in terms of the physics and physiology of mammalian vocal production.

How the Peripheral Production Mechanism Generates Nonlinear Phenomena

The world is full of oscillators: a child on a swing, a leaf in the breeze, a singer's vibrating vocal folds, or the beating of a heart. All these systems have in common the ability to sustain periodic behaviour: they exhibit self-sustained oscillations. All are also nonlinear, meaning (in the simplest case) that there is some limit on the extent of their motion. As every child discovers, if you push the swing above the horizontal, the chain buckles, and there is an abrupt discontinuity in its motion. Another type of nonlinearity is seen in the vocal folds during a crescendo, as the singer steadily increases the subglottal pressure that drives their vibration. Initially, in falsetto mode, the extent of vocal fold oscillation is closely proportional to the square root of the driving force; this is understandable from the viewpoint of linear systems theory. However, as subglottal pressure increases, the oscillation of the vocal folds reaches a natural limit imposed by the tissue properties and the absolute size of the larynx that encloses them. Any further increase in driving force will be ineffectual at increasing the singer's volume, because the vocal fold vibrations have already reached their maximum amplitude. This is due to a 'saturating nonlinearity' of a sort that typifies most real physical oscillators.

There are many other types of nonlinearities as well, so many that dividing the world into linear and nonlinear systems is akin to a taxonomic distinction between elephantine and nonelephantine mammals. However, it is often conceptually and practically useful to idealize nonlinear systems, treating them as approximately linear. This makes the mathematics simple, and often provides a reasonable approximation within some circumscribed range. Thus, one can approximately describe the motion of the swing using linear theory (as long as the child does not push too hard) or the singer's vocal folds (as long as she stays in falsetto mode between *piano* and *forte*). Thus, linear systems theory is the staple of beginning physics and engineering courses, and in some cases all that even a practicing professional in these fields requires. But in cases where systems are driven to their limits, or where multiple oscillators interact, linear approximations are no longer adequate. This is the purview of non-linear dynamics. (There is a parallel here with parametric and nonparametric statistics: the mathematical and practical properties of parametric statistics make them attractive, even in cases where the data are not precisely normal. But when the data clearly violate the assumptions of the normal distribution, nonparametric statistics become necessary.)

The branch of nonlinear dynamics most relevant in the current context concerns two or more oscillators whose motion is coupled together in some way. Picture a branch bearing several leaves, swaying in the breeze. There are several ways in which the motions of an individual leaf might influence the others. The highest leaf, exposed to the wind, might set the branch swaying and thereby induce motion in the others. Similarly, two neighbouring leaves might collide periodically, and thus entrain with one another to vibrate at the same frequency. The fascinating thing about such systems, even simple ones with just two coupled oscillators, is that they can generate highly complex patterns of motion. These complex vibratory patterns are of various qualitatively different sorts, and their variety dwarfs that observable in the same two oscillators when they are not coupled. This fundamental observation, of very complex behaviour from two coupled oscillators, is applicable to asteroids in space, pendulums mounted on a wall, or the coupled systems of heartbeat and breathing (to choose three well-studied examples). It is also applicable to the vocal apparatus, for instance to the right and left vocal folds. Let us examine the variety of behaviour that two coupled oscillators can produce, focusing on the vocal folds.

Limit cycles

In the simplest case, mechanical and aerodynamic coupling between the vocal folds will synchronize their vibrations, leading to periodic, regular oscillations. This is the case in a sustained vowel in human speech, or for a normal 'coo' call in macaques (first call in Fig. 1). Such periodic, self-sustained oscillations are technically termed a 'stable limit cycle'. A revealing way to examine such oscillations of a system is called a 'phase portrait', where the behaviour of the system is mapped out into 'phase space'. Such a representation is shown in Fig. 2, along with the equivalent and more familiar representations in the time and frequency domains. The first column illustrates a stable, periodic limit cycle, which forms a closed orbit in phase space. The system is stable because any small perturbations of the system (due to rapid fluctuations in air flow, bits of mucus, etc.) are damped out: the system tends to stay in its orbit. The limit cycle represents the most common vibratory regime for the human voice (normal speaking and singing). It represents the prototypical voiced sound (its spectrum is a fundamental frequency, with harmonics that are integer multiples of that frequency), and is in fact the only phonation regime that was considered in speech science until the 1990s. It is important to recognize that even in the case of a stable limit cycle, with regular, steady vibration, vocal fold behaviour is still nonlinear (harmonics would not otherwise be present). However, the techniques of nonlinear dynamics do not become truly indispensible until we consider more complex vibration regimes, such as subharmonics and deterministic chaos.
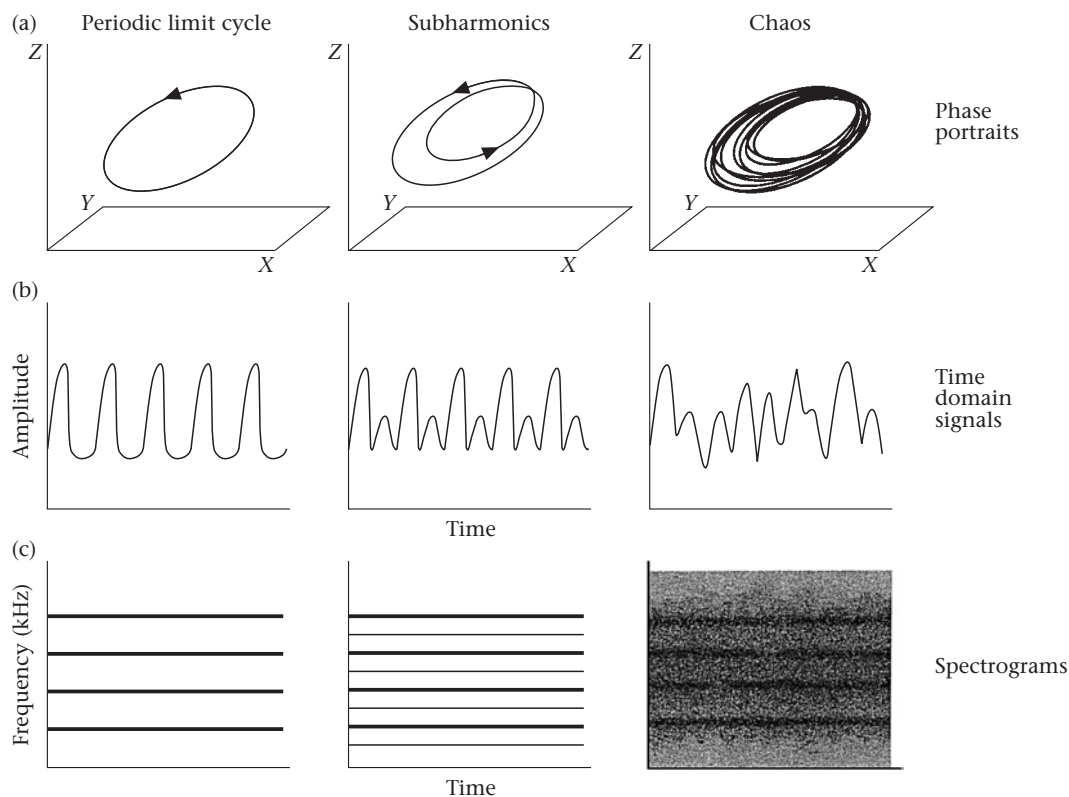
Figure 2. Nonlinear phenomena viewed in three different but equivalent ways (schematic). (a) Phase portrait; (b) time signal; (c) frequency representation. Columns from right to left: limit cycle (regular periodicity), subharmonics due to period doubling, and deterministic chaos.

Subharmonics

Sometimes, the natural vibratory frequencies of the two oscillators are quite different, for instance, if there is more tension on one vocal fold than the other. In such cases, coupling between the oscillators can still lead to synchronization or entrainment of their movements, but at different frequencies. So, for instance, one fold could go through two periods in the time it takes for the other to complete just one period. This would be termed 1:2 entrainment, since one oscillator has twice the period (half the frequency) of the other. From the viewpoint of the whole system, it now takes twice as long to repeat a cycle as it did before, and thus we observe a 'period doubling' in the time domain (or equivalently, a 'frequency halving'). In the spectral domain, this leads to the appearance of a new stack of spectral components interspersed between the previous ones; these components are termed 'subharmonics'. It is critical to realize that this phenomenon is not simply the superposition of two independent oscillators that would have this 1:2 relationship anyway: the natural frequency of each oscillator considered on its own might be some distance from this 2:1 ratio. It is the coupling between the oscillators (e.g. the collision of the two vocal folds) that forces them to assume an integer ratio, which might be quite different from what either would 'prefer' on its own. Thus, the lowest subharmonic (which now looks like a new fundamental frequency, at half the earlier one) can be considerably lower than the natural frequency of either vocal fold.

In some cases, when the coupling between the oscillators is weak, the two oscillators can vibrate freely with independent frequencies. In general there is no reason that these frequencies should be related as integer multiples: if they are independent the two folds can vibrate at any arbitrary ratio of frequencies. Such a phenomenon, called 'biphonation', can be observed in pathological voices in humans (e.g. in vocal fold paralysis), or in some unusual cases in singing by healthy subjects (Tigges et al. 1997). Biphonation is also seen occasionally in the calls of normal nonhuman primates (see Fig. 3). In general, however, the coupling between the vocal folds is quite strong, making biphonation relatively rare.

Deterministic chaos

The most surprising finding in nonlinear dynamics was the discovery in the 1970s that desynchronized coupled oscillators can generate nonperiodic, irregular vibrations termed 'deterministic chaos' or simply 'chaos' (May 1976; Bergé et al. 1984; Glass & Mackey 1988). Such aperiodic vibrations are characterized by a broadband spectrum, with energy at many different frequencies. Perceptually, such acoustic phenomena seem harsh and 'noisy'. However, there are no truly random perturbations in the system, which is still entirely deterministic. Although deterministic chaos appears superficially similar to turbulent noise (which is close to true 'white' noise, having equal energy at all frequencies), it is mechanistically, and perceptually, quite distinct. One salient characteristic of
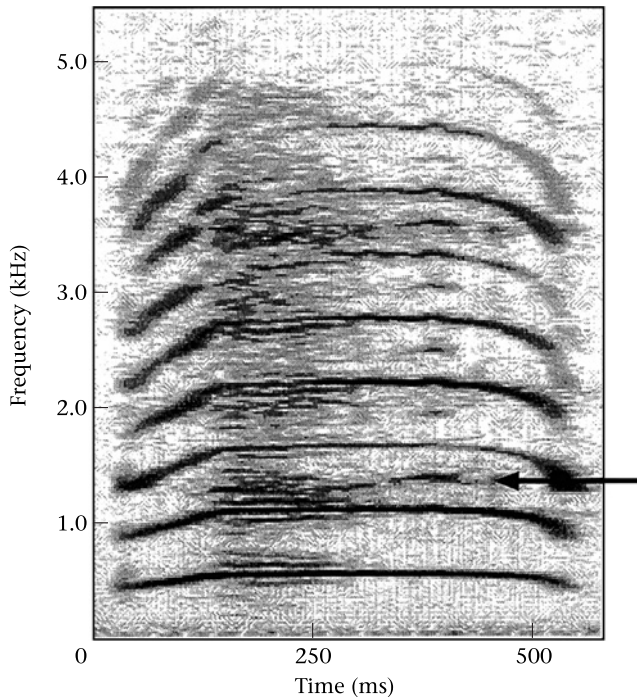
Figure 3. Biphonation in a rhesus macaque 'coo' call. The arrow indicates the second frequency component. Note the independence of the two frequency components, which is the defining feature of biphonation.

chaos is some residual periodic energy, which appears as banding in the spectrogram, and allows chaos to be readily distinguished from turbulent noise. One way of thinking about chaos is that it represents a superposition of many unstable limit cycles. The system erratically jumps from unstable orbit to orbit when in a chaotic vibratory regime.

Chaotic regimes exist, in principle, in any system of coupled nonlinear oscillators, although in practice they might be common or uncommon in any particular system. It was the recognition that broadband 'noisy' segments commonly seen in human infant cries represent deterministic chaos (Mende et al. 1990) that initiated the field of nonlinear voice research in humans. Herzel (1993) also documented the frequent occurrence of subharmonics and chaos in pathological adult voices (see Herzel et al. 1994 for a review). The construction of computer models of the vocal folds also made it possible to observe and quantify these phenomena in a system that was known to be deterministic and lack any random perturbations. Thus, the existence of chaotic vibratory regimes in the human voice is now well established. Because the physiology of the vocal folds and the basic physics underlying phonation are the same for other primates (and indeed for most mammals; see Mergell et al. 1999), these observations are also applicable to animal vocalizations. In particular, the class of calls often termed 'noisy screams' (e.g. Gouzoules et al. 1984 for rhesus macaques) bear the characteristic time and spectral domain signature of deterministic chaos. Winter (1968) termed such calls 'shrieks', and found that they occurred in 12 of the 15 nonhuman primate species whose

repertoires he reviewed from the literature. These observations suggest that the primate voice production apparatus can easily enter chaotic vibratory regimes.

Bifurcations

Thus far we have described the different types of vibratory behaviour that a system of two coupled oscillators can display, the three most prominent being limit cycles, subharmonics and chaos. Transitions between these qualitatively different vibratory regimes are termed 'bifurcations'. This term refers most obviously to the transition between a limit cycle and period doubling: such a 'period doubling bifurcation' leads to a 'splitting' of the periodic behaviour of the system (in phase space, the 'folding' of a limit cycle). However, the term is also used in a more general way, to refer to any transition between two regimes. Thus, for example, the transition from the rest state to a limit cycle is termed a 'Hopf bifurcation', which in the realm of the vocal folds corresponds to the onset of phonation. In general, once 1:1 synchronization is lost, a rich variety of transitions become possible, which depend sensitively on the details of the system. There is a relatively elaborate and complete taxonomy of the various types of bifurcations, along with an accompanying terminology. We will not pursue this technical vocabulary further in this paper (see Glass & Mackey 1988 for an introduction). Here, the critical point is that slow, gradual changes in some control parameter of the dynamical system can lead to abrupt, qualitative changes in its vibratory behaviour.

The relevance of bifurcations to primate vocal behaviour is schematically illustrated in Fig. 4. In Fig. 4a, the slow, gradual variation of some control parameter in the vocal system is illustrated. Plausible examples include vocal fold tension or subglottal pressure. As some critical threshold value for this parameter is exceeded, the system will experience a transition between qualitatively different acoustic behaviours. Exceeding the first threshold θ_1 leads to a period-doubling bifurcation, and hence the appearance of subharmonics in the acoustic signal. When the control parameter passes threshold θ_2, a transition to deterministic chaos occurs, leading to the appearance of a characteristic broadband spectrum. When the control parameter falls back below either threshold, the system returns to the previous vibratory regime, leading to characteristic episodes of a qualitatively different acoustic character in a single call. Such episodes, visible in spectrograms of vocalizations in many different mammals, can now be understood at the level of the physical sound production mechanism. Any physical system containing two (or more) coupled nonlinear oscillators can experience bifurcations between different vibratory regimes, and for a sound-generating system, spectrally disparate episodes such as those illustrated in Fig. 4 are the result.

It is worth considering in a bit more detail precisely what the coupled oscillators in the mammalian vocal production apparatus are. In this section we have used the two vocal folds as an example, both because it is conceptually simple and because a considerable body of research on the human voice indicates that all of the different vibratory regimes described above can occur for
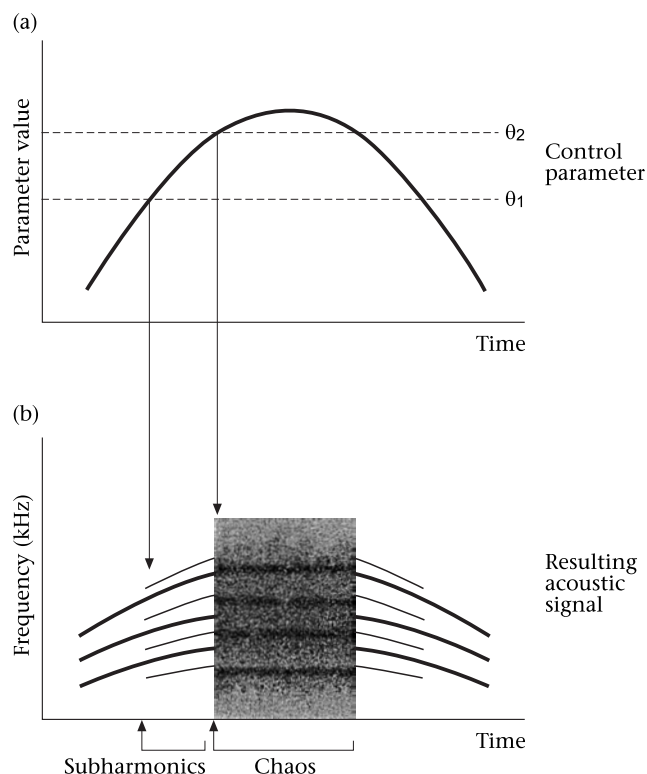
(a)

(b)

Figure 4. How simple continuous changes in a control parameter lead to complex calls in a nonlinear system: (a) Schematic view of a vocal control parameter such as subglottal pressure, or vocal fold tension; θ_1 represents the threshold to period doubling and subharmonics, θ_2 represents the threshold for chaos. (b) Schematic of the resultant acoustic signal in spectrographic form.

the simple system of two vocal folds. For instance, the two folds can be synchronized 1:1 in a stable limit cycle ('normal' phonation), they can vibrate independently at arbitrary unrelated frequencies ('biphonation': Berry et al. 1996; Tigges et al. 1997), they can entrain at ratios other than 1:1 ('subharmonics': Mende et al. 1990; Herzel et al. 1994) and they can exhibit deterministic chaos (Herzel & Wendler 1991; Herzel et al. 1991, 1995). These vibratory regimes have been documented in vivo using acoustic analysis and high-speed video of phonating patients, in vitro with high-speed observations of excised larynges, and in silico via extensive computer modelling. These observations establish beyond reasonable doubt that the full range of nonlinear phenomena can be observed in a simple system of two vocal folds, such as that possessed by all mammals.

Besides the vocal folds there are other anatomical structures in nonhuman mammals that could serve as additional oscillators, thus enriching the range of possibilities for nonlinear phenomena in vocalizations. The two most prominent are air sacs and vocal membranes. Many mammals, including most nonhuman primates, possess laryngeal air sacs: enclosed volumes of air that open into the larynx, often directly above the glottis (Schneider 1964; Fitch & Hauser 1995; Schön-Ybarra 1995). In macaques and other cercopithecids, the air sac is enclosed in the expanded bulla of the hyoid bone, with

a narrow opening directly above the anterior portion of the glottis. In great apes, the air sacs are large, flexible walled structures that extend down into the chest, and are connected by thin tubes exiting in the ventricles (lateral to the glottis). An enclosed volume of air has both mass and elasticity, and thus can vibrate at a specific well-defined frequency. The simplest case of an aerodynamic oscillator is termed a Helmholtz resonator (a familiar example is the tone created by blowing across the mouth of a bottle). Modelling studies of humans indicate the possibility for an aerodynamic coupling between a vibrating air column and the vocal folds (Mergell & Herzel 1997), and such coupling could be strong when the outlet of the aerodynamic resonator is directly at the glottis, as is typically the case with air sacs. Thus, it seems possible that some of the nonlinear phenomena observed in nonhuman primate vocalizations result from coupling in this more complex system of oscillators. This prediction has yet to be put to an empirical test.

Another likely set of coupled oscillators are the vocal membranes (also termed 'vocal lips'), thin upward extensions of the vocal folds that are found in diverse mammals including most microchiropteran bats and many primates (Griffin 1958; Schön-Ybarra 1995). These thin, lightweight structures can vibrate at very high frequencies, and subserve the production of ultrasonic vocalization by bats (Griffin 1958). Because the vocal membranes are physically attached to the vocal folds, they are strongly coupled to them. Because they are small and light, they have very different natural frequencies. Both basic principles and modelling studies (Mergell et al. 1999) suggest that this is another possible source of nonlinear phenomena in the primate voice. Some other possible vibrators within the mammalian production system include the vocal tract, the arytenoid cartilages, the ventricular folds, and the epiglottis. With so many potential oscillators available, all of them potentially coupled by mechanical or aerodynamic forces, it is no surprise that mammals can produce a rich variety of nonlinear phenomena. Indeed, from this perspective the question becomes how they can avoid such phenomena. The relevance of nonlinear phenomena to the evolution of vocal repertoires is the topic of the next section.

Evolutionary Significance: Functional Interpretations of Nonlinear Vocal Phenomena

Thus far in this paper we have provided an overview of the types of nonlinear phenomena observable in vocalizations, and offered a physical explanation of such phenomena in terms of the system of coupled oscillators comprising the vocal production mechanism. In the remainder of the paper we consider some of the evolutionary implications of these phenomena, considered as a functional component of a species' vocal communication system.

As stressed above, any system of coupled nonlinear oscillators (and thus any vertebrate vocal apparatus) has the capacity to exhibit nonlinear phenomena. Once vertebrates began to use their paired vocal folds (which

originally functioned as protective gateways to the respiratory system; Negus 1949; Hast 1985) to produce sounds, the possibility of nonlinear phenomena was automatically present. Thus, despite the complexity of the acoustic output, we cannot assume that such phenomena represent adaptations sensu stricto (Williams 1966). Indeed, one can safely assume that at least some nonlinear vocal phenomena are nonadaptive epiphenomena. For instance, the subharmonics and chaos frequently observed in diseased human voices (Herzel & Wendler 1991) are unlikely to have been shaped by natural selection (although perceptual mechanisms underlying avoidance of such voices might have been).

The inevitability of nonlinear phenomena, given the physics of vertebrate vocal production mechanisms, thus provides the first useful insight from nonlinear dynamics for the evolution of communication. Complexity is ordinarily taken as a hallmark of adaptation (despite the persistent difficulty in precisely defining 'complexity'; see e.g. Dawkins 1987; McShea 1991). But in the realm of nonlinear dynamics and vocal production, some complexity is only apparent, resulting from an underlying system that is simple. This fact warrants caution in proposing adaptationist explanations of such complexity, although of course, natural selection may still have exploited such nonlinear phenomena with neural or anatomical mechanisms that stabilize particular vibratory regimes of the dynamical system. Thus, alongside the functional hypotheses outlined below is an ever-present null hypothesis: that nonlinear phenomena may be by-products of the vocal system that neither require nor deserve adaptive explanation.

1. Individual variation due to variability in the peripheral mechanism

There is abundant evidence that the acoustic variability in calls enables listeners to identify the individual calling both in primates and other mammals. However, the physical and physiological origins of this acoustic variability is in most cases unknown. Although there is some evidence that the call variants that allow individual recognition in macaques are under neural control (e.g. Hauser 1992), many workers have hypothesized that anatomical variability in the periphery could be the primary source of cues for individual recognition (e.g. Fitch & Hauser 1995; Rendall et al. 1996). While some acoustic cues (e.g. fundamental or formant frequencies) will vary along a continuum, and thus exhibit quantitative differences, the principles of nonlinear dynamics predict another possible source of individual variability that would lead to qualitative variation in the 'same' call.

We described above how continuous variation of a control parameter in a nonlinear system can lead to a bifurcation (transition to a qualitatively different behaviour of the system) at some critical value or threshold (Fig. 4). The precise numerical value of this critical point is influenced by a host of interacting factors, both anatomical and neural, that are likely to vary between individuals. Thus, a certain call may occupy a wholly stable oscillation regime for one individual, while the same call may traverse a transition point to an unstable or chaotic regime in another individual. In Fig. 5a, we show some typical examples of a 'coo' (Hauser 1992) or 'clear call' (Rowell & Hinde 1962), each one from a different individual. Coos typically occupy a stable oscillatory regime, leading to a highly tonal call made up of a fundamental and its harmonics. However, the coos of some individuals show one or more bifurcations during the course of a call, as is shown in Fig. 5b, where three different coos from a single macaque female are shown. These calls differ qualitatively from other macaque coos, and would clearly provide a robust cue for individual recognition of this particular female.

Thus we propose that individual differences in anatomy or neural control, combined with nonlinearities in the vocal production mechanism, can lead to marked differences in call morphology between individuals. These differences might exist despite the fact that these calls are the 'same' from the viewpoint of the underlying neural control signals. While such differences are not necessarily adaptations in and of themselves, they may serve the adaptive purpose of allowing individuals to recognize one another more easily (e.g. subserving mother–infant recognition).

2. Fluctuating asymmetry in the voice

The vocal folds are paired bilaterally symmetrical structures. As long as the two folds have similar tuning frequencies (determined by their individual mass and tension), they will typically be 1:1 entrained and enter a stable, periodic limit cycle: this is normal phonation. One way of inducing nonlinear phenomena in vocal output is to desynchronize their natural frequencies, which should lead to subharmonics, or in some cases chaos. This in fact occurs in patients with unilateral vocal fold paralysis (Tigges et al. 1997), where the tension on one fold is normal and the other fold is flaccid. Models of the vocal folds show that such asymmetries provide reliable routes into subharmonics and chaos (Steinecke & Herzel 1995).

Two asymmetrical vocal folds, with unequal masses or lengths, would also induce such nonlinear phenomena. It is well known that the human larynx is typically asymmetric, often grossly so (e.g. Hirano et al. 1989). Although such asymmetries can probably be compensated for to some degree (Ludlow et al. 1997), it is clear that they also may increase the probability of nonlinear phenomena in the voice. Indeed, such asymmetries provide a plausible source of individual differences between animals that could generate clearly perceptible differences in the acoustic signal. This suggests that, in addition to the visual sources of information about symmetry, there are acoustic ones as well (Simmons & Ritchie 1996). Given the theoretical importance of fluctuating asymmetry as a potential indicator of developmental stability (see Møller & Swaddle 1997), and therefore of symmetry detection in animal mate choice (e.g. Møller 1992; Swaddle 1996; Thornhill & Gangestad 1999), the induction of nonlinear effects by anatomical asymmetry in vocal folds (or syringeal membranes in birds) is an important area for future research. The prediction here is clear: asymmetrical voices (those that have a high proportion of subharmonics, biphonation or chaos relative to normal
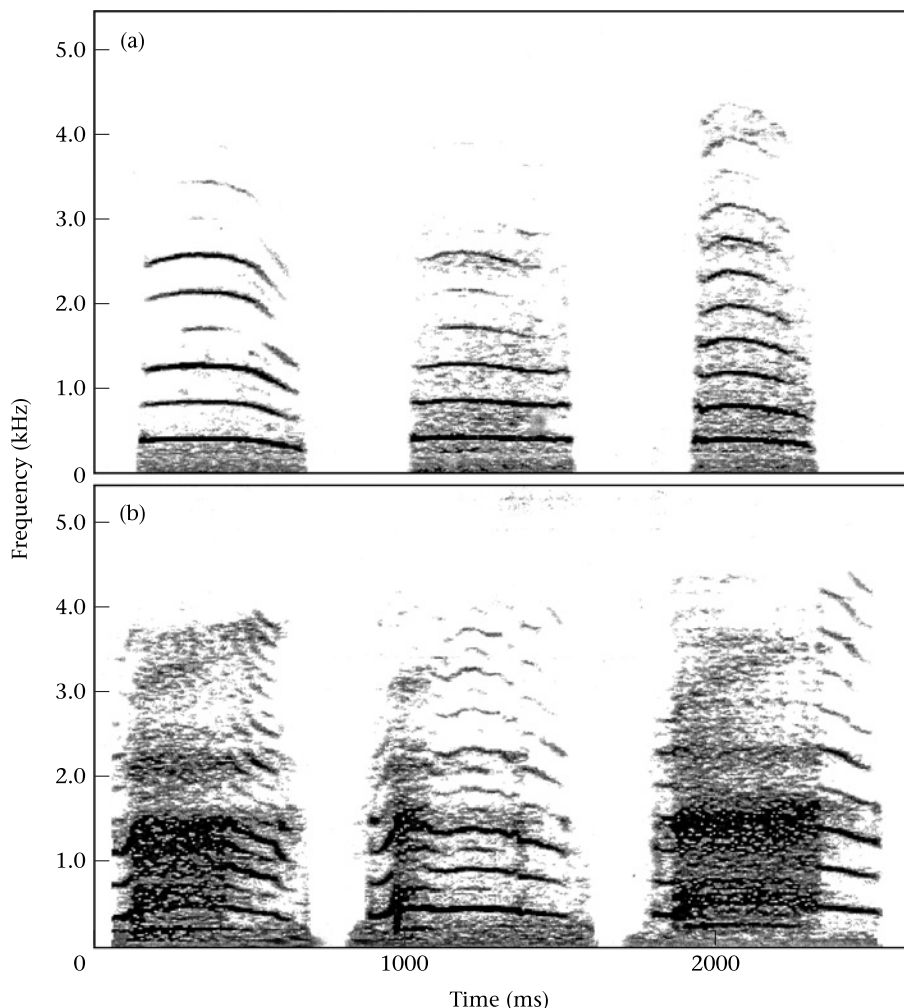
Figure 5. Nonlinear phenomena give individual variability in rhesus macaque coo calls. (a) Spectrograms of three 'normal' coos from three different individuals. (b) Three coos with nonlinear phenomena from a single female.

phonation) should be judged as unattractive by potential mates. This hypothesis does not assume selection on the producer's vocal fold symmetry (or nonlinear acoustic output), but rather selection on perceivers to notice and avoid the producers of such output. We now turn to some hypotheses for why nonlinear phenomena themselves may have been adaptive.

3. Broadband calls for outlining the vocal tract transfer function

Recent studies have shown that body size is closely correlated with the length of the vocal tract in several mammalian species (Fitch 1997; Fitch & Giedd 1999; Riede & Fitch 1999). The vocal tract is the tube of air comprising the throat, mouth and nasal passages through which sound generated in the larynx must pass on its way to the environment. Resonances of the vocal tract, termed 'formants', act as filters, shaping the spectrum of whatever sound is emitted from the laryngeal source. Because the frequencies of formants are tied to vocal tract length, low formants provide an 'honest' indication of large body size in all the mammals investigated to date. Given a proper source signal, with adequate broadband

energy, formants are highly perceptible by animals (Sommers et al. 1992; Fitch & Kelley 2000), and provide the primary phonetic cue in human speech (Lieberman & Blumstein 1988). Thus it has been suggested that formants may play an important role in size estimation or individual recognition (Fitch & Hauser 1995; Rendall et al. 1996; Fitch 1997). An animal attempting to enhance the projection of its formant frequencies should produce a loud, wideband spectrum (this provides a broad palette of frequencies and thus makes the filtering function of the formants obvious). One way to accomplish this is 'hissing': vertebrates can produce turbulent noise by making a constriction at the glottis. This sound is suitably broadband, but has low acoustic energy (in fact, this is what we call 'whispering' in speech; Tartter & Braun 1994). A better way is to induce irregular chaotic vocal fold vibrations, which produce a very broadband spectrum but can be extremely loud (as in screaming). Such a harsh-sounding signal would be an ideal way to accentuate formant information and project it over a significant distance, and could provide an adaptive function for chaos. For example, a dominant animal able to project its low formant frequencies (and thus large size) at a distant

rival could do so most effectively with an irregular chaotic 'roar'.

4. Subharmonics as a perceptual pitch-lowering device

Low-pitched voices (technically, calls with low fundamental frequency) are often deemed to sound impressive in our own species. This perceptual correlation was hypothesized by Morton (1977) to result from an inverse correlation between body size and pitch in animal voices. However, the data supporting this correlation are few: body size and pitch are related in some anurans (Davies & Halliday 1978) but not in others (see Wagner 1992). In humans, there is no correlation between adult body size and voice pitch, within a sex (Lass & Brown 1978; Cohen et al. 1980; Künzel 1989; van Dommellen 1993). None the less, perceivers still appear to respond to low-pitched voices as if they signal large size, or at least dominance or aggressiveness. The existence of subharmonics would provide a means of lowering apparent voice pitch, dropping it by an octave in the case of period doubling, without actually having an oscillator large enough to independently support such a low-frequency vibration. This would allow a small animal producing subharmonics to mimic the fundamental frequency of a larger animal phonating normally. Currently, there is not enough data on nonlinear phenomena in animal voices to evaluate this possibility, but this hypothesis strongly suggests that some species should use subharmonics during aggressive interactions.

5. Unpredictability per se as an adaptation

Group-living primates such as macaques are exposed to a large number of high-intensity calls each day, and individuals often appear to ignore calls that are of no immediate personal relevance to them. Thus, while all members of the troop will react to an alarm call, most individuals will ignore the cries of someone else's infant. Indeed, a weanling infant's own mother often appears to ignore its calls (Hauser 1993b). This poses a problem for vocalizers, who obviously are simply wasting energy if their calling falls upon deaf ears (not to mention advertising their existence to predators). In such a context, unpredictability itself could be a virtue by making calls difficult to predict and therefore difficult to habituate to and ignore (Owren & Rendall 1997). Similar ideas have been proposed regarding escape behaviour: any predictable fleeing pattern used by a particular prey species can be learned by predators and thus rendered ineffective, and the best escape strategy is therefore to be as unpredictable or 'protean' as possible (Driver & Humphries 1988). This hypothesis predicts that chaotic calls, such as noisy screams, should be harder to ignore (e.g. should take longer to habituate to in a playback experiment) than predictable calls of equal amplitude, such as coos. It also suggests that chaotic calls should be produced more frequently by animals in danger of being ignored (e.g. young and subordinate individuals). At least in the case of screams, both of these predictions seem quite likely to be upheld.

Conclusion

We suggest that an increased understanding of the vocal production mechanism leads to a better understanding of the nature of animal vocalizations, and of their evolutionary implications. In particular, we suggest that nonlinear phenomena in animal voices are common although traditionally overlooked. We have provided a brief overview of nonlinear dynamics of the voice, and have attempted to extend to animals the increased understanding of the voice mechanism gained by speech scientists in recent years. Although we have illustrated our paper with calls from nonhuman primates, there is no reason that any of the issues considered here should be limited to primates or even mammals (for examples from birds, canids and pinnipeds, respectively, see Fee et al. 1998; Wilden et al. 1998; Tyack & Miller, in press).

At a minimum, the taxonomy of nonlinear phenomena provided in this paper should make it possible for future researchers in animal communication to recognize and categorize nonlinear phenomena in vocalizations of a particular species. The conceptual tools of nonlinear dynamics also provide a means of understanding the production of such phenomena, and hopefully will encourage further research into animal vocal production in general and of nonlinear phenomena in particular. But more than this, we hope that this paper makes clear that a better understanding of vocal production at the mechanistic level allows us to generate novel hypotheses at the functional level. Combining current evolutionary theory (e.g. regarding fluctuating asymmetry, individual recognition or Morton's motivation-structural rules) with mechanistic understanding allows us to make testable predictions in the bioacoustic domain. Thus, this approach can help us to span the gap between mechanistic and functional explanation, as urged so convincingly by Tinbergen (1963).

References

Bergé, P., Pomeau, Y. & Vidal, C. 1984. *Order within Chaos: Towards a Deterministic Approach to Turbulence*. Paris: Wiley & Hermann.

Berry, D. A., Herzel, H., Titze, I. R. & Krischer, K. 1994. Interpretation of biomechanical simulations of normal and chaotic vocal fold oscillations with empirical eigenfunctions. *Journal of the Acoustical Society of America*, **95**, 3595–3604.

Berry, D. A., Herzel, H., Titze, I. R. & Story, B. 1996. Bifurcations in excised larynx experiments. *Journal of Voice*, **10**, 129–138.

Cohen, J. R., Crystal, T. H., House, A. S. & Neuburg, E. P. 1980. Weighty voices and shaky evidence: a critique. *Journal of the Acoustical Society of America*, **68**, 1884–1886.

Davies, N. B. & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, **274**, 683–685.

Dawkins, R. 1987. *The Blind Watchmaker*. New York: W. W. Norton.

von Dommelen, W. A. 1993. Speaker height and weight identification: a re-evaluation of some old data. *Journal of Phonetics*, **21**, 337–341.

Driver, P. M. & Humphries, D. A. 1988. *Protean Behaviour: the Biology of Unpredictability*. Oxford: Oxford University Press.

Fee, M. S., Shraiman, B., Pesaran, B. & Mitra, P. P. 1998. The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. *Nature*, **395**, 67–71.

Fischer, J., Hammerschmidt, K., Cheney, D. & Seyfarth, R. M. 1999. Acoustic features of female chacma baboon barks. *Ethology*, **107**, 33–54.

Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America*, **102**, 1213–1222.

Fitch, W. T. & Giedd, J. 1999. Morphology and development of the human vocal tract: a study using magnetic resonance imaging. *Journal of the Acoustical Society of America*, **106**, 1511–1522.

Fitch, W. T. & Hauser, M. D. 1995. Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on 'honest' advertisement. *American Journal of Primatology*, **37**, 191–219.

Fitch, W. T. & Kelley, J. P. 2000. Perception of vocal tract resonances by whooping cranes, *Grus americana*. *Ethology*, **106**, 559–574.

Glass, L. & Mackey, M. C. 1988. *From Clocks to Chaos: the Rhythms of Life*. Princeton, New Jersey: Princeton University Press.

Gouzoules, S., Gouzoules, H. & Marler, P. 1984. Rhesus monkey (*Macaca mulatta*) screams: representational signalling in the recruitment of agonistic aid. *Animal Behaviour*, **32**, 182–193.

Griffin, D. R. 1958. *Listening in the Dark*. New Haven, Connecticut: Yale University Press.

Hast, M. 1985. Comparative anatomy of the larynx: evolution and function. In: *Vocal Fold Physiology: Biomechanics, Acoustics and Phonatory Control* (Ed. by I. R. Titze & R. C. Scherer), pp. 3–14. Denver: Denver Center for the Performing Arts.

Hauser, M. D. 1991. Sources of acoustic variation in rhesus macaque vocalizations. *Ethology*, **89**, 29–46.

Hauser, M. D. 1992. Articulatory and social factors influence the acoustic structure of rhesus monkey vocalizations: a learned mode of production? *Journal of the Acoustical Society of America*, **91**, 2175–2179.

Hauser, M. D. 1993a. Rhesus monkey (*Macaca mulatta*) copulation calls: honest signals for female choice? *Proceedings of the Royal Society of London, Series B*, **254**, 93–96.

Hauser, M. D. 1993b. Do vervet monkey infants cry wolf? *Animal Behaviour*, **45**, 1242–1244.

Hauser, M. D., Evans, C. S. & Marler, P. 1993. The role of articulation in the production of rhesus monkey (*Macaca mulatta*) vocalizations. *Animal Behaviour*, **45**, 423–433.

Herzel, H. 1993. Bifurcations and chaos in voice signals. *Applied Mechanics Reviews*, **46**, 399–413.

Herzel, H. & Wendler, J. 1991. Evidence of chaos in phonatory samples. *Proceedings Eurospeech, Genova*, **1991**, 263–266.

Herzel, H., Steinecke, I., Mende, W. & Wermke, K. 1991. Chaos and bifurcations during voiced speech. In: *Complexity, Chaos and Biological Evolution* (Ed. by E. Mosekilde & L. Mosekilde), pp. 41–50. New York: Plenum.

Herzel, H., Berry, D., Titze, I. R. & Saleh, M. 1994. Analysis of vocal disorders with methods from nonlinear dynamics. *Journal of Speech & Hearing Research*, **37**, 1008–1019.

Herzel, H., Berry, D. A., Titze, I. R. & Steinecke, I. 1995. Nonlinear dynamics of the voice: signal analysis and biomechanical modeling. *Chaos*, **5**, 30–34.

Hirano, M., Kurita, S., Yukizane, K. & Hibi, S. 1989. Asymmetry of the laryngeal framework: a morphological study of cadaver larynges. *Annals of Otology, Rhinology and Laryngology*, **98**, 135–140.

Künzel, H. J. 1989. How well does average fundamental frequency correlate with speaker height and weight? *Phonetica*, **46**, 117–125.

Lass, N. J. & Brown, W. S. 1978. Correlational study of speakers' heights, weights, body surface areas, and speaking fundamental frequencies. *Journal of the Acoustical Society of America*, **63**, 1218–1220.

Lieberman, P. & Blumstein, S. E. 1988. *Speech Physiology, Speech Perception, and Acoustic Phonetics*. Cambridge: Cambridge University Press.

Lorenz, E. N. 1963. Deterministic nonperiodic flow. *Journal of Atmospheric Science*, **20**, 130–141.

Ludlow, C. L., Sedory Holzer, S. E. & Fujita, M. 1997. Correlations among intrinsic laryngeal muscles during speech gestures. In: *Speech Production & Language* (Ed. by S. Kiritani, H. Hirose & H. Fujisaki), pp. 9–32. New York: Mouton de Gruyter.

Mackey, M. C. & Glass, L. 1977. Oscillations and chaos in physiological control systems. *Science*, **197**, 287.

McShea, D. 1991. Complexity and evolution: what everybody knows. *Biology & Philosophy*, **6**, 303–324.

May, R. M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles and chaos. *Science*, **186**, 645–647.

May, R. M. 1976. Simple mathematical models with very complicated dynamics. *Nature*, **261**, 459–467.

Mende, W., Herzel, H. & Wermke, K. 1990. Bifurcations and chaos in newborn infant cries. *Physics Letters A*, **145**, 418–424.

Mergell, P. & Herzel, H. 1997. Modelling biphonation: the role of the vocal tract. *Speech Communication*, **22**, 141–154.

Mergell, P., Fitch, W. T. & Herzel, H. 1999. Modeling the role of non-human vocal membranes in phonation. *Journal of the Acoustical Society of America*, **105**, 2020–2028.

Møller, A. P. 1992. Female swallow preference for symmetrical male sexual ornaments. *Nature*, **357**, 238–240.

Møller, A. P. & Swaddle, J. 1997. *Asymmetry, Developmental Stability and Evolution*. New York: Oxford University Press.

Morton, E. S. 1977. On the occurrence and significance of motivation-structural rules in some birds and mammal sounds. *American Naturalist*, **111**, 855–869.

Negus, V. E. 1949. *The Comparative Anatomy and Physiology of the Larynx*. New York: Hafner.

Owren, M. J. & Rendall, D. 1997. An affect-conditioning model of nonhuman primate vocal signaling. In: *Perspectives in Ethology. Vol 12: Communication* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 299–346. New York: Plenum.

Owren, M. J., Dieter, J. A., Seyfarth, R. M. & Cheney, D. L. 1992. 'Food' calls produced by adult female rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques, their normally-raised offspring, and offspring cross-fostered between species. *Behaviour*, **120**, 218–231.

Rendall, D., Rodman, P. S. & Emond, R. E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, **51**, 1007–1015.

Riede, T. & Fitch, W. T. 1999. Vocal tract length and acoustics of vocalization in the domestic dog *Canis familiaris*. *Journal of Experimental Biology*, **202**, 2859–2867.

Robb, M. P. & Saxman, J. H. 1988. Acoustic observations in young children's non-cry vocalizations. *Journal of the Acoustical Society of America*, **83**, 1876–1882.

Rowell, T. E. & Hinde, R. A. 1962. Vocal communication by the rhesus monkey (*Macaca mulatta*). *Symposium of the Zoological Society of London*, **8**, 91–96.

Schneider, R. 1964. Der Larynx der Säugetiere. *Handbuch der Zoologie*, **5**, 1–128.

Schön Ybarra, M. 1995. A comparative approach to the nonhuman primate vocal tract: implications for sound production. In: *Frontiers in Primate Vocal Communication* (Ed. by E. Zimmerman & J. D. Newman), pp. 185–198. New York: Plenum.

Simmons, L. W. & Ritchie, M. G. 1996. Symmetry in the songs of crickets. *Proceedings of the Royal Society of London, Series B*, **263**, 305–311.

Sirviö, P. & Michelsson, K. 1976. Sound spectrographic cry analysis of normal and abnormal newborn infants. *Folia Phoniatrica*, **28**, 161–173.

Sommers, M. S., Moody, D. B., Prosen, C. A. & Stebbins, W. C. 1992. Formant frequency discrimination by Japanese macaques (*Macaca fuscata*). *Journal of the Acoustical Society of America*, **91**, 3499–3510.

Steinecke, I. & Herzel, H. 1995. Bifurcations in an asymmetric vocal-fold model. *Journal of the Acoustical Society of America*, **97**, 1874–1884.

Swaddle, J. P. 1996. Reproductive success and symmetry in zebra finches. *Animal Behaviour*, **51**, 203–210.

Tartter, V. C. & Braun, D. 1994. Hearing smiles and frowns in normal and whisper registers. *Journal of the Acoustical Society of America*, **96**, 2101–2107.

Thornhill, R. & Gangestad, S. W. 1999. Facial attractiveness. *Trends in Cognitive Sciences*, **3**, 452–460.

Tigges, M., Mergell, P., Herzel, H., Wittenberg, T. & Eysholdt, U. 1997. Observation and modelling of glottal biphonation. *Acustica*, **83**, 707–714.

Tinbergen, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, **20**, 410–33.

Truby, H. M. & Lind, J. 1965. Cry sounds of the newborn infant. In: *Newborn Infant Cry* (Ed. by J. Lind), pp. 7–59. Uppsala: Almquist & Wiksells Boktryckeri.

Tyack, P. & Miller, E. H. In press. Sound production and vocal behaviour. In: *Marine Mammal Biology: an Evolutionary Approach* (Ed. by R. Hoelzel). New York: Blackwell Scientific.

Wagner, W. E., Jr. 1992. Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. *Animal Behaviour*, **44**, 449–462.

Wilden, I., Herzel, H., Peters, G. & Tembrock, G. 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics*, **9**, 171–196.

Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, New Jersey: Princeton University Press.

Winter, P. 1968. Social communication in the squirrel monkey. In: *The Squirrel Monkey* (Ed. by L. A. Rosenblum & R. W. Cooper), pp. 235–253. New York: Academic Press.