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S26-4 Nonlinear phenomena and song evolution in *Streptopelia* doves

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Abstract The production of complex bird song is commonly achieved through neuromuscular activity of respiratory, syringeal and craniomandibular systems. According to nonlinear dynamics theory, however, complexity can also emerge spontaneously from very simple and deterministic systems, without any external control. Thus far, studies linking bird song complexity with nonlinear dynamics are very rare. Here we explore the possibility that a number of complex acoustic phenomena in vocalizations of *Streptopelia* doves are caused by nonlinear dynamics intrinsic to their vocal organ. We show that the complex acoustic phenomena in species-specific coos resemble the nonlinear phenomena described earlier for mammalian vocalizations. These phenomena include the different attractor states that have been found in mammalian phonation (limit cycle, folded limit cycle, torus, and chaos), and sudden transitions within and between those states (bifurcations). We argue that large, qualitative differences between species-specific song in *Streptopelia* doves may correspond to different attractor states of the same type of dynamic system. If so, dramatic acoustic differences between species sounds do not necessarily reflect large differences in sound production mechanisms or evolutionary differentiation, but may be due instead to relatively small differences in syringeal structure and control mechanisms.

Key words Vocal production, Nonlinear dynamics, Chaos, Syrinx, Evolution, *Streptopelia*

1 Introduction

One major challenge in the study of bird song is to explain the mechanistic origins of its complexity and diversity. Birds in general share the same basic mechanism for vocal production. The avian vocal organ, the syrinx, produces sound through the vibration of pairs of opposing labia or membranes that are driven by respiratory air flow (Larsen and Goller, 1999). Modulation of the sound generated comes about by changing the physical properties of this acoustic source, or of the vocal tract filter that shapes the source signal (Hoese et al., 2000). Such changes are often achieved through neuromuscular activity of respiratory, syringeal and craniomandibular systems. It is not surprising, then, that the identification of neuromuscular correlates of acoustic modulation in birds has received considerable attention over the years (see Suthers et al., 1999).

Recent findings, however, show that simple nonlinear systems can also exhibit complex dynamics without any external, complex control. This is true even if the underlying mechanisms are simple and completely deterministic. Systems in nature are often nonlinear, meaning that the equations describing them include squared and higher-order terms; and the study of such systems using concepts developed in nonlinear dynamics theory has led to a better understanding of their behavior in such diverse fields as ecology, physics, and economics. Because the primary sound generators in birds are nonlinear oscillators, it seems logical to hypothesize that nonlinear system dynamics also contribute to the complexity of bird vocalizations. Surprisingly, the concept of nonlinear dynamics has been mostly ignored in the study of bird song (cf. Fee et al., 1998; Fletcher, 2000).

In this paper, we explore the possibility that part of the complexity in species-distinct coo vocalizations in the genus *Streptopelia* (turtle-doves) can be explained by nonlinear dynamics intrinsic in the sound-producing organ. The genus *Streptopelia*, family Columbidae, consists of 17 species with a known phylogenetic history (Johnson et al., 2001), each of which has its own specific species perch-coo (Slabbekoorn et al., 1999). Between species, coo sounds can differ qualitatively in tonal structure, a characteristic that is used by turtle-doves to discriminate between species coos (Beckers et al., 2003), and may be used for species recognition. If qualitative differences in tonal structure represent different states of the same nonlinear dynamic system, as opposed to qualitatively different production mechanisms, this has serious implications for our understanding of the kind of mechanistic changes that may be involved in the evolution of song in these birds.

We show that acoustic characteristics of the coos of *Streptopelia* match dynamics known to occur in nonlinear systems, and resemble those found in mammalian vocalizations, the production of which is better understood in terms of the dynamics of coupled, nonlinear oscillators

(Herzel et al., 1995; Wilden et al., 1998; Riede et al., 2000; Neubauer et al., 2001). First, therefore, we recapitulate the different types of nonlinear phenomena identified in mammalian vocalizations.

2 Dynamics of nonlinear oscillators in mammalian vocalizations

The following summary of nonlinear dynamics in mammalian vocalizations is necessarily brief, and is based on Wilden et al. (1998) and Fitch et al. (2002). Voiced sounds in mammals are produced by the vocal folds, which are set into vibration by the effects of subglottal pressure, the visco-elastic properties of the vocal folds, and the Bernoulli effect (Titze, 1994). Nonlinearities in glottal pressure-flow relations, stress-strain-relations of vocal fold tissue, and the collision of vocal folds into each other constitute the nonlinearities of the system. This system consists of multiple coupled, nonlinear oscillators, and has been shown to exhibit qualitatively different types of vibratory dynamics that correspond to three different attractor types in nonlinear dynamics theory (Wilden et al., 1998): limit cycle, torus, and chaos attractors.

2.1 Limit cycle

In the simplest state, the behavior of the system is periodic, i.e. repeats itself in time. The resulting sounds are called harmonic sounds in acoustics, and correspond to a limit cycle in nonlinear dynamics theory. This is the normal state: vocal folds vibrate synchronously and periodically, and produce voiced sounds in humans and other mammals. Spectrographic representation of harmonic sounds shows acoustic energy in discrete bands, composed of a fundamental frequency, corresponding to the inverse of the vibration period, and zero or more integer multiples of the fundamental frequency. Sometimes, additional spectral components called subharmonics appear in the harmonic stack, usually at multiples of 1/2 or 1/3 of the fundamental frequency. Subharmonic regimes correspond to folded limit cycles, and occur, for example, when one of two vocal folds oscillates at exactly half or one-third the frequency of the other.

2.2 Torus

In a more complex attractor, there are two oscillations that are not harmonically related. In human vocal production this has been termed biphonation, and the corresponding object in nonlinear systems theory is a torus. Biphonation can be identified in a spectrogram as two simultaneous, non-parallel energy bands, and occurs, for example, when two vocals folds that are normally entrained to vibrate harmonically at the same frequency, become desynchronized and vibrate at their own individual, different frequencies (Neubauer et al., 2001). In nonlinear systems, this not only gives rise to two independent frequencies f and g, but also to linear combinations of these frequencies: $n \cdot f + m \cdot g$, where n and m are integer numbers.

2.3 Chaos

In a very complex attractor called a chaotic state, or ‘chaos’, oscillations are very irregular. This results in particularly complex sounds, the spectrographic representation of which exhibits irregular patterns of energy over wide frequency bands, even though some residual energy may still be concentrated in discrete bands. It is easy to misidentify chaotic sounds as noise, because chaos and noise resemble each other superficially in spectrograms. Mechanistically, however, they are very different (Tokuda et al., 2002). The complexity of chaotic sounds originates from the intrinsic behavior of a low-dimensional dynamics system (say, less than 10 components), and is completely deterministic. Noise, in contrast, originates from a very high-dimensional system of random components. Noise is a normal component of human speech, and is not produced by vibrating vocal folds but by a vocal tract constriction that creates turbulence in the flow of air (Stevens, 1998). Deterministic chaos, in contrast, is produced by vibrating vocal folds, in pathological human speech and in the normal vocalizations of other mammals (Wilden et al., 1998; Fitch et al., 2002).

2.4 Bifurcations

Apart from the above qualitatively different dynamical states, coupled nonlinear oscillators can also exhibit another characteristic behavior, namely sudden transitions from one dynamic state to another. These are called bifurcations. Typical examples in mammalian vocalizations are the sudden transitions from harmonic to subharmonic regimes (period-doubling bifurcation), from harmonic to biphonation (secondary Hopf bifurcation), or from harmonic to chaotic regimes. Sudden transitions within one type of attractor are also bifurcations. Examples of this are mode-locking transitions, in which harmonic vibrations instantaneously jump from one frequency to another. Mode locking occurs when a nonlinear interaction constrains two oscillating components of a system to maintain a small integer ratio of frequencies; it is known to occur in the song of zebra finches (Fee et al., 1998). Mode-locking transitions may arise when the characteristic frequency of one component is changed relative to the other, and the oscillation frequency suddenly jumps to achieve a new stable integer ratio.

3 Nonlinear dynamics in the song of *Streptopelia* doves

We used recordings of perch-coo vocalizations that had been collected for earlier studies (Slabbekoorn et al., 1999; Beckers et al., 2003) to search for phenomena linked to nonlinear dynamics. All of the above-described nonlinear phenomena in mammalian vocalizations (Wilden et al., 1998; Fitch et al., 2002) appear in the perch-coo vocalizations of *Streptopelia* doves.

3.1 Limit cycles

Fourteen of the seventeen species have pure-tonal perch-coos, the simplest form of a limit cycle (Fig. 1a). Seven of these have trill-like coos, which consist of fast, repetitive pulses of pure-tone sound, and could therefore be regarded as amplitude-modulated and interpreted as a torus in nonlinear dynamics theory. The repetition rate of these pulses, however, is relatively low (< 30 Hz); they do not give rise to multiple frequencies in human and probably dove perception, and their production may not be intrinsic to the dynamics of the syrinx.

Subharmonics (folded limit cycles) do not occur normally in coo sounds emitted by *Streptopelia* doves, but vocalizations recorded in the interclavicular air sac of ring doves, *S. risoria*, occasionally do (Fig. 1b; Beckers et al., 2003), even though the harmonic and subharmonic components are filtered out before the sound radiates.

3.2 Torus

Two harmonically unrelated frequencies, "biphonation", occur in the normal perch-coos of at least one species, *S. orientalis*. An example is the third sound element, labeled "B" in Fig. 2. In this example, a multi-harmonic signal with a fundamental frequency of 460 Hz (*f*) is modulated by a lower signal (*g*) of about 180 Hz, leading to the "side-bands" of 180 Hz at each harmonic of *f*.

3.3 Chaos

In three species (*S. orientalis, S. tranquebarica* and *S. lugens*), normal coo vocalizations consist completely or partly of elements with a chaotic structure. The *S. orientalis* sound elements labeled "C" in Fig. 3 are examples. Slabbekoorn et al. (1999) classified these vocalizations as "noisy", but we believe that they are true chaotic sounds because there is often some harmonic structure within the irregular patterns, as described for mammalian chaotic sounds by Wilden et al. (1998). The regular sudden transitions from harmonic or biphonic sound to very irregular regimes (element 'B/C" in Fig. 2), and the varying degrees of irregularity in time-frequency patterns, are consistent with this interpretation. In an exceptional case, we found short chaotic regimes in the perch-coos of *S. risoria*, a species that normally produces harmonic coos. Although it is hard to prove the chaotic nature of sounds from acoustic analysis alone, some mathematical tools can be helpful in its identification (Fletcher, 2000; Tokuda, 2002).

3.4 Bifurcations

Frequency jumps are common sudden dynamic state transitions in all *Streptopelia* species with harmonic vocalizations. At these transitions, the gradual time-frequency contour is momentarily disrupted, as the fundamental frequency jumps almost instantaneously to a different frequency range without interrupting phonation (the first element in Fig. 1b). Such frequency shifts probably reflect mode-locking dynamics. In *S. orientalis*, transitions from harmonic to chaotic states are common (Fig. 2), and in *S. risoria*, coos showing subharmonics, transitions from harmonic to subharmonic regimes, and vice versa, occur suddenly without a stop in phonation.

4 Implications for evolution of song

One of the key features of nonlinear systems is that small and gradual changes in control parameters can cause large, sudden, and qualitative changes in dynamics. If true in bird song, the intrinsic dynamics of the sound production organ itself would provide a source of major and qualitative acoustic variation. Presence of transitions within species shows that these can be readily achieved. Such transitions may also be at the basis of vocal differences between species. Seemingly strong interspecific differences, e.g. between the tonal coos of *S. risoria* and the noisy ones of *S. orientalis* or *S. tranquebarica*, might thus have resulted from minor changes in underlying mechanisms of vocalization, without the need for large changes in syringeal structure or control mechanisms.

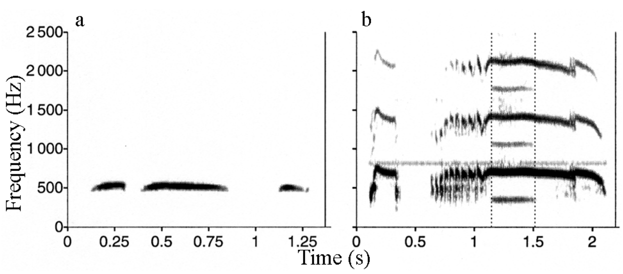

Fig. 1 Perch-coos of *Streptopelia decaocto* (a) and of *S. risoria* (b)
Perch-coo (a) is harmonic sound corresponding to a limit cycle. Perch-coo (b) is recorded in the interclavicular air sac inside the vocalizing dove, near the syringeal sound source. Normally this source sound is a multi-harmonic signal, only the fundamental frequency (300 < f < 800 Hz) radiating from the dove. This particular individual (b) shows subharmonic regimes (between dotted lines) in its perch-coos, corresponding to a folded limit cycle. The continuous frequency band around 825 Hz is an artifact due to electronic interference during recording.

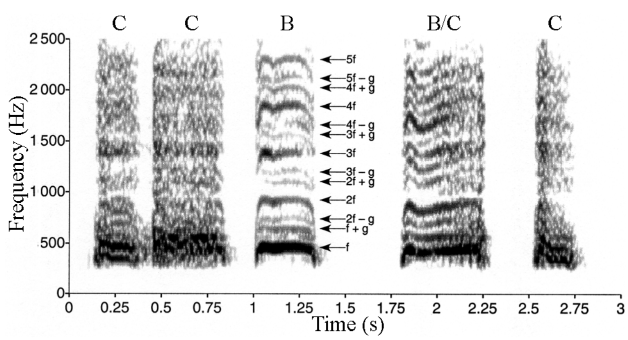

Fig. 2 Part of a coo bout of *Streptopelia orientalis*
C = chaotic regime, B = biphonation regime. In the third element, a harmonic signal (f, first five harmonics shown) is modulated by a lower frequency component (g), which causes a side-band pattern around each harmonic of f. Note that in the fourth element, the regime changes from biphonation (or perhaps subharmonic) to chaotic.

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