Supplemental Material

Smooth Operator: Avoidance of Subharmonic Bifurcations through Mechanical Mechanisms simplifies Song Motor Control in Adult Zebra Finches

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Topological analysis

The theory of nonlinear dynamics established that the long-term behavior of a dynamical system depends on the geometry of the underlying attractor (Strogatz, 1994). Many different utterances in voiced sound production by vertebrates are represented by distinct dynamical attractors: the silent organ (a constant value) is represented by a fixed point; a pure tone or a harmonic stack (a periodic oscillation) are represented by a limit cycle; amplitude-modulated sounds are represented by a torus; and “noisy” or harsh sounds (nonperiodic oscillations) are represented by a chaotic attractor. All stable and unstable periodic orbits in the phase space of a system are geometrically arranged in a particular way, like many different (closed) threads entangled in a twisted skein.

Topological methods have relatively recently been developed for the analysis of three-dimensional dissipative dynamical systems. Topological methods possess three very useful features: 1) they describe how to model the dynamics, 2) they allow validation of the models so developed, and 3) the topological invariants are robust under changes in control-parameter values (Gilmore 1998). A topological approach to the study of a dynamical system is based precisely on finding the geometrical arrangement of the periodic orbits of the system.

The topological structure of a system is identified by a set of integer invariants. One of the truly remarkable results of the topological-analysis procedure is that these integer invariants can be extracted from the time series. These integers can be used to determine whether or not two dynamical systems are equivalent. In particular, they can determine whether a model developed from time-series data is an accurate representation of a physical system. Conversely, these integers can be used to provide a mathematical model for the dynamical mechanisms that generated the experimental data (Gilmore 1998).

There is a topological invariant, the Linking Number (LN), which describes how two closed curves (periodic orbits) are linked or intertwined. The LN is an integer and it remains invariant as the orbits are deformed, as long as the deformation does not involve the orbits crossing through each other. Two different periodic orbits can never intersect, for that would violate the uniqueness theorem: the intersection point would have two possible futures. The only exception is an intersection on a fixed point, where the velocity is zero.

The orbits in a specific bifurcation are constrained to have a specific set of topological indices. Any departure from these values should cast serious doubt on the identity of the bifurcation. Consider a period doubling bifurcation: a stable limit cycle abruptly becomes unstable and at the same time a related, stable limit cycle is created that has twice the period (**Fig. S1A**). Just before the bifurcation, the organization of the phase space in the vicinity of the period-1 orbit (i.e. the stable manifold) takes the form of a Moebius band, such that any initial condition on one side of the limit cycle will be on the other side after one period, alternatively switching sides as the trajectory asymptotically approaches the limit cycle. This Moebius-like geometrical organization is preserved at the moment of the bifurcation, such that the newly created period-2 orbit and the now unstable period-1 orbit are intertwined in a very particular way: the period-2 orbit should be twisted around the period-1 orbit an odd number of half-turns. This leads to an odd LN. The orbits in **Fig. S1C**, **D** are not topologically related as it should be for a true period doubling, and indeed their LNs are not odd, but even in both cases.

Fig. S2 shows a more complicated set of orbits in a period doubling bifurcation p1→p2. These schematic orbits are representing the reconstruction from the time series $x(t)$ through a time-delayed embedding. Note the Moebius-like organization of the period-2 orbit around the period-1 orbit. Study of even more complicated orbits (**Figs. 2** and **3** in the main text) needs 3D visualization tools, or computational implementation of an algorithm as described below.

The LN of two orbits embedded in a three-dimensional phase space can be computed through the following algorithm (Gilmore 1998):

1. Project the orbits A and B onto a two-dimensional subspace. This can be done simply by plotting any two variables of the phase space or embedding ($x(t)$ vs. $x(t-\tau)$ in our case) for both orbits.

2. Determine the sign of every crossing between orbit A and orbit B. Right-handed crossings are assigned a value +1, left-handed crossings are assigned a value -1.

3. The linking number of A and B, LN(A,B), is half the sum of the signed crossings between A and B.

In general a candidate for period doubling bifurcation can be discarded by an even LN, but the LN alone is not sufficient for proving a period doubling bifurcation of arbitrary period and thus one has to compute a more detailed set of indices known as the Relative Rotation Rates (RRR) (Gilmore 1998, Solari and Gilmore 1988). However, in the particular case of a period doubling bifurcation between periods 1 and 2, the topological organization of the orbits is completely described by the LN, and there is no need to resort to the RRR (Solari and Gilmore 1988). As all candidates in this study were period doubling bifurcation between periods 1 and 2, in our case, a presumed period doubling bifurcation could be either discarded or proved by looking only at the LN. An odd LN is strongly supportive of a period doubling bifurcation, while the bifurcation can be discarded if the LN is even.

Close-returns (CR) plots are a powerful tool for finding periodic orbits (either stable or unstable) in a time series. For a time series $x(t)$, the CR plot is based on the observation that the difference $|x(t) - x(t+T)|$ remains smaller than a given threshold ε when $x(t)$ is near a periodic orbit of period T (Gilmore, 1998). The CR plot contains a mesh plot as a function of time t and period T, where the pixel (t,T) is plotted black when $|x(t) - x(t+T)| < \varepsilon$. A periodic orbit appears as a set of parallel, continuous, horizontal line segments in the CR plot. The period of the orbit is reflected in the value of the lowest segment. Additional line segments always appear at multiples of the lowest value—a signal that is periodic at T is also periodic at mT. An abrupt end of a segment while a harmonically related segment continues (i.e. a multiple) is indicative of a subharmonic bifurcation. In a period doubling bifurcation every other segment disappears (**Fig. S2C**, black arrowhead).

REFERENCES

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Solari HG, Gilmore R (1988) Relative rotation rates for driven dynamical systems. *Physical Review A* **37**, 3096-3109.

Supplemental Fig.S1

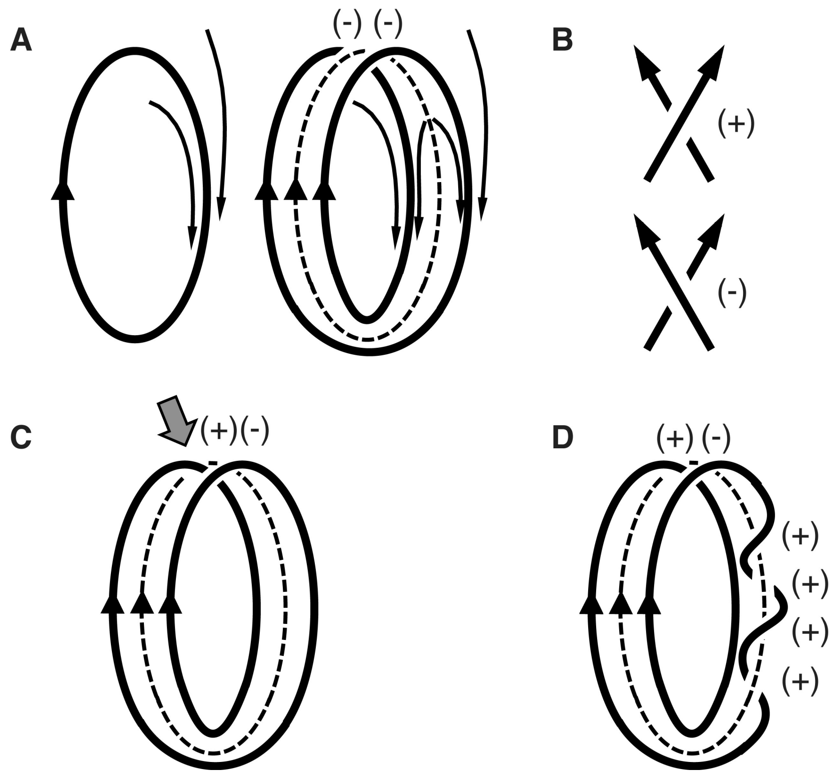

FIGURE LEGENDS

Figure S1. Linking number and signed crossings.

(A) Schematic drawing of a period doubling bifurcation in phase space. Before the bifurcation (left) a stable limit cycle is present, corresponding to a periodic time series with frequency *f*. After the bifurcation (right) the original limit cycle has become unstable (dashed line) and the system abandons it for a new stable solution: a related limit cycle with frequency *f*/2 (solid line). The signed crossings count is -2, so the linking number for these two orbits is LN = -1. A period doubling bifurcation has an odd LN (either positive or negative). (B) Definition of signed crossings. A right-handed crossing in the direction of the flow is positive, while a left-handed crossing is negative. (C) Two orbits p1 and p2 very similar to the orbits in (A), that nonetheless are not related through a period doubling bifurcation. Compare the crossing marked with the grey arrow. Note that the orbits in this case can be “disentagled” from each other. The count for signed crossings is zero; LN = 0 and so a period doubling is discarded. (D) A more complicated pair or orbits. Signed crossings +4, which gives LN = +2, so a period doubling is discarded.

Supplemental Fig.S2

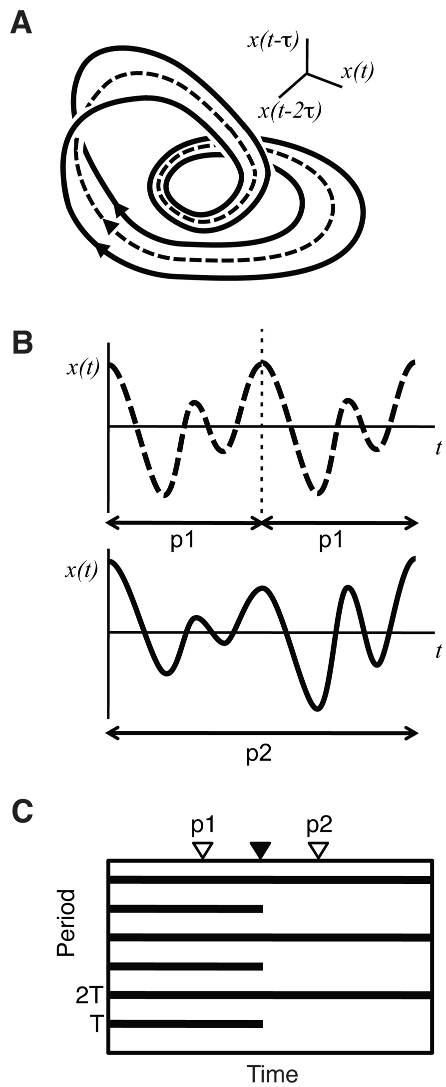

Figure S2. The orbits of a period doubling bifurcation p1→p2 in phase-space embedding. (A) The two orbits reconstructed by embedding the original time series $x(t)$ in a three-dimensional phase space $[x(t), x(t-\tau), x(t-2\tau)]$. Very near the bifurcation, orbit p2 (solid line) is close to orbit p1 (dashed line) and it lies on the edge of a Moebius band around p1. All crossings between the orbits (solid-dashed intersections, not shown for visual clarity, six total) are positive, and then LN = +3. (B) Segments of the original time series: p1 (dashed) and p2 (solid), corresponding to the open arrowheads in (C). Segment p1 is plotted twice for comparison with each half of p2. The slight differences explain the longer period of p2 (exactly twice that of p1). (C) Close-returns plot. The period of a signal at any given time is read from the value of the lowest horizontal line segment at that time. In a period doubling bifurcation (black arrowhead) the period abruptly jumps to twice the value before.