Introduction to Focus Issue: Mixed Mode Oscillations: Experiment, Computation, and Analysis

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Mixed mode oscillations (MMOs) occur when a dynamical system switches between fast and slow motion and small and large amplitude. MMOs appear in a variety of systems in nature, and may be simple or complex. This focus issue presents a series of articles on theoretical, numerical, and experimental aspects of MMOs. The applications cover physical, chemical, and biological systems. © *2008 American Institute of Physics*. [DOI: 10.1063/1.2903177]

An oscillator is a dynamical system which goes through the same—or almost the same—states again and again. Oscillators occur everywhere in nature as rhythms and vibrations. Simple oscillators are based on a single mechanism, but in more complex systems different mechanisms are active during different phases of the oscillation. This can give rise to oscillations which shift between slow and fast motion and small and large amplitude. Such mixed mode oscillations (MMOs) are the subject of a substantial current research effort, and include experimental, computational, and theoretical approaches which shed light on important issues in physics, chemistry, and biology.

Oscillatory behavior occurs everywhere in nature. The harmonic oscillator is a fundamental mathematical structure that any science student meets. Real world oscillators do, however, rarely possess the uniformity of the harmonic oscillator but typically switch between slow and fast motion and small and large amplitudes, and, hence, display MMOs. Here we make a slightly narrower definition of MMOs. We primarily refer to MMOs as complex patterns that arise in dynamical systems, in which oscillations with different amplitudes are interspersed. These amplitude regimes differ roughly by an order of magnitude. In each regime, oscillations are created by a different mechanism and their amplitudes may have small variations. Additional mechanisms govern the transition among regimes. MMOs of this type are ubiquitous in nature, and have first been observed in chemical reactions more than 100 years ago,[1] with the Belouzov–Zhabotinsky (BZ) reaction discovered in the 1970s being the most thoroughly studied example.[2–5] MMOs are also found in surface chemical reactions,[6–9] electrochemical systems,[10–12] neural systems,[13–16] calcium dynamics,[17,18] electrocardiac dynamics,[19] and laser dynamics[20] to name but a few fields.

The mathematical modeling of systems where MMOs occur result in nonlinear ordinary or partial differential equations. In such systems, several mechanisms which can produce MMOs have been identified: Slow passage through a Hopf bifurcation,[21–25] breakup of an invariant torus,[26] breakup (loss) of stability of a Shilnikov homoclinic orbit,[27,10] and subcritical Hopf-homoclinic bifurcation.[28,29]

MMOs may also occur through the canard phenomenon, first discovered in the van der Pol equation.[30,31] Here a limit cycle born in a Hopf bifurcation experiences the transition from a small, almost harmonic cycle to a large relaxation oscillation in a narrow parameter interval. The intermediate limit cycles existing during the transition are the *canard cycles* which are characterized by following a slow manifold for a substantial time and distance on its unstable part. The canard phenomenon occurs in the parameter range of the system where it is a singular perturbation problem, and it has subsequently been identified in a number of other 2D singularly perturbed oscillators.[5,12] If such a system is modified either by adding further variables or by noise MMOs may occur in larger regions as the dynamics switches between small amplitude oscillations (SAOs) and large amplitude oscillations (LAOs). Dynamics related to canards is a connecting theme for most of the papers in this Focus Issue.

THIS FOCUS ISSUE

In the last years, considerable progress has been made towards the understanding of MMO patterns. Several papers have been published and results have been presented in various ad hoc meetings. The purpose of this Focus Issue is to bring together researchers working in various disparate aspects related to the mechanisms of generation and control (dynamic, biological, chemical, physical, etc.) of MMOs. We hope this Focus Issue serves as a framework for both the exchange of ideas and cross-fertilization among the various apparently disparate fields that, although their objects of study and scientific terminology are different, they share mathematical models with common underlying dynamic structures.

Bakeš *et al.*[32] present an experimental study of oscillations in a homogeneous chemical reaction. The *p*H varies significantly and allows a detailed examination of the dynamics of the system. As the flow rate is varied, the system transitions from a periodic regime into a chaotic regime, via a series of bifurcations that involve MMOs in the *p*H.

Baba and Krisher[33] provide numerical results on pattern formation in a prototypical electrochemical model with global coupling, where the underlying homogeneous system displays MMOs. The distributed system exhibits a complex pattern of clusters with a dynamics related both to the underlying MMOs and the global coupling.

Higuera *et al.*[34] investigate computationally a single-mode expansion model for Faraday waves occurring on the surface of a fluid in an elliptical container. The model is a singular perturbation problem, where the small parameter is the ratio of the evolution time of the surface waves and the evolution time of the streaming flow. Periodic and nonperiodic MMOs are observed in the amplitudes of the surface waves, and they arise due to the slow drift through Hopf bifurcations.

Rubin and Wechselberger[35] investigate, analytically and numerically, the mechanism of the generation of MMOs in a modified 3D version of the classical Hodgkin–Huxley neuron model. The membrane potential and ionic current gating variables exhibit MMOs, with a varying pattern of oscillations consisting of a number of LAOs followed by a number of SAOs.

Krupa *et al.*[36] investigate analytically the mechanism of generation of MMOs in a two-compartmental model of the dopaminergic neuron in the mammalian brain stem. In this model, each compartment is a 2D oscillator describing the dynamics of the membrane potential and calcium concentration, and the two compartments are strongly electrically coupled. It is shown that a slowly varying canard structure is responsible for the observed MMOs.

Desroches *et al.*[37] developed a computational method to investigate the mechanism of generation of MMOs in a self-coupled FitzHugh–Nagumo (FHN) model. The FHN model has been used as a simplified two-dimensional model for the description of neural oscillations and of other phenomena in fast–slow systems. In their model, the self-coupling is provided by an extra synaptic variable whose evolution alternates between fast and slow modes. The new method enables one to represent the relevant manifolds with sufficient accuracy to find the different canard solutions and MMOs, and it can be used and extended for a variety of systems with MMOs.

The article by Guckenheimer[38] shows how chaotic dynamics and MMOs arise near folded nodes and folded saddle-nodes on slow manifolds. It focuses on the global return maps for trajectories passing near such equilibria on two-dimensional slow manifolds, showing how they may be approximated by 1D maps. These 1D maps have multiple discontinuities and turning points due to the twisting of solutions about the primary canard, and these features generate interesting chaotic dynamics. The general ideas are illustrated on a variant of the classical forced van der Pol equation, and this example is chosen so that the MMOs and chaos exist in large regions of parameter space and so that it is easy to tune the system parameters to control the number of twists the trajectories make.

Bouse *et al.*[39] study general fast–slow systems possessing coexisting stable limit cycles. One branch of limit cycles represents SAOs, and the other represents LAOs. In the bifurcation diagram, where the norms of the solutions are plotted as functions of the bifurcation parameter, these branches are S-shaped, with three regimes: a central bistable regime with monostable regimes on either side. As the control parameter is varied, MMOs exhibiting alternation between SAOs and LAOs can arise. The authors present analytically verifiable criteria that enable one to detect whether or not this S-shaped bifurcation structure exists in a given problem.

A new control method is introduced by Durham and Moehlis in Ref. 40 to drive planar fast-slow systems to the regime of canard solutions near supercritical Hopf bifurcations. Within the context of these classical types of planar problems in which canards were first discovered, such as the FHN and the van der Pol equation, it is challenging to detect numerically the canards due to the narrowness of the parameter intervals in which they exist. The strategy underlying the new control scheme is inspired by the dynamics of MMOs, exploiting the differences between SAOs and LAOs on either side of the canard regime.

Noise can create MMOs, as is shown in the article by Muratov and Vanden-Eijnden.[41] These authors study a fast–slow Morris–Lecar model in the vicinity of a supercritical Hopf bifurcation point. During the transition between excitable kinetics and relaxation oscillations, a variety of dynamically distinct behaviors are observed as the amplitude of Gaussian white noise is decreased in a manner depending on the small parameter measuring the separation of time scales in the deterministic system. These dynamics include MMO states, self-induced stochastic resonance, coherence resonance, bursting relaxation oscillations, and rare clusters of spikes. In addition, it is shown how these results generalize to other fast–slow systems.

Noise can also induce MMOs in systems of coupled oscillators, as is demonstrated numerically for a system of two coupled Morris–Lecar equations and analytically for a system of two coupled λ-ω systems, in the article by Yu *et al.*[42] The MMOs arise in those regimes in which the deterministic system has coexisting stable oscillatory states, including when both equations exhibit LAOs, and localized states in which one oscillator exhibits LAOs and the other SAOs. The noise causes the system to randomly visit these different oscillatory states, and hence to exhibit MMOs. This analysis is also applied to analyze the impact of noise on the phase dynamics of moderate-size networks of 20 neuronal oscillators in the weak coupling regime.

When electrical activity in the brain is recorded experimentally, it is the result of synchronized oscillations in a network of many neurons. Single neurons typically fire at rates which are much lower than the frequencies found in the electric potential. Brunel and Hakim[43] review their numerical and theoretical work on models where a fast collective synchronized oscillation results from a network of neurons firing stochastically at a low rate.

As a simple example of a network of oscillators which share a common resource which controls the individual oscillator, Postnov *et al.*[44] consider a network of electric oscillators with a common power supply. Depending on the coupling strength, the system exhibits a range of different MMOs.

The article by Erchova and McGonigle,[45] presents an overview of transmembrane voltage dynamics in some paradigm neuronal systems, especially the entorhinal cortex. This overview should be useful for general neuroscientists to see what role mathematical modeling in general, and dynamical systems techniques in particular, can play in understanding rhythmic behavior. A number of possible neurophysiological interpretations are given for the roles of MMOs, including those with regular and irregular alternations between different states.

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