

## Introduction to Focus Issue: Nonlinear and Stochastic Physics in Biology

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## Introduction to Focus Issue: Nonlinear and Stochastic Physics in Biology

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Frank Moss was a leading figure in the study of nonlinear and stochastic processes in biological systems. His work, particularly in the area of stochastic resonance, has been highly influential to the interdisciplinary scientific community. This Focus Issue pays tribute to Moss with articles that describe the most recent advances in the field he helped to create. In this Introduction, we review Moss's seminal scientific contributions and introduce the articles that make up this Focus Issue.

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**Biological systems are complex, nonlinear and, in many cases, subject to various kinds of noise. Concepts of nonlinear dynamics and stochastic processes have been transformational for the study and understanding of biological systems on all organizational scales, from single molecules to swarms of organisms. This Focus Issue provides an overview of current research at the interface of nonlinear and stochastic physics with biology. This volume also pays tribute to Frank E. Moss, whose work in this area was profoundly influential and who will be greatly missed. In this Introduction, we review briefly Moss's most influential works.**

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Frank Moss made numerous and fundamental contributions to the field of nonlinear physics. But in both the physics and biophysics communities, the name Frank Moss is most strongly associated with the phenomenon of stochastic resonance. Frank's unique intuition and deep knowledge of physics were critical in extending this interesting effect, observed first in physical systems, to biological systems, sparking world-wide interest.

Frank's interest in nonlinear stochastic processes probably began with his work from the 1960s to the 1980s on turbulence in superfluid helium. In a 1975 *Physical Review Letter*, he provided the first measurements of fluctuations in turbulent He II.<sup>1</sup> One of the aims of that paper was to verify Vinen's dimensional theory of liquid He turbulence. An equation describing the growth of vortex-line density, Vinen's equation, is a first-order nonlinear differential equation with several parameters that are likely to fluctuate in a physical experiment. This led Moss to use the concept of *multiplicative* (or parametric) noise, which could alter qualitatively the dynamics of a nonlinear system. Indeed, in 1982 Moss theoretically predicted that noise modulation of the counterflow velocity in superfluid He (a control parameter in

Vinen's theory) shifts the critical velocity of the turbulence onset towards higher values.<sup>2</sup>

Having a strong background in electrical engineering, Moss soon realized that analog models provide an effective way to study the dynamics of systems perturbed by noise. Such approaches were particularly important, since only a limited class of nonlinear stochastic dynamical systems allows for exact analytical evaluations of their statistical properties, such as probability density, power spectrum, and relaxation times. The analog simulations of stochastic nonlinear systems developed by Moss and Peter McClintock provided a platform for testing various theories for non-equilibrium nonlinear stochastic dynamics. For example, in Ref. 3 the first measurement of the phase diagram of a noise-induced phase transition was presented. Another representative example was the use of an analog simulation to attack the problem of evaluating the statistical properties of nonlinear systems driven by colored noise, i.e., noise with finite correlation time.

The problem of finding the escape rate from a potential well arises in many areas of physics, chemistry, and biology, e.g., the firing rate of an excitable cell. Several approximate theories of stochastic dynamics with colored noise were developed and tested with the use of analog simulators, such as in the highly cited Ref. 4. Note that even now, in the days of fast and inexpensive computers, these works are of high value, as the noise used in Moss's experiments came from *physical* sources rather than being obtained with pseudo-random number generators.

Moss also used analog simulations to study bifurcations of nonlinear oscillators in the presence of noise. These works provided the first experimental observations of many interesting effects, such as noise-induced postponement of bifurcations and noise-induced shaping of two-dimensional stationary probability densities.<sup>5-7</sup> Growing interest in the dynamics of non-equilibrium stochastic systems led to

publication of the famous three-volume book “Noise in Non-linear Dynamical Systems” by Cambridge University Press, which Frank co-edited with Peter McClintock.<sup>8–10</sup> This collection of theoretical and experimental papers by the leading experts in the field is still a desk book for many researchers and graduate students.

As mentioned above, many of Frank’s best known contributions are in the field of stochastic resonance. Stochastic resonance (SR) describes a phenomenon where the addition of noise to a system results in enhancement of its sensitivity to a weak, subthreshold external signal. Various measures characterizing input-output relations have been used to quantify SR, such as signal-to-noise ratio (SNR), spectral power amplification, distributions of residence times, mutual information rate, signal discriminability, etc. The hallmark of SR is the existence of a maximum of some SR measure as a function of the noise intensity, indicating optimal transmission of information at a non-zero noise intensity.

Stochastic resonance was first discovered and proposed to explain periodic recurrence of earth’s ice ages.<sup>11,12</sup> It was subsequently observed in experiments with several physical systems such as lasers,<sup>13</sup> electron paramagnetic resonance (EPR) systems,<sup>14</sup> and tunnel diodes.<sup>15</sup> A canonical model for SR is an overdamped bistable system driven by noise and a weak periodic force. In the absence of noise, this weak periodic drive is not sufficient to switch the system from one potential well to another. Addition of noise allows for switching between the states and an optimal noise intensity at which the noise-controlled switching time approaches the period of the signal. At this optimal noise intensity, the signal-to-noise ratio or other SR measures are maximized. The probability density of escape times from a potential well of a periodically modulated stochastic bistable system shows multiple peaks centered at the half period of the driving force, a structure remarkably similar to an interspike interval histogram of a neuron with periodically modulated firing rate, as was pointed out by Longtin, Bulsara, and Moss in Ref. 16.

Moss and colleagues soon realized that the phenomenon of stochastic resonance might be important for sensory neurons, which are known to be noisy and in many cases are excitable. Moss speculated that the theory of SR developed for physical systems could be applied to neuronal models in order to investigate the possible benefits of noise in sensory information processing.<sup>17–20</sup> Consider a canonical example of an excitable neuron, which is silent in the absence of noise and fires an action potential spike in response to a strong depolarizing stimulus. A weak subthreshold stimulus, however, keeps the neuron silent, so that it does not convey information about the stimulus. When noise is present, the neuron fires spikes, encoding the stimulus in a sequence of interspike intervals. For weak stimuli and large noise strengths, the neuron’s firing is dominated by fluctuations, and the efficiency of information encoding (quantified, for example, by the signal-to-noise ratio) is small. At an optimal noise intensity, the information transmission becomes maximal, a clear manifestation of the phenomenon of stochastic resonance. Moss established a collaboration with the neurobiologist Lon Wilkens to perform the first experiment on sto-

chastic resonance in a biological system, using the crayfish mechanoreceptor system. Their 1993 *Nature* paper<sup>21</sup> opened up stochastic resonance to the neuroscience community, sparking great interest in this phenomenon, and in the role of noise in sensory neurobiology in general. Using a carefully designed experiment, whereby single mechanoreceptor neurons were stimulated by a combination of mechanical noise and periodic vibration, they demonstrated a maximum in the signal-to-noise ratio derived from a mechanoreceptor neuron’s spike train. This clearly demonstrated the positive role that noise might play in a sensory nervous system and led to many follow-up studies of SR in other single-neuron preparations. Moss and Wilkens then extended their experimental studies to a light-sensitive interneuron in the crayfish mechanosensory system, the caudal photoreceptor. This interneuron integrates outputs from an array of peripheral mechanoreceptors, but also responds directly to light. An SR-like phenomenon was documented from the recording of spiking activity of a caudal photoreceptor when weak periodic mechanical vibrations were applied to the crayfish tail-fan mechanoreceptors. Just as the signal-to-noise ratio increased in the mechanoreceptor spike trains in the presence of mechanical noise, the signal-to-noise ratio increased in the photoreceptors when the photoreceptor was stimulated by light, mimicking injection of noise.<sup>22</sup> Other studies from Moss’s group later showed various phase-locking regimes as the photoreceptor/mechanoreceptor system was driven with various frequencies and intensities of mechanical vibration; essentially, these experiments recreated the passage of the synchronizing system through a series of Arnol’d tongues.<sup>23</sup> Moss and colleagues also demonstrated that the synchronization index between the periodic drive and the photoreceptor spike train could be optimized as a function of light intensity, as the SNR is optimized as a function of noise in “classical” SR experiments.<sup>24</sup> In parallel, Gingl, Kiss, and Moss developed the concept of non-dynamical stochastic resonance, i.e., stochastic resonance for threshold-like nonlinear elements which offered a simple, general, and transparent description of the essence of SR (Ref. 25; see also Refs. 26 and 27).

To foster interdisciplinary collaboration, Moss and Wilkens founded the Center for Neurodynamics in 1996 at the University of Missouri at St. Louis. The Center was supported by a University Research Instrumentation Program (URIP) grant from the Office of Naval Research. In this new collaborative setting, Moss and Wilkens set out to address a fundamental, but still unanswered, question about stochastic resonance in biology. Experimental evidence of SR in a single neuron did not answer the question of whether biological organisms actually exploit noise in order to perform useful tasks, such as locating prey for feeding. To attack this fundamental problem, the Center used another animal model, the paddlefish. Paddlefish inhabit the muddy waters of the Mississippi, Missouri, and Ohio rivers and use a passive electro-sense to feed on zooplankton prey such as *Daphnia*. In fact, electro-sense largely substitutes for vision in this animal. Moss and colleagues posed the question of whether addition of noise in the water can help paddlefish to better locate and feed on *Daphnia*. In a series of unique behavioral

experiments, Russell, Wilkens, and Moss showed that the addition of weak electrical noise to a swim mill in which a paddlefish is feeding results in a wider distribution of distances of successful feeding strikes. Thus, in the presence of a small electrical noise, the paddlefish was able to detect prey at longer distances as compared to a noise-free control condition. This result, published in 1999 in *Nature*,<sup>28</sup> was the first experimental observation and verification of *behavioral* stochastic resonance. This study gave a strong argument in favor of the hypothesis that sensory nervous systems have evolved to take advantage of inevitable environmental fluctuations.

Another transformative study initiated by Moss involved visual perception of stochastic resonance. In a 1997 *Physical Review Letter*,<sup>29</sup> Moss and colleagues showed that SR can be used as an assay to study the ability of the human brain to interpret visual stimuli. They used psychophysics experiments where noise-contaminated images were presented to human subjects; a perceptive contrast threshold was determined for various levels of noise strengths and correlation times. The perceptive contrast threshold was consistently minimal for an optimal (intermediate) noise strength and followed non-dynamical SR theory,<sup>25,27</sup> which allowed the authors to identify a measurable sensitivity parameter for the human visual system. This paper opened up a new avenue for SR studies in psychophysics and in medical physics.

Another project actively pursued in the Center was devoted to the development of methods for detection of low-dimensional dynamics from biological data.<sup>30–33</sup> Moss established active collaborations with many research groups world-wide, sharing his ideas and inspiring research projects on various aspects of fluctuations and noise in biological systems. He wrote several highly cited reviews on stochastic resonance,<sup>34–38</sup> as well as many *News and Views* articles in *Nature* and articles in other journals highlighting and promoting research of other groups.<sup>39–47</sup>

The behavioral stochastic resonance paper<sup>28</sup> suggested a biologically plausible source of noise: the electric field from the collective motion of many *Daphnia* forming a swarm. Observation of a swarm in an aquarium triggered Moss's interest in the area of collective animal motion, and he turned his attention away from the paddlefish and toward its noisy prey. This led to the development of theoretical models for the detection of a noisy *Daphnia* swarm.<sup>48,49</sup> But Moss was soon drawn away from the study of *Daphnia* as prey, and began to study how these small creatures searched for their own food. Following a detailed experimental investigation in collaboration with Ai Nihongi and Rudi Strickler at the Great Lakes WATER Institute,<sup>50</sup> he began to investigate the various theoretical models that might be applied to *Daphnia* foraging.<sup>50,51</sup> Questions of foraging not only interested Moss because of their deep relation to fundamental problems of nonlinear dynamics, random walks, fractal search strategies, and statistical physics; Moss was perhaps even more intrigued by the question of how evolution might have shaped optimal foraging strategies. In his last paper, he demonstrated how a simple model of natural selection could be used to “evolve” step length and turning angle distributions quite similar to those found in actual *Daphnia*.<sup>52</sup> Already in ailing health, Moss had no hesitation about taking a leap into

the unknown and beginning to explore a new scientific field. It is that intellectual courage, perhaps even more than his pioneering scientific contributions, which made Frank Moss such an inspiring figure to colleagues, students, and friends around the world.

In this issue, we bring together a collection of papers reflecting the state of the art in the application of nonlinear and stochastic processes to biological systems. The authors of the papers included here have all had their lives and their work shaped in some way by the inspiration of Frank Moss. A number of papers included here address the phenomenon of SR, a central theme in Moss's work. Yu *et al.*<sup>53</sup> investigate the phenomenon of SR on a modular neuronal network consisting of several small-world subnetworks with a sub-threshold periodic pacemaker. They show that the correlation between the pacemaker frequency and the dynamical response of the network is resonantly dependent on the intensity of additive spatiotemporal noise. Turning to the interaction between Brownian motors and stochastic resonance, Mateos and Alariste<sup>54</sup> study the transport properties of a Brownian walker on a ratchet potential, finding an optimal amount of noise for which the amplitude of the system's periodic response is maximum, a hallmark of SR. They also show that, precisely for this optimal noise, the average velocity of the walker is maximal, implying a strong link between SR and the ratchet effect.

Other contributors address aspects of dynamics and synchronization in experimental neural systems. Hofmann and Wilkens<sup>55</sup> report on the original experimental finding of a new kind of skin potential in paddlefish. The voltage pulses are triggered by external electric fields, and propagate from the tip of the rostrum towards the gill covers. The authors show that the skin potentials are closely akin to neuronal action potentials, following an all-or-nothing rule and requiring a refractory period before their next initiation. The response to and encoding of time-varying stimuli in paddlefish electroreceptors are studied by Neiman and Russell.<sup>56</sup> Coherence analysis demonstrates that weak stimuli, with waveforms derived from zooplankton prey, are encoded to a high degree into afferent spike trains, transmitting information at  $\sim 30$  bits/s. When the stimulus strength is increased to induce bursting firing, the stimulus transfer to afferent spike timing becomes nonlinear. Takeshita and Bahar<sup>57</sup> investigate synchronization during seizures in an *in vivo* model of focal neocortical epilepsy in the rat neocortex. Using voltage sensitive dye imaging and stochastic phase synchronization analysis, they demonstrate a significant rise in synchrony during seizure events.

Turning to computational studies of neural systems, Yu and Longtin<sup>58</sup> study how quasiperiodic stimuli composed of two sinusoids, one with noise-modulated amplitude, are encoded by generic leaky integrate-and-fire neuron models. The authors study how the coherence between modulation and response spike trains (a measure of linear stimulus encoding) depends on the frequency content of the stimulus, versus the intrinsic firing rate of the neuron. They showed that a neuron model with an adaptive threshold can improve the coherence, providing a better linear encoding of modulation. However, the coherence is depressed by noise when the

beat frequency and the intrinsic neuronal firing rate overlap. Van Hemmen and collaborators<sup>59</sup> explore a frequently-used method in neuroscience to detect periodicities in neuronal spike trains: a geometric interpretation of the Fourier transformation called the vector strength, which has some similarities to standard stochastic phase synchronization techniques. The timing of each neuronal spiking event is mapped onto the simultaneous phase of a harmonic with variable frequency, denoting the putative frequency of the neuronal spike train. If, for a given frequency, the events cluster on the unit circle, the vectors corresponding to the spiking events add constructively, like waves emerging from a coherently driven periodic diffraction grating in certain directions, to yield a large vector strength. Van Hemmen and collaborators generalize this method, address the influence of noise, and apply it to spike trains from the auditory system of the cat and from the electrosensitive fish.

Transitions from tonic spiking to bursting regimes are often observed in neurons from various areas of the central nervous system (CNS). Unraveling the detailed mechanisms leading to such transitions is a subject of current research in computational neuroscience and requires the knowledge of a model, e.g., in the form of a system of nonlinear ordinary differential equations (ODEs). However, Braun *et al.*<sup>60</sup> show that the tonic spiking to bursting transition, via a period-doubling bifurcation, can be anticipated from experimental sequences of interspike intervals, using a method previously developed for the detection of unstable periodic orbits. The method is based on detection of specific patterns (encounters) in the first return map of interspike intervals and a further assessment of the statistical significance of these patterns. The authors apply this method to experimental data and verify the nature of correlated patterns of interspike intervals with a noisy conductance-based neuron model.

Finke *et al.*<sup>61</sup> study the stochastic dynamics of a thermoreceptor neuron model. This conductance-based model, developed by Huber and Braun, demonstrates the rich variety of periodic spiking and chaotic bursting patterns when the control parameter, the temperature, is varied. The authors consider two distinct sources of noise: a fluctuating synaptic current and a fluctuating activation kinetic variable; they show that the effect of these two types of noises on neuronal responses is dramatically different in the low temperature region of the model. Yanchuk *et al.*<sup>62</sup> show that a ring of unidirectionally delay-coupled spiking neurons may possess a multitude of stable spiking patterns and provide a constructive algorithm for generating a desired spiking pattern. Such multistability significantly enhances the coding capability of oscillatory neuronal loops. In the paper by Quan *et al.*,<sup>63</sup> resonance phenomena in a two-neuron model with mutual time-delayed inhibitory feedback are investigated. These authors discuss delay-induced oscillations in the noise-free as well as in the noisy case, and construct a Markov chain model for their dynamics. Astakhov *et al.*<sup>64</sup> investigate the synchronization of noise-induced oscillations over a range of frequencies, using the FitzHugh-Nagumo neural model. They demonstrate that this excitable system undergoes the same frequency lockings as a self-sustained quasiperiodic oscillator, and discuss noise-induced stable and unstable limit cycles and tori, as well as bifurcations between these states.

Noisy dynamics in biologically-inspired ODEs is not limited to the neural realm, however, as Bashkirtseva and Ryashko<sup>65</sup> remind us when they apply the novel tool of stochastic sensitivity functions to study dynamics in a noise perturbed predator-prey model with the Allee effect. Their computational method allows constructing so-called confidence ellipses, providing a geometrical description of noise-forced dynamics. In particular, for the stochastic predator-prey model this method allows estimation of a threshold value of noise intensity resulting in a transition from coexistence to extinction states of the model. Wiesenfeld and Borrero-Echeverry<sup>66</sup> address more general problems of synchronization, with applications to neural systems and beyond, developing a generic iterative map model of coupled oscillators. The model enhances our understanding of the original synchronization experiments by Huygens, and modern realizations of his two coupled clocks, from a unified perspective.

Other contributors address problems of collective behavior in active Brownian particles and other aspects of noisy Brownian motion. The motion of a Brownian particle in a double-well potential, driven by a periodic force, is analyzed by Jung and Marchesoni.<sup>67</sup> They show that the power delivered by the periodic force is controlled by the strength of the noise, while the power delivered by the noise is independent of the amplitude and frequency of the periodic force. The implications of these findings to the mechanism of stochastic resonance are discussed. Romanczuk *et al.*<sup>68</sup> look back on their creative cooperation with Frank Moss, and discuss how an oscillating internal degree of freedom may act as an effective bridge between an internal energy depot and macroscopic propulsion of an active particle. Martens *et al.*<sup>69</sup> consider biased Brownian motion of point-size particles in a three-dimensional tube with smoothly varying cross-section. They employ an asymptotic analysis of the stationary probability distribution of a geometric parameter and calculate from this the mobility and diffusion coefficient of the Brownian particle as a function of the geometry and of the applied force. Berezhkovskii and Bezrukov<sup>70</sup> remind us of how Frank Moss was able to merge his enjoyment of science with his enjoyment of life in their paper on the movement of a spherical Brownian particle, by pointing out that the Wiener sausage is not only an Austrian culinary delicacy made from beef and pork, but it also denotes the neighborhood of a spherical Brownian particle it has visited during a time interval. Since Brownian trajectories are stochastic, so is the Wiener sausage! Berezhkovskii and Bezrukov provide a simple and intuitive method to calculate surface area and the stochastic variations of the Wiener sausage with important implications for enzyme binding kinetics.

Kia *et al.*<sup>71</sup> take us in a different direction and return to some of the fundamental problems of chaotic dynamics, with applications to chaos computing. These contributors employ unstable periodic orbits, which form the skeleton of any chaotic system, to build a model for the chaotic system in order to measure the sensitivity of each orbit to noise, and to select the orbits whose symbolic representations are relatively robust against the existence of noise.

Dynamics and stochastic processes in biology were first explored, by Moss and his colleagues, in single cells and in

multi-cellular organisms. The inclusion of several studies in this issue applying stochastic dynamics to gene networks and systems biology is indicative of the extent to which stochastic dynamics has extended its reach in recent years. Dari *et al.*<sup>72</sup> offer a genetic module that can perform the AND/OR gate functionalities in the presence of noise, following the logical stochastic resonance paradigm. The effects of connection topology and time-delayed coupling on the dynamics of genetic regulatory small-world networks are studied by Yang *et al.*<sup>73</sup> For a fixed network topology, the phenomenon of delay-induced resonance is revealed. Tuning the time-delay and connection topology gives rise to optimal spatial synchrony, while temporal resonance is always reduced by time-delay with large rewiring probability. The issue concludes with an investigation by Stamatakis *et al.*<sup>74</sup> of the role of noise in gene expression. They investigate the common assumption that extrinsic noise acts as a pure input on a gene of interest, which exerts no feedback on the extrinsic noise source, and demonstrate that this assumption falls short when multiple genes share a common pool of regulatory molecules. Due to competitive utilization of the molecules existing in this pool, genes cease to be uniformly influenced by the extrinsic noise source, and begin to exert negative regulatory effects on each other, rendering it impossible to determine the extrinsic noise source by currently established methods. What better way to close this special issue than to show how Frank Moss's influence carries us into the future via the emerging fields of genomics and systems biology?

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