Interaction of noise with excitable dynamics

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In this paper, the interaction of noise with excitable dynamics of a three-electrode electrochemical cell is examined. Different scenarios involving both external and internal noise sources are considered. In the case of external noise, aperiodic stochastic resonance and regulation of the noise-induced spiking behaviour are investigated. In the case of internal noise, the interaction of intrinsic electrochemical noise with autonomous nonlinear dynamics is studied. The amplitude of this internal noise, determined by the concentration of chloride ions, is monotonically increased and the provoked dynamics are analysed. Our results indicate that internal noise, similar to its external counterpart, is able to induce regularity in the system response.

Keywords: noise; excitable dynamics; stochastic resonance

1. Introduction

The interaction of noise with nonlinear dynamics has become an extremely active field of research. Most studies of this phenomenon, known as stochastic resonance (SR), have been on the noise-enhanced system response to subthreshold periodic signals (Benzi et al. 1981, 1982, 1983; Nicolis & Nicolis 1981; Nicolis 1982; Gammanitoni et al. 1998). SR has been explored in a wide variety of physical, chemical and biological systems (Longtin et al. 1991; Moss et al. 1993; Ditzinger et al. 1994; Föster et al. 1996; Amemiya et al. 1998; Escalera Santos & Parmananda 2002) and has been proposed as an instrument for improving signal detection and enhancing information transfer (Hanggi 2002; Lindner et al. 2002, 2003). While studies of SR typically focus on periodic subthreshold signals, some investigations have examined more complex signals such as aperiodic signals (Gang et al. 1992; Collins et al. 1995, 1996). As in SR, there exists an optimal noise level for information transfer in aperiodic stochastic resonance (ASR; Collins et al. 1996). The fidelity between the aperiodic input stimulus and the system response in such situations can be quantified by determining the cross-correlation coefficient (power norm; Collins et al. 1996; Eichwald & Walleczek 1997). Another one of these noise-provoked effects, namely coherence resonance (CR; Gang et al. 1993; Pikovsky & Kurths 1997), involves the inception of almost periodic oscillations supported by purely stochastic fluctuations and is attributed to an interplay between the nonlinear nature of the deterministic systems and random driving forces.

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In comparison, the role of internal noise and its interaction with nonlinear dynamics (Jung & Shuai 2001; Schmid et al. 2001; Stacey & Durand 2001) are less well understood. Since it is possible to envisage numerous real systems with intrinsic noise, the question whether internal noise, similar to its external counterpart, plays a constructive role in nonlinear systems has tremendous validity and applicability. For example, it has been categorically shown that synaptic noise improves the detection of subthreshold signals in hippocampal CA1 neurons (Stacey & Durand 2001). Moreover, it has been demonstrated numerically by Schmid et al. (2001), using the Hodgkin–Huxley model (Hodgkin & Huxley 1952), that internal noise caused by the fluctuations of individual channels in an assembly of ion channels can induce intrinsic coherence resonance (ICR). Consequently, for optimum levels of internal noise, the regularity of the observed spike sequence is augmented (Schmid et al. 2001).

In this present contribution, we characterize different resonances invoked by both external and internal noise sources. The electrochemical cell used for the experiments is described in §2. In §3, results involving the inception of ASR in experiments are presented. This involves characterizing the noise-induced system response to subthreshold spike trains with aperiodic interspike intervals. Experimental results involving the manipulation of the spike sequence regularity (Janson et al. 2004) using a delayed feedback method (Pyragas 1992) are presented in §4. They indicate the effectiveness of the delayed feedback technique in controlling noise-induced motion. In §5, results involving the emergence of ICR in the presence of internal noise are discussed. The amount of internal noise in these experiments is dictated by the concentration of chloride ions in the electrolyte solution. This inception of ICR, evident from the enhanced regularity of the invoked time series of anodic current \( I \) at optimum levels of intrinsic noise, is furthermore verified quantitatively by calculating the coherence factor \( \beta \) (Gang et al. 1992, 1993). Finally, scanning electron microscope (SEM) imaging of the anode is carried out to visualize the surface morphology of the anode undergoing pitting corrosion. This is, in part, done in an effort to correlate the regularity observed in the time series with the spatial organization of the pitting centres on the anodic surface. A summary of the presented results is furnished in §6.

2. Electrochemical cell

Experiments were carried out in a three-electrode electrochemical cell, configured to study the potentiostatic electrodissolution of iron in a mixture of copper sulphate and sulphuric acid. The anode was a pure iron (Sigma Aldrich 99.98% purity) disc (6.3 mm diameter) shrouded by epoxy. The electrolyte solution was a mixture of 1.0 M sulphuric acid and 0.4 M copper sulphate. A volume of approximately 500 ml was maintained in the cell. The anodic potential \( V \), measured relative to a saturated calomel reference electrode (SCE), was used as the control (bifurcation) parameter on to which the external perturbations were superimposed. The cathode was a 5 mm diameter copper rod. Oscillations in anodic current \( I \) (the current between the anode and the cathode) were recorded using a 12 bit data acquisition card at a sampling rate of 250 Hz. The external noise used in the experiments (Escalera Santos et al. 2004a,b; Parmananda et al. 2005; Rivera et al. 2005) was derived from a random number generator consistent with white noise with a Gaussian distribution (Press et al. 1992). This output was converted to an analogue
signal and superimposed on to the anodic voltage via a potentiostat (PINE Model AFRDE5). The frequency at which the noise amplitude was varied is approximately 1.25 Hz. A schematic of the experimental set-up is shown in figure 1.

Figure 1. Schematic of the electrochemical cell with iron, copper and saturated calomel electrodes, being the anode, cathode and reference, respectively. The electrolytic solution is a mixture of 1.0 M sulphuric acid and 0.4 M copper sulphate.

The details of the autonomous behaviour exhibited by this electrochemical cell have been reported previously (Escalera Santos et al. 2004a, b; Parmananda et al. 2005; Rivera et al. 2005) and can be summarized as follows: varying anodic voltage \( V \) as the bifurcation parameter, two different dynamical responses of the anodic current \( I \) were observed, namely a stationary-state behaviour (constant current response) and period-1 oscillations emerging from a supercritical Hopf bifurcation at approximately 175 mV. At anodic voltages slightly above the Hopf bifurcation, small harmonic oscillations were observed. At higher voltages, the experimental system exhibited relaxation oscillations whose period augmented with increasing voltage. In our earlier studies (Escalera Santos et al. 2004a,b; Parmananda et al. 2005; Rivera et al. 2005), we noted that this period of lengthening occurs until the oscillations died at the homoclinic bifurcation point \( V_{hc} \) at approximately 216 mV. Consequently, for anodic voltages \( V > V_{hc} \), the autonomous dynamics exhibit an excitable fixed point behaviour.

### 3. Aperiodic stochastic resonance

ASR in an electrochemical system with excitable dynamics was characterized experimentally. Two different spike trains, one with stochastic and the other with chaotic interspike intervals, were imposed on the system as subthreshold aperiodic signals.
The experiments were carried out in the electrochemical cell described in §2. In our experiments on ASR, the reference voltage \( V_0 \) was chosen such that \( V_0 > V_{hc} \) and the experimental dynamics exhibit an excitable steady-state behaviour. The anodic voltage \( V_z \) was then defined as \( V_z = V_0 + C_S(t) \), where \( V_0 \) (set-point) and the subthreshold aperiodic pulse train \( S(t) \) were set such that \( V_0 > V_{hc} \), i.e. the subthreshold signal never perturbed the system into the oscillatory regime.

Subsequently, the system’s response as a function of the noise (Gaussian white) amplitude \( D \) was analysed. To quantify the information transfer, we use the power norm defined by Eichwald & Walleczek (1997),

\[
C_0 = \langle (x_1 - \langle x_1 \rangle_t)(x_2 - \langle x_2 \rangle_t) \rangle_t, \tag{3.1}
\]

where \( x_1 \) represents the time series of the aperiodic input signal, \( x_2 \) represents the noise-induced response of the electrochemical system and \( \langle \rangle_t \) denotes the respective time averages. The power norm is a measure of the coincidence fidelity between the subthreshold aperiodic input signal and the noise-induced system response.

In our first set of experiments, the subthreshold aperiodic pulse train was constructed by using a random number generator (Press et al. 1992) that yields uniform random deviates in the interval \([0,1]\). These numbers were subsequently rescaled to provide appropriate interspike intervals suitable for our experiments. The pulse amplitude was chosen to be \(-100\) mV and the pulse duration as \(8.0\) s. Thus, while the amplitude and pulse duration remained constant, the interspike interval varied stochastically.

Figure 2a–c shows the time series of the system response with identical subthreshold spike trains for three different amplitudes of imposed noise. We see in

![Figure 2](image-url)
that there is little correspondence between the subthreshold signal and the system response at a low noise amplitude, while there is excellent correspondence at an intermediate noise amplitude (figure 2b). In figure 2c, the subthreshold signal is lost in the system response to the high-amplitude noise. Figure 2d shows the power norm $|C_0|$ as a function of the noise amplitude $D$ for two experimental runs with identical reference voltages $V_0$. The two curves exhibit a unimodal structure, where the maxima reveal the optimal noise level for maximum information transfer.

In our second set of experiments, we used a deterministic model that simulates irregular neural spiking (Baier et al. 2000) as the subthreshold aperiodic signal. The spikes of the chaotic time series have a relatively constant amplitude of approximately 100 mV. Although the origin of the irregular spiking is purely deterministic, the histogram for the spike sequence fits well with a Poisson distribution (Baier et al. 2000). Incrementing the noise amplitude $D$ monotonically, the provoked system response was analysed. Figure 3a–c shows the stimulus–response time series for (a) low-, (b) medium- and (c) high-amplitude noise. Analogous to the previous results, there exists an intermediate noise amplitude, figure 3b, that gives rise to an excellent stimulus–response correspondence, while lower- and higher-amplitude noise produces little overlap. The upper traces in figure 3a–c correspond to the subthreshold aperiodic spike train and the lower traces correspond to the induced system response. Figure 3d shows $|C_0|$ as a function of $D$, quantifying the input–output correlation for two different experiments with the same reference voltage $V_0$. The $|C_0|$ power norm...
curves have a unimodal shape implying the existence of an optimum noise level for which maximum information transfer was achieved.

4. Coherence resonance control

In CR systems, by virtue of the underlying mechanisms, regularity of the induced spike sequences is significantly less in comparison to that for SR systems. Even for the optimum noise level, the maximal periodicity obtained is quite low. However, it was recently realized in numerical simulations that, by using a feedback control technique (Janson et al. 2004), it is possible to augment the coherence of the noise-invoked spiking.

Using the electrochemical cell described in §2, the set-point for the control parameter (anodic voltage) $V$ was chosen such that $V_0 > V_{hc}$. Consequently the anodic current ($I$), the system observable, exhibited excitatory fixed point behaviour. The anodic voltage $V$ was then defined as $V = V_0 + D\xi$, where the amplitude of the imposed Gaussian white noise $\xi$ is $D$. We studied the system response as a function of the noise amplitude $D$. Normalized variance (NV), defined as $\text{NV} = \sqrt{\text{Var}(t_p)}/(t_p)$, where $t_p$ is the time between successive peaks, was used to quantify the extent of induced regularity. It is evident that, the more regular the dynamics, the lower the value of the computed NV. The dotted curve in figure 4e was obtained by plotting the NV values, calculated using experimental data, as a function of the noise amplitude $D$. Time series for three of the imposed noise amplitudes, figure 4a–c corresponding to low, optimum and high noise levels, respectively, are also shown.

The second set of experiments involved the inception of the CR effect in conjunction with delayed feedback control. The superimposed control should alter the dotted NV curve of figure 4. The anodic voltage for this set of experiments was modulated as $V = V_0 + D\xi + \gamma(I(t) - I(t - \tau))$, where $\gamma(I(t) - I(t - \tau))$ was the feedback term intended to enhance the regularity of the spike trains. The control amplitude $\gamma$ and the delay time $\tau$ were determined as follows (Parmananda et al. 1999; Escalera Santos et al. 2006). Using the time series provoked by the noise amplitude in figure 4b, a return map (not shown) was constructed by plotting successive interspike intervals ($t_{p+1}$ versus $t_p$). Subsequently, a linear regression of this apparently structureless return map was obtained. The intersection of this regression line with the line of identity provides the appropriate delay $\tau$ used in the feedback term. The CR experiments performed in the presence of feedback control yielded the solid NV curve presented in figure 4e. It is evident, by visual inspection, that the maximum attainable regularity of the spike train was enhanced (manifested by a deeper minima) owing to the superimposed delayed feedback control. Moreover the NV values, for the controlled system, calculated at other noise amplitudes were also reduced. This lowering of the NV curve points to the effectiveness of the delayed feedback control strategy. Figure 4a–d also shows the noise-invoked time series in the presence of delayed feedback control. The trace of figure 4d shows the time series for the noise amplitude corresponding to the solid curve of figure 4e (optimum noise level for the controlled NV curve). When compared to the time series corresponding to label (b) of the dotted curve (optimum noise level for the uncontrolled NV curve), the enhanced regularity observed by virtue of the superimposed feedback is revealed.
5. Intrinsic coherence resonance

To study experimentally the interaction of internal noise with nonlinear dynamics, the electrochemical cell of §2 had to be modified slightly. In this new configuration, the electrolyte solution was a mixture of 1.0 M sulphuric acid and 0.6 M potassium sulphate. A volume of 500 ml was maintained in the electrochemical cell. The anodic potential $V$, measured relative to a saturated calomel electrode (SCE), was used as the control parameter. The cathode was a graphite rod, 5.0 mm in diameter and 2 cm long, immersed in the electrolyte solution. The following protocol was implemented as a precursor to each experimental run.

(i) The anode surface was polished with sand paper of 600 grade and rinsed thoroughly with distilled water before being mounted in the electrochemical cell.

Figure 4. ($a$–$c$) The experimental time series of the anodic current ($I$) provoked by noise amplitudes labelled ($a$–$c$) on the dotted curve in ($e$). ($d$) The noise-induced time series, in the presence of the delayed feedback control, for the noise amplitude corresponding to label ($d$) on the solid curve. ($e$) The experimentally computed NV curves without (dotted) and with (solid) delayed feedback control. The set-point ($V_0$) was chosen to be 360 mV such that the autonomous dynamics exhibited excitable fixed point behaviour. The amplitude $\gamma$ of the delayed feedback control term was fixed at 100 mV and $\tau$ was calculated, as explained in the text, to be $\tau = 16.428$ s.

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Nitrogen gas was pumped into the cell for about 15 min to cleanse the electrochemical cell of oxygen gas.

Subsequently, a fixed amount of potassium chloride, our source of chloride ions (internal noise; Bertocci 1979; Lalvani & Zhang 1995), was added to the electrolyte solution without changing the volume maintained in the electrochemical cell. After waiting for approximately 15 min, wherein the transient behaviour is observed and therefore neglected, the anodic current $I$ data (the current between the anode and the cathode) were recorded for analysis using a 12 bit data acquisition card at a sampling frequency of 200 Hz. This entire procedure is repeated for different (increasing) concentrations of chloride ions added to the electrolyte solution, analogous to monotonically increasing the amplitude of the internal noise, and the experimental $\beta$ curve is constructed.

The principle of this modified electrochemical cell was qualitatively similar to the earlier experimental set-up. Again, two basic types of dynamics were observed: steady-state fixed point behaviour with a constant current response and period-1 oscillations emerging from a supercritical Hopf bifurcation, where $V_H$ is approximately 140 mV. At anodic voltages slightly above the Hopf bifurcation, small, sinusoidal oscillations were observed. At higher voltages, relaxation oscillations were observed in which the period increased with an increase in voltage. This period lengthening occurs until oscillations cease at the homoclinic bifurcation point $V_{hc}$ at approximately 250 mV.

In our experiments on ICR, the set-point for the autonomous system was chosen to be 700 mV such that a constant anodic current $I$ (fixed point) of approximately 0 mA was observed. This set-point, maintained constant for all experimental runs, was chosen far away from the bifurcation point in an effort to minimize the effects of small variations in the autonomous dynamics. Under these experimental conditions, the anode is susceptible to pitting corrosion (Bertocci 1979; Lalvani & Zhang 1995) in the presence of chloride ions, our source of internal noise. Thereafter, potassium chloride is added to the electrolytic solution in order to analyse the effect of noise on the autonomous fixed point dynamics. It is observed that, up until a certain concentration (0.025 M) of added potassium chloride, the value of the anodic current $I$ increases, reaching a value of approximately 100 mA. However, the anodic current time series continues to exhibit fixed point behaviour. This concentration of potassium chloride where the anodic current $I$ exhibits fixed point behaviour at approximately 100 mA is chosen to be the first point of the experimental $\beta$ curve presented later. For subsequent experimental runs, each one was started with fresh electrolyte solution and polished electrodes, the concentration of the added chloride ions was systematically increased and the asymptotic time series of the anodic current (recorded for each experimental run) was used to calculate the coherence factor $\beta$. Furthermore, the surface morphology of the anode, subsequent to some experimental runs, was analysed using the scanning electron microscope (SEM). Figure 5f shows the experimentally generated coherence factor ($\tilde{\beta}$) versus concentration of the chloride ions (internal noise amplitude) curve. Time series corresponding to some of the experimental data points are shown in figure 5a–e. The computed $\beta$ curve has a unimodal shape indicating the observation of ICR. It implies that, for some optimum levels of internal noise, the interplay of stochastic pitting process, provoked by the chloride ions, and
autonomous nonlinear dynamics invokes enhanced coherence. This is manifested by the emergence of increased regularity for oscillations presented in the time series (figure 5c). In contrast, at low levels of chloride concentrations, the noise-provoked dynamics are devoid of any periodic features and for the most part exhibit fixed point direct current response at approximately 100 mA. Furthermore, at high levels of chloride concentrations, the dynamics are dominated by the stochastic pitting process resulting in the observation of a noisy fixed point behaviour. The profiles of the provoked time series in figure 5a–e vary as different parameter domains are visited for distinct noise strengths. It is interesting to observe that the average value of the fixed point current value for both low and high levels of internal noise remains nearly the same (100 mA).

We also tried to correlate the enhanced periodicity of the time series to the spatial organization of the anode morphology undergoing pitting corrosion. For these purposes, after some experimental runs, the anode was dismounted from the electrochemical cell and taken over to the SEM laboratory for imaging purposes. Figure 6 shows the images of the anode surface obtained, using the
SEM, corresponding to points (a), (c) and (e) of the β curve shown in figure 5f. It is observed that the anode surface corresponding to data point (c) of the β curve, where maximum coherence in the noise-induced time series is observed, exhibits increased homogeneity (smoothness) in the surface morphology. This could be due to a more regular spatial distribution of the pitting centres at this optimum level of internal noise. In contrast, the images corresponding to low (figure 5a) and high (figure 5e) levels of internal noise exhibit a substantially rougher morphology for the anode surface. It needs to be clarified that, while it is interesting to detect qualitatively that SEM images indicate enhanced levels of spatial organization for optimum levels of noise, it is by no means a conclusive proof for the emergence of ICR. It is the experimentally generated β curve that provides quantitative and therefore more reliable evidence for the existence of ICR in our experiments.

6. Summary

Our experiments establish the emergence of SR for aperiodic subthreshold signals in excitable systems. The observed ASR occurs near an infinite-period homoclinic bifurcation. The ASR in our system differs from previous studies in which the aperiodicity arises in the interspike interval rather than in the amplitude. In neurophysiological sensory systems, the stimuli often comprise aperiodic spike trains, and ASR could provide a means for enhanced information transmission in these noisy systems. Then, we verify the regulation of the noise-provoked dynamics using a delayed feedback control strategy. The effectiveness of this feedback method is manifested by its ability to control the different spike sequences induced by distinct amplitudes of random forcings. The control of noise-induced motion, apart from being a challenging scientific problem, could be of relevance to threshold systems subjected to internal/external noise. For example, usually, in threshold systems with internal noise, one has no control over the intensity of the existing noise. Consequently, regulating the characteristics of the
noise-provoked spike sequences is not possible. However, in such scenarios, judicious implementation (suitable choice of $\gamma$ and $\tau$) of the delayed feedback control strategy could alter/regulate the properties of the observed spike trains. Finally, our observation of ICR renders the noise- (external and/or internal) induced resonance phenomena ubiquitous. The results of this section are of immense relevance to biological systems in general and neuronal systems in particular. For example, internal noise provoked by the fluctuation of individual channels in an assembly of ion channels induces neuronal firing (Hanggi 2002). In the framework of our results, this would imply that, as the amplitude of the internal noise is varied, different profiles of spike sequences (and consequently different interspike intervals) are generated, yielding the most regular firing pattern at an optimum value of internal noise.

References


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