

Coherence and Stochastic Resonance in Nonlinear Dynamical Systems

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Zusammenfassung

Diese Arbeit ist der Untersuchung zweier rauschinduzierter Phänomene, der kohärenten und der stochastischen Resonanz in nichtlinearen dynamischen Systemen gewidmet. Theoretisch untersucht werden diese Effekte in zwei Modellen aus der Neurobiologie, dem Integratorneuron mit Leckstrom (LIF - engl.: leaky integrate-and-fire neuron) und dem FitzHugh-Nagumo (FN) Modell, sowie in einem klassischen System der statistischen Physik, der Brownschen Bewegung im geneigten periodischen Potential. Kohärente Resonanz beobachtet man in anregbaren dynamischen Systemen, die mit Rauschen (einem Zufallsprozeß) getrieben werden. Bei einer optimalen *endlichen* Stärke der treibenden Fluktuationen treten reguläre, rein rauschinduzierte Oszillationen auf - das System zeigt eine *rauschinduzierte Eigenfrequenz*. Im ersten Teil der Arbeit wird dieser Effekt in den Neuronenmodellen mittels charakteristischer Maße (Koeffizient der Variation, Diffusionskoeffizienten der Pulszahl und Leistungsspektrum des neuronalen Pulszuges) analytisch nachgewiesen. Während die Resultate für das LIF Modell exakt sind, beruhen sie im Fall des zweidimensionalen FN Systems auf einem neuartigen Verfahren der adiabatischen Eliminierung, das es erlaubt, im Fall einer ausgeprägten Zeitskalenseparation zwischen den Systemvariablen, die oben genannten Maße der kohärenten Resonanz als auch Pulsraten und marginale Wahrscheinlichkeitsdichten zu berechnen. Eine rauschinduzierte Eigenfrequenz wird für das anregbare und das bistabile dynamische Regime des FN Modells gefunden, im oszillatorischen (Grenzzyklus-) Regime hingegen verschlechtert endliches Rauschen die Kohärenz der neuronalen Dynamik.

Für die überdämpfte Brownsche Bewegung im geneigten periodischen Potential beliebiger Form werden exakte analytische Ausdrücke für den effektiven Diffusionskoeffizienten und die Péclet Zahl abgeleitet. Anhand dieser Größen kann ein weiterer rauschinduzierter Effekt, der *kohärente Transport* Brownscher Teilchen quantifiziert werden. Für bestimmte Potentialformen ergibt sich der erstaunliche Befund, daß eine *Verstärkung der thermischen Fluktuationen* zu einer *Verringerung des Diffusionskoeffizienten* führen kann.

Stochastische Resonanz bezeichnet den Effekt einer verbesserten Signalübertragung mittels endlicher Fluktuationen und wird in einer Vielzahl nichtlinearer Dynamiken beobachtet, die mit periodischen Kräften und Rauschen getrieben werden. Im zweiten Teil der Arbeit wird der Einfluß der stochastischen und der kohärenten Resonanz auf die Signalübertragung durch periodisch getriebene Neuronenmodelle (LIF und FN) studiert. Die lineare Antwort der Systeme auf schwache Signale für beliebige Signalfrequenzen und Rauschintensitäten wird analytisch berechnet, spektrale Maße wie die Leistungsverstärkung und das Signal-Rausch Verhältnis werden ebenfalls abgeleitet. In den rauschaktivierten (anregbaren und bistabilen) dynamischen Regimen beider Systeme wird stochastische Resonanz nachgewiesen. Weiterhin wird gezeigt, daß eine nichtmonotone Abhängigkeit der neuronalen Antwort von der Signalfrequenz auftreten

kann und daß das globale Optimum der Transmission somit bei endlicher Rauschstärke als auch endlicher Signalfrequenz angenommen wird (stochastische Doppelresonanz). Der Effekt kann aufgrund der Vorarbeit zur kohärenten Resonanz als eine gewöhnliche Resonanz mit der rauschinduzierten Eigenfrequenz verstanden werden.

Auch im oszillatorische Regime der LIF und FN Modelle kann für spezifische Signalfrequenzen eine Art stochastischer Resonanz auftreten. Dieser Effekt wird diskutiert und auf die erhöhte Variabilität der Pulszeiten durch Einwirkung von Fluktuationen zurückgeführt.

Wie in der Einführung der Arbeit gezeigt wird, müssen für Neuronen, die pulskodiert von anderen Neuronen stimuliert werden, außer *additiven* Signalen (periodische Modulation des Basisstroms) auch *rauschkodierte* Signale (Modulation der Intensität der treibenden Fluktuationen) in Betracht gezogen werden. Im LIF Modell wird ein detaillierter Vergleich der neuronalen Antwort auf beide Signale vorgenommen. Es zeigt sich, daß hochfrequente rauschkodierte Signale vom LIF Neuron effizient (mit endlicher Amplitude und verschwindender Phasenverschiebung) übertragen werden. Dieses Ergebnis impliziert eine schnelle Signaltransmission durch neuronale *Populationen*. Physikalische Beschränkungen, die sich aus modellierungsbedingten Vereinfachungen ergeben, werden ebenfalls diskutiert.

Abstract

This thesis is devoted to the theoretical investigation of noise-induced resonance phenomena in three different systems. *Coherence resonance* (CR) and *stochastic resonance* (SR) are studied in two excitable model neurons, namely, the leaky integrate-and-fire (LIF) neuron and the stochastic FitzHugh-Nagumo (FN) system. Furthermore, noise-induced *coherent transport* of Brownian particles in a tilted periodic potential is examined and related to the CR phenomenon occurring in excitable systems.

Coherence resonance, a noise-induced regularity in the output of a noise driven excitable system can be quantified by the coefficient of variation, the spike count diffusion coefficient, and by the power spectrum. Analytical expressions for these measures are derived for the LIF and FN models and applied to demonstrate the occurrence of CR in different dynamical regimes of those models. Exact solutions are obtained for the LIF model. Results for the two-dimensional FN system are based on a novel approximation scheme that is applicable in case of a well-established time scale separation between the system's variables.

The examination of the overdamped Brownian motion in a tilted periodic potential reveals another form of noise-induced regularity that can be quantified by diffusion coefficient and Péclet number. Exact formulae for these quantities are derived that allow a closer inspection of the *coherent transport* phenomenon appearing at finite noise intensity. Most notably, it is shown that an *increase in thermal noise* may cause a *decrease in spatial diffusion*.

The second main part of this work deals with noise-enhanced signal transmission by means of stochastic resonance in periodically driven neuron models. SR is established by spectral measures (power amplification, signal-to-noise ratio) in both LIF and FN model neurons. For the LIF model, linear response theory can be immediately applied. In case of the FN model spectral measures can only be obtained in a two-state approximation that nevertheless captures the main features of signal transmission in *all dynamical regimes* of the original system. By means of this *nonadiabatic* theory that is valid for arbitrary noise strength and driving frequency it is possible to show that coherence resonance introduces a nonmonotonous dependence of the spectral response on the signal frequency.

Particular emphasis is put on the comparison between the transmission of additive and noise coded signals by the LIF model. As outlined in the introduction the latter type of signal appears naturally in the neuronal dynamics. While for both kinds of signals the transmission exhibits stochastic resonance, solely the noise coded signal leads to an efficient high frequency transmission (finite response amplitude, vanishing phase shift). Implications for a possible *fast* signal transmission through *neuronal ensembles* are discussed as well.

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List of symbols

Mathematical notation

$\delta(x)$	Dirac function
$\Theta(x)$	Heaviside's jump function
$\langle \cdot \rangle$	Ensemble average
$\langle \Delta x^2 \rangle = \langle (x - \langle x \rangle)^2 \rangle$	Variance of the random variable
$\xi(t)$	White Gaussian noise of unit intensity
$f'(x)$ or $\frac{df}{dx}$	Derivative with respect to x
$[f]_x = \lim_{\varepsilon \rightarrow 0} (f(x + \varepsilon) - f(x - \varepsilon))$	Jump of a function
$f _x = f(x)$	Value of function f at x
$\text{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x dz e^{-z^2}$	Error function
$\text{erfc}(x) = 1 - \text{erf}(x)$	Complementary error function
$\mathcal{D}_a(z)$	Parabolic cylinder function

Physical measures

$P(x, t)$ or $P(x, y, t)$	Probability density for x or x and y
$J(x, t)$	Probability current
$r(t)$	Spike rate
R	coefficient of variation
D_{eff}	Diffusion coefficient of spike count <i>or</i> spatial diffusion coefficient (chapter 4)
$S(\omega)$	power spectral density
η	Spectral power amplification
SNR	Signal-to-noise ratio

List of Symbols

An index “+” or “-” indicates that the function or the jump of the function is taken at x_+ or x_- , respectively. Stationary values or functions are labelled with index “0”. All quantities considered in this work are non-dimensional unless stated otherwise. Throughout this work, the numerical error of results obtained by computer simulations is within symbol size, unless error bars are shown.

1. Introduction

Noise-induced phenomena in nonlinear dynamical systems are nowadays popular topics in statistical physics with applications in many other scientific fields, too. One guiding idea behind much of the current research is the notion that fluctuations can be more than a nuisance but may play a constructive (“ordering”) role in systems far from thermodynamic equilibrium. Two manifestations of this principle are *coherence* and *stochastic resonance* that are the subjects of the present work.

Coherence resonance (CR) occurs in excitable systems that are driven by noise. The system’s output appears to be most regular (most coherent) when the level of input noise attains a certain *finite* value. In this case, the system possesses a noise induced eigenfrequency that becomes apparent in the power spectral density of the output. In the first main part of this work we shall study this phenomenon in two neuron models, namely, the leaky integrate-and-fire (LIF) neuron and the FitzHugh-Nagumo (FN) model. Furthermore, we will explore *coherent motion* of Brownian particles in a tilted periodic potential - an effect that is closely related to coherence resonance.

Stochastic resonance (SR) is observed in a broad class of nonlinear systems that are driven by a signal and noise. Here, the optimal (finite) noise intensity results in a maximal response of the system to the signal. In other words, the system is looked upon as a *signal detector* and the detection is enhanced by the assistance of fluctuations. This scheme is most natural for *neurons* - stochastic units subject to various sources of noise and to signals they are supposed to transmit and/or process. The second main part of this work is devoted to stochastic resonance in the LIF and FN models driven by noise and periodic signals. A question of particular interest will be how the noise-induced eigenfrequency and hence coherence resonance influences the SR features of these systems. Furthermore, in case of the LIF model we do not restrict ourselves to an additive periodic forcing and noise. In contrast to this conventional scheme of SR we shall also take account of possible signal dependent modulations of the amplitude of fluctuations. The latter is called a *noise coded* signal and appears quite natural in the neuronal context.

Most of the findings in this thesis are based on analytical results that might be important also for other physical phenomena encountered in the considered systems. We would like to draw the reader’s attention to the following main results the detailed derivation of which she or he may find here. These are analytical expressions for

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1. the power spectrum of the white noise driven leaky integrate-and-fire (LIF) model,
2. the linear response function of the LIF model driven by an additive signal,
3. the linear response function of the LIF model driven by a noise coded signal,
4. the effective diffusion coefficient and the Péclet number for the overdamped Brownian motion in a tilted washboard.

Furthermore, some approximate results are achieved for

5. an adiabatic elimination procedure for a two-dimensional excitable system driven by white noise,
6. power spectrum and linear response function of a piecewise linear FN model in the absence and presence of an additive signal, respectively.

Note that two of our results (2 and 4) have been very recently obtained by other groups (Brunel et al., 2001; Reimann et al., 2001). Furthermore, we would like to remark that some results (1,2 and 6) were achieved applying and extending a method developed by Melnikov (1993). A reader with inclination towards calculation technics for stochastic systems should certainly consult this paper.

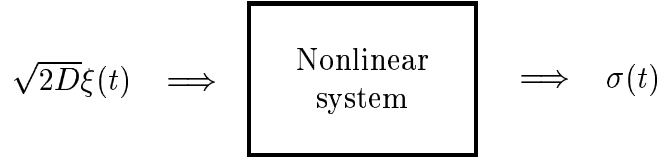
Most of the relevant results presented here have been published in four papers. As an exception to this, chapter 2 covers unpublished results on the white noise driven LIF model and coherence resonance in this system. Chapter 3 details the findings on the stochastic FitzHugh-Nagumo model published in Lindner and Schimansky-Geier (1999, 2000). In chapter 4 we present the results on coherent particle transport in periodic potentials (Lindner et al., 2001) supplemented by some additional comments. The signal transmission through leaky integrate-and-fire models discussed in chapter 5 is an extensive reanalysis of the issues addressed in Lindner and Schimansky-Geier (2001). Finally, in chapter 6 we reconsider the periodically driven stochastic FitzHugh-Nagumo system based on the results from (Lindner and Schimansky-Geier, 2000). We conclude in chapter 7 with some remarks about the potential meaning of our results for neuronal signal transmission.

Throughout this work, computer simulations are mainly employed for the validation of theoretical findings. Particular emphasis is put on the explanation of the analytical approaches and detailed derivation of the results. References to previous work on specific models are given in the beginning of each chapter.

Here, we proceed with a more general introduction of coherence and stochastic resonance stressing specific aspects addressed in this work. The last section gives a brief overview of the neuronal dynamics and, furthermore, deals with noise and different kinds of signals in simple model neurons.

1.1. Coherence resonance - basic effect and measures

Consider a nonlinear dynamical system driven by external fluctuations with intensity D .



If the noise is uncorrelated it does not directly introduce a new time scale in the system. However, there are generically different time scales within the system itself that dominate the system's dynamics depending on the noise level D . In certain dynamical systems the output $\sigma(t)$ may look *most regular* neither at vanishing nor at infinite D but at a finite noise intensity. Put differently, adding noise to this system increases - a little surprisingly at the first glance - the order of the output. As a consequence of the regularity, there exist a noise-induced peak in the power spectrum of the output variable. One may also speak of noise induced oscillations - a term that was already introduced in the 1980's (Wiesenfeld, 1985; Ebeling et al., 1986).

The effect has been differently named: *stochastic resonance without external periodic driving* (Gang et al., 1993), *internal* (Neiman et al., 1997a) or *autonomous stochastic resonance* (Longtin, 1997) and *coherence resonance* (Pikovsky and Kurths, 1997). In the following we will use exclusively the latter denotation that has been widely accepted within the recent past.

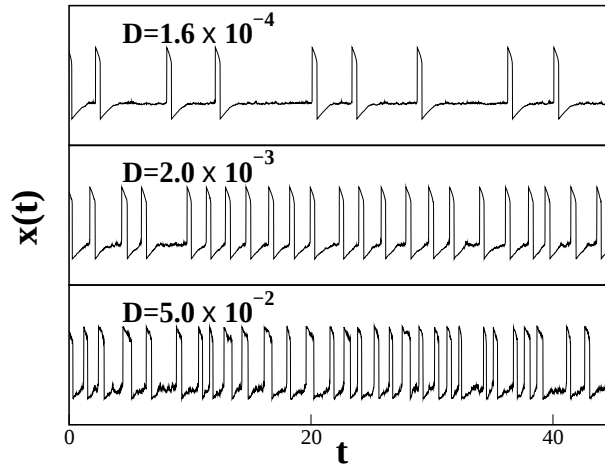


Figure 1.1.: Coherence resonance in the FitzHugh-Nagumo model. Numerical simulations of the stochastic dynamics eq. (3.4) introduced in chapter 3 with $\gamma = 1.5$, $b = 0.6$, $\epsilon = 10^{-3}$.

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An example for coherence resonance is shown in Fig. 1.1. Here, the nonlinear system is the FitzHugh-Nagumo model driven by noise. This model generates a spike train that mimics the spontaneous electric activity of an excitable nerve cell. The crucial point is that this spike train is most regular for the intermediate noise intensity corresponding to the trace in the mid panel. In the following we describe in which systems this effect has been encountered and by which measures it can be quantified.

First of all, the CR phenomenon has been found in a number of theoretical models. Gang et al. (1993) studied a system in which a limit cycle appears via a saddle-node bifurcation by tuning of a control parameter (see also Rappel and Strogatz, 1994). They demonstrated that for the control parameter being at its critical value the system exhibits a most regular behavior when a finite noise is added.

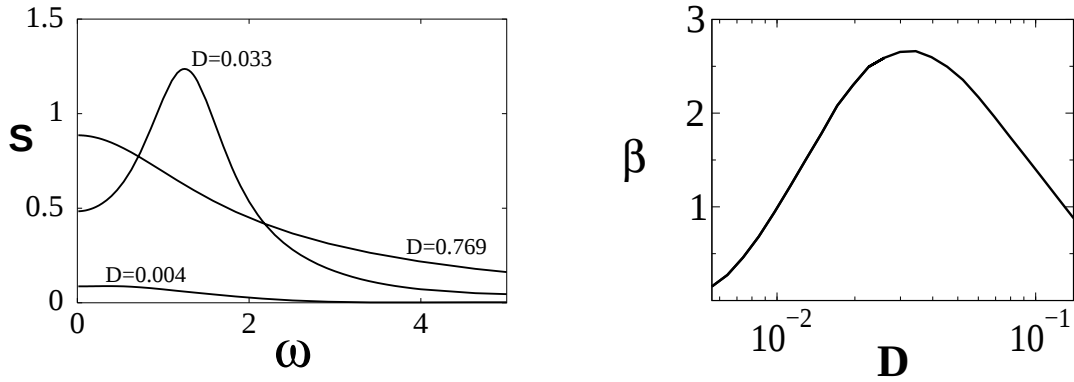


Figure 1.2.: Coherence resonance quantified by the power spectrum. For a certain range of noise intensities a peak at finite frequency appears (l.h.s.) that can be described by the degree of coherence β (r.h.s.). Data result from a theory for a piecewise linear FitzHugh-Nagumo model studied in chapter 3 but are very similar to the numerical findings in Gang et al. (1993).

This became evident by looking at the power spectrum of one of the variables $x(t)$

$$S(\omega) = \int_{-\infty}^{\infty} d\tau \langle x(t)x(t+\tau) \rangle e^{i\omega\tau} \quad (1.1)$$

that measures - roughly speaking - the periodic components in the stochastic trajectory. Here, the angular brackets indicate the average over a stationary ensemble.

As common in the literature, we used in eq. (1.1) the Wiener-Khintchine theorem (Risken, 1984) for introducing the power spectrum. Actually, it is defined by means of the *random spectrum* $\tilde{x}(\omega)$ of the variable $x(t)$ within the observation time $(0, T)$ (Stratonovich, 1967)

$$S(\omega) = \lim_{T \rightarrow \infty} \frac{\langle |\tilde{x}(\omega)|^2 \rangle}{T}, \quad \tilde{x}(\omega) = \int_0^T dt x(t) e^{i\omega t}. \quad (1.2)$$

It can be readily seen by both definitions that the integrated spectrum yields, apart from a prefactor, the total “power” of the process, i.e., its variance

$$\int_{-\infty}^{\infty} d\omega S(\omega) = 2\pi \langle x^2(t) \rangle. \quad (1.3)$$

Indeed, due to coherence resonance the spectrum exhibits a peak at finite frequency for a certain range of noise intensities (cf. Fig. 1.2, l.h.s.). The peak height and width depends nonmonotonously on the intensity of the applied noise. In order to quantify the resonance Gang et al. (1993) used the *degree of coherence*

$$\beta = \frac{S(\omega_{\max})}{\Delta\omega/\omega_{\max}} \quad (1.4)$$

where $S(\omega_{\max})$ is the height of the spectral peak at the frequency $\omega_{\max}$, while $\Delta\omega$ is the typical width of the peak and, consequently, $\Delta\omega/\omega_{\max}$ is a *relative* width. Usually, $\Delta\omega$ is the difference between the frequencies for which the spectrum has dropped to a certain fraction $1/a$ of $S(\omega_{\max})$, e.g., $a = 2$ (half width) or $a = e$. The function β was shown to pass through a maximum as a function of noise intensity (cf. Fig. 1.2, r.h.s.) thus exhibiting a resonance like behavior. Note once more that the oscillation that manifests itself in the spectral peak has an *internal* origin since the system is only driven by noise. External periodic forcing, being a prerequisite for classic stochastic resonance, is absent.

A similar effect has been found in the above mentioned FitzHugh-Nagumo (FN) model by Pikovsky and Kurths (1997). This two-dimensional dynamical model (introduced and studied in detail in chapter 3) exhibits also a bifurcation although a supercritical Hopf instead of a saddle node bifurcation like in Gang et al. (1993). Below the bifurcation point the system shows *excitability*, i.e., an external perturbation driving the system beyond a certain region results in an over proportional stereotype response of the system. Noise induces repeatedly these excitation events, that are seen in the phase plane as the motion of the state point on a *noise-induced limit cycle*. Projected onto a single variable as a function of time this limit cycle motion reduces to a fluctuation around a mean value interrupted by occasional spikes. It was already shown in Fig. 1.1 that this spike train is most regular for a moderate noise intensity. Pikovsky and Kurths (1997) did not use the power spectrum but two other measures to quantify the effect: the coefficient of variation (CV) and the correlation time. The former is the relative standard deviation of the intervals between spikes

$$R = \frac{\sqrt{\langle \Delta T^2 \rangle}}{\langle T \rangle}. \quad (1.5)$$

For a Poissonian spike sequence, the CV is one, for a strictly periodic train it vanishes. Noise induced coherent spike timing like in Fig. 1.1 yields a value in between these limits. The correlation time was defined by the integral over the square of the normalized

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auto correlation function of one stochastic variable $y(t)$ of the FN model.

$$\tau_{\text{corr}} = \int_0^\infty d\tau C^2(\tau), \quad C(\tau) = \frac{\langle (y(t) - \langle y \rangle)(y(t + \tau) - \langle y \rangle) \rangle}{\langle y^2 \rangle} \quad (1.6)$$

A rather regular spike train certainly exhibits a slowly decaying and possibly oscillating correlation function that yields a large correlation time.

It is intuitively clear that R and τ_{corr} both quantify the regularity of the spike train. As a manifestation of coherence resonance the CV attains a minimum (shown in Fig. 1.3, r.h.s.) and the correlation time a maximum at roughly the same noise intensity (Pikovsky and Kurths, 1997). These numerical findings were accompanied by a qualitative explanation based on the presence and distinct noise dependence of two different time scales in the system. These are the activation time the system needs to get excited by the noisy input and the excursion time taken by the system's response (the spike) including the times spent in firing and refractory state. Both (stochastic) time intervals are illustrated in Fig. 1.3 (l.h.s.). In the noise-free case the activation time is infinite while the excursion time (measured by a single external perturbation) takes a finite value. With growing noise intensity, the activation time drops strongly whereas the excursion time decreases only slightly and exhibits also only a small jitter. Eventually, for large noise intensity the activation time becomes negligible while the excursion time exhibits a considerable variance - here, the noise simply dominates the dynamics and internal time scales become less important. Coherence resonance occurs for intermediate values of the noise intensity where the activation time is rather short (compared to the excursion time) and the variance of the excursion time is still small.

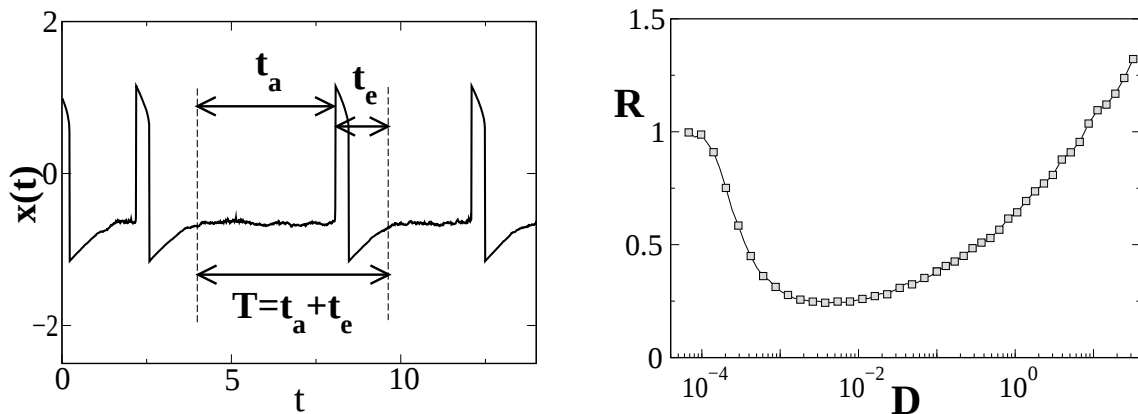


Figure 1.3.: Left: the interval between two spikes consist of two distinct times: the activation time t_a and the excursion time t_e (suboptimal case Fig. 1.1, upper trace). Right: coherence resonance quantified by the coefficient of variation R . Numerical simulation of the FitzHugh-Nagumo model with $\gamma = 1.5, b = 0.6, \epsilon = 10^{-3}$, see chapter 3 for details of the dynamics.

This can be seen by a simple consideration of the squared coefficient R^2 that becomes

minimal at the same noise intensity like R . Assuming statistical independence between the two times we obtain for the squared coefficient of variation

$$R^2 = \frac{\langle \Delta(t_a + t_e)^2 \rangle}{\langle T \rangle^2} = \frac{\langle \Delta t_a^2 \rangle \langle t_a \rangle^2}{\langle t_a \rangle^2 \langle T \rangle^2} + \frac{\langle \Delta t_e^2 \rangle \langle t_e \rangle^2}{\langle t_e \rangle^2 \langle T \rangle^2} = R_a^2 \left(\frac{\langle t_a \rangle}{\langle T \rangle} \right)^2 + R_e^2 \left(\frac{\langle t_e \rangle}{\langle T \rangle} \right)^2 \quad (1.7)$$

where R_a and R_e denote the coefficients of variation of activation and excursion time, respectively. If we assume a Poissonian process for t_a , the coefficient R_a is one and the first term will be the squared ratio of activation time and interspike interval. For increasing noise intensity this term drops rapidly from one to almost zero, while the second term increases in both factors: the jitter of the excursion time R_e as well as the ratio $\langle t_e \rangle / \langle T \rangle$ both starting at zero for vanishing noise increase with noise intensity. The minimum in R^2 (and hence in R) appears as a compromise at a noise intensity where both terms are just small, i.e., the noise strength suffices to generate a small activation time compared to the excursion time, while it is still weak enough to introduce only a small jitter in the excursion time. In this case the noise induced oscillations are mainly determined by the rather regular excursion time and may thus look regular itself. In general, the effect is the more pronounced the larger the ratio between excursion and activation time at moderate noise is.

There are, however, many more systems that exhibit the effect. Longtin (1997) found coherence resonance (which he called autonomous stochastic resonance) in Plant and Hindmarsh-Rose models of bursting neurons. In the Plant model the effect is mainly based on a subthreshold oscillation of a slow variable in the model, i.e., coherence resonance appears as a synchronization with the internal clock at a moderate noise intensity. In contrast, the CR effect in the Hindmarsh-Rose model was again due to a saddle node bifurcation. In both cases the degree of coherence β as well as the signal-to-noise ratio (SNR) were maximal at finite noise intensity. Here, the SNR was defined by the ratio of integrated power to the noisy background and turned out to be more suitable to quantify CR in the Hindmarsh-Rose model.

Further evidence of CR was found by Neiman et al. (1997a) for the noisy Feigenbaum map, for two coupled maps of this kind and for the three dimensional Rössler system. All three systems undergo a period doubling bifurcation if a control parameter is tuned. The authors interpreted CR as a noisy precursor of this bifurcation at subcritical control parameter value. In other words, in the presence of noise, deterministic eigenfrequencies may become visible already in a parameter range where the deterministic system does not exhibit them (see also Wiesenfeld, 1985).

Coherence resonance was further observed in the stochastic Hodgkin-Huxley model (Lee et al., 1998), in a model laser with saturable absorber (Dubbeldam et al., 1999), in a noisy prey-predator model (Rai and Singh, 2000), and in a pair of coupled chaotic oscillators (Liu and Lai, 2001). It has been furthermore reported for models of excitable biomembranes (Zhong and Xin, 2000), for a unidirectionally coupled chain of Brusselator models (Jiang and Xin, 2000), for the Adler equation (Qian et al., 2000), and for a

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chemical model system (Zhong and Xin, 2001). Makarov et al. (2001) found CR in the FN model in a regime where subthreshold oscillations occur (Canard phenomenon) and the model exhibits excitable as well as oscillatory properties. Katsev and L’Heureux (2000) proposed that CR may be a formation mechanism for the regular variations of chemical composition (regular zoning) occurring in many natural minerals. CR like effects in spatial extended systems were studied in Neiman et al. (1999); Hempel et al. (1999); Wang et al. (2000); Hu and Zhou (2000), demonstrating generally that CR is improved by coupling and may result in a synchronization of the elements. Other studies have focused on the role of possible correlations of the noise (neglected in most of the above work), using e.g., colored Ornstein-Uhlenbeck (Casado, 1997) or harmonic noise¹ (Wu et al., 2001) as a source of fluctuations in the FitzHugh-Nagumo and the Hindmarsh-Rose models, respectively. Since by such fluctuations additional time scales are introduced one also finds “resonances” by tuning the correlation time of the noise. The first experimental observation of coherence resonance was reported for a weakly ionized magnetoplasma in I and Liu (1995). Postnov et al. (1999) found the effect occurring in an electronic circuit (monovibrator) with noise input and examined the enhancement of the coherence if the output of a noise driven circuit is used as the input for a whole cascade of such circuits. Coupled monovibrators were investigated in Han et al. (1999) revealing a phase locking between the coherent resonance oscillators. Furthermore, CR was found for a semiconductor laser diode subject to optical feedback (Giacomelli et al., 2000). Here, the coherence of the output was quantified by an entropy that took a minimal value at finite noise intensity. Eventually, evidence has been given that CR may explain oscillation features of an atomic cloud which is optically trapped (Wilkowski et al., 2000).

Turning back to the theory, we would like to point out that most of the quoted work employed numerical simulations to explore the CR phenomenon. Some analytical results for coherence resonance in the FitzHugh-Nagumo system were presented in Lindner and Schimansky-Geier (1999, 2000). The approximation used in this work is based on a perfect time scale separation between the two variables of the system. In this case the two-dimensional excitable dynamics separates into *two* one dimensional subsystems coupled by currents of probability. By this approach the probability flux around the noise-induced limit cycle is still captured and stationary probability densities, the spike rate and the coefficient of variation can be calculated. By further reasonable simplifications it is also possible to calculate the power spectrum of the fast variable. All this will be detailed and supplemented by some novel findings in chapter 3.

Besides the above discussed two and three-dimensional systems there are actually two simpler dynamical models in which CR or a CR-like effect can be found. The first is the leaky integrate-and-fire (LIF) neuron model, an one-dimensional system with threshold and reset conditions that is used in neurobiology as a spike generator model.

¹These are fluctuations with a preferred frequency band generated by the dynamics of a white noise driven harmonic oscillator. For more details, see (Schimansky-Geier and Zülicke, 1990).

In chapter 2 we will show by different measures that the output of the model, i.e., the generated spike train exhibits a noise induced eigenfrequency and increased regularity at a finite optimal noise intensity. We stress that the effect is different from the noise-induced coherence found in coupled networks of integrate-and-fire neurons reported by Rappel and Karma (1996).

The second simple model exhibiting a CR like effect is the overdamped motion of a Brownian particle in a tilted periodic potential (“washboard”) (Lindner et al., 2001) - one of the classics in the theory of stochastic processes (Stratonovich, 1967; Risken, 1984) that is still the topic of many investigations (see, e.g., Costantini and Marchesoni, 1999; Reimann et al., 2001). The phase dynamics of some of the above mentioned two-dimensional dynamical systems (Gang et al., 1993; Pikovsky and Kurths, 1997) correspond in a way to the washboard dynamics (Kurrer and Schulten, 1995; Rappel and Strogatz, 1994), i.e., to the position of the particle. The phase in the FitzHugh-Nagumo model, for instance, is given by the angular variable that parameterize the noise-induced limit cycle while the stable and unstable fixed points on the cycle determine the minima and maxima of the periodic potential. One may ask whether the coherence resonance observed in the excitable system possesses a counterpart in the particle motion on the washboard potential. This will be explored in chapter 4 by means of mean velocity v , effective diffusion coefficient D_{eff} and Péclet number Pe given by

$$v = \lim_{t \rightarrow \infty} \frac{\langle x(t) - x(0) \rangle}{t}, \quad D_{\text{eff}} = \lim_{t \rightarrow \infty} \frac{d \langle \Delta x^2 \rangle}{dt} \frac{1}{2}, \quad Pe = \frac{vL}{D_{\text{eff}}} \quad (1.8)$$

with $x(t)$ denoting the particle position and $\Delta x^2 = x^2(t) - \langle x(t) \rangle^2$ the square displacement. The Peclet number characterizes the regularity of motion. It will turn out in chapter 4 that this number goes through a maximum as a function of noise which is a manifestation of *coherent transport* of particles that is in close relation to the coherence resonance phenomenon. Moreover, for a specific shape of the potential also the effective diffusion coefficient may attain a minimal value - a much more pronounced coherence than found for the typical cosine potential. Put differently, in this case *an increase in thermal noise causes a decrease in particle diffusion*.

We will adopt the diffusion coefficient also as a measure for coherence resonance in FN and LIF models. In these systems, the number of excitations or spikes appearing in a certain time, the so-called spike count undergoes a dispersion that grows linearly with time and can thus be characterized by a diffusion coefficient. Moreover, by a formula from renewal theory this diffusion coefficient can be expressed by means of stationary excitation rate and coefficient of variation R . This and other relations between the different measures are briefly discussed in the following.

Some remarks on the measures of coherence resonance

We have introduced the power spectrum, the coefficient of variation R , the correlation time τ_{corr} and the spike count diffusion coefficient D_{eff} as measures for coherence reso-

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nance. Here, we discuss relations between these measures and attempt to distinguish between weak and strong criteria for the CR effect. First, we will try to estimate the correlation time by means of the coefficient of variation. Second, we show that a mere minimum in the coefficient of variation does not suffice to speak of an noise induced eigenfrequency. It will emerge that among the characteristic R , D_{eff} and τ_{corr} , the CV is the weakest and the diffusion coefficient the strongest criterion for coherence resonance.

We consider a point process for a sort of events called *spikes*. For the LIF neuron this process is simply given by the generated spike train. In case of the FN model one may define it by the instances at which a certain variable crosses a fixed level from below. This is actually the way in which interspike intervals are determined in neuron models like the FN or Hodgkin-Huxley model. If the continuous variable shows a regular spiking behavior this will be certainly reflected in the point process. Furthermore, for the LIF and FN models driven by fluctuations, the resulting point process will be a *renewal process* (Cox, 1962), i.e., intervals between subsequent points are statistically independent of each other. If this is so, how can the process be regular? It can be quite regular if the distribution of interspike intervals is peaked around a certain finite interval τ . The extreme case would be a δ function at τ . Formally, we draw independent realizations from this “distribution” and get always the same interval. The resulting spike train is completely periodic and the correlation time of it should be infinite. The trivial example shows that independence of the *intervals* does not necessarily imply independence of the *firing times*.

For a renewal process the variance of the spike count will grow linear in time. The prefactor of this relation is determined by mean and variance of the interspike interval (Cox, 1962) leading to the following relation between diffusion coefficient D_{eff} coefficient of variation R and spike rate r_0

$$D_{\text{eff}} = \lim_{t \rightarrow \infty} \frac{d}{dt} \frac{\langle n^2(t) - \langle n(t) \rangle^2 \rangle}{2} = \frac{1}{2} \frac{\langle \Delta T^2 \rangle}{\langle T \rangle^3} = \frac{1}{2} R^2 r_0. \quad (1.9)$$

From the definition of the correlation time eq. (1.6) it is not straightforward how to define an equivalent for the point process. One might possibly define it by the spike-spike correlation function (Stratonovich, 1967; Jung, 1994) or by means of the distribution functions for the process (Stratonovich, 1967). However, here we content ourselves with a simple estimate that can be expressed by the diffusion coefficient and the firing rate.

Provided that we know about the occurrence of a spike at a certain time, how much can we say about the timing of subsequent events? The drawing in Fig. 1.4 shows the initial spike and the expected adjacent spikes. The respective standard deviation around the expected position will be $\sqrt{n \langle \Delta T^2 \rangle}$ and grow with the distance to the initial spike. If the window given by the standard deviation is much smaller than the mean interval the spike can be obviously looked upon as still correlated to the initial spike. The correlation is certainly lost if the standard deviation is equal to the mean interval.

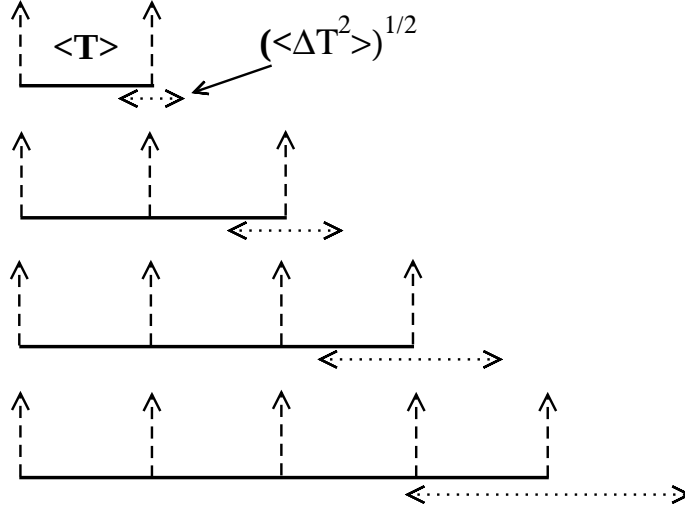


Figure 1.4.: Illustration of the correlations of spiking times for a renewal process. Given the position of the initial spike at t_0 , the next spike is expected at $t_0 + \langle T \rangle$ with the uncertainty determined by the jitter, i.e., the standard deviation of the interval T (upper row). Since the intervals are independent the uncertainty for the next but one spike will be $\sqrt{2}$ times the jitter of a single interval and so forth (lower rows). The growth of the jitter in the drawing is only schematic.

For this spike number n_{uncorr} one finds (expressing the standard deviation by CV and mean interval)

$$\sqrt{n_{uncorr}} R \langle T \rangle = \langle T \rangle. \quad (1.10)$$

Now, assume that the preceding spike is just correlated, then we get as an upper limit for the correlation time

$$\tau_{corr} \approx (n_{uncorr} - 1) \langle T \rangle = \left(\frac{1}{R^2} - 1 \right) \langle T \rangle = \frac{1}{2D_{eff}} - \frac{1}{r_0}. \quad (1.11)$$

This tells us that the correlation time is zero for a Poisson process ($R = 1$) and infinity for a strictly periodic (i.e., deterministic) process ($R = 0$), as expected². Clearly, the above line of reasoning is by no means a strict derivation of a correlation time, however, under certain soft assumptions eq. (1.11) should yield a rough estimate for the order of magnitude of the correlation time. One of these assumption is that the process is more regular than a Poisson process ($R < 1$), otherwise the estimate eq. (1.11) will be negative and therefore senseless.

Provided that the derivative of the mean interval (i.e., that of $1/r_0$) is monotonously decreasing (as it is indeed the case for LIF and FN model) one may show that a local minimum in the diffusion coefficient (i.e., a maximum in $1/D_{eff}$) implies a maximum

²Note that the first term in the r.h.s. of eq. (1.11) equals the time during which the variance (and also the standard deviation) of the *spike count* increases by one.

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in the correlation time. This does not hold vice versa, in general. For this reason, in this work we use the diffusion coefficient but not the correlation time as a measure of coherence resonance.

One of the most frequently employed quantities in characterizing coherence resonance is the coefficient of variation eq. (1.5). We conclude this section with the question: Does a minimum in the coefficient of variation suffice as a criterion for a noise-induced eigenfrequency? We give here a simple example where this is *not* the case.

Consider the bistable system depicted in Fig. 1.5. An overdamped Brownian particle is subjected to the potential force of a double well and to thermal fluctuations with different intensities (temperatures) in both wells.

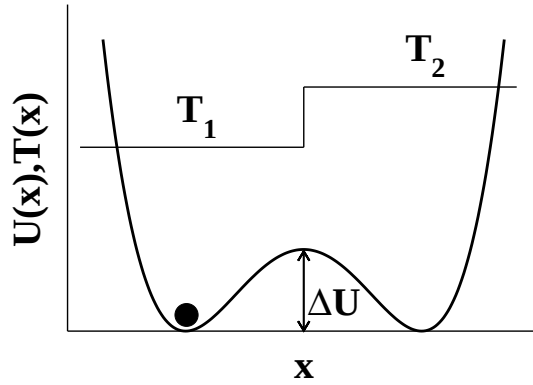


Figure 1.5.: Brownian particle in double well potential with different temperatures.

For this *Kramers oscillator with multiplicative noise* the corresponding point process can be defined, for instance, by the transition times from left to right. We assume low temperatures at which the dynamics can be approximated by a Poissonian two state process with the transition rates from left to right

$$r_1(T_1) = ae^{-\Delta U/(k_B T_1)} \quad (1.12)$$

and vice versa

$$r_2(T_2) = ae^{-\Delta U/(k_B T_2)}. \quad (1.13)$$

where ΔU , k_B and a stand for the potential barrier, the Boltzmann constant and the inverse relaxation time, respectively.

Now, fix T_1 and vary T_2 which implies a variation of r_2 at fixed r_1 since r_1 and r_2 are monotonous functions of T_1 and T_2 . Because of the Poissonian approximation and the statistical independence of the two subsequent escape processes belonging to one cycle we obtain

$$\begin{aligned} \langle T \rangle &= \langle T_1 \rangle + \langle T_2 \rangle = \frac{1}{r_1} + \frac{1}{r_2} \\ \langle \Delta T^2 \rangle &= \langle \Delta T_1^2 \rangle + \langle \Delta T_2^2 \rangle = \langle T_1 \rangle^2 + \langle T_2 \rangle^2 = \frac{1}{r_1^2} + \frac{1}{r_2^2} \end{aligned}$$

and thus

$$R = \frac{\sqrt{r_2^2/r_1^2 + 1}}{r_2/r_1 + 1}. \quad (1.14)$$

The function R tends to one in the limit $r_2 \rightarrow 0$ ($T_2 \rightarrow 0$) and for $r_2 \rightarrow \infty$ ($T_2 \rightarrow \infty$) to

$$\sqrt{1 - \frac{1}{2 \cosh(\Delta U/(2k_B T_1))}} \quad (1.15)$$

which is practically also one for sufficiently small T_1 . In both limits the process is thus reduced to effectively *one* state - that one with a smaller rate while the other state is left very fast and not important for the interval statistics. Between these limits there exists a minimum attained at

$$\frac{dR}{dr_2} = 0 \Rightarrow r_2 = r_1 \rightsquigarrow R_{min} = 1/\sqrt{2}, \quad (1.16)$$

i.e., in case of equal temperatures. Thus, we have tuned the “noise intensity” (temperature T_2) such that the system is symmetric and obtained a minimum in R . But the symmetric system in the above two state approximation corresponds to one of the standard stochastic processes, namely, the random telegraph noise, commonly looked upon as a rather irregular process. First of all, the diffusion coefficient

$$D_{\text{eff}} = \frac{r_2}{2} \frac{r_2^2/r_1^2 + 1}{(r_2/r_1 + 1)^3} \quad (1.17)$$

is monotonous in r_2 (and T_2) as can be shown by inspection of its derivative. Furthermore, within the two-state approximation we may readily calculate the other characteristics of the process. Its power spectrum exhibits the well known Lorentz shape without any noise induced eigenfrequency for arbitrary rates and also at $r_1 = r_2$. From the normalized auto correlation function (e.g., in Gardiner, 1985, p. 79)

$$C(\tau) = \exp[-(r_1 + r_2)\tau] \quad (1.18)$$

we find the correlation time according to the definition eq. (1.6)

$$\tau_{\text{corr}} = \int_0^\infty d\tau C^2(\tau) = \frac{1}{2(r_1 + r_2)} \quad (1.19)$$

that is clearly a monotonic function of T_2 .

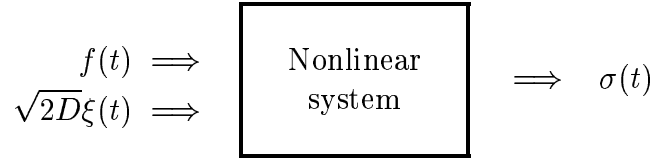
The minimum of R is merely a consequence of the fact that we have considered a process which at equal temperatures consists of *two* subsequent equal Poisson steps. Such a process and also its generalization to n steps (cf. the Gamma function in probability theory) are known to be more regular than a single Poisson process. By our scaling of the rates (dictated by the physics illustrated in Fig. 1.5) we go with

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increasing temperature from one state to two states and again back to one state. The conclusion drawn from the above example is simple - a shallow minimum in the coefficient of variation is not sufficient to speak of a noise-induced eigenfrequency. The coefficient of variation is therefore compared to the correlation time, the spectrum and the diffusion coefficient the weakest criterion for coherence resonance. We will refer to the case where only the function R attains a minimum as *weak coherence resonance* since also in this case a small noise-induced increase in regularity of the system's output is present.

1.2. Stochastic resonance

Consider a system that is driven by two components: one denoted by $f(t)$ is a “signal”, the other $\xi(t)$ is a noise term.



The box in the above sketch represents either a dynamical system or a map driven by the input, an integral operator or simply a function of the input. The signal $f(t)$ can be a deterministic or stochastic function, a typical choice is a simple cosine function $f(t) = \varepsilon \cos(\omega t)$.

In general, the output will consist of a signal correlated and a noisy component. We may look upon the system as a signal transmission device. This poses the following questions.

1. How well is the input signal $f(t)$ reproduced by the output?

$\Rightarrow$ Output signal strength

2. How well can the output signal be separated from the noisy component?

$\Rightarrow$ Signal-to-noise ratio

We have included noise in the input (actually, this could be as well *internal* noise inherent to the system), so we may ask what the optimal noise intensity with regard to signal transmission is. One might be tempted to think that *vanishing noise* is obviously the correct answer. However, in a broad class of nonlinear systems this is *not true*. These systems exhibit an increased signal strength and signal-to-noise ratio at *finite* noise intensity. Furthermore, too large noise destroys the cooperative effect and we may thus conclude that there is a *finite optimal* noise level D for which output signal strength and signal-to-noise ratio attain maximal values. This is (in a broader sense) the celebrated stochastic resonance (SR) effect.

Since stochastic resonance was proposed as a possible mechanism for the recurrences of the ice ages by Benzi et al. (1981, 1982) and Nicolis (1982) it has been found in a variety of theoretical models as well as experiments in diverse scientific fields. Extensive reviews were given by Gammaitoni et al. (1998) and Anishchenko et al. (1999), more specific issues are addressed in the proceedings of two conferences on the topic (Moss et al., 1993; Bulsara et al., 1995). Here, we restrict ourselves to some simple examples and measures of SR and will point out the issues that are relevant in this work.

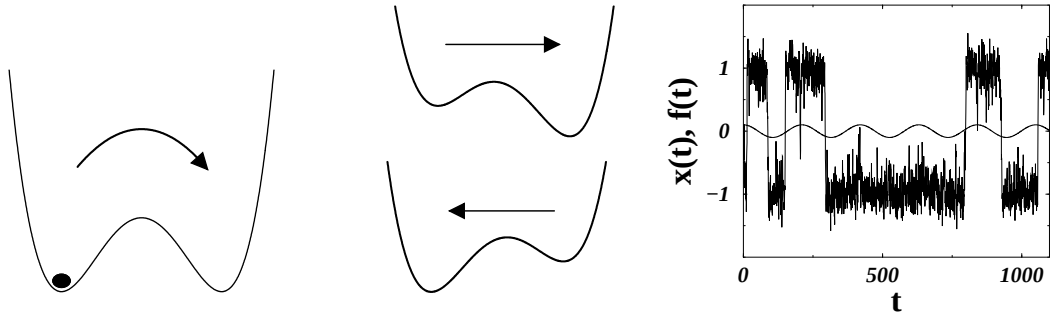


Figure 1.6.: Brownian motion in a quartic potential. Left: The potential $U(x)$. Middle: The effective potential at different instances, e.g., at $t = 0$ (above) and $t = \pi/\omega$ (below). Right: Signal and output (trajectory $x(t)$) of the system.

The mechanism for SR can be readily understood in systems with a barrier or threshold in which a *weak* deterministic signal cannot evoke a finite response in the absence of noise. An instructive example is the periodically forced Brownian motion in a bistable potential. Here, the periodic driving and the thermal fluctuations play the role of signal and noise, respectively, while the transitions from one well to the other determine the output³. In the high-friction limit this dynamics is (after a proper scaling) given by the stochastic differential equation

$$\dot{x} = -U'(x) + \varepsilon \cos(\omega t) + \sqrt{2D}\xi(t), \quad U(x) = \frac{x^4}{4} - \frac{x^2}{2}. \quad (1.20)$$

The force $-U'(x)$ and the signal $\varepsilon \cos(\omega t)$ can be lumped into one force resulting from the time dependent potential $U(x) - \varepsilon \cos(\omega t)x$. For a weak signal ($\varepsilon \ll 1$) and zero noise the particle oscillates within the well but does not jump into the other well since the time dependent potential barrier remains finite during the entire signal period (cf. Fig. 1.6, mid panel). The output is thus simply constant and does not reflect the periodic forcing. This changes if noise is finite. Escapes from one well to the other become possible, moreover, due to the time dependent asymmetry of the potential one of these transitions is favored at given signal phase (i.e., at a given time). Consequently,

³The particle dynamics within the single well (intrawell motion) is not considered because in most cases the hopping between the wells (interwell motion) is of more physical relevance (e.g., the transitions between ice and warm ages in Benzi et al. (1981)).

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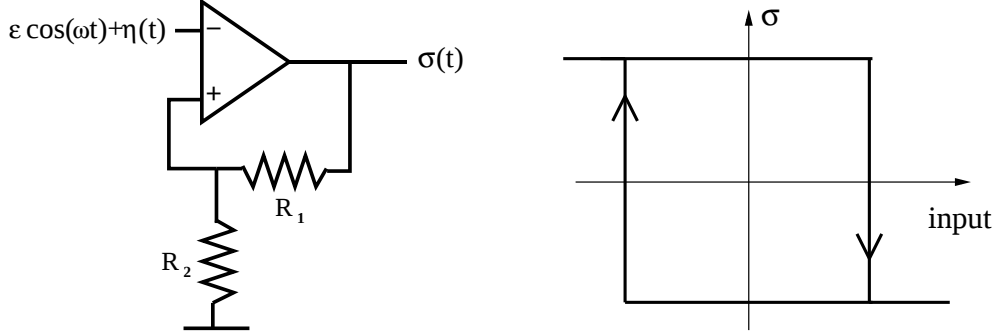


Figure 1.7.: Left: the circuit diagram of the Schmitt trigger. Signal and noise $V_-(t) = \varepsilon \cos(\omega t) + \eta(t)$ are applied to the non inverting terminal of the operational amplifier (OP) while the output of the OP is feed back into the inverting terminal via a voltage divider, i.e., $V_+ = R_2\sigma/(R_1 + R_2)$. The output of the OP $\sigma(t)$ is either $+V_0$ or $-V_0$ depending on the sign of the difference of its two inputs ($V_+ - V_-$). Starting with a $V_- < V_+$ and $\sigma = +V_0$, this state remains stable as long as these conditions hold. When $V_+ > V_-$ the trigger switches instantaneously into the other state $\sigma = -V_0$ and resides in this state as long as $V_- > V_+$. The resulting transfer function showing hysteresis is depicted in the right panel.

the hopping events are correlated with the input signal (cf. Fig. 1.6, right panel). One may expect that this is most pronounced if the mean transition time (i.e., the inverse hopping rate) matches the half period of the signal. This can be expressed by rate and signal frequency as follows

$$r_0(D) = \omega/\pi. \quad (1.21)$$

This is the time scale matching condition for stochastic resonance in symmetric bistable systems (Benzi et al., 1981; Gammaitoni et al., 1998). The trajectory $x(t)$ will behave in the following way: the hopping events are synchronized to the signal but with occasional dropouts and apparently uncorrelated transitions during the respective “negative” half period of the signal. We stress that the relation eq. (1.21) is not exact (Fox and Lu, 1993), in particular, the resonance condition holds approximately only for varying D at given frequency. The spectral response to the periodic forcing (see below), for instance, drops always with increasing frequency what underlines the statistical nature of stochastic resonance.

First experimental evidence for the effect was given by Fauve and Heslot (1983) who studied the spectral response of a Schmitt trigger driven by a periodic signal and noise. The circuit diagram and the transfer function are depicted in Fig. 1.7. The device is for a limited (subthreshold) range of input bistable and shows hysteresis. The output $\sigma(t)$ is discrete and switches between the two stable states like the Brownian particle in the above example between the potential wells. If the input signal’s amplitude is below a critical value the weak signal itself cannot evoke transitions. Again a finite amount of noise increases the probability of switching events that are most synchronized with

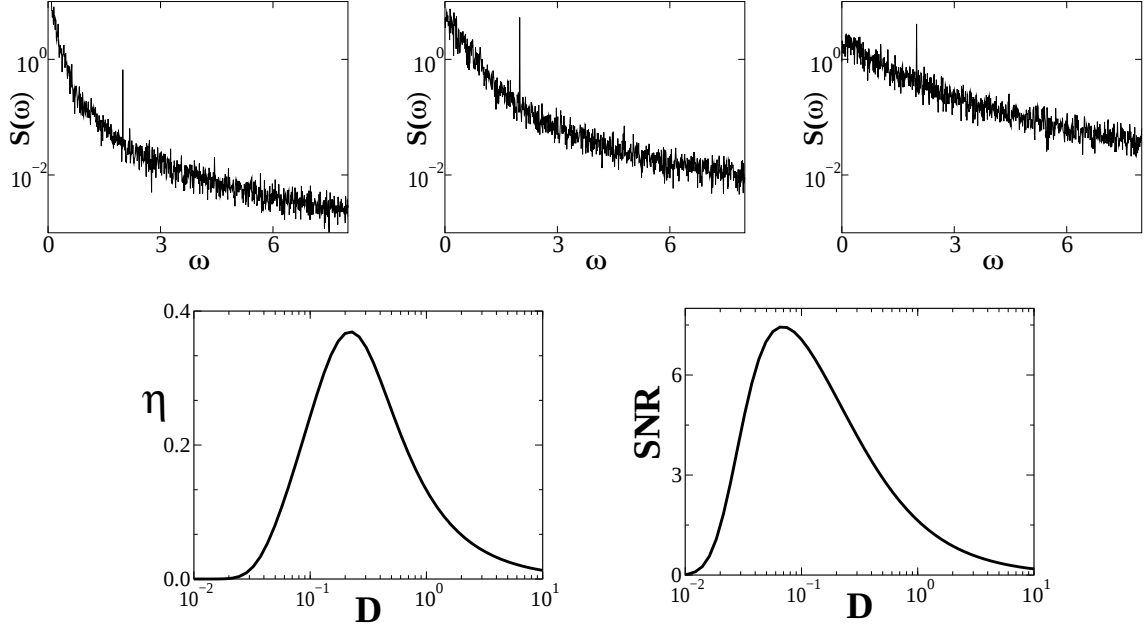


Figure 1.8.: Top: Power spectra of an ideal Schmitt trigger (results of a computer simulation) driven by a harmonic signal and Ornstein-Uhlenbeck noise with correlation time one. Driving frequency in all panels $\omega = 2$ while the noise intensity is $D = 0.03$ (left), $D = 0.1$ (middle), and $D = 1.0$ (right). Bottom: The spectral power amplification (left) and the signal-to-noise ratio (right) versus noise intensity D for a Schmitt trigger driven by a weak harmonic signal and Ornstein-Uhlenbeck noise with correlation time one. The curves are analytical results of a calculation by Melnikov (1993).

the output for a certain noise level.

These features are clearly seen in the power spectrum (Fauve and Heslot, 1983). Three spectra obtained by a computer simulation of an ideal Schmitt trigger are shown in Fig. 1.8. The spectrum consists of a peak at driving frequency superimposed on a continuous background (for larger signal amplitudes also peaks at higher harmonics may be observed). The peak height as well as its ratio to the noise background (in the logarithmic scale given as the peak height over the noise floor) are largest in the middle panel, i.e., for intermediated noise strength. To quantify this we consider the theoretical spectrum in which the spectral peak tends to a δ function because the observation time is infinite

$$S(\omega) = S_{\text{bg}}(\omega) + \frac{A_{\text{out}}}{2} [\delta(\omega - \omega_s) + \delta(\omega + \omega_s)]. \quad (1.22)$$

The output intensity is usually described by the spectral power amplification that is the ratio of output and input intensity

$$\eta = \frac{A_{\text{out}}}{A_{\text{in}}}. \quad (1.23)$$

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One advantage of this function is that it does not (at least for weak signals) depend on the signal amplitude. Likewise, we use here a scaled variant of the signal-to-noise ratio

$$\text{SNR} = \frac{\eta}{S_{\text{bg}}(\omega_{\text{sig}})}. \quad (1.24)$$

The Schmitt trigger is one of the rare examples of SR in dynamical systems for which both quantities in case of a weak signal can be exactly calculated (Melnikov, 1993). The resulting curves are shown in Fig. 1.8 (bottom) and reveal indeed maxima of the response and SNR with respect to the noise intensity. The maxima are attained at slightly different noise levels since the background spectrum contributes its own dependence on noise. Spectra and resonance curves of the forced Brownian particle as well as of other bistable systems are similar provided the output is two-state filtered (elimination of intrawell motion). Note that the frequency dependence of the response quantities is monotonously decreasing as above mentioned.

This is typical for bistable systems, however, two exceptions should be mentioned: If in a bistable system the depth of only one potential minimum is modulated, the SNR can exhibit a non-monotonous dependence on the driving frequency (Berdichevsky and Gitterman, 1996). The same feature is observed for certain globally coupled bistable systems (Gang et al., 1996).

We mention briefly, that the description of SR is not restricted to spectral measures. One may also use the distribution function for the escape times out of one stable state that displays a multimodal shape with peaks at multiples of the half driving period. Other measures come from information theory (see, for instance, Stemmler, 1996; Neiman et al., 1996) that are in part simply related to the spectral ones discussed above. For SR with stronger signal amplitude the notion of synchronization has turned out to be useful (Neiman et al., 1998). Here, we restrict ourselves to the spectral measures of stochastic resonance.

The signal has not to be additive and/or periodic nor should the dynamics be necessarily bistable in order to exhibit the SR phenomenon. One may consider, for instance, only one input, namely, a noise with signal dependent intensity ($\sqrt{2D[1+f(t)]} \xi(t)$) instead of additive signal and noise with a constant intensity. Stochastic resonance by tuning of the overall noise intensity D can be observed if the system displays a spatial asymmetry as was shown by Dykman et al. (1992) for the Brownian motion in an asymmetric bistable potential.

One may also consider a system where the periodic signal is replaced by a stochastic input. One example is a signal with finite spectral line width, e.g., a harmonic noise like in Neiman and Schimansky-Geier (1994). Furthermore, also entirely aperiodic signals may be used (Collins et al., 1995a). This *aperiodic* stochastic resonance can be quantified by either the spectral coherence function (Neiman et al., 1997b) or by the cross correlation coefficient also called the power norm (Collins et al., 1995a).

Most notably, SR can be observed in non bistable systems. The first example was the excitable dynamics of the FitzHugh-Nagumo model (Longtin, 1993; Wiesenfeld et al.,

1994; Longtin, 1995b). The research in this direction was much stimulated by experimental findings showing that *sensory neurons may benefit from noise* in their ability to detect weak signals. In these investigations sensory neurons of the crayfish (Douglass et al., 1993), the cercal system of the cricket (Levin and Miller, 1996), and of the rat (Nozaki et al., 1999) were stimulated with external noise and periodic or aperiodic signals. The signal-to-noise ratio or information theoretic measures passed through maxima by increasing the noise level. Similar findings were made in experiments on slices of the mammalian brain (Gluckman et al., 1996), on human muscle spindles (Cordo et al., 1996), and on human tactile sensation (Collins et al., 1996). Recently, also *behavioral stochastic resonance* could be verified (Russell et al., 1999): the juvenile paddlefish prey upon zoo plankton by detecting weak electric signals generated by the prey. The capture rate can be significantly enhanced by adding electrical noise from outside. Freund et al. (2001) gave theoretical evidence that in reality the required noise might be generated by a background swarm of plankton. All these findings demonstrate clear-cut evidence for stochastic resonance in biological systems and especially in living sensory neurons.

From a theoretical point of view the essential difference between the previously considered bistable systems and the neuronal dynamics is that the latter shows excitability and possesses only one stable (resting) state, while other states (firing and refractory) are unstable and left also in the absence of external perturbations and noise. However, the mechanism for SR is not much different in principal from that in bistable systems: a weak signal that alone cannot trigger escapes from the stable state and thus excitation events (i.e., action potentials), may induce them with a signal dependent probability if noise is present. The output of the neuron, that is the spike train will in this case exhibit a correlation to the weak signal which is impossible in the absence of noise. Obviously, at large noise the dynamics is - as in the bistable case - determined by noise alone, i.e., there is a finite optimal noise level as it has been also established in the aforementioned experiments.

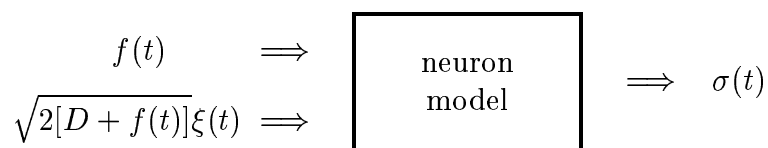
These features are also captured by nondynamical threshold models (Jung, 1994; Gingl et al., 1995; Chapeau-Blondeau, 1996; Gammaitoni, 1995; Chapeau-Blondeau and Godivier, 1997), given either by a function of the input (e.g., the Heaviside jump function of the input) or a detector that marks up-crossings for the input variable (i.e., signal plus noise). Gammaitoni (1995) has pointed out that SR in such systems is based on the *linearization of the transfer function by noise* or simply the *dithering effect* known from electronics: adding a small amount of noise to an input signal enhances the performances of analog-to-digital converters since it decreases (statistically) the *quantization error*.

The description of neurons by a transfer function and hence effectively by a non-dynamical threshold device seems to be in some way justified for very slow (adiabatic) signals. It must obviously fail if the neuronal dynamics and its internal time scales come into play. This is important for the following: in contrast to the bistable dynamics, the excitable neuronal dynamics displays besides the typical life time of the

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stable state also a quasi deterministic time scale associated with the decay of the unstable states. In the previous section we referred to them as activation and excursion times and mentioned that the presence of these time scales may introduce a certain order in the output even in absence of periodic stimulation, i.e., it results in coherence resonance and in a noise-induced eigenfrequency. This poses the question how the regularity of the neuronal output due to CR influences the SR features of neurons and other excitable dynamics. Numerical simulations by Massanés and Vicente (1999); Liu et al. (1999) and Kanamaru et al. (1999) indicate that in contrast to bistable systems the spectral response may be enhanced by tuning of the driving frequency, an effect referred to as *stochastic double resonance* (Plesser and Geisel, 1999b). If the driving frequency matches the noise induced eigenfrequency a classic resonance occurs. The first analytical results that confirmed these numerical findings were achieved in Lindner and Schimansky-Geier (2000) for the periodically driven FitzHugh-Nagumo system. These will be detailed in chapter 6.

The FitzHugh-Nagumo model is not the only neural model that has been investigated in detail in the context of stochastic resonance. A simpler model (already mentioned in the previous section) that exhibits stochastic resonance as well is the leaky integrate-and-fire neuron (Bulsara et al., 1996; Stemmler, 1996; Plesser and Tanaka, 1997; Plesser and Geisel, 1999b; Shimokawa et al., 1999b; Lindner and Schimansky-Geier, 2001). Here, we will study the impact of coherence resonance on the SR features of the transmission. It will be shown that - as in the FN model - the noise-induced eigenfrequency leads to a nonmonotonous dependence of the spectral response on the driving frequency of a periodic stimulation. Moreover, we will also investigate the response of the model to a signal dependent modulation of the noise intensity (noise coded signal). In the neuronal context the scheme is different from the above mentioned bistable one explored by Dykman et al. (1992).



First, in general both additive and noise coded signals are present. Second, the scaling of signal and overall noise intensity differs from that in Dykman et al. (1992). Due to this difference and due to the different nature of asymmetric bistable and LIF model it is not clear at all whether stochastic resonance is present for noise coded signals transmitted by the LIF model. By means of the analytical solutions for the linear response to additive and noise coded signals (Lindner and Schimansky-Geier, 2001) we will be able to compare the responses to both kinds of signal in chapter 5. The reason for the occurrence of these signals are elucidated in the next section.

1.3. Neurons and neuronal models - origins of noise and signals

Since we deal with two neuron models in this work a brief sketch of the (rather complicated) neuronal dynamics is indicated. Detailed surveys of neuronal models were given, for instance, by Holden (1976); Ricciardi (1977); Tuckwell (1988, 1989); Koch (1999).

A typical neuron consists of three components: the soma (cell body) and extending from the soma the dendritic branches and the axon. In all three parts the electric potential is not the same as in the surrounding medium, there is a *potential difference* or voltage across the nerve membrane. The latter is a lipid bilayer that is almost impenetrable for ions and acts thus as a capacitor. However, there are also *ion pumps* and *ion channels* within the membrane that maintain the aforementioned voltage or may change it, respectively

The neuron receives input from other neurons via *synaptic connections* (order of magnitude 10^4 on average) located in the dendritic branches and at the soma. A pulse of electric activity (spike) at the presynaptic neuron induces a release of *neurotransmitters*⁴ that diffuse across the *synaptic cleft* and cause a short-time opening of certain ion channels at the postsynaptic side. This conductance change in the postsynaptic membrane leads to a change in the membrane voltage. Under certain conditions (Koch, 1999) - assumed throughout the following - this may be approximated by a small current pulse that propagates (and decays) along the dendrite towards the soma. Depending on the nature of the synapse (*excitatory* or *inhibitory*) the current pulse is either positive or negative. In the soma all pulses are summed up (integrated) and lead to a voltage change across the nerve membrane in the *axon hillock* (spike initiating zone) that is, a particular excitable patch of the soma. In experiment the spikes from the dendrite can be mimicked by current injections into the soma or the axon.

If no currents are present, the voltage at the *axon hillock* is at rest which is for a typical neuron about $V_{rest} = -70mV$ with the exterior as a reference point. A small current induces also only small changes in the voltage. However, if the voltage reaches a certain threshold, a strongly nonlinear mechanism results in a fast (over proportional) raise of the voltage such that the membrane is *discharged* and becomes *depolarized*. Other mechanisms cause a *repolarisation* of the membrane which goes even beyond the resting value ($V < V_{rest}$) (*hyperpolarization*). The entire process is called an action potential or spike. Once a spike sets in, the shape of it does not depend on the details of the stimulus - the neuron performs an *all-or-none* response to current stimulation. Repeated stimulation will not cause an arbitrary large number of action potentials in a given time window - there exists a certain refractory period after spike generation in which the membrane cannot be discharged (*absolute* refractory period) or a larger current is required to evoke a spike (*relative* refractory period). Once a spike is gener-

⁴We restrict ourselves to the consideration of chemical synapses.

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ated it propagates down the axon and may cause itself a release of neurotransmitters at synaptic connections to other neurons. In this way, neurons communicate with each other. Because of the stereotype shape of the action potential, the whole information is carried by the timing of spikes (Rieke et al., 1996).

The nonlinear mechanism responsible for spike generation is due to specific ion channels with voltage-dependent opening probabilities in the cell membrane. In the celebrated model of the giant axon of squid by Hodgkin and Huxley (1952), the voltage-dependent conductances are two sorts of ion channels selective for sodium and potassium, respectively. The voltage dependencies of the conductances are governed by so-called gating variables m, n and h . The voltage dynamics is given by equation

$$C \frac{dV}{dt} = I_{Na} + I_K + I_{leak} + I_{syn}(t) \\ = \bar{g}_{Na} m^3 h (V - E_{Na}) + \bar{g}_K n^4 (V - E_K) + \bar{g}_{leak} (V - E_{leak}) + I_{syn}(t). \quad (1.25)$$

Here, C is the membrane capacity, the E_i and $\bar{g}_i$ are the reversal potentials and maximal conductances of the ion and ion channels, respectively. The gating variables are governed by first-order equations whose right-hand sides depend only but highly nonlinear on the voltage and the respective gating variable itself. In total this constitutes a four-dimensional dynamical system complicated to solve even for simple synaptic inputs. The Hodgkin-Huxley model, i.e., eq. (1.25) supplemented by the mentioned equations for the gating variables reproduce in detail features of the action potential generation in the squid axon due to current injections. In the same spirit, models have been designed that involve far more sorts of ion channels and are used for other specific neurons.

Most of the more tractable neuron models result from simplifications of the HH model and its modern variants. In the leaky integrate-and-fire (LIF) neuron, for instance, the voltage dependence of the conductances is completely ignored such that the whole equation becomes linear in V . It is convenient to write the equation for the deviation from the resting value and to normalize it by some constant V_0 (e.g., an effective threshold voltage) in order to get a non-dimensional variable, i.e., $v = (V - V_{rest})/V_0$

$$\tau_m \dot{v} = -v + R \tilde{I}_{syn}(t). \quad (1.26)$$

Here, $\tau_m = RC$ is the membrane time constant and R is an effective leak resistance. In order to reduce parameter redundancy, in chapter 2 and chapter 5 we will measure time in units of τ_m , i.e., we deal with a non-dimensional time and set $\tau_m = 1$, while the constant resistance R is always lumped into the effective input. The nonlinear spike generation mechanism mediated by the gating variables is replaced by a simple threshold condition. If a certain (constant) value v_T is reached a δ spike is generated that represents the onset of the action potential. After the spike generation, the neuron is in an absolute refractory state standing for the sum of both the duration of the action potential and the physiologically observed absolute refractory period. Then, the

voltage is reset to a value v_R that is not necessarily equal to the resting value. Note that in spite of the linearity of eq. (1.26) the threshold condition implies a strong non-linearity of this model. Although the approximations made are rather crude, the LIF model has been successfully applied in various situations and is the working horse of many theoretical investigations in neurobiology, in particular when networks of neurons are considered. For an impressive convergence of experimental data (monkey auditory neuron) and results obtained using the LIF model, see (Plesser, 1999).

Another approximation, the FitzHugh-Nagumo model (FitzHugh, 1961; Nagumo et al., 1962) is based upon the observation that the four variables of the Hodgkin-Huxley dynamics can be subdivided into two slow (sodium inactivation h and potassium activation n) and two fast variables (voltage V and sodium activation m). So one may combine the two slow and the two fast variables into a single voltage-like variable x and a recovery-like variable y . The qualitative behavior for these new variables is captured by the FitzHugh-Nagumo model that can be written as follows

$$\begin{aligned}\epsilon \dot{x} &= x - x^3 - y + I_{syn} \\ \dot{y} &= \gamma x - y + b.\end{aligned}\tag{1.27}$$

Here, ϵ stands for the ratio of the time scales of both variables and γ and b are some positive parameters that have to be in a certain range for the system to be excitable. The specific form of the nonlinearity in the first equation is not important - any other N-shaped function can also be used, in particular, a piecewise linear function does not need to be a bad choice (Abbott and Kepler, 1990). Contrary to the LIF model, the FN system generates an action potential the shape of which resembles much that of a real neuron. An advantage of the model as opposed to the HH system is that it is only two dimensional and can be analyzed by phase-space technics. Furthermore, regions in the phase plane can be identified with certain physiological states (FitzHugh, 1961). For more details see chapter 3.

We turn now to the question, how fluctuations enter the dynamics of the neuron and how one may account for them in theory. There are various sources of fluctuations that impact on a neuron. First, the opening and closure of the above mentioned ion channels that mediate the excitability of the membrane are probabilistic events. Although, by the large number of channels the resulting fluctuations (channel noise) are averaged out to a large extent one cannot ultimately exclude that they introduce some noise. Second, the release of a certain number of neurotransmitters from chemical synapses is also stochastic and obeys a Poisson law. The third and probably most important noise source is random synaptic input from other neurons. The second and third sources of fluctuations are relevant only for higher order sensory or cortical neurons and not for receptors that respond to changes of physical quantities in the environment of the organism. In the latter case, short correlated input that is not relevant for the organism can be also interpreted and modeled as noise.

Channel noise may be incorporated through transforming the HH system into a stochastic one by adding noise terms to all four equations (Fox, 1997). In conjunction with

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stochastic synaptic input this will result approximately in noise terms in the equation of the LIF model and in those of both variables in the FN model. While in the former system we will focus on the synaptic input noise (see the discussion below) for the FN model we will assume that the fluctuations (white Gaussian noise) act only on the dynamics of the recovery variable y . The reason to do so is only a technical one - the approximation we have developed can be applied only in this case. However, since the model is qualitative rather than quantitative, it does not matter in principal in which of the equations fluctuations are added. Indeed, there is much numerical evidence that the features we are interested in, namely, coherence and stochastic resonance do not depend much on whether noise is added to the dynamics of the fast voltage variable x like in Longtin (1993, 1995b) and Collins et al. (1995a) or of the slow recovery variable y like in Wiesenfeld et al. (1994); Pei et al. (1995) and Pikovsky and Kurths (1997). The next question, how signals have to be incorporated in the neuron models described above is closely related to the occurrence of fluctuations. It will turn out that in a simple model of a neuron receiving spike train input, there are two kinds of signals: *additive* and *noise coded* signals that will be introduced now. We stress that in the following discussion no realistic modeling of physiological parameters is intended. Rather, generic situations are considered with parameter sets as simple as possible in order to elucidate the principal origin of additive and noise coded signals. For receptors and their subsequent stage of sensory neurons, the input can be assumed as a smoothly varying function of time. Thus, a signal from the environment (e.g., change in mechanical pressure or electrical field) is transformed to a smooth change of base current and is called an *additive signal*. In this case we may write

$$I(t) = \mu(t) + \sqrt{2D}\xi(t) \quad (1.28)$$

where $\mu(t)$ stands for the signal and the second term takes account of fluctuations with intensity D stemming also from the environment or from internal noise sources. Such input was considered in most of the theoretical work on SR in neural systems. The same scheme was also used in several experiments where an additive signal contaminated by noise with a constant intensity was externally presented to a neuron. For higher stages of neural processing and in particular for cortical neurons this picture of a smoothly varying input changes drastically. These neurons receive trains of action potentials (usually approximated by δ spike trains) from many other ($10^3 - 10^5$) neurons (input neurons). As mentioned above each spike train enters the target neuron via one particular synapse. The current I_k injected by spikes at the k -th synapse due to the k -th neuron⁵ can be roughly described by a linear filter dynamics (see, e.g., Brunel and Sergi, 1998)

$$\tau_s \dot{I}_k = -I_k \pm a_{e,i} \sum_l \delta(t - t_{l,k}). \quad (1.29)$$

⁵For simplicity of presentation we assume that any input neuron synapses but once on the target neuron.

where τ_s is the synaptic filter constant and a_e and a_i are excitatory and inhibitory amplitudes, respectively. For simplicity, these parameters are assumed to be identical for all synapses. Furthermore, $t_{l,k}$ is the l -th firing time of the k -th input neuron and the sign on the r.h.s. has to be positive or negative for excitatory or inhibitory synaptic connections. The total current $I(t) = \sum I_k(t)$ that acts on the voltage dynamics in the spike generating zone depends crucially on the numbers and amplitudes of excitatory and inhibitory connections as well as on the statistics (in simplest case the firing rate) of the spike times. Here, we make the following assumptions.

1. The input is nearly balanced between excitatory and inhibitory currents, i.e., the mean value of the total current $\langle I(t) \rangle$ is small with respect to the spiking threshold of the voltage dynamics. This can be realized by proper ratios of numbers and/or amplitudes of excitatory and inhibitory spikes.
2. Spike trains arriving at different synapses are statistically independent.

While the first assumption seems to be realistic in many cases (Shadlen and Newsome, 1998; van Vreeswijk and Sompolinsky, 1996), the latter is only an approximation (Feng and Titozzi, 2000).

A signal may be conveyed by a time dependent spike rate common to a large subgroup of input neurons (note that this does not necessarily violate the assumed independence of input spike trains!). This is a simple example for a so called *population code* (see, e.g., Gerstner, 1995).

Besides such a stimulation encoding signals, neurons are also subject to massive input from the *neuronal background* (Koch, 1999), that is, the contribution by incoherently firing neurons from regions that are (functionally) far apart from each other. The firing rates of these neurons can be assumed as temporally constant.

Letting aside for the moment this background contribution, we consider the current $I(t)$ for an input consisting solely of spike trains with a periodically modulated rate. For simplicity, the synaptic amplitudes are set equal and the input trains are generated by Poisson processes. How does the total current look like if the input ensemble consists of *equal* numbers of excitatory and inhibitory neurons? This is illustrated in Fig. 1.9 where the rates, two single current traces according to eq. (1.29), and the total current $I(t)$ are shown. The summation of independent currents I_k yields a rather continuous random process with periodically modulated variance. This is an example for a *noise coded* signal - after the synaptic transmission the information (here, simply the signal frequency) carried by a population code in the activity of the input ensemble is coded by the intensity of noise. Put differently, noise becomes a *signal carrier*.

There is no reason to believe that the input will be always balanced such that the numbers and amplitudes of excitatory and inhibitory contributions are equal. In Fig. 1.10 we demonstrate what happens when an excess of excitatory neurons is given. In this case the current $I(t)$ is a random process with both signal dependent mean and variance. In addition to the noise coded signal, there appears also an additive signal

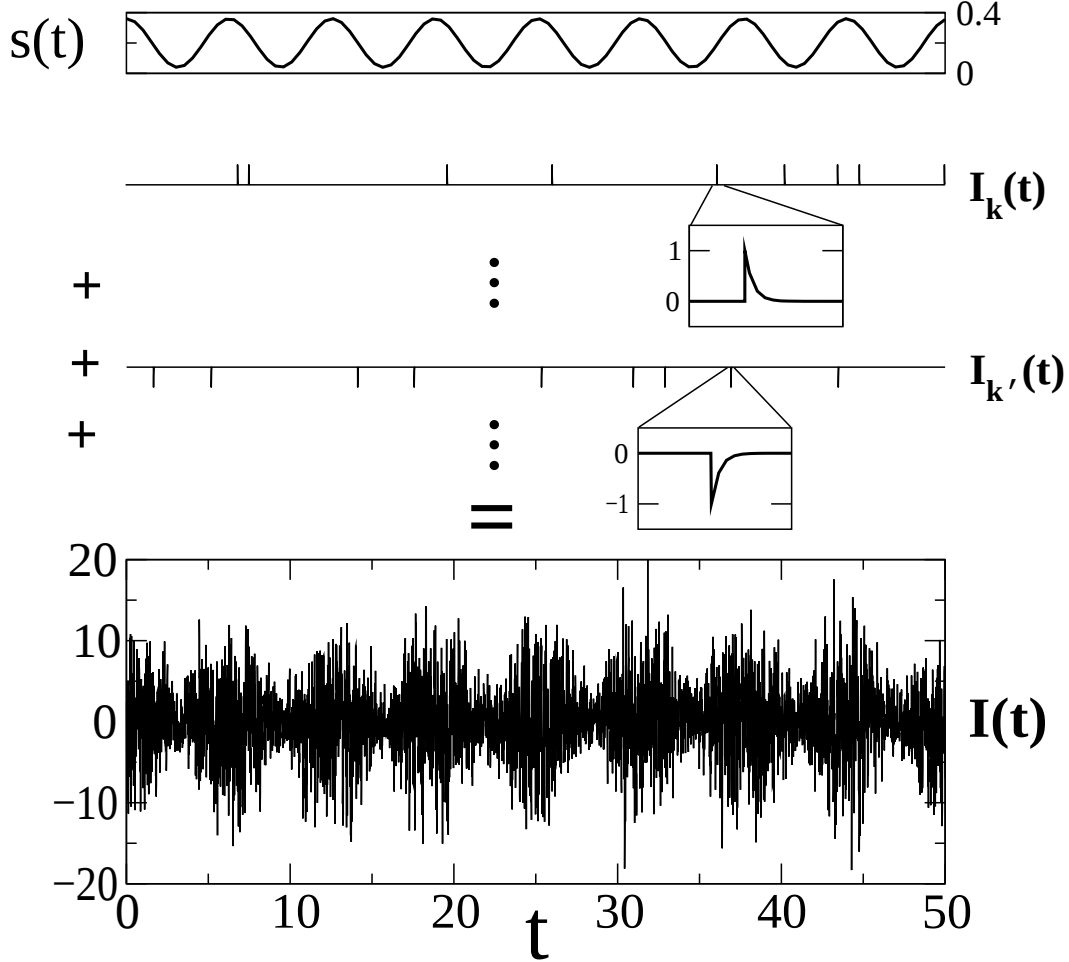


Figure 1.9.: Postsynaptic current (lower panel) resulting from spike trains with rate $s(t) = 0.2[1 + 0.8 \cos(t)]$ generated by 10^4 excitatory and 10^4 inhibitory neurons. The current $I(t)$ resembles much a short-correlated Ornstein-Uhlenbeck process with periodically modulated noise intensity (pure noise coded signal). Parameters of the synaptic filter are $a_e = a_i = 0.01$ and $\tau_s = 0.01$. The traces above $I(t)$ show single postsynaptic currents either from excitatory (positive amplitude) or inhibitory (negative amplitude) synapses. Insets give an expanded view of the response to a single input spike (exponential decay with time constant τ_s).

which can be well separated from the pure fluctuations. The current looks somewhat asymmetric with respect to the ordinate because mean and variance are increased or decreased at the same time.

Can we achieve a pure additive signal as in case of the receptor neuron considered above? For reasons that will become apparent below, this case is realized if only excitatory (or only inhibitory) neurons with time dependent rates are present in the input ensemble. In order to keep the input almost balanced (first assumption above) we

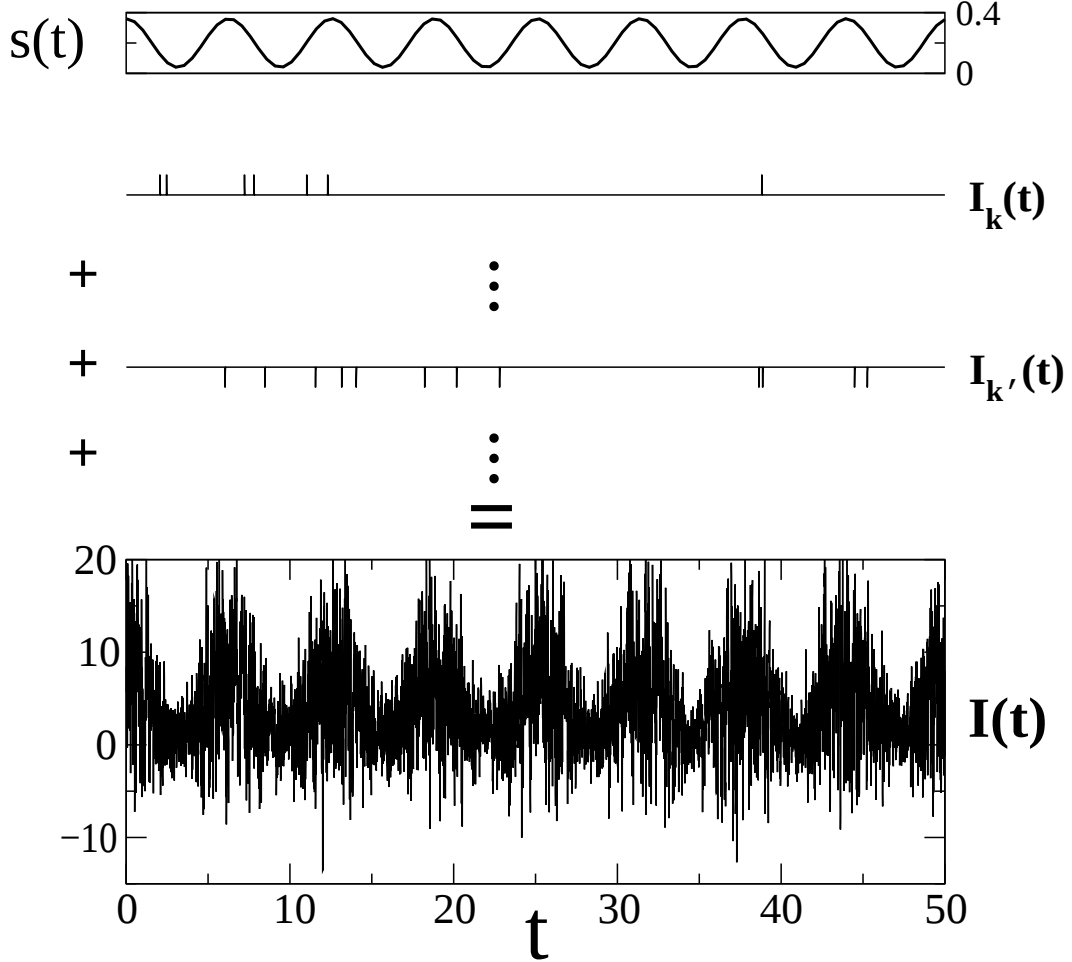


Figure 1.10.: Same as in Fig. 1.9 but with 1.2×10^4 excitatory and 10^4 inhibitory neurons. The result is now an Ornstein-Uhlenbeck process with time dependent mean and variance, i.e., both additive and noise coded signal are present.

add a large number of excitatory and inhibitory neurons with a *constant* rate standing for the background contributions. Doing so, we obtain indeed a total input current $I(t)$ that is apparently a noise with constant intensity but time dependent mean value. Only in this case, noise and signal can be separated. The resulting input is thus similar to that one assumed for the receptor neuron eq. (1.28).

A simple model for a transmission scheme including all of the considered cases is depicted in Fig. 1.12. The target neuron on the r.h.s. is subject to spike train input generated by n_e excitatory and n_i inhibitory neurons sharing a common harmonically modulated rate $s(t)$. As in the latter example (Fig. 1.11) background activity contributing with effective constant rates is taken into account. For this model we know already that in general ($n_e \neq n_i$ and $n_e, n_i > 0$) both additive and noise coded signals will be present in the total current resulting from synaptic transmission.

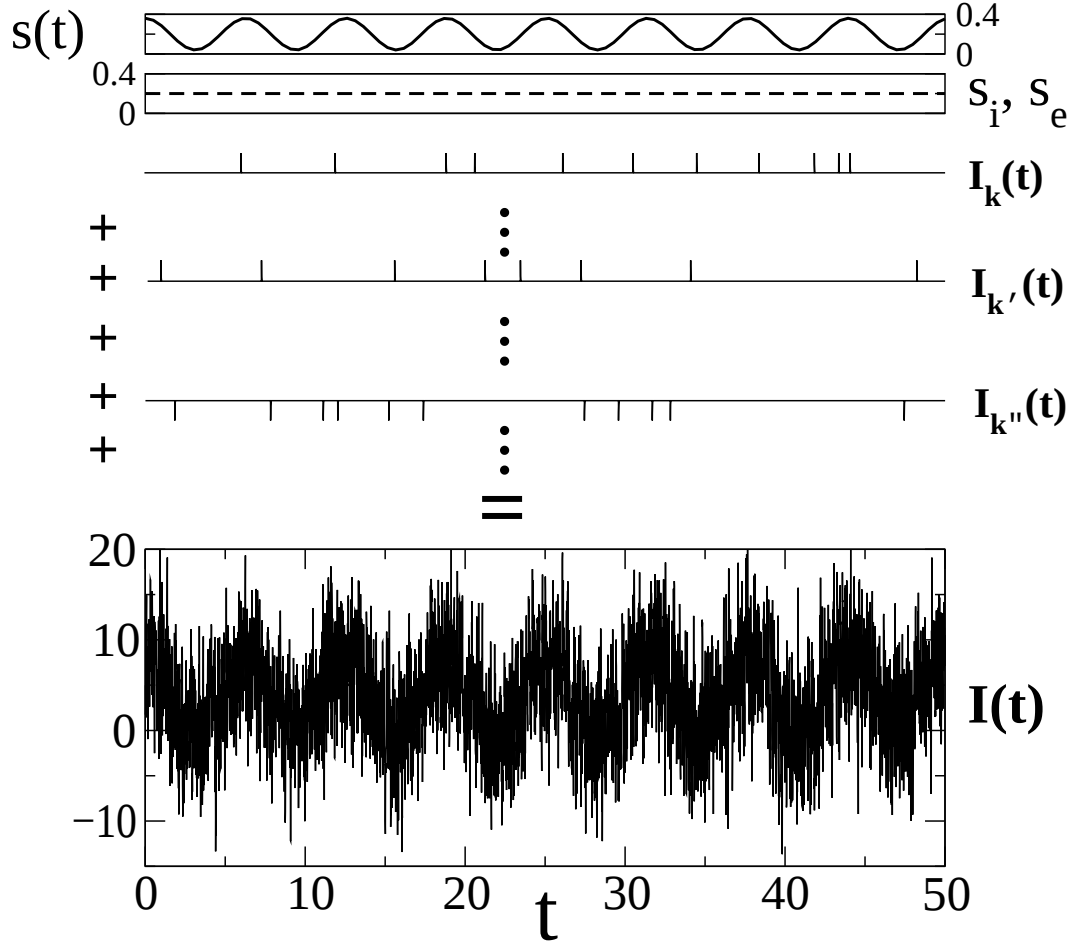


Figure 1.11.: Same as in Fig. 1.9 but with 10^4 excitatory and 10^4 inhibitory neurons firing with a constant rate $s_e = s_i = 0.2$ (indicated by dashed lines) and 2×10^3 excitatory neurons firing with the time dependent rate $s(t) = 0.2[1 + 0.8 \cos(t)]$ (solid line in the upper panel). This case corresponds to the derivation in Lánský (1997), the summed process is approximated by an Ornstein-Uhlenbeck process with only time dependent mean (pure additive signal).

The apparent continuity of the total current (which is, of course, only approximate for a finite number of input neurons) was due to the fact that we used massive synaptic input at rather small amplitudes $a_{e,i}$. In this limit case the diffusion approximation of spike train input (Ricciardi, 1977; Lánský, 1984; Tuckwell, 1988) applies, i.e., the spike train can be replaced by a white noise input with the same mean and intensity. The linear synaptic dynamics driven by such an input corresponds to an Ornstein-Uhlenbeck process, i.e., to the continuous current $I(t)$ observed in the computer simulations. We will outline the main steps of the diffusion approximation in order to accomplish this effective input.

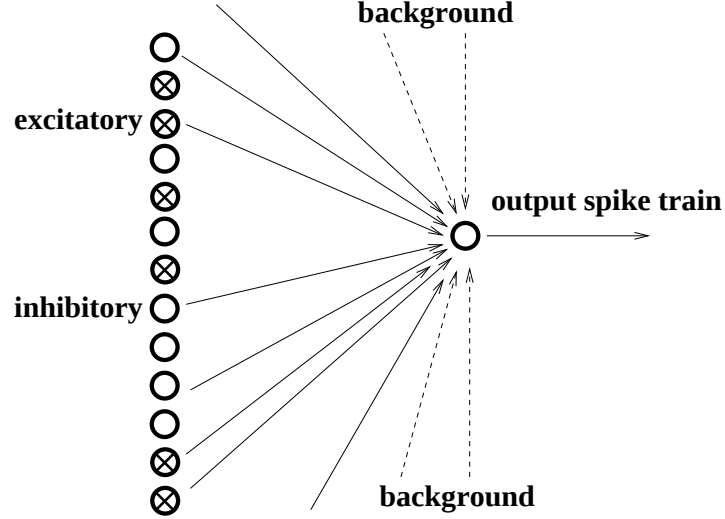


Figure 1.12.: Scheme of input generation for a single target neuron. The neurons within the input ensemble (l.h.s.) share a time dependent spike rate $s(t)$.

The first step is to write down the effective filter equation for the total current taking the sum over all the linear equations for the single currents. Next we note that for a large number of independent spike trains with a common rate $s(t)$ the sum of either excitatory or inhibitory trains will approach a Poissonian spike train (Cox, 1962) with the rate $R_e(t) = n_e s(t)$ and $R_i(t) = n_i s(t)$, respectively. A similar line of reasoning applies in case of the background contributions with the important difference that the *constant* rates $R_{e,bg} = n_{e,bg} s_e$ and $R_{i,bg} = n_{i,bg} s_i$ are expressed by the *average* rates of the background neurons s_e or s_i . Thus the total current dynamics is driven by only a few independent Poissonian spike trains standing for excitatory and inhibitory input from different subgroups of input neurons that share a common rate. For our specific model (Fig. 1.12) the dynamics is described by

$$\tau_s \dot{I} = -I + a_e \left(\frac{dN_e}{dt} + \frac{dN_{e,bg}}{dt} \right) - a_i \left(\frac{dN_i}{dt} + \frac{dN_{i,bg}}{dt} \right). \quad (1.30)$$

Here, N_e , $N_{e,bg}$, N_i and $N_{i,bg}$ are independent Poisson (step) processes with the respective rates introduced above. The derivatives of the processes yield the desired spike trains. Eq. (1.30) is very similar to Stein's model for the voltage in the spike generating zone (instead of the synaptic current) given by the leaky integrate-and-fire neuron driven by Poissonian spike trains with constant rates (Stein, 1965).

In the diffusion approximation the Poisson input is replaced by its mean value and a white Gaussian noise such that the infinitesimal moments

$$\gamma_n = \lim_{\epsilon \rightarrow 0} \frac{\langle (I(t + \epsilon) - I(t))^n \rangle}{\epsilon}. \quad (1.31)$$

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remain the same as for the original process, i.e.,

$$\dot{I} = \gamma_1(t) + \sqrt{\gamma_2(t)}\xi(t). \quad (1.32)$$

Using the statistical properties of the Poisson process one obtains for the moments of the original process $I(t)$ (see, e.g., Ricciardi, 1977; Lánský, 1984; Tuckwell, 1988)

$$\begin{aligned} \gamma_1 &= [-I + a_e(R_e(t) + R_{e,bg}) - a_i(R_i(t) + R_{i,bg})]/\tau_s, \\ \gamma_2 &= [a_e^2(R_e(t) + R_{e,bg}) + a_i^2(R_i(t) + R_{i,bg})]/\tau_s^2, \\ \gamma_n &= [a_e^n(R_e(t) + R_{e,bg}) + (-a_i)^n(R_i(t) + R_{i,bg})]/\tau_s^n, \quad n \geq 3. \end{aligned} \quad (1.33)$$

Although this has been considered mostly for constant rates, the expressions for the moments do not change if time dependent rates are involved (Lánský, 1997; Plesser, 1999).

By a certain scaling of amplitudes and rates the diffusion approximation becomes exact. Letting aside the background contributions (for which an analog calculation can be carried out), suppose that rates and amplitudes for the time dependent input ensemble are given by

$$n_e = an + bn^2, \quad n_i = bn^2, \quad a_e = a_i = \frac{1}{n}. \quad (1.34)$$

Here, a denotes an excess of excitatory neurons and n is related to the ensemble size. In the above scaling, the parameters a and b represent also the strength of the influence the input ensemble exerts on the target neuron. Note that we might introduce as well two parameters in the amplitudes which would be equivalent to a and b (in this case $a_e \neq a_i$), however, for the ease of notation, we use only the free parameters a and b but keep in mind that they quantify the general impact of the input ensemble rather than solely the numbers of excitatory and inhibitory neurons.

Now, for $n \rightarrow \infty$ which means the limit of an infinite input ensemble (infinite rates of the Poisson processes) and vanishing amplitudes we obtain

$$\begin{aligned} \gamma_1 &= [-I + as(t)]/\tau_s, \\ \gamma_2 &= [2bs(t)]/\tau_s^2, \\ \gamma_n &= 0 \quad n \geq 3. \end{aligned} \quad (1.35)$$

i.e., indeed all higher moments than the first two vanish as it is the case also for the diffusion process described by the stochastic differential equation eq. (1.32). Using the limiting relations above we may readily understand what we have obtained by the different parameter sets used for the results in Figs. 1.9, 1.10, and 1.11. An additive signal is associated with the unbalanced periodically modulated part of the input, setting $a = 0$ yields a pure noise coded signal. On the other hand, if only excitatory neurons are present ($b = 0$) the second moment vanishes and a pure additive signal is

left. In general we have to deal with both kinds of signals.

For the background noise we make no further specific assumptions regarding the input rates and numbers but assume simple constant contributions to the first two moments $\gamma_{1,\text{bg}} = \mu_{\text{bg}}/\tau_s$ and $\gamma_{2,\text{bg}} = 2D_{\text{bg}}/\tau_s^2$. The synaptic dynamics for the current reads now

$$\tau_s \dot{I} = -I + \mu_{\text{bg}} + as(t) + \sqrt{2[D_{\text{bg}} + bs(t)]}\xi(t). \quad (1.36)$$

This equation describes an Ornstein-Uhlenbeck process (OUP) with time dependent mean and variance. This linear equation can be solved immediately, however, we won't do so, but neglect throughout this work the synaptic filtering we have considered so far completely by setting $\tau_s = 0$. This means that we replace the colored noise current (i.e., the OUP with correlation time τ_s) by a combination of time dependent base current and white noise with signal dependent intensity⁶. Furthermore, we will restrict ourselves to the consideration of weak periodically modulated signals $s(t) = 1 + \varepsilon \cos(\omega_s t)$ with $\varepsilon \ll 1$ (because of parameter redundancy we set the constant part of the rate one). With the new constant parameters

$$\mu = \mu_{\text{bg}} + a, \quad D = D_{\text{bg}} + b, \quad \varepsilon_\alpha = a\varepsilon, \quad \varepsilon_\beta = b\varepsilon. \quad (1.37)$$

that are, the base current, the noise intensity and the amplitudes of additive and noise coded signal, respectively the input current reads

$$I(t) = \mu + \varepsilon_\alpha \cos(\omega_s t) + \sqrt{2[D + \varepsilon_\beta \cos(\omega_s t)]}\xi(t). \quad (1.38)$$

In chapter 5 we shall study the linear response of the LIF neuron to this kind of input. In particular, the transmission features for additive and noise coded signals will be compared. When exploring a possibly occurring stochastic resonance with respect to the noise level D this might be well interpreted as a resonance with respect to the background noise D_{bg} . In other words, the parameters a and b are arbitrary small but fixed hence also the strength of the signal carrying noise is fixed. The question implicitly posed in this way is whether the signal transmission of additive and noise coded signals is enhanced by the spontaneous activity of the neuronal background.

At least for additive signals, a number of recent numerical findings support this conjecture. Without applying the diffusion approximation SR could be found in neural networks where the target neuron was a LIF model (Mato, 1999), a Hindmarsh-Rose model (Wang and Wang, 1997) or even a sophisticated biophysical compartment model (Rudolph and Destexhe, 2001).

Features of the response to a noise coded signal that are beyond stochastic resonance

⁶The reader might wonder why we have considered the synaptic dynamics if we finally neglect it.

First, we wanted to point out just a few of the crude approximations one has to make to obtain the “usual” input (signal plus white noise) considered in most work on SR in neuronal models. Second, a practical reason was that a noise coded signal is somewhat uncomfortable to illustrate if we deal with white noise.

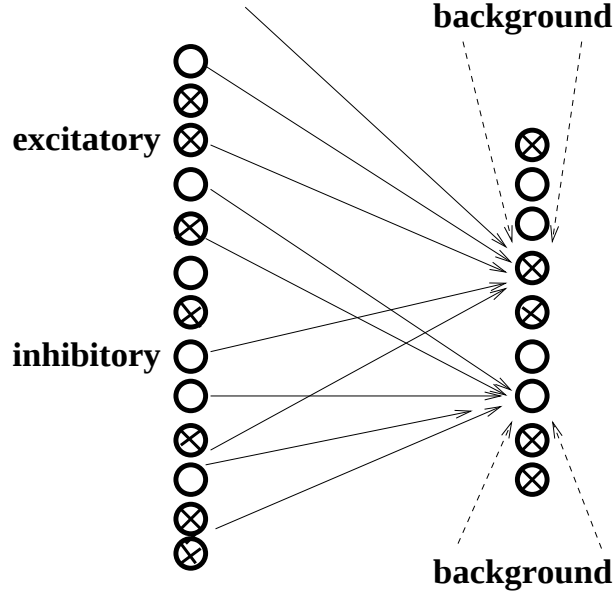


Figure 1.13.: Generation of periodic input by an input ensemble of excitatory and inhibitory neurons (l.h.s.) and by the neuronal background that stimulates an ensemble of target neurons (r.h.s.).

will turn out to be more relevant for the transmission through an *ensemble* of neurons. For this reason, in section 5.3 we will extend the scheme of Fig. 1.12 to an ensemble-ensemble transmission as illustrated in Fig. 1.13. We will focus on the case that the input neurons share only a small number of common input neurons that can be neglected. In this case we may immediately adopt the analytical results for the single-neuron transmission.

In the study of the periodically driven FN model carried out in chapter 6 we will content ourselves with the case of a pure additive signal. Here, emphasis is put on how coherence resonance influences the signal transmission. Two different driving modes are investigated, namely, the cases of a periodic driving in either the equation of the recovery (driving mode I) or of the voltage variable (driving mode II). Furthermore, nonadiabatic response features in all dynamical regimes (excitable, bistable and oscillatory) are also studied.

2. Coherence resonance in the leaky integrate-and-fire neuron

The leaky integrate-and-fire (LIF) model of the neuronal activity dates back as far as to a paper by Lapicque (1907). It became very popular by two papers of Knight (1972a,b) and, since then, it has found wide applications as a model that captures essential features of the neuronal spiking (for reviews see Ricciardi (1977); Tuckwell (1988) and Lánský and Rospars (1995)). The interest in the single LIF dynamics has been revived during the 1990's in the context of stochastic resonance (Bulsara et al., 1994, 1996; Plesser and Geisel, 1999b; Shimokawa et al., 1999b). Furthermore, the integrate-and-fire neuron is nowadays frequently used, in particular, for analytical and numerical studies of neural networks (see Diesmann et al., 1999; Mueller and Herz, 1999; Shimokawa et al., 1999c; Brunel, 2000).

Here, we study the single LIF neuron driven by a constant input and white Gaussian noise. For this simple case, a number of analytical results are already known for a long time. For example, the calculation of the moments of the interspike interval is actually a first passage time problem, for which quadrature formulae have been found already in 1933 by Pontryagin et al. (1933) (later independently derived by Siegert (1951)). A solution for the first passage time density (FPTD), i.e., the interspike interval density, for a special case goes back to Wang and Uhlenbeck (1945). The Laplace transform of the FPTD was found by Darling and Siegert (1953) and was several times recovered during the late sixties. Ricciardi and Sacerdote (1979) have derived by means of this transform alternative expressions for mean and variance of the interspike interval. Concerning the stationary probability density for the voltage variable, we are not aware of any publication prior to that by Ricciardi et al. (1992). Here, we discuss the stationary density and firing rate, derive a convenient expression for the variance of the interspike interval by means of which coefficient of variation (CV) and phase diffusion coefficient D_{eff} can be determined and give an analytic expression for the power spectrum of the spike train generated by the LIF model that is to our knowledge new. The main focus is again on the coherence resonance phenomenon that is discussed by means of CV, D_{eff} and power spectral density.

2.1. Description of the model and Fokker-Planck equation

The LIF model describes the voltage across the nerve membrane by a simple electric circuit consisting of an Ohmic resistor, a capacitor, a battery (ion pumps maintaining a resting potential difference) and a nonlinear threshold element. As mentioned above, we will assume the input as an additive white Gaussian noise and a constant base current according to the diffusion approximation. In this case, the model is sometimes also referred to as Ornstein-Uhlenbeck neuron (Lánský and Rospars, 1995) since the deviation of the voltage from the resting level obeys the linear stochastic differential equation

$$\dot{v} = -v + \mu + \sqrt{2D}\xi(t), \quad (2.1)$$

originally introduced by Langevin for the velocity of a Brownian particle¹ and later treated in detail by Uhlenbeck and Ornstein (1930).

In eq. (2.1) time is measured in units of the membrane time $\tau_m = RC$. The parameter μ denotes base current while the Gaussian white noise is completely characterized by its intensity D .

Eq. (2.1) describes only the neuron's dynamics between subsequent excitations. Whenever the voltage v reaches the threshold value v_T the neuron fires a δ spike, followed by an absolute refractory period of time τ and is then reset to the value v_R . More formal, we may write (Plesser, 1999)

$$\begin{aligned} \dot{v} &= -v + \mu + \sqrt{2D}\xi(t), \\ v = v_T &\implies t_i := t, \quad v(t + \tau) = v_R, \end{aligned} \quad (2.2)$$

$$\mathcal{T} = \{.., t_{i-1}, t_i, t_{i+1}, ..\}.$$

Thus, the *output* of the neuron consists of a spike sequence that is completely characterized by the ordered set of spiking times $\mathcal{T}$

$$\sigma(t) = \sum_{t_i \in \mathcal{T}} \delta(t - t_i). \quad (2.3)$$

Note that $\sigma(t)$ is only indirectly connected to the voltage variable v . The threshold condition makes the system highly nonlinear in spite of the apparent simplicity of eq. (2.1). This becomes also evident by looking at the example trajectory shown in Fig. 2.1.

¹Actually, the equation for the velocity reads $m\dot{v} = -\gamma v + \sqrt{2\gamma k_B T}\xi(t)$ (m -mass, γ -friction coefficient, $k_B T$ -thermal energy). Thus, $\mu \neq 0$ would mean an additional constant force.

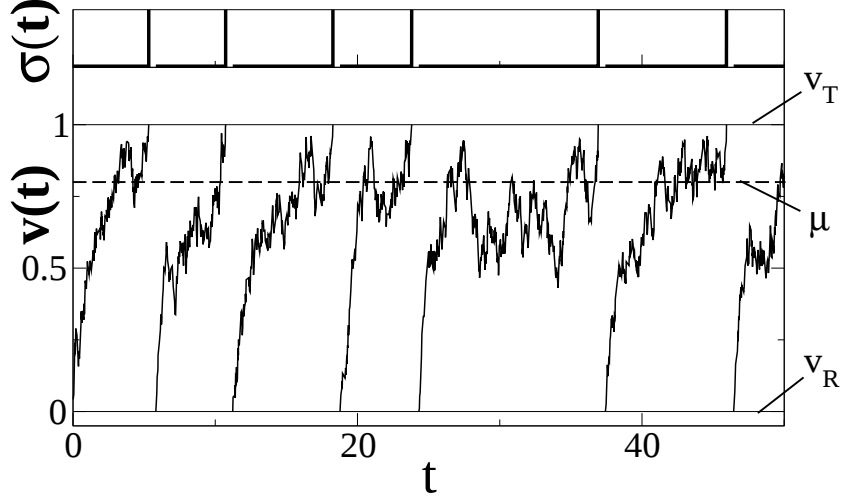


Figure 2.1.: Trajectory of the voltage variable $v(t)$ and generated spike train for $\mu = 0.8$, $D = 0.015$, $v_T = 1$, $v_R = 0$, $\tau = 0.5$. The gaps in the spike train have no physical meaning ($\sigma = 0$ there) but indicate the absolute refractory period τ . The Langevin equation was integrated by a simple Euler procedure with time step $\Delta t = 10^{-3}$.

We define the instantaneous firing rate of the neuron by an average over different realizations

$$r(t) = \lim_{\Delta \rightarrow 0} \frac{1}{\Delta} \left\langle \int_{t-\Delta/2}^{t+\Delta/2} dt' \sum \delta(t' - t_i) \right\rangle = \lim_{\Delta \rightarrow 0} \frac{1}{\Delta} \int_{t-\Delta/2}^{t+\Delta/2} dt' \langle \sigma(t') \rangle = \langle \sigma(t) \rangle. \quad (2.4)$$

The latter step was possible since the mean value is a continuous function (at finite noise, the instants t_i are not sharp). Hence, one sees that the instantaneous rate is nothing but the time dependent mean output of the neuron.

A firing rate can be also defined for a single spike train by averaging over a *finite* time window. Then, the firing rate will be a stochastic quantity, unless the time window is extended to infinity. In this case, features resulting from non-stationary stimulation are generally not reflected by this time averaged rate while in the stationary case the two different rates coincide.

One might ask for the spike count $n(t)$ for a certain time interval, e.g., for $(0, t)$. This stochastic variable is given by

$$n(t) = \int_0^t dt' \sigma(t'). \quad (2.5)$$

The mean value reads

$$\langle n(t) \rangle = \int_0^t dt' \langle \sigma(t') \rangle = \int_0^t dt' r(t') \quad (2.6)$$

2. Coherence resonance in the leaky integrate-and-fire neuron

which leads in the stationary case to

$$\langle n(t) \rangle = tr_0 \quad (2.7)$$

where r_0 is the stationary spike rate. Furthermore, the spike count is characterized by a spreading: its number will differ among a set of spike trains and the difference will grow in the course of time. This can be quantified by the diffusion coefficient for the spike count that is

$$D_{\text{eff}} = \frac{1}{2} \lim_{t \rightarrow \infty} \frac{d}{dt} \langle n^2(t) - \langle n(t) \rangle^2 \rangle. \quad (2.8)$$

As was pointed out in the introduction, the diffusion coefficient is also a measure for the regularity of the single spike train. A low value of it indicates either that the neuron is silent which is a rather trivial kind of regularity or that the output is close to a periodic spike train.

Further important quantities are given by the interspike interval (ISI)

$$T_i = t_i - t_{i-1}, \quad (2.9)$$

the first two central moments of which, namely mean ISI and variance can be determined from the firing times as follows

$$\langle T \rangle = \lim_{N \rightarrow \infty} \frac{1}{N} \sum_{i=0}^N t_i - t_{i-1}, \quad \langle \Delta T^2 \rangle = \lim_{N \rightarrow \infty} \frac{1}{N} \sum_{i=0}^N (t_i - t_{i-1})^2 - \langle T \rangle^2. \quad (2.10)$$

Equivalently, they can be expressed by the interspike interval *probability density* $\rho(T)$.

$$\langle T \rangle = \int_0^\infty dT T \rho(T), \quad \langle \Delta T^2 \rangle = \int_0^\infty dT (T^2 - \langle T \rangle^2) \rho(T). \quad (2.11)$$

From eq. (2.10) it becomes apparent that the time average of the rate $r(t)$ is related to the mean ISI.

$$\langle T \rangle = \lim_{N \rightarrow \infty} (N / \sum_{i=0}^N T_i)^{-1} = \lim_{t \rightarrow \infty} \left(\frac{1}{t} \int_0^t dt' \sigma(t') \right)^{-1} = \lim_{t \rightarrow \infty} \left(\frac{1}{t} \int_0^t dt' r(t') \right)^{-1}. \quad (2.12)$$

Replacing the output $\sigma(t)$ by the instantaneous rate (its mean) is of course only permitted for $(N, t \rightarrow \infty)$ and corresponds to a time average. In particular in the stationary case studied in the remainder of the chapter it follows from eq. (2.12) that

$$\langle T \rangle = \frac{1}{r_0}. \quad (2.13)$$

Therefore, it is sufficient to study either the mean ISI or the stationary rate in this case since both carry the same information.

Another quantity that characterizes the regularity of the spike train is the coefficient of variation (CV)

$$R = \frac{\sqrt{\langle \Delta T^2 \rangle}}{\langle T \rangle} \quad (2.14)$$

that is the relative standard deviation of the interspike intervals. As discussed in the introduction it is a rather weak criterion for coherence resonance.

For the system studied in this chapter, evidently, all interspike intervals of the spike train are independent of each other since after a reset the LIF model has completely “forgotten” previous realizations of the voltage variable. Furthermore, all intervals are drawn from the same ISI density $\rho(T)$ as we have already tacitly assumed in eq. (2.11). Under these conditions it is evident that the neuronal spiking is described by a *renewal point process* (Cox, 1962). Hence, the diffusion coefficient given by eq. (2.8) is simply related to spike rate and coefficient of variation according to eq. (1.9).

Besides the velocity of a free Brownian particle, there is another more instructive mechanical analogy that is extensively used in the following (cf. Fig. 2.2). Eq. (2.1) describes the dynamics of an overdamped Brownian particle subjected to a parabolic potential with an absorbing boundary. Hence, in this terminology (introduced by Bulsara et al. (1996)) we can say that the escape of the particle via the absorbing boundary v_T generates a spike. After a “time-out” τ (refractory period) it is injected at v_R from where it may diffuse and possibly reach the threshold again.

With a look at Fig. 2.2 we can now distinguish between two different regimes. Depending on the value of the base current μ , there exist a stable fixed point, i.e.,

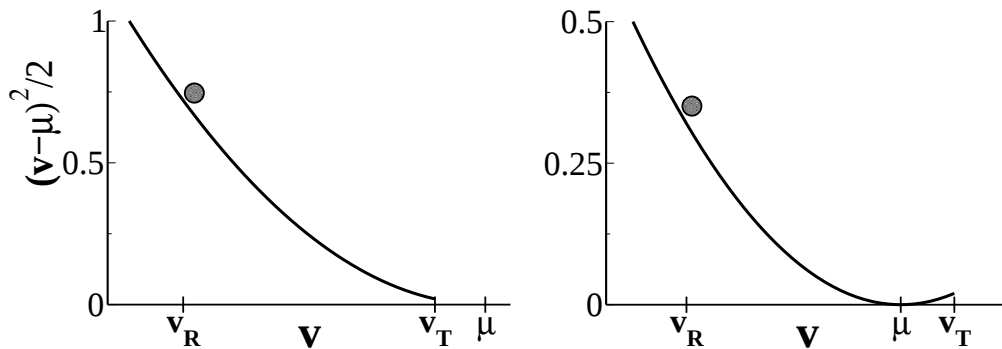


Figure 2.2.: Mechanical analogy for the voltage dynamics eq. (2.1). A Brownian particle (circle) moves in a parabolic potential possessing a minimum at $v = \mu$ and is absorbed when it hits the boundary $v = v_T$ (threshold). At the very same time a spike is generated. After time τ the particle is reset to the voltage $v = v_R$ (reset point). Left: deterministic (oscillatory) firing regime ($v_T < \mu$), for which an example trajectory is depicted in Fig. 2.3. Right: noise activated (excitable) firing regime ($v_T > \mu$) - a corresponding example trajectory was given in Fig. 2.1.

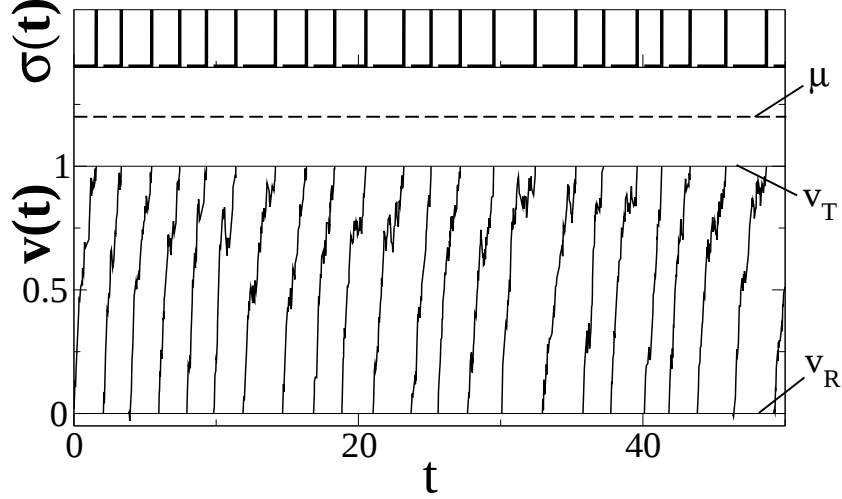


Figure 2.3.: Trajectory of the voltage variable $v(t)$ for the same parameter as in Fig. 2.1 but with $\mu = 1.2$. This corresponds to the situation sketched in Fig. 2.2 (l.h.s.).

a potential minimum is present ($\mu < v_T$, Fig. 2.2, r.h.s.) or absent ($\mu > v_T$, Fig. 2.2, l.h.s.). In the latter case, the particle will simply go “downhill” and reach the threshold even in the absence of noise resulting in a strictly periodic firing of the neuron. For this reason the case $\mu > v_T$ is called the *deterministic* or *oscillatory firing regime*. Small fluctuations will, of course, lead to a small irregularity of the generated spike train (cf. Fig. 2.3), thus, the system resembles much a noisy oscillator².

This is completely different for the case $\mu < v_T$ which is more relevant from the biological point of view. Without noise ($D = 0$), the particle is bound to the minimum and persists in this state forever - no spikes at all. By the assistance of a finite noise, the particle may overcome the *barrier* at the threshold (for an example consider once more the trajectory depicted in Fig. 2.1 where $\mu < v_T$ holds true). Therefore, one refers to the case $\mu < v_T$ as the *noise-activated* or *excitable firing regime*. At weak noise, these escapes via the absorbing boundary are governed by a Kramers rate that grows in proportion to $\exp[-\Delta V/D]$. Here, $\Delta V = (v_T - \mu)^2/2$ is the potential difference between minimum and threshold. At strong noise, this barrier will be less important, the variance of the variable v will be large so that the particle frequently hits the boundary at v_T and will be absorbed.

Up to this point, we have only discussed the escape from minimum to threshold. There is, however, another process to take into account, in particular, if the system is close to the transition from one regime to the other. For a value of μ smaller than but close to v_T , the time for relaxation from reset point into the potential minimum will be relevant and contribute essentially to the total interspike interval. This process can be

²The trivial difference to the oscillator is that the considered output takes only the values 0 and ∞ instead of a continuous range like, for instance, the coordinate of a harmonic oscillator.

looked upon as a *relative refractory period* since during this time firings of the neuron are unlikely. A precondition for an appreciable influence of the refractory period is, of course, a finite and not too small noise intensity that permits a fast escape via the fairly small barrier at v_T . This situation is in a way the counterpart to the escape via a large barrier usually considered in the escape problem according to Kramers. And it is exactly the parameter regime where coherence resonance is expected to occur. In terms of (Neiman et al., 1997a), CR appears simply as a precursor of the bifurcation of the firing rate (escape rate) for $\mu = v_T$.

Dwelling further on the mechanical analogy, we may also consider an ensemble of N particles corresponding to a pool of independent, i.e., non-interacting neurons. These particles are described by a density $P^N(v, t)$ obtained by counting how many of them are in a certain interval $v, v + dv$. Additionally, some particles will be “on vacation” in the refractory state since they have crossed the threshold recently. Their number is denoted by $P_\tau^N(t)$. Clearly, by integrating the density over the valid range of the coordinate (voltage) and adding $P_\tau^N(t)$ we find the conserved total number N . Furthermore, if we divide by the total number of particles and go to the limit $N \rightarrow \infty$ we obtain the probability density $P(v, t) = P^N(v, t)/N$ and the probability for the refractory state $P_\tau(t) = P_\tau^N(t)/N$. Now, particles that leave the interval via the threshold within the span $t, t + dt$ give rise to firing events. By dividing the number of these particles by N we may estimate the instantaneous firing rate $r(t)$. The current of particles via the threshold $J^N(v_T, t)dt$ has also a probabilistic counterpart, namely, the *probability current* $J(v_T, t) = J^N(v_T, t)/N$ at the threshold. But this is obviously the same as our estimate of the instantaneous firing rate in the limit $N \rightarrow \infty$ where it becomes an exact average. Thus, we have found the important relation

$$r(t) = J(v_T, t). \quad (2.15)$$

This holds true in general, i.e., also if time dependent parameters (μ, D) are involved. The probability density $P(v, t)$ is governed by a Fokker-Planck equation (FPE). While deriving this equation and the boundary conditions we have to bear in mind not only the Langevin equation but also the reset mechanism. This is illustrated in Fig. 2.4.

The absorption at the threshold leads clearly to a classic absorbing boundary condition,

$$P(v_T, t) = 0. \quad (2.16)$$

Since the the temporal derivative of v is proportional to a white noise (that - roughly speaking - oscillates between $\pm\infty$) a particle arbitrary close to v_T crosses that point infinitely often in a finite time, however, it is, of course, absorbed when reaching v_T for the first time. Hence, there is no particle that is arbitrary close to the threshold what is expressed by the above condition.

At the reset point in turn, there is no absorption but an influx of probability that may be expressed by an additional source term in the FPE

$$\partial_t P(v, t) = \partial_v (v - \mu + D\partial_v) P(v, t) + J_+(t)\delta(v - v_R) = -\partial_v J(v, t) \quad (2.17)$$

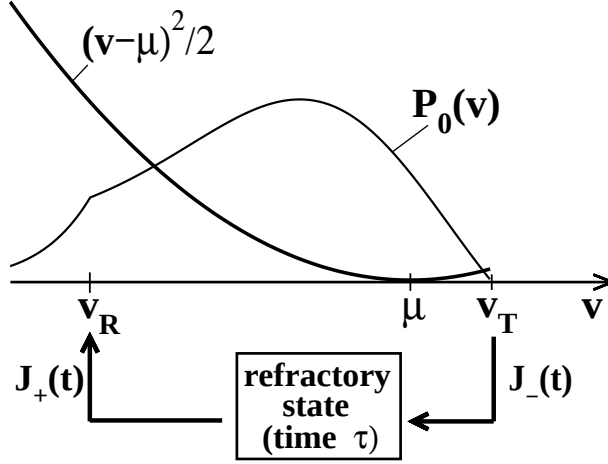


Figure 2.4.: Probability flow in the leaky integrator model with absolute refractory state. At the threshold, probability leaves the interval and enters the refractory state (box). After a delay of time τ the probability is reinjected into the reset point. As an example we show the shape of the *stationary* density ($\mu = 0.8, D = 0.1$) that illustrates the boundary and jump conditions: it vanishes at $v = v_T$ and possesses a jump in its derivative at $v = v_R$. Note that the scheme sketched below the v axis applies also in case of an explicit time dependence of the density (initial value problem or case of time dependent driving).

with $J(v, t)$ being the probability current at v . The influx $J_+(t)$ at the reset point is given by the outflux from the absolute refractory state. Since this state is occupied for a fixed (deterministic) time, the mentioned outflux equals the influx delayed by the refractory period τ . The latter influx in turn equals the outflux at the threshold (cf. Fig. 2.4). Explicitly,

$$J_+(t) = J_-(t - \tau) = J(v_T, t - \tau) = -D \left. \frac{\partial P(v, t - \tau)}{\partial v} \right|_{v=v_T} \quad (2.18)$$

where we have used the FPE eq. (2.17) and the absorbing boundary condition (2.16). Also, as should be clear from the above line of reasoning, the probability of the absolute refractory state can be expressed by the integrated influx of probability from v_T

$$P_\tau(t) = \int_{t-\tau}^t dt' J(v_T, t') = -D \int_{t-\tau}^t dt' \left. \frac{\partial P(v, t')}{\partial v} \right|_{v=v_T}. \quad (2.19)$$

The same diffusion effect responsible for the absorbing boundary condition implies that in spite of the influx at v_R the density has to be continuous also at this point

$$[P(v, t)]_{v_R} = 0 \quad (2.20)$$

where the square bracket with index denotes the jump of the function. As was mentioned by Melnikov (1993) for a similar problem, one may go back to the usual form of the FPE

$$\partial_t P(v, t) = \partial_v (v - \mu + D \partial_v) P(v, t) = -\partial_v J(v, t) \quad (2.21)$$

excluding the reset point v_R if the following condition is fulfilled

$$\left[\frac{\partial P(v, t)}{\partial v} \right]_{v_R} = \frac{\partial P(v, t - \tau)}{\partial v} \Big|_{v_T}. \quad (2.22)$$

For all values of v with $v \neq v_R$ we get trivially eq. (2.21) from eq. (2.17). Regarding the excluded point, note that a jump in the derivative implies a δ function component in the second derivative.

By virtue of eq. (2.22), this component cancels the δ function in (2.17).

Furthermore, in order to exclude unphysical solutions we demand that the density vanishes at infinity

$$\lim_{v \rightarrow -\infty} P(v, t) = 0. \quad (2.23)$$

Eventually, the normalization condition reads

$$\int_{-\infty}^{v_T} dv P(v, t) + P_\tau = \int_{-\infty}^{v_T} dv P(v, t) - D \int_{t-\tau}^t dt' \frac{\partial P(v, t')}{\partial v} \Big|_{v=v_T} = 1. \quad (2.24)$$

For the calculations in the following, it is convenient to use the variable $x = v - \mu$ that shifts the potential minimum to the origin. The FPE for the new density $P(x, t) = P(v + \mu, t)$ reads³

$$\partial_t P(x, t) = \partial_x (x + D \partial_x) P(x, t) = -\partial_x J(x, t). \quad (2.25)$$

The new reset and threshold points are denoted by $x_+ = v_R - \mu$ and $x_- = v_T - \mu$, respectively, while the boundary conditions are easily obtained from the eqs. (2.16), (2.20), (2.22) and (2.23)

$$P(x_-, t) = 0, \quad (2.26)$$

$$[P(x, t)]_{x_+} = 0, \quad (2.27)$$

$$\left[\frac{\partial P(x, t)}{\partial x} \right]_{x_+} = \frac{\partial P(x, t - \tau)}{\partial x} \Big|_{x_-}, \quad (2.28)$$

$$\lim_{x \rightarrow -\infty} P(x, t) = 0. \quad (2.29)$$

All quantities will be given in terms of the original variable v and the parameters v_T and v_R . Unless stated otherwise, for numerical evaluation we use the standard values $v_T = 1$, $v_R = 0$ and $\tau = 0.1$.

³For the ease of notation, we distinguish between the two different functions only by the different arguments.

2.2. The stationary density

The stationary density $P_0(x)$ is obtained if we set $\partial_t P(x, t) = 0$ in eq. (2.25). Then, the probability current $J(x, t)$ must be constant, i.e., $J(x, t) \equiv J_0$. A first obvious solution is obtained for vanishing probability current $J_0 = 0$

$$(x + D\partial_x) P(x, t) = 0. \quad (2.30)$$

The solution is the Gaussian density $\exp[-x^2/(2D)]$ which, however, does neither satisfy the absorbing boundary condition nor the jump condition for the derivative. Assuming a finite current, leads by elementary methods to

$$P_0(x) = c_1 e^{-x^2/(2D)} \int_x^{c_2} dy e^{y^2/(2D)} \quad (2.31)$$

where c_1 and c_2 are free constants. Condition (2.26) is met by choosing $c_2 = x_-$ since then the integral vanishes at the boundary. Furthermore, the derivative of the density at x_- is

$$P'_0|_{x_-} = -c_1 = -\frac{J_0}{D} = -\frac{r_0}{D} \quad (2.32)$$

where we have introduced the stationary spike rate r_0 that is equal to the current at the boundary according to eq. (2.15). Now we have

$$P_0(x) = \frac{r_0}{D} e^{-x^2/(2D)} \int_x^{x_-} dy e^{y^2/(2D)} \quad (2.33)$$

but this cannot be the full solution because of the jump condition (2.28). What we expect for the current in the stationary case according to Fig. 2.4: the probability flows out at x_- into the refractory state. From there it flows into x_+ and further to x_- again - a simple circuit for the probability current. However, there is no finite current for points to the left of x_+ . Hence, the solution above showing a finite current applies only for the interval (x_+, x_-) and for the other region we may use the Gaussian solution

$$P_0(x) = c_3 e^{-x^2/(2D)} \quad (2.34)$$

that is also consistent with the condition (2.29). The jump condition (2.28) requires that

$$-\frac{r_0 x_+}{D^2} e^{-x_+^2/(2D)} \int_{x_+}^{x_-} dy e^{y^2/(2D)} - \frac{r_0}{D} + \frac{c_3 x_+}{D} e^{-x_+^2/(2D)} = P'_0|_{x_-} = -\frac{r_0}{D}. \quad (2.35)$$

Hence,

$$c_3 = \frac{r_0}{D} \int_{x_+}^{x_-} dy e^{y^2/(2D)} \quad (2.36)$$

and the solution thus reads

$$\begin{aligned}
 P_0(x) &= \frac{r_0}{D} e^{-x^2/(2D)} \int_x^{x_-} dy e^{y^2/(2D)} \Theta(y - x_+) \\
 &= \frac{r_0}{D} e^{-x^2/(2D)} \begin{cases} \int_{x_+}^{x_-} dy e^{y^2/(2D)} & , \quad x < x_+ \\ \int_x^{x_-} dy e^{y^2/(2D)} & , \quad x_+ < x < x_- \end{cases}. \quad (2.37)
 \end{aligned}$$

Note, that the density is continuous at x_+ as demanded by condition (2.27).

In addition, we have to determine the probability of the absolute refractory state. Using eq. (2.19) with $J(v_T, t) = J_0 = r_0$ we obtain

$$P_\tau = r_0 \tau. \quad (2.38)$$

The rate r_0 is determined by the normalization condition (2.24) that reads by means of (2.38)

$$r_0 = \frac{D}{\tau D + \int_{-\infty}^{x_+} dx e^{-x^2/(2D)} \int_{x_+}^{x_-} dy e^{y^2/(2D)} + \int_{x_+}^{x_-} dv e^{-x^2/(2D)} \int_x^{x_-} dy e^{y^2/(2D)}}. \quad (2.39)$$

This expression can be further simplified to

$$r_0 = (\tau + \sqrt{\pi} \int_{-x_-/\sqrt{2D}}^{-x_+/\sqrt{2D}} dz e^{z^2} \operatorname{erfc}(z))^{-1} \quad (2.40)$$

where $\operatorname{erfc}(z)$ is the complementary error function (Abramowitz and Stegun, 1970).

Plotting the total region of integration for the two integrals in eq. (2.39) reveals that they can be combined by a change of integration order.

$$\int_{-\infty}^{x_+} dx e^{-x^2/(2D)} \int_{x_+}^{x_-} dy e^{y^2/(2D)} + \int_{x_+}^{x_-} dv e^{-x^2/(2D)} \int_x^{x_-} dy e^{y^2/(2D)} = \int_{x_+}^{x_-} dy e^{y^2/(2D)} \int_{-\infty}^y dx e^{-x^2/(2D)}.$$

Now, changing the variables to $z = -y/\sqrt{2D}$ and $u = -x/\sqrt{2D}$ yields

$$\begin{aligned}
 &\int_{x_+}^{x_-} dy e^{y^2/(2D)} \int_{-\infty}^y dx e^{-x^2/(2D)} = \int_{x_+}^{x_-} dy e^{y^2/(2D)} \int_{-y/\sqrt{2D}}^{\infty} du \sqrt{2D} e^{-u^2} \\
 &= \sqrt{2D} \int_{x_+}^{x_-} dy e^{y^2/(2D)} \operatorname{erfc}(-y/\sqrt{2D}) \sqrt{\pi}/2 = \frac{2D\sqrt{\pi}}{2} \int_{-x_-/\sqrt{2D}}^{-x_+/\sqrt{2D}} dz e^{z^2} \operatorname{erfc}(z).
 \end{aligned}$$

from which we obtain (2.40).

2. Coherence resonance in the leaky integrate-and-fire neuron

Apart from the latter simplifications of the spike rate, all we have done can be repeated in the same way for a general potential $V(x)$, that grows unbounded for $x \rightarrow -\infty$. The solution for this case we will need in the subsequent chapters. It is given here with explicit notation of the parametric dependence on x_+ , x_- and τ .

$$P_0^g(x; x_+, x_-, \tau) = \frac{r_0^g}{D} e^{-V(x)/D} \begin{cases} \int_{x_+}^{x_-} dy e^{V(y)/D}, & x < x_+ \\ \int_x^{x_-} dy e^{V(y)/D}, & x_+ < x < x_- \end{cases} \quad (2.41)$$

The corresponding rate can be written

$$r_0^g(x_+, x_-, \tau) = \left(\tau + \frac{1}{D} \int_{x_+}^{x_-} dy e^{V(y)/D} \int_{-\infty}^y dx e^{-V(x)/D} \right)^{-1}. \quad (2.42)$$

Returning to the LIF model and the original variable v we obtain the density

$$P_0(v) = \frac{r_0}{D} e^{-(v-\mu)^2/(2D)} \begin{cases} \int_{v_R}^{v_T} dy e^{(y-\mu)^2/(2D)}, & v < v_R \\ \int_v^{v_T} dy e^{(y-\mu)^2/(2D)}, & v_R < v < v_T \end{cases} \quad (2.43)$$

and the stationary instantaneous firing rate is simply

$$r_0 = \left(\tau + \sqrt{\pi} \int_{(\mu-v_T)/\sqrt{2D}}^{(\mu-v_R)/\sqrt{2D}} dz e^{z^2} \operatorname{erfc}(z) \right)^{-1}. \quad (2.44)$$

In the noise-activated firing regime ($\mu < v_T$) we obtain from this the small noise limit

$$r_0(D) = \sqrt{\frac{\Delta U}{\pi D}} e^{-\Delta U/D} \quad \mu < v_T, \quad D \ll \Delta U \quad (2.45)$$

where $\Delta U = (v_T - \mu)^2/2$ is the height of the effective potential barrier at the threshold. This Arrhenius like exponential dependence on the noise intensity and especially the prefactor were first derived by Kramers (1940) for a general cusp potential. In the deterministic firing regime in turn the rate does not vanish for $D \rightarrow 0$. The correction in D is only linear (Arecchi, 1981)

$$r_0(D) = (\tau + \ln[(\mu - v_R)/(\mu - v_T)])^{-1} + \frac{D}{2} \left(\frac{1}{(\mu - v_T)^2} - \frac{1}{(\mu - v_R)^2} \right) (\tau + \ln[(\mu - v_R)/(\mu - v_T)])^{-2}. \quad (2.46)$$

One sees that noise increases the firing rate in the deterministic firing regime, too. For the sake of completeness we give also the expressions for the derivatives of r_0 with respect to base current μ and noise intensity D which will be needed in chapter 5.

$$\frac{dr_0}{d\mu} = r_0^2 \sqrt{\frac{\pi}{2D}} \left[e^{(\mu-v_T)^2/(2D)} \operatorname{erfc}\left(\frac{\mu-v_T}{\sqrt{2D}}\right) - e^{(\mu-v_R)^2/(2D)} \operatorname{erfc}\left(\frac{\mu-v_R}{\sqrt{2D}}\right) \right]. \quad (2.47)$$

$$\begin{aligned} \frac{dr_0}{dD} = \frac{r_0^2}{2} \sqrt{\frac{\pi}{2D^3}} & \left[(\mu-v_R) e^{(\mu-v_R)^2/(2D)} \operatorname{erfc}\left(\frac{\mu-v_R}{\sqrt{2D}}\right) - \right. \\ & \left. (\mu-v_T) e^{(\mu-v_T)^2/(2D)} \operatorname{erfc}\left(\frac{\mu-v_T}{\sqrt{2D}}\right) \right]. \end{aligned} \quad (2.48)$$

For a discussion of the density, one has to distinguish between the noise activated and deterministic firing regime. We show examples for the density at different parameters in Fig. 2.5 for the first (upper rows) and the second case (lower row), respectively.

In the noise activated firing regime and for small noise, the density resembles much the usual density $\exp[-V(x)/D]$ since out- and influxes of probability are weak. The larger the base current is the larger are the deviations from the Gaussian density. For growing noise, the density attains its maximum at smaller voltage than $v = \mu$ where the potential minimum is located. Here (middle column), the jump of the derivative as well as the vanishing at the threshold are clearly seen. For even stronger noise (rightmost column), the maximum of the density is shifted to the reset point since due to the increased firing rate much probability flows into that point and is quickly spread and/or absorbed at $v_T = 1$.

In the deterministic firing regime (lower row), we find essentially the same features at moderate to large noise intensity. The main difference to the above case appears in the small noise limit. Here, the density does not tend to a Gaussian but to a density that is obviously restricted to the range (v_R, v_T) and can be calculated by a time average of the deterministic trajectory.

Suppose $D = 0+$. The density at v is then proportional to the time the particle spends at v

$$P_0(v)dv = a dt(v) = \frac{a}{\mu - v} dv$$

where a is a constant that is determined by the normalization condition. Obviously, we have

$$\frac{\int dv P_0(v)}{P_\tau} = \frac{T}{\tau} \quad \text{with} \quad T := T(v_R \rightarrow v_T) = \ln \frac{\mu - v_R}{\mu - v_T}$$

and thus

$$\frac{aT}{\tau/(T+\tau)} = \frac{T}{\tau} \rightarrow a = \frac{1}{T+\tau} \rightarrow P_0(v) = \frac{1}{\tau + \ln[(\mu - v_R)/(\mu - v_T)]} \frac{1}{\mu - v}$$

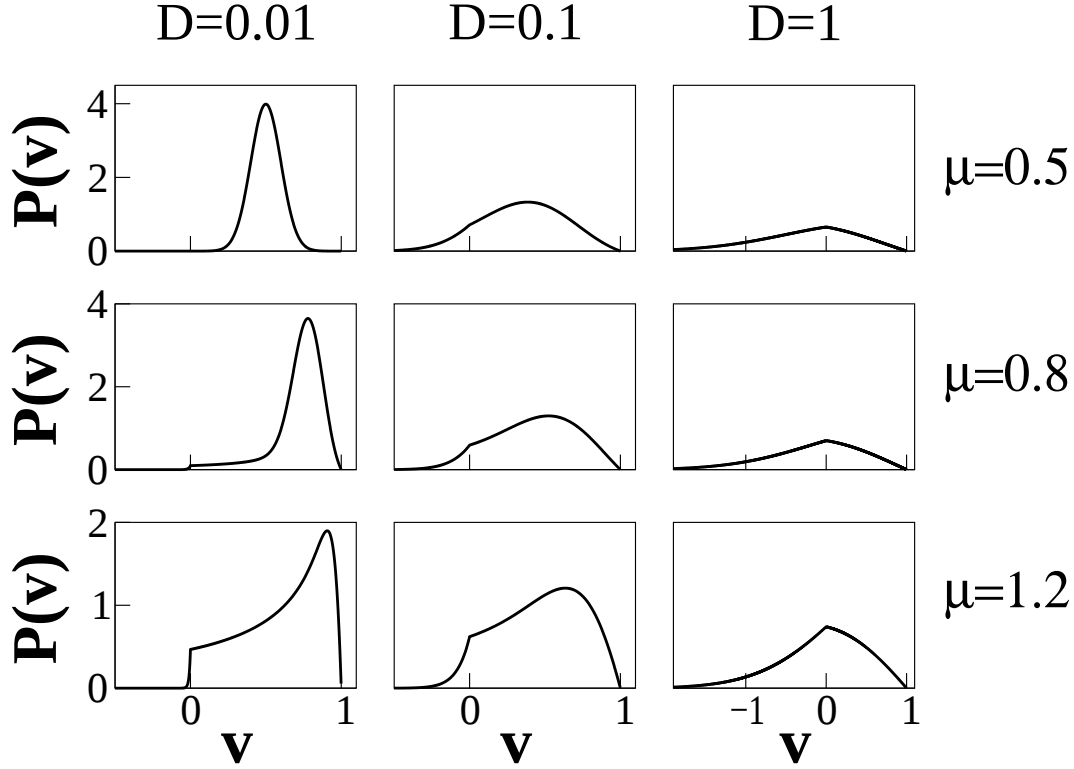


Figure 2.5.: Stationary density $P(v)$ for different values of noise intensity D and base current μ . Upper rows: noise activated firing regime. Lower row: deterministic firing regime.

Finally, it is maybe necessary to mention that coherence resonance cannot be investigated by means of the stationary density. The only relevant quantity for the spike train that can be inferred from the stationary solution is the firing rate r_0 , a first order quantity that does not tell us anything about the *regularity* of the spiking. Hence, we have to explore second order quantities like the coefficient of variation, the diffusion coefficient or the power spectrum in order to gain some insight in the coherence resonance phenomenon of the leaky integrate-and-fire neuron. The density $P_0(v)$ will be nonetheless needed and will play an important role in the linear response theory of chapter 5.

2.3. Central moments, coefficient of variation and phase diffusion coefficient

Apart from the absolute refractory period, the central moments of the interspike interval are given by the moments of the first passage time from reset point to threshold

$$\langle T \rangle = \tau + \langle T_{FP}(v_R \rightarrow v_T) \rangle, \quad (2.49)$$

$$\langle \Delta T^2 \rangle = \langle \Delta T_{FP}^2(v_R \rightarrow v_T) \rangle = \langle T_{FP}^2(v_R \rightarrow v_T) \rangle - \langle T_{FP}(v_R \rightarrow v_T) \rangle^2. \quad (2.50)$$

The latter relation holds true because the variance of the first passage time does not depend on τ and the absolute refractory period is a deterministic time.

For a general potential $V(x)$ as well as initial and final points a and b , the first two moments read

$$\langle T_{FP}(a \rightarrow b) \rangle = \frac{1}{D} \int_a^b dx e^{V(x)/D} \int_{-\infty}^x dy e^{-V(y)/D}, \quad (2.51)$$

$$\langle T_{FP}^2(a \rightarrow b) \rangle = \frac{2}{D^2} \int_a^b dx e^{V(x)/D} \int_{-\infty}^x dy e^{-V(y)/D} \int_y^b du e^{V(u)/D} \int_{-\infty}^u dv e^{-V(v)/D} \quad (2.52)$$

The variance $\langle \Delta T_{FP}^2 \rangle$ calculated from these formulae is a rather lengthy expression. In addition, the *four* quadratures required by the second moment are hard to tackle numerically, in particular, for small noise intensity D . The expression for $\langle \Delta T_{FP}^2 \rangle$ can be, however, analytically simplified.

First, we introduce the quantity

$$I(x) = \frac{1}{D} e^{V(x)/D} \int_{-\infty}^x dy e^{-V(y)/D}$$

by means of which we find

$$\langle T_{FP} \rangle = \int_a^b dx I(x). \quad (2.53)$$

Furthermore, we may write

$$\langle T_{FP}^2 \rangle = \frac{2}{D} \int_a^b dx e^{V(x)/D} \int_{-\infty}^x dy e^{-V(y)/D} \int_y^x dz I(z) + \mathcal{R} \quad (2.54)$$

with

$$\begin{aligned} \mathcal{R} &= \frac{2}{D} \int_a^b dx e^{V(x)/D} \int_{-\infty}^x dy e^{-V(y)/D} \int_x^b dz I(z) = 2 \int_a^b dx I(x) \int_x^b dy I(y) \\ &= 2 \int_a^b dy I(y) \int_a^y dx I(x) = 2 \int_a^b dx I(x) \int_a^b dy I(y) - 2 \int_a^b dx I(x) \int_x^b dy I(y) = 2 \langle T_{FP} \rangle^2 - \mathcal{R} \\ &\rightarrow \mathcal{R} = \langle T_{FP} \rangle^2 \end{aligned}$$

where we have interchanged the boundaries of integration and the names of variables. Now, the variance reads

$$\langle \Delta T_{FP}^2 \rangle = \frac{2}{D} \int_a^b dx e^{V(x)/D} \int_{-\infty}^x dy e^{-V(y)/D} \int_y^x dz I(z)$$

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$$\begin{aligned}
&= \frac{2}{D} \int_a^b dx e^{V(x)/D} \int_{-\infty}^x dz I(z) \int_{-\infty}^z dy e^{-V(y)/D} \\
&= 2 \int_a^b dx e^{V(x)/D} \int_{-\infty}^x dz e^{-V(z)/D} [I(z)]^2.
\end{aligned}$$

This result is due to Reimann et al. (2001) who have simplified the formulae for the special case of a periodic potential (see chapter 4). Now, another interchange of the integrations yields

$$\begin{aligned}
\langle \Delta T_{FP}^2 \rangle &= 2 \left\{ \int_{-\infty}^a dz [I(z)]^2 e^{-V(z)/D} \int_a^b dx e^{V(x)/D} + \int_a^b dz [I(z)]^2 e^{-V(z)/D} \int_z^b dx e^{V(x)/D} \right\} \\
\langle \Delta T_{FP}^2 \rangle &= 2 \int_{-\infty}^b dz [I(z)]^2 e^{-V(z)/D} \int_z^b dx \Theta(x-a) e^{V(x)/D}. \tag{2.55}
\end{aligned}$$

With a look at eq. (2.41) one finds that the respective second integral can be expressed by the special stationary density $p_{st}(x)$ with $x_+ = a$, $x_- = b$ and $\tau = 0$.

For a general potential $V(x)$ the variance of the first passage time from a to b can be written in the following appealing form

$$\langle \Delta T_{FP}^2 \rangle = 2D \langle T_{FP} \rangle \int_{-\infty}^b dx [I(x)]^2 P_0^g(x, a, b, 0) \tag{2.56}$$

$$I(x) = \frac{1}{D} e^{V(x)/D} \int_{-\infty}^x dy e^{-V(y)/D}$$

where P_0^g is given by eq. (2.41).

Turning to the parabolic potential $V(x) = x^2/2$, we find after some straightforward manipulations

$$\langle T_{FP} \rangle = \sqrt{\pi} \int_{(\mu-v_T)/\sqrt{2D}}^{(\mu-v_R)/\sqrt{2D}} dx e^{x^2} \operatorname{erfc}(x), \tag{2.57}$$

$$\langle \Delta T_{FP}^2 \rangle = 2\pi \int_{(\mu-v_T)/\sqrt{2D}}^{\infty} dx e^{x^2} [\operatorname{erfc}(x)]^2 \int_{(\mu-v_T)/\sqrt{2D}}^x dy e^{y^2} \Theta\left(\frac{\mu-v_R}{\sqrt{2D}} - y\right). \tag{2.58}$$

From (2.57) one recovers $r_0 = 1/(\langle T_{FP} \rangle + \tau)$.

Formulae (2.57) and (2.58) can be easily evaluated numerically, except for small values of D and a long lasting relaxation time, i.e., the integration within the positive x range can hardly be performed when $\mu - v_R \gg \sqrt{2D}$ (note that we have inverted the direction of integration such that for $\mu < v_T$ the threshold is at negative and the reset point at positive values). However, just for the relaxation process from one unstable point b to another unstable point a ($a > b$ and

2.3. Central moments, coefficient of variation and phase diffusion coefficient

no attracting point between them) the following small D approximations can be made (Arecchi, 1981)

$$\langle T_{FP} \rangle(a \rightarrow b) \approx \int_b^a \frac{dx}{x} - D \int_b^a \frac{dx}{x^3} = \ln\left(\frac{b}{a}\right) - \frac{D}{2} \left(\frac{1}{b^2} - \frac{1}{a^2}\right), \quad (2.59)$$

$$\langle \Delta T_{FP}^2 \rangle(a \rightarrow b) \approx 2D \int_b^a \frac{dx}{x^3} = D \left(\frac{1}{b^2} - \frac{1}{a^2}\right). \quad (2.60)$$

Since for $a > b > c$

$$\langle T_{FP} \rangle(a \rightarrow c) = \langle T_{FP} \rangle(a \rightarrow b) + \langle T_{FP} \rangle(b \rightarrow c)$$

and

$$\langle \Delta T_{FP}^2 \rangle(a \rightarrow c) = \langle \Delta T_{FP}^2 \rangle(a \rightarrow b) + \langle \Delta T_{FP}^2 \rangle(b \rightarrow c),$$

one may divide mean and variance into two contributions corresponding to the relaxation from the reset point to an auxiliary point and the motion from this auxiliary point to the threshold. The first part can be treated by the above expressions while the second part is obtained by (2.57) and (2.58), respectively.

The approximation had to be used in order to obtain the data shown in Fig. 2.6 (r.h.s.) where $\mu = 0.99$, $v_T = 1$, and $v_R = 0$. It provided a curve agreeing in line thickness with the exact integration for a range of noise intensities where the latter is still feasible.

The coefficient of variation and the diffusion coefficient can be calculated from (2.57) and (2.58) using eq. (1.9) as follows

$$R = \frac{\sqrt{\langle \Delta T_{FP}^2 \rangle}}{\langle T_{FP} \rangle + \tau}, \quad (2.61)$$

$$D_{\text{eff}} = \frac{1}{2} \frac{\langle \Delta T_{FP}^2 \rangle}{(\langle T_{FP} \rangle + \tau)^3} = \frac{1}{2} R^2 r_0. \quad (2.62)$$

Note in the last line the relation between diffusion coefficient and coefficient of variation that was also discussed in the introduction. We remark that another expression for the diffusion coefficient can be found in terms of the spectrum (see next section).

Certainly, in the context of coherence resonance, the most interesting features become apparent in the noise activated firing regime plotting the characteristics r_0 , R and D_{eff} versus noise intensity. We show them in Fig. 2.6 (l.h.s.) for different values of a subthreshold base current and $\tau = 0$ (the influence of a finite absolute refractory period is discussed below). While the rate exhibits the common monotonously increasing behavior, the coefficient of variation displays a minimum at moderate values of D . *Weak* coherence resonance is present already for a vanishing base current indicating that the pure escape process out of the minimum is not a perfect Poisson process. Increasing the base current deepens the minimum and shifts it to smaller values of the noise strength. The different curves never cross what implies that the coherence is always improved if μ is increased.

According to the mentioned relation between coefficient of variation and phase diffusion one might expect that a minimum in R results in a minimum of D_{eff} as well.

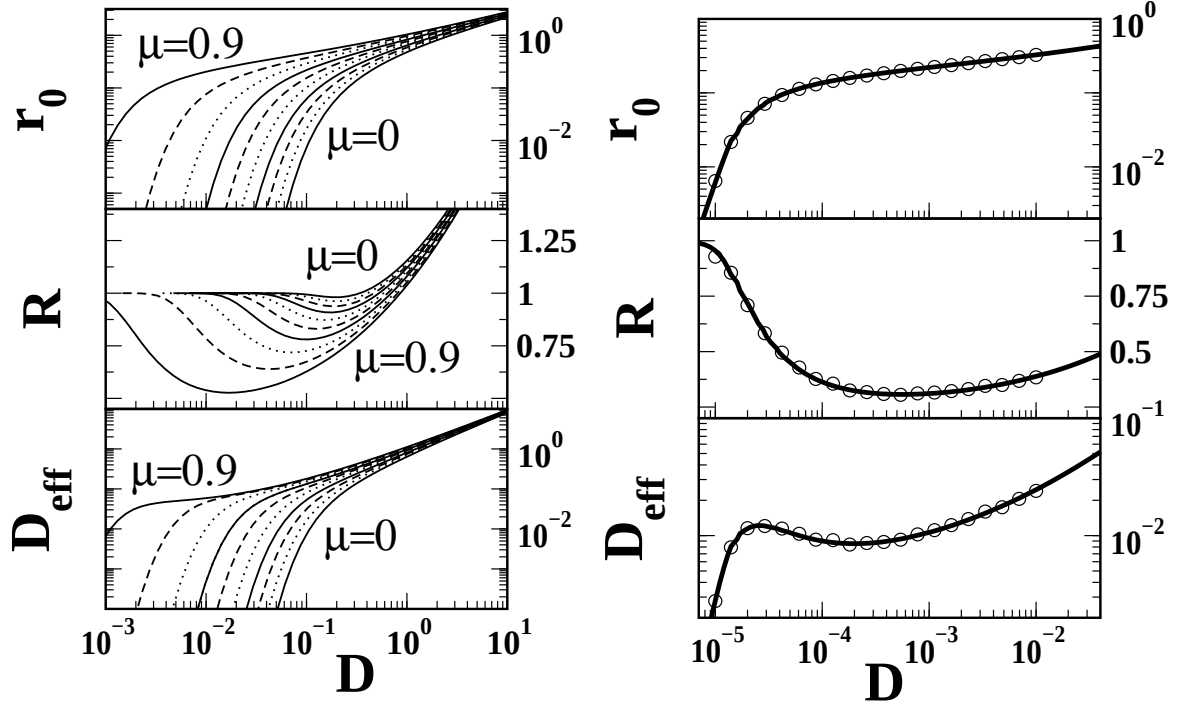


Figure 2.6.: Rate r_0 , coefficient of variation and diffusion coefficient according to eqs. (2.44),(2.61),(2.62) versus noise intensity for $\tau = 0$. Left: The parameter μ is varied from 0 to 0.9 in steps of 0.1 (subthreshold base current μ , i.e., noise activated firing regime). Right: For $\mu = 0.99$, the characteristics are compared to results (circles) from a numerical simulation of eq. (2.1) (Euler procedure with time step 10^{-4} , error bars are within symbol size).

Setting the derivative of (2.62) equals zero yields

$$\frac{dD_{\text{eff}}}{dD} = Rr_0 \frac{dR}{dD} + \frac{R^2}{2} \frac{dr_0}{dD} = 0$$

$$\frac{dR}{dD} = -\frac{R}{2r_0} \frac{dr_0}{dD}$$

Since the derivative of the rate is positive a potential minimum of D_{eff} versus D can only appear for values at which R drops, i.e., for values smaller than the one at which R becomes minimal.

For the data shown ($\mu \leq 0.9, \tau = 0$) no minima occur. The rate grows too strongly in the respective ranges of D allowing only for a flattening of the diffusion coefficient most pronounced for $\mu = 0.9$.

Moving closer to the transition point, for instance, to $\mu = 0.99$ (Fig. 2.6, r.h.s.) we find a minimum in the diffusion coefficient. This finding is confirmed by results of numerical simulations which are shown as circles. The minimum indicates a much more pronounced coherence resonance. It implies, for instance, that a neuronal ensemble

being initially in a synchronized state can maintain this synchronization longest when the noise strength has a certain *finite* value.

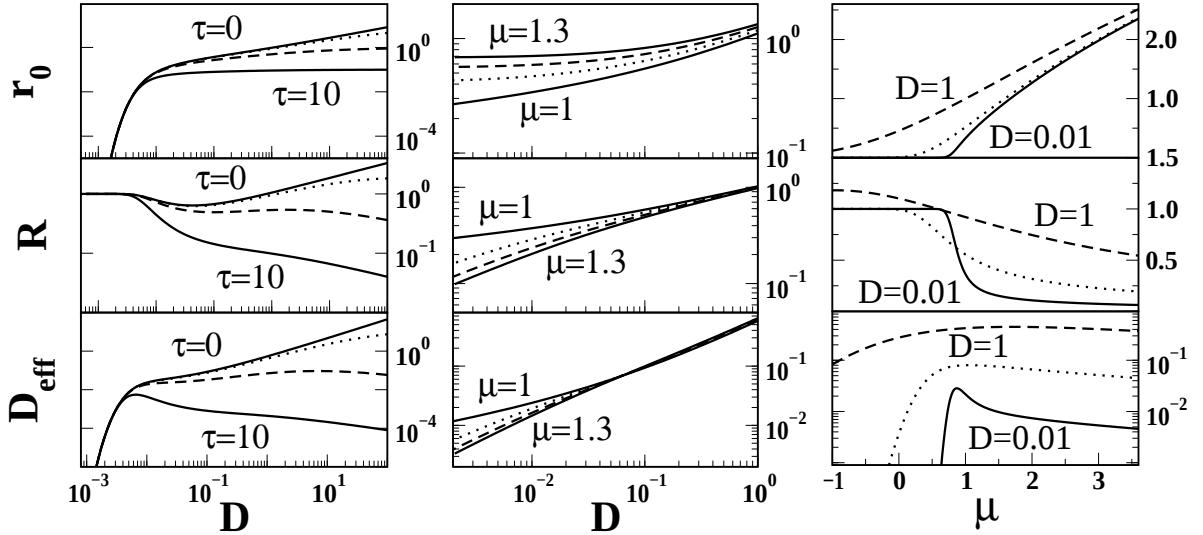


Figure 2.7.: Rate r_0 , coefficient of variation and diffusion coefficient according to eqs. (2.44),(2.61),(2.62) versus noise intensity (left and middle) and versus base current (right), respectively. Left: Variation of τ (0, 0.1, 1, 10), $\mu = 0.8$ (noise activated firing regime). Middle: The parameter μ is varied from 1 to 1.3 in steps of 0.1 (deterministic firing regime), $\tau = 0$. Right: Variation of D (0.01, 0.1, 1), $\tau = 0.1$.

The influence of a finite absolute refractory period is explored in Fig. 2.7 (l.h.s.). Generally, it becomes only relevant at large noise strength. First of all, at finite τ the rate does not grow unbounded but saturates for large D at $1/\tau$. In this trivial limit, the neuron fires regularly with period τ and hence R and D_{eff} , both characterizing the irregularity of the spike train, must drop for $D \rightarrow \infty$ and arbitrary but finite τ . The resulting maxima of R and D_{eff} versus D are shown for the rather non-physiological values $\tau = 1$ and 10 by dashed and solid lines, respectively. However, for a realistic value $\tau = 0.1$ we find only slightly smaller rates, coefficient of variation and phase diffusion coefficient within a reasonable range of noise intensities⁴.

We remark that in the deterministic firing regime (Fig. 2.7, middle), all quantities exhibit a monotonous shape. In the small noise limit, the rate saturates at the deterministic value $(\tau + \ln[(\mu - v_R)/(\mu - v_T)])^{-1}$ while R and D_{eff} decrease. At the critical value $\mu = 1$ (also in Fig. 2.7, middle), all three characteristics decrease for $D \rightarrow 0$. More common than a plot versus noise intensity is one versus the base current that can also be understood as a static signal. The rate is seen as a transfer or transduction

⁴Values of the noise strength that result in a saturation of the rate seem to be very unrealistic both with respect to physiological data and to the validity of assumptions made in the derivation of the LIF model

function with a typically sigmoidal shape resulting from the saturation at zero and $1/\tau$ for small and large noise strength, respectively. In Fig. 2.7 (r.h.s.), we show the rate for a slightly smaller range of μ (the saturation occurs at $r_0 = 10$). In particular at low noise ($D = 0.01$), the typical change of the rate in the vicinity of the transition point $\mu = 1$ is clearly seen. Here, the rate starts a more rapid growth and the coefficient of variation drops from unity (Poisson limit) to rather small values. At the first glance surprisingly, the effective diffusion coefficient attains a maximum shortly before the critical value is reached. This effect is caused by the rapid increase of the rate near the transition point. While the rate is large the statistics of the interspike interval is still mainly determined by the escape over the barrier, i.e., by a rather irregular process. Some neurons of an ensemble may fire in quick succession, others may be silent meanwhile. This gives rise to a large spreading in the spike count of the ensemble. Note that this effect corresponds in a way to the *maximum* of the diffusion coefficient with respect to D and is, though parametrically close to the CR phenomenon, the counterpart to the increased regularity at larger noise strength. Furthermore, we notice that a similar effect was found in Costantini and Marchesoni (1999) for the overdamped motion in a washboard potential which is also the subject of chapter 4.

2.4. The power spectrum

Since the LIF generates a renewal sequence of δ spikes we can apply a formula which connects the power spectral density and the characteristic function of the interspike interval (see, e.g. Stratonovich, 1967)

$$S_\sigma(\omega) = \int_{-\infty}^{\infty} d\tilde{\tau} \langle \sigma(t) \sigma(t + \tilde{\tau}) \rangle e^{i\omega\tilde{\tau}} = \frac{1}{\langle t \rangle} \frac{1 - |\varrho(\omega)|^2}{|1 - \varrho(\omega)|^2} + \frac{2\pi}{\langle t \rangle^2} \delta(\omega). \quad (2.63)$$

The characteristic function is equal to the Fourier transform of the interspike interval density $\rho(t)$

$$\begin{aligned} \varrho(\omega) &= \int_{-\infty}^{\infty} dt \rho(t) e^{i\omega t} = \int_0^{\infty} dt \rho(t) e^{i\omega t} \\ &= \int_0^{\infty} dt \rho(t) e^{-st} \Big|_{s=-i\omega} \\ &= L[-i\omega, \rho(t)]. \end{aligned} \quad (2.64)$$

It is given by the product $L[-i\omega, \delta(t - \tau)]L[-i\omega, \rho_{FP}]$ of the Laplace transform of the (deterministic) absolute refractory period τ

$$L[-i\omega, \delta(t - \tau)] = e^{i\omega\tau} \quad (2.65)$$

and the Laplace transform of the first passage time density of an OUP to an absorbing boundary that reads in our notation

$$L[-i\omega, \rho_{FP}] = e^{\Delta} \frac{\mathcal{D}_{i\omega}(\frac{\mu-v_R}{\sqrt{D}})}{\mathcal{D}_{i\omega}(\frac{\mu-v_T}{\sqrt{D}})} \quad (2.66)$$

where $\mathcal{D}_a(z)$ denotes the parabolic cylinder function (see appendix) and Δ is given by

$$\Delta = \frac{v_R^2 - v_T^2 + 2\mu(v_T - v_R)}{4D}. \quad (2.67)$$

The result (2.66) is due to Darling and Siegert (1953) and has been several times rederived (see, e.g., Gluss, 1967; Roy and Smith, 1969; Capocelli and Ricciardi, 1971; Melnikov, 1993). In respect of the calculations carried out in chapter 5 it might be useful to show briefly our own derivation of formula (2.66) which is close to that by Melnikov (1993).

Let $P(x, t)$ a probability density governed by the FPE (2.25) and at $t = 0$ be localized at x_+ . The reader may imagine an ensemble of particles started at this position. Then, if no influx of probability is present, the outflux of probability at the absorbing boundary x_- yields exactly the first passage time density (Tuckwell, 1988). To illustrate that point: in a numerical experiment one might start non-interacting particles at x_+ which diffuse in the parabolic potential and are taken “out of the game” when they reach the threshold. The number of particles reaching the threshold between t and $t + \Delta t$ gives then an estimate of the first passage time density multiplied by the total number of particles.

The outflux of probability has to be calculated from the time dependent solution $P(x, t)$ with the initial condition $P(x, 0) = \delta(x - x_+)$ and the boundary conditions (2.26), (2.27) and (2.29). Note, that in this case neither condition (2.28) nor a normalization of probability do apply since no influx at x_+ is considered.

The special Laplace transform

$$p(x, s) = e^{-(x_+^2 - x^2)/(4D)} \int_0^\infty dt e^{-st} P(x, t) \quad (2.68)$$

applied to the FPE (2.25) yields the ordinary differential equation

$$\hat{L}p(x, s) := Dp''(x, s) - \left(\frac{x^2}{4D} + s - \frac{1}{2} \right) p(x, s) = -\delta(x - x_+). \quad (2.69)$$

This equation can be solved provided we know a solution of the *homogeneous* problem $\hat{L}p(x, s) = 0$. The δ function in (2.69) leads to another jump condition for $p(x, s)$. In addition to the boundary conditions (2.26), (2.27) and (2.29), the solution of (2.69) must fulfill

$$[p'(x, s)]_{x_+} = -\frac{1}{D}. \quad (2.70)$$

This cancels by the second derivative the δ function in the right hand side of (2.69).

Solutions of the *homogeneous* problem $\hat{L}p(x, s) = 0$ are given by the parabolic cylinder functions.

We will use

$$\psi(x) = U\left(-i\omega - \frac{1}{2}, -\frac{x}{\sqrt{D}}\right) = \mathcal{D}_{i\omega}\left(-\frac{x}{\sqrt{D}}\right) \quad (2.71)$$

2. Coherence resonance in the leaky integrate-and-fire neuron

that approaches zero for $x \rightarrow -\infty$ and thus, possesses the correct asymptotic behavior (boundary condition (2.29)). An additional independent solution $\psi_2(x)$ that is not needed in the final result is scaled such that

$$\psi'(x)\psi_2(x) - \psi(x)\psi_2'(x) = 1. \quad (2.72)$$

In general, the left hand side is independent of x as can be readily verified taking the derivative and using the FPE (2.69). Next, we introduce the auxiliary function

$$Y(x) = \psi(x)\psi_{2-} - \psi_{-}\psi_2(x) \quad (2.73)$$

that obeys $Y_- = 0$ and $Y'_+ = 1$ by virtue of (2.72). A solution that satisfies the homogeneous equation and the boundary conditions (2.26), (2.27) and (2.29) is given by

$$p(x, s) = k \begin{cases} Y_+ \psi(x) , & x < x_+ \\ Y(x) \psi_+ , & x_+ < x < x_- \end{cases}. \quad (2.74)$$

The constant k can be determined by the jump condition (2.70).

$$\begin{aligned} [p']_+ &= k (Y'_+ \psi_+ - Y_+ \psi'_+) = k \left(\underline{\psi'_+ \psi_{2-} \psi_+} - \psi_- \underline{\psi'_{2+} \psi_+} - \underline{\psi_+ \psi_{2-} \psi'_+} + \psi_- \underline{\psi_{2+} \psi'_+} \right) \\ &= k \psi_- (\psi'_+ \psi_{2+} - \psi_+ \psi'_{2+}) = -\frac{1}{D} \\ &\leadsto \quad k = -\frac{1}{D\psi_-} \end{aligned}$$

where the underlined terms cancel each other and we have made use of relation (2.72). For the derivative of $p(x, s)$ at the absorbing boundary we obtain

$$p'_- = -\frac{\psi_+}{D\psi_-}. \quad (2.75)$$

We recall that the first passage time density was given by the probability current at the absorbing boundary the Laplace transform of which reads

$$\varrho_{FP}(s) = J(x_-, s) = \int_0^\infty dt e^{-st} j(x_-, t) = -D \int_0^\infty dt e^{-st} \left. \frac{\partial P}{\partial x} \right|_{x_-} = -D e^{\frac{x_+^2 - x_-^2}{4D}} p'_- = e^{\frac{x_+^2 - x_-^2}{4D}} \frac{\psi_+}{\psi_-}.$$

By inserting $x_\pm = v_{R,T} - \mu$ into eq. (2.63) we obtain eq. (2.66).

Combining eqs. (2.63) and (2.66) we obtain the power spectrum for the leaky integrate and fire neuron

$$S_\sigma(\omega) = r_0 \frac{\left| \mathcal{D}_{i\omega} \left(\frac{\mu - v_T}{\sqrt{D}} \right) \right|^2 - e^{2\Delta} \left| \mathcal{D}_{i\omega} \left(\frac{\mu - v_R}{\sqrt{D}} \right) \right|^2}{\left| \mathcal{D}_{i\omega} \left(\frac{\mu - v_T}{\sqrt{D}} \right) - e^{\Delta} e^{i\omega\tau} \mathcal{D}_{i\omega} \left(\frac{\mu - v_R}{\sqrt{D}} \right) \right|^2} + 2\pi r_0^2 \delta(\omega). \quad (2.76)$$

Although both relations (2.63) and (2.66) are well known for decades, we are not aware⁵ of any explicit formula for the power spectrum like in eq. (2.76).

⁵Note, however, that Holden (1976) mentioned the possibility to achieve the power spectrum for $\tau = 0$ by the Laplace transform eq. (2.66) and the appropriate formula from renewal theory (i.e., eq. (2.63)).

In the following, we will use the spectrum for the process with zero mean, in other words, we ignore the second term appearing in eq. (2.76) and consider

$$S(\omega) := S_{\sigma-\langle\sigma\rangle}(\omega) = r_0 \frac{\left| \mathcal{D}_{i\omega}(\frac{\mu-v_T}{\sqrt{D}}) \right|^2 - e^{2\Delta} \left| \mathcal{D}_{i\omega}(\frac{\mu-v_R}{\sqrt{D}}) \right|^2}{\left| \mathcal{D}_{i\omega}(\frac{\mu-v_T}{\sqrt{D}}) - e^{\Delta} e^{i\omega\tau} \mathcal{D}_{i\omega}(\frac{\mu-v_R}{\sqrt{D}}) \right|^2}. \quad (2.77)$$

The first somewhat surprising property of the spectrum $S(\omega)$ at finite frequencies is that it does not decay in the high frequency limit but saturates at r_0 .

$$\lim_{\omega \rightarrow \infty} S(\omega) = r_0. \quad (2.78)$$

Since we deal with a train of δ spikes the neuronal output possesses an infinite variance.

The second moment of $\sigma(t)$ can be written as the limit

$$\begin{aligned} \lim_{\bar{\tau} \rightarrow 0} \langle \sigma(t) \sigma(t + \bar{\tau}) \rangle &= \lim_{\bar{\tau} \rightarrow 0} \left\langle \sum_{t_i, t_j \in \mathcal{T}} \delta(t - t_i) \delta(t - t_j + \bar{\tau}) \right\rangle \\ &= \lim_{\bar{\tau} \rightarrow 0} \left\langle \sum_{t_i \in \mathcal{T}} \delta(t - t_i) \delta(t - t_i + \bar{\tau}) + \sum_{t_i \neq t_j \in \mathcal{T}} \delta(t - t_i) \delta(t - t_j + \bar{\tau}) \right\rangle. \end{aligned}$$

The first term gives rise to a singularity for $\bar{\tau} \rightarrow 0$ since

$$\lim_{\bar{\tau} \rightarrow 0} \left\langle \sum_{t_i \in \mathcal{T}} \delta(t - t_i) \delta(t - t_i + \bar{\tau}) \right\rangle = \delta(\bar{\tau}) \left\langle \sum_{t_i \in \mathcal{T}} \delta(t - t_i) \right\rangle = r_0 \delta(\bar{\tau}).$$

The second term yields only a finite contribution (squared mean value and spike-spike correlation function at vanishing argument, see (Stratonovich, 1967), Vol.I, pp. 152, formula (6.28)). As a consequence of the above relation, the integral over the spectrum that gives the value of the correlation function at $\bar{\tau} = 0$ diverges.

The dependence of the rate r_0 on the system's parameters was discussed in the previous section, thus, the high frequency limit is already understood. Another simple limit is the spectral density for vanishing frequency where we obtain

$$\lim_{\omega \rightarrow 0} S(\omega) = 2D_{\text{eff}} = R^2 r_0. \quad (2.79)$$

One concludes that for a CV below one the low frequency limit is below the high frequency limit, there is a dip at low frequencies that is caused by the refractory period as was also pointed out by Franklin and Bair (1995).

One way to derive this limit is the expansion of the characteristic function for $\omega \rightarrow 0$

$$\rho(\omega) = \langle e^{i\omega T} \rangle = 1 + i\langle T \rangle \omega - \langle T^2 \rangle \omega^2 / 2 + \dots \quad (2.80)$$

Inserting this into eq. (2.63) one finds (Franklin and Bair, 1995)

$$\lim_{\omega \rightarrow 0} S(\omega) = \frac{\langle \Delta T^2 \rangle}{\langle T \rangle^3}. \quad (2.81)$$

2. Coherence resonance in the leaky integrate-and-fire neuron

A comparison with the general expression for the renewal process (1.9) then yields (2.79). Another way is the usage of the Kubo formula. By means of eq. (2.8) we find

$$\begin{aligned} D_{\text{eff}} &= \frac{1}{2} \lim_{t \rightarrow \infty} 2 \langle \dot{n}(t) n(t) - \langle \dot{n}(t) \rangle \langle n(t) \rangle \rangle = \lim_{t \rightarrow \infty} \int_0^t dt' \langle \sigma(t) \sigma(t') - \langle \sigma(t) \rangle \langle \sigma(t') \rangle \rangle \\ &= \int_0^t dt' C(t, t') = \lim_{t \rightarrow \infty} \int_0^t d\bar{\tau} C(t, t - \bar{\tau}) \end{aligned}$$

where $C(t, t')$ is the correlation function that tends for large t to the stationary function $C(t - t')$ which depends only on the difference of its arguments. Using furthermore the Wiener-Khintchine theorem we obtain

$$D_{\text{eff}} = \lim_{t \rightarrow \infty} \int_0^t d\bar{\tau} C(\bar{\tau}) = \int_0^\infty d\bar{\tau} C(\bar{\tau}) = \frac{1}{2} S_{\sigma - \langle \sigma \rangle}(\omega = 0)$$

from which eq. (2.79) follows.

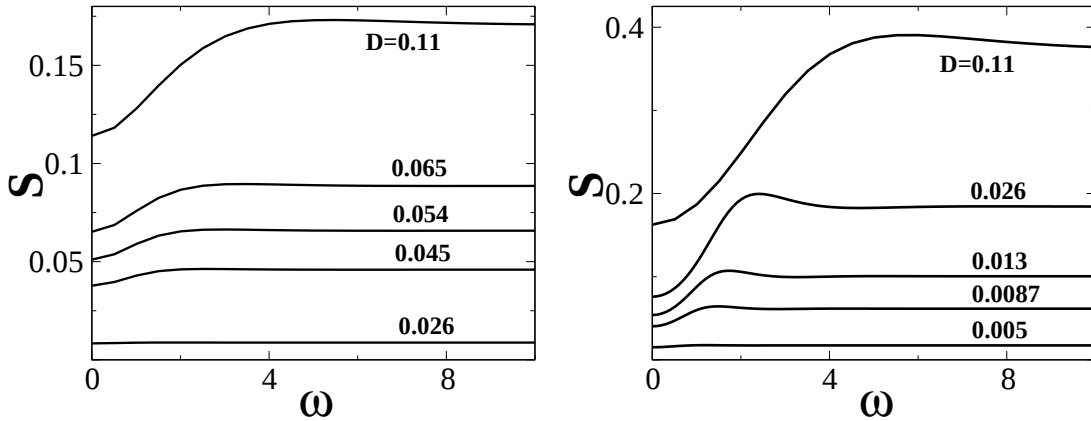


Figure 2.8.: Power spectra in the noise activated firing regime for different noise intensities at $\tau = 0.1$. Left: $\mu = 0.5$. Right: $\mu = 0.8$.

New details about the neuronal dynamics are revealed if we consider low to moderate frequencies. From Figs. 2.8, 2.9, and 2.10 it becomes apparent that the spectral shape depends strongly on base current and noise intensity. First, we focus on the noise activated firing regime at small to moderate D , then we discuss briefly the deterministic firing regime and the strong noise limit that is essentially the same in both regimes. At low base current and moderate noise intensity ($\mu = 0.5$, $D < 1$, Fig. 2.8, l.h.s.), the spectrum starts at low values for $\omega = 0$, increases, passes through a small maximum and saturates eventually at r_0 . As mentioned above, the dip at low frequencies is due to the finite refractory period (relative and absolute) and was found also in former studies (Franklin and Bair, 1995; Plesser and Geisel, 1999b) as well as in experimental spectra (Bair et al., 1994). Going to smaller noise intensity yields a weaker dip - in this

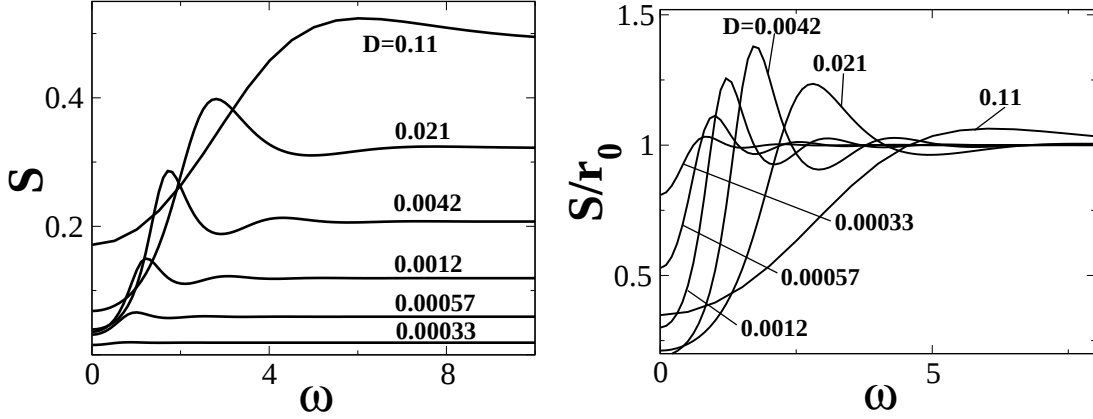


Figure 2.9.: Left: Power spectra in the noise activated firing regime for different noise intensities at $\mu = 0.95$, $\tau = 0.1$. Right: Normalized Power spectra $S(\omega)/r_0$ at same parameters.

limit we obtain eventually a flat Poissonian spectrum as can be also inferred from the low frequency limit eq. (2.79) that approaches r_0 (because of $R(D \rightarrow 0) = 1$) which in turn coincides with the high frequency limit. This behavior is due to the fact that refractoriness (i.e., the “passage” from reset to resting level) becomes irrelevant if the neuron needs a very long time on average to reach the threshold.

For larger as well as for small noise intensity this picture does not change in principle if we go to larger but still subthreshold base currents ($\mu = 0.8$, Fig. 2.8, r.h.s. and $\mu = 0.95$, Fig. 2.9, l.h.s.). The novel feature appearing at moderate D due to coherence resonance is a pronounced hump at finite frequencies. Clearly, for $\mu = 0.95$ this maximum is largest and even accompanied by higher harmonics at roughly twice the frequency of the first peak. The effect is best seen, if the normalized spectrum S/r_0 is plotted (Fig. 2.9, r.h.s.).

In the deterministic firing regime, the small noise limit is completely different from the flat Poissonian spectrum. Recall that in this regime and for $D \rightarrow 0$ the neuron fires strictly periodically with a finite rate $r_0 = (\tau + \ln[(\mu - v_R)/(\mu - v_T)])^{-1}$. Hence, for a small noise intensity we expect high peaks close to $2\pi r_0$ and its multiples that are indeed present in Fig. 2.10 (l.h.s.). Note, however, that for $D = 0.11$ the shape of the spectrum does not differ significantly from the corresponding spectra in the noise activated firing regime.

For large noise ($D > 1$), the spectrum exhibits also an oscillatory behavior (Fig. 2.10, r.h.s.) regardless of the value of μ . This is again the trivial limit in which the absolute refractory period dominates and the noise driven escape via the threshold is very fast. Accordingly, one finds peaks at $2\pi/\tau$ and for strong noise also at the higher harmonics. Let us discuss more in detail the coherence resonance effect in the noise driven firing regime. How can the hump of the spectrum be quantified? One might compute the height of the peak and divide by its quality factor. However this is inappropriate since

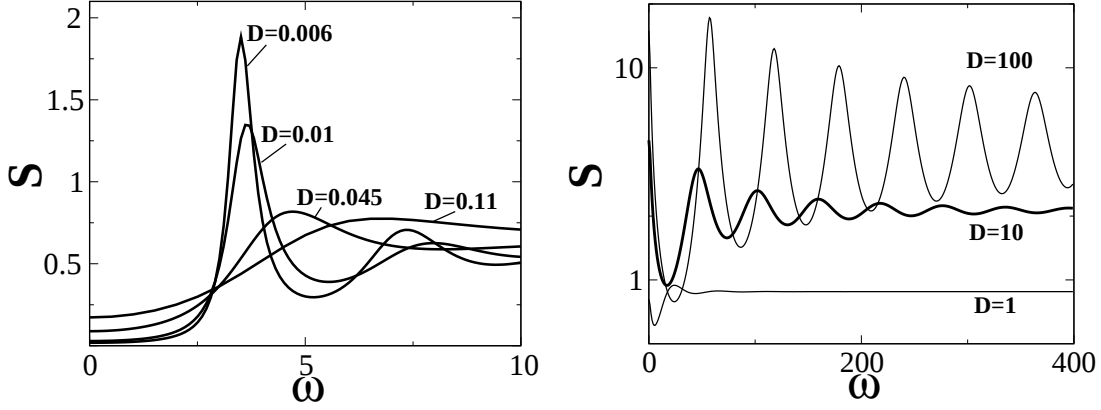


Figure 2.10.: Left: Power spectra (deterministic firing regime) for different noise intensities at $\mu = 1.2$. Right: Power spectra (noise activated firing regime) for different large noise intensities at $\mu = 0.8$.

the hump is not very pronounced in all cases and the spectrum does not decay for large ω . Here, we will use another quantity, namely the value by which the spectrum exceeds its high frequency limit r_0 divided by that value

$$\beta = \frac{S(\omega_{max}) - r_0}{r_0} \quad (2.82)$$

where we consider only the first (highest) peak at finite frequency. The function β is depicted in Fig.2.11 and shows a maximum with respect to the noise intensity - another manifestation of coherence resonance. The comparison to the CV reveals that the maximum occurs at smaller D than the minimum in R does. This difference decreases the closer we get to the bifurcation point $\mu = 1$.

One may ask for the frequency at which the spectrum attains its maximum. Is it simply related to the firing rate like for the deterministic firing regime in the small noise limit? This is obviously not the case as revealed by Fig. 2.11 (r.h.s.). The frequency ω_{max} is always larger than the firing frequency $2\pi r_0$. The former is rather related to the most probable interspike interval. This is the so called mode, i.e., the time where the ISI density $\rho(t)$ attains its maximum.

It is clear that for a coherent output mode and mean of $\rho(t)$ are close to each other. Thus, we can look upon Fig. 2.11 (r.h.s.) as another manifestation of coherence resonance: the mutual distance of ω_{max} and $2\pi r_0$ is apparently smallest for the noise intensity at which β becomes maximal. Consequently, for this value of D , the difference between mode and mean of $\rho(t)$ is minimal and hence the neuronal output is closest to a periodic one.

What does the spike train look like if the CR effect is present? In Fig. 2.12 we show the voltage dynamics and the resulting spike trains for three different noise levels (small, optimal and large intensities) for $\mu = 0.95$. Although some regularity can be seen by

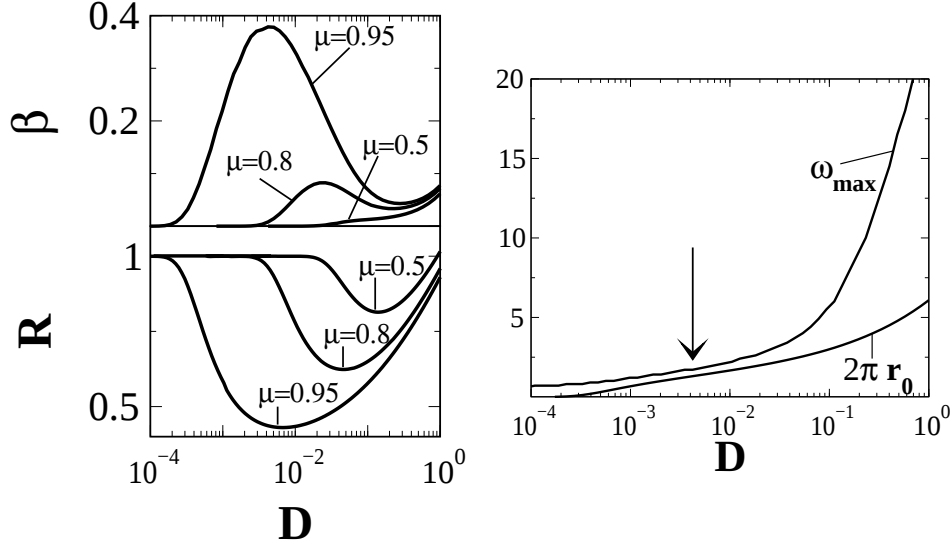


Figure 2.11.: Left: The function $\beta(D)$, eq. (2.82) is compared with the CV for different values of μ (noise activated firing regime), $\tau = 0.1$. Right: The frequency where the power spectrum attains its maximum is compared to the mean firing rate (cycle frequency) for $\mu = 0.95$ and $\tau = 0.1$. The arrow indicates the noise strength where the mutual distance of both frequencies is minimal.

eye in the spike train generated at the optimal noise level, the effect is not pronounced to a great extent.

Of course we may choose a value of μ closer to the bifurcation point (here $v_T = 1$) and obtain a practically perfect regularity for say $\mu = 1 - 10^{-10}$ and a proper noise intensity. However, this has not much importance in our opinion. First, for such small values of μ the CR effect would occur at a tiny noise level that cannot be observed in real neurons since they are subject to several (internal and external) sources of noise and it is hard to imagine a situation where their overall noise level is very close to zero. Second, the LIF model is, of course, only an approximation and it is more than questionable whether predictions of it that depend to a great extent on a fine tuning of parameters are meaningful. Hence, what remains is that coherence resonance in the LIF model is a markedly statistical effect that is present for a reasonable range of the base current but becomes visible rather in the power spectrum and CV than directly in the spike train.

2.5. Summary

We have shown by different measures that the leaky integrate-and-fire neuron exhibits coherence resonance. Novel formulae for the power spectrum and the variance of the interspike interval have been derived. We have thus understood the simple mechanism

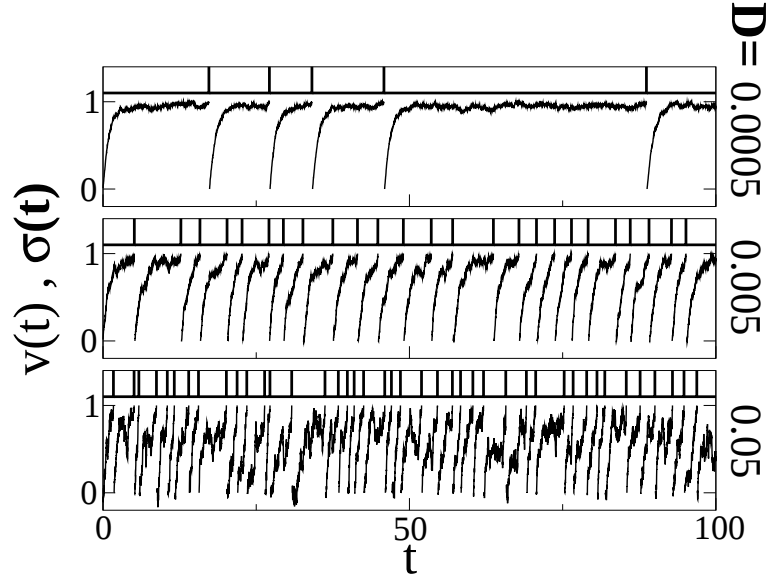


Figure 2.12.: Voltage dynamics and generated spike trains for three noise levels indicated at the r.h.s. The middle panel corresponds (roughly) to the value of D that maximizes β (cf. Fig. 2.11, l.h.s.). Remaining parameters: $\mu = 0.95, \tau = 0.1$.

that underlies the noise induced eigenfrequency at moderate noise intensity. The consequences of this phenomenon for the signal transmission through a single LIF neuron or a neuronal ensemble will be explored in chapter 5.

3. The stochastic FitzHugh-Nagumo model and coherence resonance

The FitzHugh-Nagumo (FN) model sometimes also called the Bonhoeffer-Van der Pol (BVP) model is a simple example for a two-dimensional excitable dynamics. Proposed by FitzHugh (1961) as a simplification of the famous model by Hodgkin and Huxley (1952) it describes (qualitatively rather than quantitatively) the response of an excitable nerve membrane to external current stimuli. Important features found also in experiments on real neurons include a recovery mechanism and different refractory states after excitation as well as states of enhanced and depressed excitability depending on the time course of external stimulation. In a spatial extended version with diffusion in the fast voltage variable the model displays traveling pulses, i.e. it reproduces the propagation of an action potential (spike) down the neuronal axon (Scott, 1975). This extended version is sometimes also referred to as FN model, it will be, however, not considered here.

Because of its generic excitability mechanism, the model has found applications in other fields, too. In physical chemistry, for instance, it has been frequently used in the spatial extended version for the modeling of spiral waves. From a more mathematical point of view, several authors have focused on different kinds of external deterministic stimulation, as for instance, periodic (Alexander et al., 1990; Chou and Lin, 1996) and chaotic forcing (Longtin, 1995a).

A stochastic version of the model was explored for the first time by Treutlein and Schulten (1986). Here the notion of noise induced limit cycles were introduced for the FN model. The system driven by white noise and a (periodic or aperiodic) signal became popular during the 1990's in context of stochastic resonance (Longtin, 1993; Pei et al., 1995; Longtin, 1995b; Collins et al., 1995b; Wiesenfeld et al., 1994; Collins et al., 1995a; Chialvo et al., 1997; Longtin and Chialvo, 1998, see also chapter 6). Furthermore, in a spatial extended version (in this case also called a noisy excitable medium) it has also attracted much attention in the last decade (see, for instance, Jung et al., 1998; Neiman et al., 1999; Hempel et al., 1999).

In this chapter, we address the FN model driven by white noise - a seemingly simple case that is nonetheless still the topic of many investigations.

On the one hand, the FN system driven by white noise exhibits coherence resonance (Pikovsky and Kurths, 1997; Casado, 1997; Massanés and Vicente, 1999; Lindner and

Schimansky-Geier, 1999; Makarov et al., 2001). Due to the presence of quasi deterministic time scales in the dynamics the model exhibits an enhanced regularity and quasi oscillations at an optimal finite noise level.

On the other hand, from the theoretical point of view it is still a challenge to determine conventional probability measures like probability densities or correlation functions of the stochastic system. Even the calculation of the stationary probability density is in general a nontrivial (and still unsolved) problem. The reason for this is that the FN model is a so called non-potential system. For certain parameter sets one may achieve expressions for the density (Izús et al., 1998) using non-equilibrium potential theory (see, e.g., Graham and Tél, 1986). Unfortunately, these parameter sets are not typical for physiological applications of the model and hence this method will not be used in the following.

Here, we will derive approximate expressions for the stationary marginal densities of the two variables and the pulse or spike rate of the model that coincides with the rotational flux of probability. The results are based on the assumption of a perfect time scale separation between the two dynamical variables. We will show that in this limit the two-dimensional stochastic system separates into *two* one dimensional subsystems which exchange probability by instantaneous currents. Furthermore, in the same limit also higher moments of the interspike interval are found in terms of quadratures¹. Hence, the CV and the spike count diffusion can be quantified in order to explore the coherence resonance features of the system.

After the investigation of the conventional FN system with a cubic null cline we will use a piecewise linear version of it that is further reduced to a two-state system. The output of this system corresponds to a two-state filtering of the voltage variable. Its power spectrum can be exactly calculated for arbitrary frequency and noise intensity applying a method that is due to Melnikov (1993). We shall study this power spectrum not only in the excitable case but also in the bistable and oscillatory (limit cycle) regime of the FN model.

3.1. The FitzHugh-Nagumo model with cubic nonlinearity

3.1.1. Deterministic and stochastic model

Before turning to the stochastic version of the FitzHugh-Nagumo model we discuss the deterministic version that can be written in the symmetric form

$$\begin{aligned}\epsilon \dot{x} &= x - x^3 - y + s, \\ \dot{y} &= \gamma x - y + b.\end{aligned}\tag{3.1}$$

¹A similar calculation of higher moments was carried out by Grasman and Roerdink (1989) for the noisy Van der Pol oscillator.

Here, x stands for the voltage variable (corresponding up to a constant to the variable $v(t)$ in the LIF model from the previous section) while y is the so called recovery variable. ϵ determines the time scale separation between x and y . The stimulus parameter $s = \text{const}$ in the first equation can be easily lumped into b by the transformation $\tilde{y} = y - s$, therefore we set $s = 0$ in the following. In most applications of the model (e.g. also in the neuronal context) one assumes

$$\epsilon \ll 1 \text{ and } \epsilon \ll 1/\gamma. \quad (3.2)$$

The condition on the right hand side is needed since the time scale of y being the slow variable is also influenced by γ .

Another popular version of the model used, e.g., in Longtin (1993); Wiesenfeld et al. (1994); Collins et al. (1995a); Pei et al. (1995) reads in the most general (noiseless) form

$$\tau_v \dot{v} = v(v - A)(1 - v) - w, \quad \tau_w \dot{w} = v - dw - B. \quad (3.3)$$

The transformation to new variables and time

$$v = \alpha x + \beta, \quad w = \Gamma y + \Delta, \quad \tilde{t} = t/\tau$$

with

$$\alpha = \sqrt{\frac{A^2 - A + 1}{3}}, \quad \beta = \frac{1 + A}{3}, \quad \Gamma = \left(\frac{A^2 - A + 1}{3} \right)^{\frac{3}{2}}, \quad \Delta = \frac{(A + 1)(2A - 1)(A - 2)}{3^3}, \quad \tau = \frac{\tau_w}{d}$$

leads to the dynamics eq. (3.1) with b , γ and ϵ expressed by the above constants.

$$\gamma = \frac{1}{d\alpha^2}, \quad b = \frac{1}{d\Gamma}(\beta - B - d\Delta), \quad \epsilon = \frac{d\tau_v}{\alpha^2\tau_w}$$

For typical parameter values (Longtin, 1993)

$$A = \frac{1}{2}, \quad d = 1, \quad B = 0.15, \quad \tau_w = 1, \quad \tau_v = 0.005$$

one finds

$$\alpha = \beta = 0.5, \quad \Gamma = \frac{1}{8}, \quad \Delta = 0 \quad \rightsquigarrow \quad \gamma = 4, \quad b = 2.8, \quad \epsilon = 0.02$$

The null clines of the model (curves with $\dot{x} = 0, \dot{y} = 0$) are a cubic function $y_{\dot{x}=0}(x)$ for the voltage variable with minimum and maximum at $(x_{\mp}, y_{\mp})$, respectively and a linear function $y_{\dot{y}=0}(x)$ for the refractory variable. The latter is determined by the parameters γ and b . Depending upon their values we will have different numbers and kinds of fixed points in the phase plane (x, y) , i.e. intersection points of the null clines. For sufficiently small ϵ there are basically three dynamical regimes of interest illustrated in Fig. 3.1.

1. One unstable fixed point at the middle branch - called the oscillatory regime (limit cycle system, for small ϵ also called a relaxation oscillator).

3. The stochastic FitzHugh-Nagumo model and coherence resonance

2. Two stable and one unstable fixed point - the bistable regime.
3. One stable fixed point, for reasons of symmetry assumed at the left stable branch of the cubic null cline - this is the excitable regime.

We note that the transition between excitable and oscillatory regime occurs by changing b via a supercritical Hopf bifurcation. However, we do not go into the details of the bifurcation analysis (for this, see, e.g. FitzHugh (1961); Grasman (1989)) because it is not needed in the following.

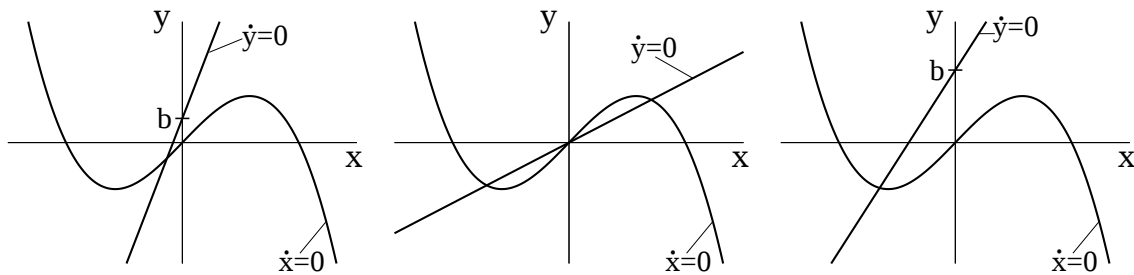


Figure 3.1.: Three different dynamical regimes of the FitzHugh-Nagumo model with null-clines of the x and y dynamics. Left panel: oscillatory regime ($\gamma = 2.5, b = 0.2$). Middle panel: bistable regime ($\gamma = 0.5, b = 0$). Right panel: excitable regime ($\gamma = 1.5, b = 0.6$).

In the oscillatory regime, a state point $(x(t), y(t))$ will move on a *limit cycle* close to the left and right branches of the cubic null cline. Since $\epsilon \ll 1$ the period is mainly given by the slow motion along the branches. In this regime the system is not much different from the Van der Pol oscillator that is a generic model for relaxation oscillations in electronics and other fields. It also corresponds in some way to the leaky integrate-and-fire neuron in the deterministic firing regime at zero noise except that the FN model yields directly a series of action potentials in $x(t)$ whereas the LIF model generates only the firing times and the action potential is represented by a δ spike.

In the bistable regime the state point will simply relax to one of the stable fixed points (which one depends, of course, on the initial conditions). This regime might be of some importance in the neuronal context since also the more realistic Hodgkin-Huxley model as well as some real neurons display such bistability for certain stimulus parameters (Longtin, 1993).

In the following we will focus on the excitable regime and return to the other two regimes when considering a simplified FN model in section 3.2.

The excitable regime captures some important features of the action potential generation by real excitable neurons. This is illustrated in Fig. 3.2 closely following FitzHugh (1961). The phase plane and the motion of the state point is interpreted in physiological terms. Starting the system at the fixed point, that is, the resting point of the neuron, leaves it there forever. In contrary, a “proper” initial condition for the state

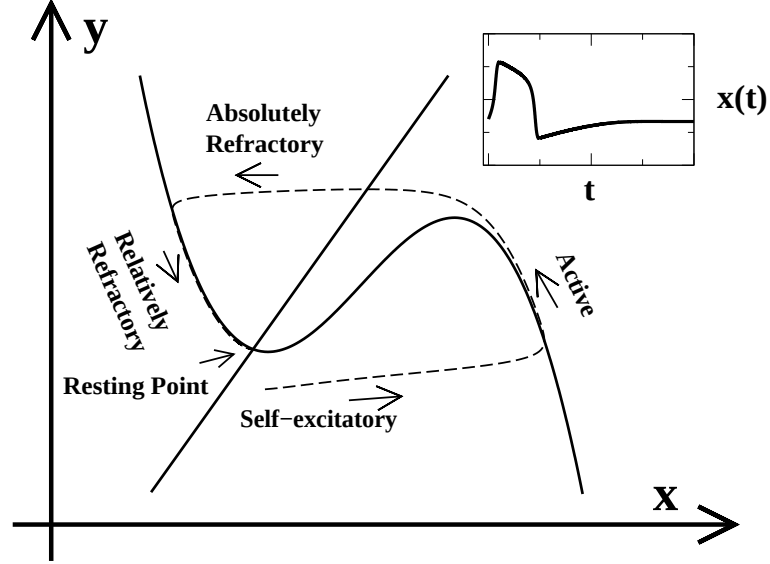


Figure 3.2.: Physiological phase diagram (excitable regime). Regions of particular neuronal states are indicated and related to the motion of the state point (trajectory of eq. (3.1)). The inset shows the shape of the resulting action potential $x(t)$.

point (see below) leads to a long excursion through the phase plane. This initial condition placed in the region labeled as “self excitatory” can be realized by a perturbation in the voltage or the recovery variable or by perturbing both. In the beginning of the mentioned excursion the state point moves from the initial position rapidly to the right branch of the cubic null cline and passes it upwards till it reaches the local maximum of the cubic function. This is the firing or active state. Around the top the dynamics becomes unstable and the state point switches to the left branch. During this time a further excitation through a pulse in x is impossible, therefore this region of the phase plane can be identified with the absolute refractory period. Finally, the point relaxes into the fixed point (resting state) and is (if not already very close to the fixed point) during this time not to such an extent excitable as in the resting state, therefore the slow passage along the left branch represents the relative refractory period. The relaxation takes infinitely long time and this is all what happens in the deterministic system if no external excitation takes place. The shape of the voltage variable as a function of time is illustrated in the inset of Fig. 3.2. Qualitatively, it resembles an action potential as observed in real neurons.

Now we specify what is meant with ‘proper initial condition’. As FitzHugh (1961) noted there is a line in $x - y$ plane separating trajectories that starting from the lower left region either diverge to the right (generating a spike) or to the left (generating a subthreshold excursions). This line that FitzHugh (1961) called a “quasi type point” separatrix is in general not uniquely defined but hinges upon what we define as a spike. In fact, by a fine tuning of the initial position around the separatrix one may produce

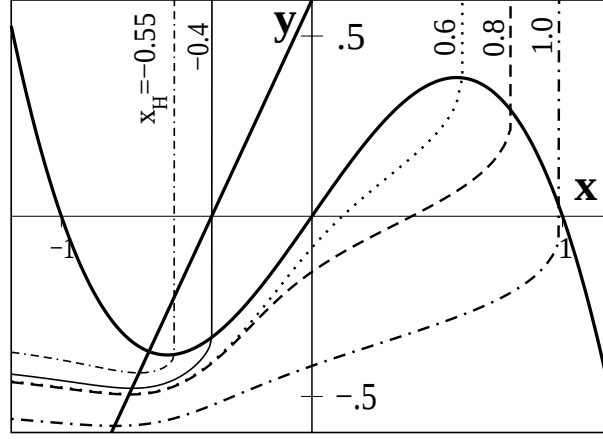


Figure 3.3.: Separatrix lines for $\epsilon = .1, \gamma = 1.5, b = 0.6$ and the indicated pulse heights that define a spike. All initial points below the respective line will result in a pulse of minimum height x_H .

‘all intermediates between “all” and “none” responses’ (FitzHugh, 1961). If we define a spike as a pulse in $x(t)$ of minimum height x_H the separating line is well defined and may be numerically determined. Such lines for different x_H values are shown in Figs. 3.3 and 3.4 for $\epsilon = 10^{-1}$ and $\epsilon = 10^{-2}$, respectively. Initial points below the respective line yield spikes of minimum height x_H . First of all, points with $x > x_H$ result trivially in spikes of the desired height. More important in the following is the run of the curves close to the fixed point and the minimum of the cubic null cline. The question is whether the different lines are well separated or not. This depends strongly on the value of ϵ . For $\epsilon = 10^{-1}$ the lines for $x_H = 0.6$ and 0.8 are close by. Spikes of minimum height $x_H = 1$ in turn require a slightly lower y value. The curves for $x_H = -0.55$ and -0.4 are well separated - these result clearly in subthreshold pulses the amplitude of which can be tuned in a finite range. For the more realistic value $\epsilon = 10^{-2}$ (Fig. 3.4) all lines with $x_H \geq -0.4$ are practically indistinguishable in the region of interest. This is also shown in an expanded view of the region around the minimum (inset of Fig. 3.4). Although this set of lines is still a whole array of close-by curves one may look upon them as one single line that is, the separatrix for excitations of action potentials. An excursion of the state point from the resting point due to an external perturbation will either result in a subthreshold pulse or in an action potential - a pulse of intermediated height is very unlikely since it would require an accurate placing of the state point within the array of curves. The mentioned subthreshold excursion may occur if the initial value is within the region between the lines for $x_H = -0.55$ and the separatrix (inset of Fig. 3.4). Its amplitude can be obviously well distinguished from that of a full action potential. In this way, the FN model generates for sufficiently small ϵ an all-or-none response as it is also typical for neurons.

Perturbations driving the state point repeatedly out of the vicinity of the fixed point

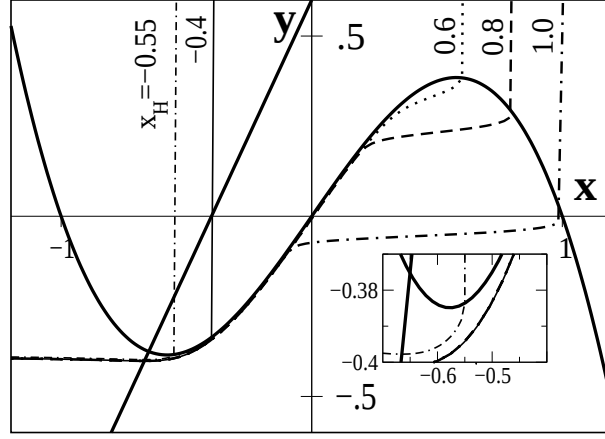


Figure 3.4.: Separatrix lines for $\epsilon = .01, \gamma = 1.5, b = 0.6$. The inset shows an expanded view of the lower left region. The line for $x_H = -0.55$ (dashed-dotted) is separated from the others that cannot be distinguished in the given resolution.

can be introduced either by deterministic forcing or by fluctuations of the system's parameters. Here we consider the latter case since neurons as well as many other excitable systems are inherently noisy (Tuckwell, 1989). As outlined in the introduction, conductance and synaptic fluctuations as well as random synaptic input have to be taken into account. The simplest way to do this is to add noise terms to eq. (3.1). Several authors have considered white noise or short correlated colored noise sources in the equations of **1**) both variables (Treutlein and Schulten, 1986; Kurrer and Schulten, 1991; Izús et al., 1998), **2**) in the voltage variable (Longtin, 1993, 1995b; Collins et al., 1995a) or **3**) in the recovery variable (Wiesenfeld et al., 1994; Pei et al., 1995; Pikovsky and Kurths, 1997). All these variants might be appropriate depending on the noise sources considered. According to the picture drawn in the previous chapter on the LIF model, the main contribution originates in random synaptic input, thus a noise term in the voltage equation is appropriate. However, one outcome of the cited papers is that important features like coherence and stochastic resonance apparently do not depend on to which equation noise is added. In view of this we will restrict our consideration to the case that white Gaussian noise of intensity D acts on the recovery variable y , i.e., eq. (3.1) becomes

$$\begin{aligned}\epsilon \dot{x} &= x - x^3 - y \\ \dot{y} &= \gamma x - y + b + \sqrt{2D}\xi(t)\end{aligned}\tag{3.4}$$

A certain limit case of this variant can be treated analytically as we will see in the following. Approximations are also possible for the other variants (see, e.g., Collins et al., 1995a), however, these do not take account of the refractory period that is essential for the occurrence of coherence resonance.

It is maybe worth mentioning that eq. (3.4) is equivalent to the situation where a

3. The stochastic FitzHugh-Nagumo model and coherence resonance

colored noise with correlation time one acts on the voltage variable.

Introducing two new variables by $y(t) = z(t) - \eta(t)$ we may write (because the second equation in eq. (3.4) is linear)

$$\begin{aligned}\epsilon \dot{x} &= x - x^3 - z + \eta(t) \\ \dot{z} &= \gamma x - z + b \\ \dot{\eta} &= -\eta - \sqrt{2D}\xi(t)\end{aligned}\tag{3.5}$$

The sign of the noise term $\sqrt{2D}\xi(t)$ is only a matter of convention, thus, the third equation in eq. (3.5) describes obviously an Ornstein-Uhlenbeck process with correlation time one, while $z(t)$ is the new recovery variable that is stochastic only due to $x(t)$.

The Ornstein-Uhlenbeck process generates a colored noise that is independent of x and z and possesses correlation function and spectrum

$$\langle \eta(t)\eta(t') \rangle = De^{-|t-t'|}, \quad S(\omega) = 2D/(1 + \omega^2).\tag{3.6}$$

The latter shows a cut-off at high frequencies what explains the name “colored” (sometimes also “red”) noise as opposed to the white noise with constant spectrum $S = 2D$.

A colored noise in the input to the voltage variable takes account of synaptic filtering of random input spikes. However, it is unfortunately quite unrealistic that the synaptic dynamics should be much *slower* than the voltage dynamics. Usually, one assumes that the first order dynamics that governs the synaptic transmission is much smaller or at most equal to the time scale of the voltage variable (Longtin, 1995b; Brunel et al., 2001). The transformation might have nevertheless relevance for other excitable systems with different time scale ratios.

Now, what is the effect of noise in the excitable system? First of all, the infinitely long lasting deterministic relaxation into the fixed point is replaced by a random motion of the state point around the stable fixed point. Furthermore, a large fluctuation may “kick” the state point towards the separatrix and beyond of it. Then the deterministic mechanism described above leads to an action potential. The process will be repeated, of course, at random times and every realization of it is obviously independent of the others. The stochastic FN model hence generates a renewal spike train characterized by spontaneous activity as it is observed in many real neurons (Tuckwell, 1988; Rieke et al., 1996, for examples of phase space trajectories and spike trains $x(t)$ see Fig. 3.5). A common criterion for the onset of a spike is an up crossing of $x(t)$ through a certain x level, e.g., $x = 0$. Using this one may estimate the intervals between spikes as well as the spike rate and the coefficient of variation. Regarding the rate, note that this is *not* given by the probability of finding a firing neuron in the interval $(t, t + dt)$. This probability is finite irrespective of the time span dt since the firing state is obviously occupied for a finite time. The rate is here the infinitesimal probability of finding a neuron *generating* a spike, thus we may rather use the term “spike generating rate” to avoid confusion.

As pointed out in the introduction, the interspike interval consists of two different times: the activation time needed for the escape from the fixed point to the separatrix and

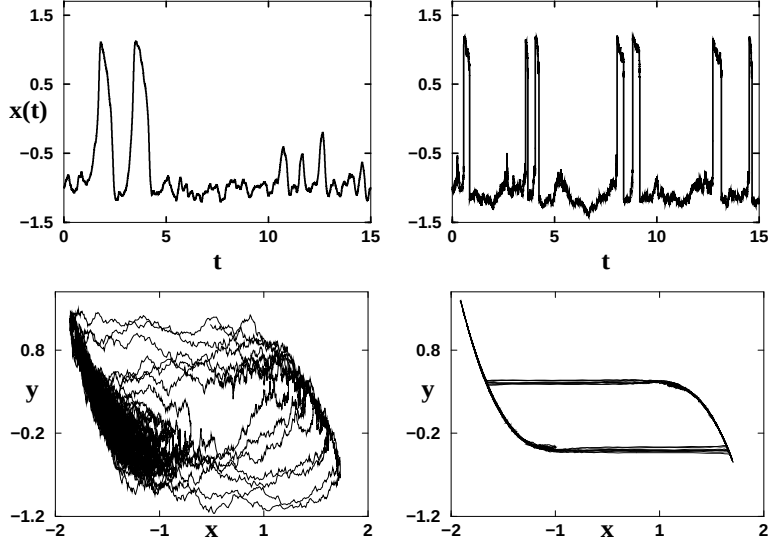


Figure 3.5.: Simulations of the stochastic differential equations. Voltage variable versus time and the corresponding trajectory in phase space for $\gamma = b = 1.5, D = 0.3$; left: $\epsilon = 10^{-1}$ right: $\epsilon = 10^{-4}$.

the excursion time for the passage of firing and refractory states. Both times will be stochastic quantities, however, they exhibit different dependences on the noise strength. While the noise adds a small jitter to the excursion time and may also weakly modify the mean value of it, the activation time depends strongly on noise. Recall that there is no activation (escape via the separatrix) in the deterministic system, hence a very small noise will result in a huge activation time. On the other hand for large noise the typical deviations from the fixed point due to noise are much larger than the distance to the separatrix and, hence, a fast escape and small activation time is expected. As pointed out already by Pikovsky and Kurths (1997) the presence of two time scales with such a way different noise dependences gives rise to coherence resonance.

Returning to the stochastic motion in phase space we note that in analogy to the oscillatory regime of the deterministic model, it is often referred to as a motion on a noise induced limit cycle. Treutlein and Schulten (1986) showed that the stationary probability density $P(x, y)$ for the stochastic variables exhibits a crater like structure, i.e., the probability is distributed along the noise induced limit cycle. Additionally, the probability current does not vanish like in so called potential systems (Risken, 1984) but exhibits a rotational component. Similar findings were made for the Duffing-Van der Pol oscillator (Ebeling et al., 1986) that is closely related to the FN model.

As mentioned above, the calculation of the stationary probability density is a nontrivial task. The system described by (3.4) is a “non-potential” one, i.e., the corresponding

Fokker-Planck-equation (FPE) for the probability density $P(x, y)$

$$\partial_t P = -\frac{1}{\epsilon} \partial_x (x - x^3 - y)P + \partial_y (y - \gamma x - b + D \partial_y)P \quad (3.7)$$

cannot be solved, even in the stationary case. Likewise not available are the marginal densities

$$\rho(x) = \int_{-\infty}^{+\infty} dy P(x, y), \quad p(y) = \int_{-\infty}^{+\infty} dx P(x, y),$$

which reveal how an ensemble of independent neurons is distributed over the excited and the resting state or the recovery variable, respectively.

With a look at the simulations at $\epsilon = 10^{-4}$ in Fig. 3.5 one notes that the dynamics becomes effectively one-dimensional in the limit $\epsilon \rightarrow 0$. This is the case of a perfect time scale separation between fast voltage and slow recovery variable². The stochastic motion of the state point is in this limit restricted to the stable (leftmost and rightmost) branches of the cubic null cline. The effective separatrix considered above approaches the middle branch, however, this unstable branch is not occupied by the state point. Therefore, the separatrix reduces to two points, namely, the matching points of stable and unstable branches, i.e., the local minimum and maximum of the cubic null cline. Going beyond these points results in an infinitely fast switch to the other branch, hence these points are now absorbing boundaries for the trajectories on the stable branches. During the switch the value of the slow variable y obviously cannot change. At the level of probability, the reset is nothing other than an efflux and influx of probability at absorbing boundary and reset point, respectively. A similar flow of probability was already discussed in the consideration of the LIF model. In fact, it will turn out that we may apply the same calculus like in the previous chapter in order to achieve $p(y), \rho(x)$ as well as the spike rate, coefficient of variation, and diffusion coefficient of the spike count for the FN model in the limit $\epsilon \rightarrow 0$.

3.1.2. Probability densities and rate

Minimum P_- and maximum P_+ of the cubic null cline are given by the coordinates (cf. Fig. 3.6)

$$x_{\pm} = \pm \frac{1}{\sqrt{3}}, \quad y_{\pm} = \pm \frac{2}{3\sqrt{3}}. \quad (3.8)$$

Since the motion of the state point is governed by the value of the slow variable y we are forced to express x by y . Cardan's formulae yield after some additional manipulations

$$\begin{aligned} x_l(y) &= 3y_- \cosh\left(\frac{1}{3} \operatorname{arccosh}(y/y_+)\right) \\ x_r(y) &= 3y_+ \cosh\left(\frac{1}{3} \operatorname{arccosh}(y/y_-)\right) \end{aligned} \quad (3.9)$$

²In the deterministic theory this limit is also known as singular perturbation limit (Jackson, 1989).

where $x_l(y)$ and $x_r(y)$ is the inverse of the cubic function at the left and right branch, respectively. We note that

$$x_l(-y) = -x_r(y) \quad (3.10)$$

holds true.

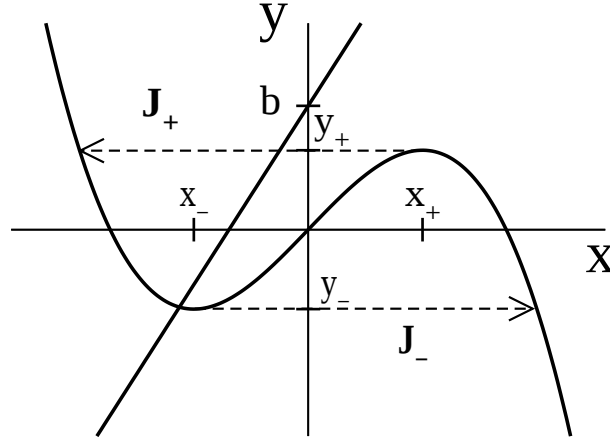


Figure 3.6.: Null clines of the system and some particular points used in the calculations. For $\epsilon = 0$ the probability currents J_+ and J_- flow on the straight dashed lines and the separatrix coincides with the middle branch of the cubic x null cline.

Now, we may insert these functions into the Langevin equation for y as in a usual adiabatic elimination procedure. However, because there are two stable branches we obtain *two* Langevin equations. This means that in the limit $\epsilon \rightarrow 0$ the two-dimensional Markovian system described by the Langevin equations eq. (3.4) and the FPE (3.7) separates into *two* one-dimensional subsystems. On the level of the Fokker-Planck equation these subsystems exchange probability by currents J_- , J_+ infinitely fast via the dashed lines indicated in Fig. 3.6. Hence, the probability on every branch is governed by a Fokker-Planck equation and these equations are coupled through currents of probability. A similar system of FPE's were obtained for the first time by Melnikov (1993) who considered the stochastic Schmitt trigger.

The FPEs of the two systems do not only contain the usual drift and diffusion terms, but additional sources and sinks of probability, similar to the FPE for the LIF model (cf. eq. (2.17)). They read

$$\begin{aligned} \partial_t P_l(y) &= \partial_y(y - b - \gamma x_l(y) + D \partial_y) P_l + J_+ \delta(y - y_+) \\ \partial_t P_r(y) &= \partial_y(y - b - \gamma x_r(y) + D \partial_y) P_r + J_- \delta(y - y_-). \end{aligned} \quad (3.11)$$

The currents that were chosen to be positive are given by those at the absorbing boundaries of the respective opposite branch, i.e., by

$$J_- = D \frac{\partial P_l(y)}{\partial y} \Big|_{y_-}, \quad J_+ = -D \frac{\partial P_r(y)}{\partial y} \Big|_{y_+}. \quad (3.12)$$

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At the reset points, the densities have to be continuous

$$[P_l(y, t)]_{y_+} = 0, \quad [P_r(y, t)]_{y_-} = 0 \quad (3.13)$$

and they vanish at the absorbing boundaries as well as at $\pm\infty$

$$P_l(y, t)|_{y_-} = 0, \quad P_r(y, t)|_{y_+} = 0, \quad (3.14)$$

$$\lim_{y \rightarrow \infty} P_l(y, t) = 0, \quad \lim_{y \rightarrow -\infty} P_r(y, t) = 0. \quad (3.15)$$

Like in case of the FPE for the LIF model we may exclude the points of probability influxes y_+ and y_- and write the FPE's without the δ functions.

$$\begin{aligned} \partial_t P_l(y) &= \partial_y(y - b - \gamma x_l(y) + D\partial_y)P_l \\ \partial_t P_r(y) &= \partial_y(y - b - \gamma x_r(y) + D\partial_y)P_r. \end{aligned} \quad (3.16)$$

Then we have to take into account the influxes by a jump condition for the derivatives of the probability densities at the reset points, that reads

$$\left[\frac{\partial P_l(y, t)}{\partial x} \right]_{y_+} = + \frac{\partial P_r(y, t)}{\partial y} \Big|_{y_+}, \quad (3.17)$$

$$\left[\frac{\partial P_r(y, t)}{\partial x} \right]_{y_-} = - \frac{\partial P_l(y, t)}{\partial y} \Big|_{y_-}. \quad (3.18)$$

The latter relations are the only coupling between the two subsystems. Eventually, the the sum of probabilities on both sides is conserved

$$\int_{y_-}^{\infty} P_l(y) dy + \int_{-\infty}^{y_+} P_r(y) dy = 1. \quad (3.19)$$

The evolution of the probability densities is entirely determined by the FPE (3.16) together with the conditions (3.13), (3.14), (3.15) (3.17), (3.18) and (3.19).

It should have become apparent that the FN model for perfect time scale separation resembles in some ways the LIF model. There we considered a reset of probability from an absorbing boundary (the threshold voltage) via the absolute refractory state to a reset voltage. In the FN model for $\epsilon \rightarrow 0$ the probability is absorbed and reinjected into another neuronal state (the right branch corresponding to the firing state) and from there it returns to the original state by a similar procedure. This flow of probability is illustrated in Fig. 3.7. Formally, the dynamics of the lower state (that represents resting and relative refractory states) resembles a LIF model in the noise activated firing regime, while the dynamics on the right branch (firing state) is more

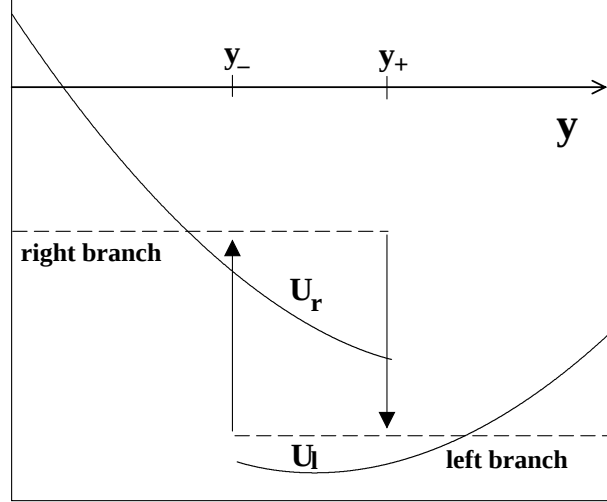


Figure 3.7.: Schematic picture of the system for $\epsilon \rightarrow 0$. Depicted are the effective potentials $U_l(y), U_r(y)$ (solid lines) for $\gamma = b = 1.5$ and the absorption points y_+, y_- , the dashed lines indicate the two branches. Although the scheme resembles a Schmitt trigger, note that in this case the output depends on the slow variable y and is not a constant.

like the deterministic firing regime. Note that the effective potentials (which will be derived in the following) are not parabolic as for the LIF model.

Furthermore, in the considered limit the FN model resembles also a Schmitt trigger driven by an Ornstein-Uhlenbeck-process (OUP) (Melnikov, 1993). The recovery variable y replaces the input variable of a Schmitt trigger (ST). Due to the nonlinear terms $x_{l,r}(y)$ the input is **1)** not a true OUP and **2)** an asymmetry of the absorbing and reset points is introduced such that only one state is stable while the other is left even in the absence of noise. The latter feature makes the main difference to the ST that is always bistable, i.e., both states can be only left by the assistance of noise or suprathreshold deterministic input. A further difference to the ST is that the output of the FN model i.e., the voltage variable $x(t)$ is a continuous variable whereas the output of the ST is a discrete variable $\sigma = \pm V_{out}$ (see introduction, Fig. 1.7) that depends only on the state or branch that is currently occupied.

Before we come to the solution of the stationary problem we clarify the relation of the spike generating rate to the probability measures. The line of reasoning is the same as in the previous chapter. Suppose we have fixed the voltage level for which up crossings are counted as the onset of a spike to $x = a$. Consider further an ensemble of FN neurons that is in the phase plane an ensemble of state points, a fraction of which crosses the line $x = a$ from left within $(t, t + dt)$. Then this fraction (number of crossings divided by total number of neurons) gives the spike generating rate and obviously also the current through the half line $y < 0$ at $x = a$. In the limit $\epsilon \rightarrow 0$ all probability flows just through one point of this line (which is y_-) and the rate equals

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therefore this probability current through the point, i.e., $J_-(t)$.

$$r(t) = J_-(t). \quad (3.20)$$

Concerning the mean interspike interval in the stationary case we may adopt eq. (2.13) from the previous chapter, i.e.,

$$\langle T \rangle = \frac{1}{r_0}. \quad (3.21)$$

In the steady state the currents have to be constant and coincide to each other and to the spike rate.

$$J_+ = J_- = r_0. \quad (3.22)$$

Otherwise, more probability would be injected into than absorbed from one of the branches and hence the probability on that branch would change in time.

Now each of the branches can be considered separately. The stationary problem for a one-dimensional system with constant influx and efflux at two points was solved in the previous chapter by eq. (2.41). Applying this formula yields

$$P_l(y) = \frac{r_0}{D} e^{-U_l(y)/D} \int_{y_-}^y dz e^{U_l(z)/D} \cdot \Theta(y_+ - z) \quad (3.23)$$

$$P_r(y) = \frac{r_0}{D} e^{-U_r(y)/D} \int_y^{y_+} dz e^{U_r(z)/D} \cdot \Theta(z - y_-) \quad (3.24)$$

The effective potentials $U_l(y), U_r(y)$ are obtained by integration of the drift terms

$$\begin{aligned} U_l(y) &= \frac{(y-b)^2}{2} - \gamma \frac{x_l(y)}{4} (3y - x_l(y)) \\ U_r(y) &= \frac{(y-b)^2}{2} - \gamma \frac{x_r(y)}{4} (3y - x_r(y)). \end{aligned} \quad (3.25)$$

The potential $U_l(y)$, for instance, is obtained as follows (integration constants are set zero)

$$\begin{aligned} U_l(y) &= - \int_c^y dy (\gamma x_l(y) - y + b) = \frac{(y-b)^2}{2} - \gamma \int_c^{x_l(y)} dx \frac{dy}{dx} x = \frac{(y-b)^2}{2} - \gamma \int_c^{x_l(y)} dx (x - 3x^3) \\ &= \frac{(y-b)^2}{2} - \gamma \frac{x_l(y)}{4} (3[x_l(y) - x_l^3(y)] - x_l(y)) \end{aligned}$$

$U_l(y)$ and $U_r(y)$ are depicted in Fig. 3.7 for a certain parameter set. As already mentioned the potential at the left branch possesses a minimum at the fixed point, while the other potential is only decreasing. The spike rate r_0 is obtained from the normalization condition eq. (3.19)

$$r_0 = D \left[\int_{y_-}^{y_+} du \int_u^\infty dv e^{\frac{U_l(u) - U_l(v)}{D}} + \int_{y_-}^{y_+} du \int_{-\infty}^u dv e^{\frac{U_r(u) - U_r(v)}{D}} \right]^{-1}. \quad (3.26)$$

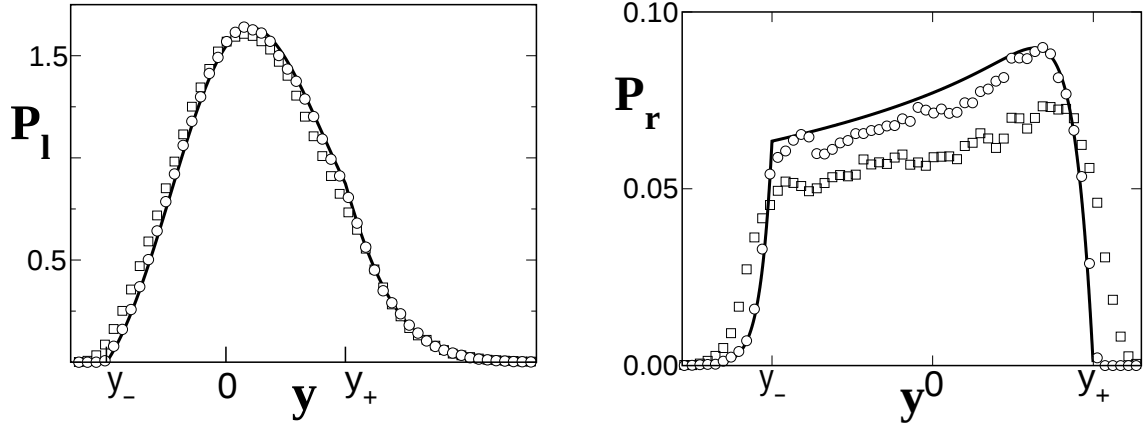


Figure 3.8.: Probability densities on the left (l.h.s.) and right branch (r.h.s.). The approximations (solid lines) given by eq. (3.23) and eq. (3.24) are compared to simulations of the Langevin-equations (squares and circles). Parameters: $D = 0.1, \gamma = 1.5, b = 1.5, \epsilon = 10^{-3}$ (squares) and $\epsilon = 10^{-5}$ (circles)

The marginal density $p(y)$ is given as the sum of the densities on the left and right branch

$$p(y) = P_l(y) + P_r(y) \quad (3.27)$$

with $P_{l,r} = 0$ for $y < y_-$ and $y > y_+$, respectively. The marginal density with respect to the voltage variable in turn can be achieved by a transformation of $p(y)$ to this variable

$$\rho(x) = p(y) \left| \frac{dy}{dx} \right| \quad (3.28)$$

From the above calculation it should be obvious that in the limit considered the two-dimensional density is a δ like function along the left and right branches. Apart from the fact that the function is somewhat uncomfortable to represent, it obviously does not carry more information than the marginal densities and is therefore not considered. Now, we compare the analytical approximations for the densities and the spike rate for $\epsilon = 0$ with results from simulations at a finite ϵ .

In general, the densities at the left and right branches are similar to those of the LIF model in the noise-activated and deterministic firing regime, respectively (cf. Fig. 2.5 in chapter 2).

Since the rate is always positive it can be shown that the maximum of the density $P_l(y)$ occurs above the position of the fixed point. On the other hand there exists at least one maximum on the right branch (Fig. 3.8, r.h.s.), which can never be outside $[y_-, y_+]$. The total probability on this branch is comparable small (note the different scales in the two panels of Fig. 3.8). The comparison to the simulations reveals a satisfactory agreement for $\epsilon = 10^{-5}$, while for a larger value the assumed absorbing boundary condition fails significantly and the total probability on the right branch is smaller than predicted.

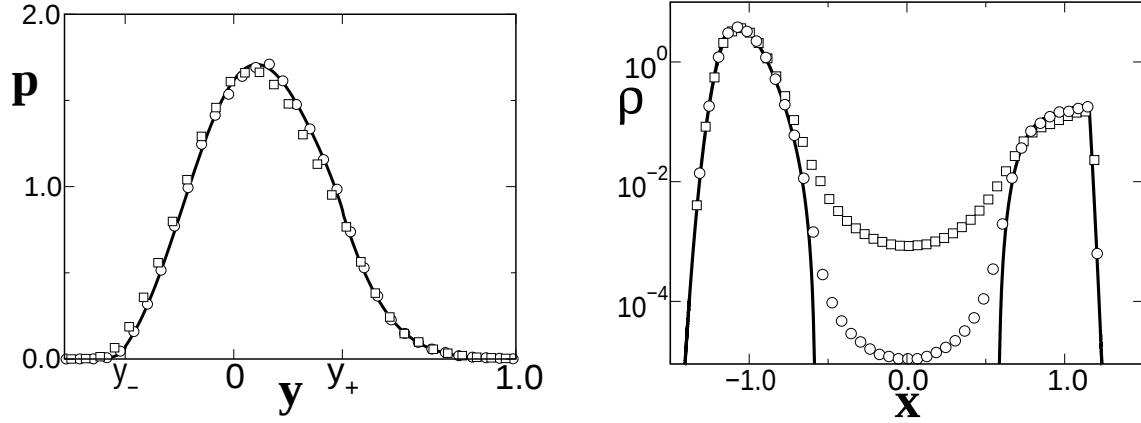


Figure 3.9.: Marginal density $p(y)$ (l.h.s.) and a log plot of the marginal density $\rho(x)$ (r.h.s.). Theory (solid lines) given by eq. (3.27) and eq. (3.28), respectively compared to results of simulations at different values of ϵ . Parameters like in Fig. 3.8.

For a finite ϵ , the separatrix does not intersect the minimum of the cubic null cline but is somewhat below this point. Therefore, the noise must kick the state point in a region below y_- in order to elicit a transition to the right branch and thus a spike. This explains why for a small ϵ there is still a finite amount of probability in this region in contrary to the absorbing boundary condition for $\epsilon = 0$. It makes furthermore evident that the spike rate is at finite ϵ smaller than the approximate result eq. (3.26) and that consequently also the firing state (the right branch) is less populated than predicted by the theory. Additionally, the probability to find the state point on the connecting lines between the branches is small but finite in the simulations. This part contributes also to the regions around the absorbing points where the approximate densities are just zero.

The marginal densities $p(y)$ and $\rho(x)$ are depicted in Fig. 3.9. The main contribution to $p(y)$ comes from the left branch, therefore $p(y)$ looks similar to $P_l(y)$. There is one maximum and the discontinuities that were apparent in the densities on the left and right branches are hardly visible in $p(y)$. The marginal density $\rho(x)$ of the voltage variable is bimodal what reflects the distribution of probability over the silent and excited state. The theoretical result for $\epsilon = 0$ does not exhibit any contribution between x_{min} and x_{max} , since as supposed in our approach, there is no probability on the straight lines between the branches. In contrast, simulations at finite ϵ provide a small amount of probability within that range. This part can be made visible only in a logarithmic plot (Fig. 3.9, r.h.s.). The density around the maxima agrees fairly well with the numerical data in this kind of presentation.

The spike rate (3.26) can be evaluated numerically and results are presented in Figs. 3.10 and 3.11. We first note that our formulae (3.26) is clearly an overestimation of the rate at finite ϵ for the above mentioned reasons: first, the motion between the branches takes obviously a finite time. Second, a finite ϵ limits the effect of the noisy

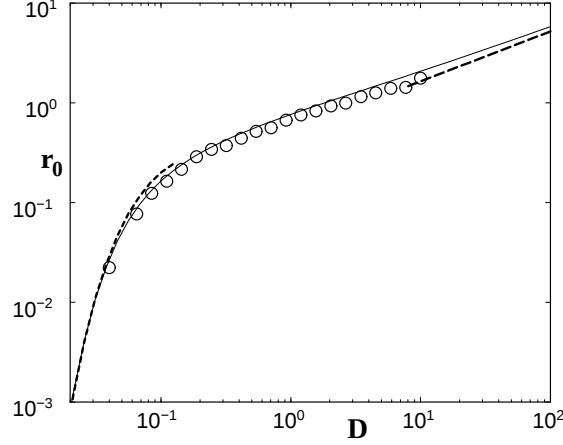


Figure 3.10.: Rate versus noise intensity D , with $\gamma = 0.8, b = 0.9, \epsilon = 10^{-4}$. Approximation (solid line) compared to simulations (circles) and to the simplified expressions (3.29)(dashed) and (3.30) (long dashed).

driving since the separatrix is lowered and not all trajectories on the left branch that reach y_- elicit a spike. Nevertheless the approximation is confirmed quantitatively by the simulations at sufficiently small ϵ , apart from the case of large γ , to which we shall return below.

Estimations for the rate can be made for small and large noise intensities. For small D eq. (3.26) may be simplified to (Kramers, 1940)

$$r_0 \approx U_l''(y_{fix}) \sqrt{\frac{\Delta U_l}{\pi D}} e^{-\frac{\Delta U_l}{D}}, \quad D \ll \Delta U_l \quad (3.29)$$

with $\Delta U_l = U_l(y_-) - U_l(y_{fix})$ being the potential barrier between the fixed point and the absorbing boundary. For large D the rate approaches

$$r_0 \approx \frac{\sqrt{2D}}{4y_+ \sqrt{\pi}}, \quad D \gg \Delta U_l. \quad (3.30)$$

In general, a monotonous behavior is obtained by increase of the noise strength (Fig. 3.10). Trajectories reach more often the absorbing boundaries and the rate increases with growing noise. The simulation is compared to the expressions (3.29), (3.30) for small and large D too showing the validity of those formulae.

The impact of the slope γ is illustrated in Fig. 3.11 (l.h.s.), where we have chosen $b = y_{fix} - \gamma x_{fix}$. The fixed point remains at the same position, increase of γ turns the null cline of y in positive sense. Note that at γ close to zero ($\gamma < 0.53$) the system is actually in the bistable regime. Increasing slope has two effects: on the one hand, the excursion time is reduced yielding an increase of the rate for small γ . At the same time the effective barrier (see Eq. (3.25)) is enlarged decreasing the rate for large γ .

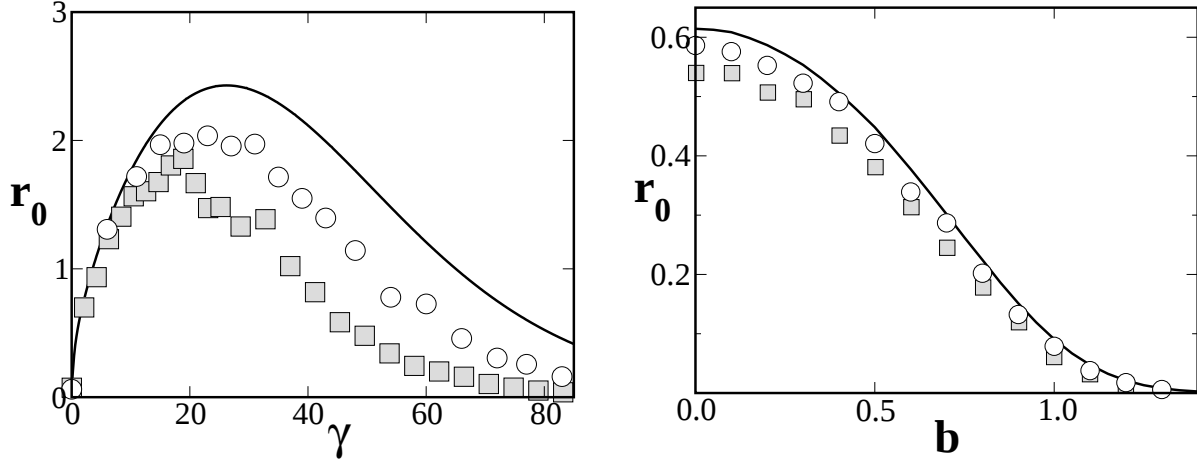


Figure 3.11.: Left: Rate versus the slope γ , while $D = 0.1$ and the fixed point is constant $x_{fix} = -0.8$, therefore $b = b(\gamma)$. Approximation eq. (3.26) (solid line) compared to simulations with $\epsilon = 10^{-4}$ (squares) and $\epsilon = 10^{-5}$ (circles). Right: Rate versus b for $D = 0.05, \gamma = 1.0$. Approximation Eq. (3.26) compared to simulations with $\epsilon = 10^{-3}$ (squares) and $\epsilon = 10^{-4}$ (circles).

Thus, a maximum of the rate with respect to γ is observed in Fig. 3.11 (l.h.s.). Since the slope has no obvious physiological meaning this effect might be of minor relevance. For other excitable systems described by a FN like dynamics this may be different. In the context of our approximation scheme, it is worth mentioning that for growing γ the deviations of the predicted rate from the simulation data become stronger. The reason for this is that the assumed time scale separation between voltage and recovery variable (eq. (3.2)) is weakened.

Eventually, a variation of the parameter b is considered in the right panel of Fig. 3.11. An increase of b enlarges the distance of the fixed point to the threshold and diminishes therefore monotonously the rate. As pointed out above a change in b is equivalent to a change in the input current s . Hence, the dependence shown in Fig. 3.11 (r.h.s.) is nothing but the transfer function of the neuron with respect to a negative input.

3.1.3. The coefficient of variation and the diffusion coefficient of the spike count - coherence resonance in the FN model

In the approximation $\epsilon = 0$ it is also possible to calculate the higher moments of the interspike interval (ISI). Since one ISI consists of the statistically independent passages along the left and right branch we may express mean and variance of the interval by the sums of means and variances of the single times, respectively.

$$\langle T \rangle = \langle T_l \rangle + \langle T_r \rangle, \quad \langle \Delta T^2 \rangle = \langle \Delta T_l^2 \rangle + \langle \Delta T_r^2 \rangle. \quad (3.31)$$

Given these central moments, the coefficient of variation and the diffusion coefficient of the spike count can be calculated employing for the latter again the formula from renewal theory (Cox, 1962).

$$R = \frac{\sqrt{\langle \Delta T^2 \rangle}}{\langle T \rangle}, \quad D_{\text{eff}} = \frac{1}{2} R^2 r_0. \quad (3.32)$$

Now, the passage along the left and right branch from y_- to y_+ and vice versa, respectively, is for $\epsilon = 0$ a simple *one* dimensional problem for which we may use eqs. (2.53), (2.55) from the previous chapter, i.e.

$$\langle T_{l,r} \rangle = \int_{y_-}^{y_+} dx I_{l,r}(x), \quad I_{l,r}(x) = \frac{1}{D} e^{V_{l,r}(x)/D} \int_{-\infty}^x dy e^{-V_{l,r}(y)/D} \quad (3.33)$$

and

$$\langle \Delta T_{l,r}^2 \rangle = 2 \int_{-\infty}^{y_+} dz [I_{l,r}(z)]^2 e^{-V_{l,r}(z)/D} \int_z^{y_+} dx \Theta(x - y_-) e^{V_{l,r}(x)/D}. \quad (3.34)$$

For the right branch we have simply to insert $V_r = U_r$ from eq. (3.25) while for the left branch one may change the variable $y \rightarrow -y$ such that the passage on that branch is also “from left to right”. Using eq. (3.10) it is readily verified that we can utilize eqs. (3.33), (3.34) with the following potential

$$V_l(y) = U_l(-y) = \frac{(y+b)^2}{2} - \gamma \frac{x_r(y)}{4} (3y - x_r(y)). \quad (3.35)$$

By means of these potentials, eq. (3.33) and eq. (3.31) lead on comparing with eq. (3.26) to the relation eq. (3.21), i.e., the rate is indeed given by the inverse of the mean interspike interval.

Regarding the problem of numerically evaluating eq. (3.33) and eq. (3.34) we refer to the procedure explained on page 48 and remark that it is in general slightly more complicated than for the LIF model because of the strong nonlinearity of the potentials $V_{l,r}(y)$.

We first discuss CV and diffusion coefficient given by the quadrature formulae and eq. (3.32) for the case $\gamma = 0.8, b = 0.9$ that corresponds to the rate versus noise strength shown in Fig. 3.10. Here the fixed point is not close to the separatrix but appears even above the x axis. Nevertheless, the coefficient of variation (Fig. 3.12, l.h.s.) shows a minimum versus noise intensity although a weak one ($R \geq 0.8$). Deviations to simulation data obtained for finite ϵ are small. At finite ϵ the minimum appears at slightly larger noise intensity and is also somewhat deeper than predicted by the theory. The diffusion coefficient of the spike count in turn shows only a monotonous behavior by increasing noise strength (Fig. 3.12, r.h.s.) both in theory and at finite ϵ . Recall that D_{eff} was the stronger criterion for coherence resonance. Because a minimum in

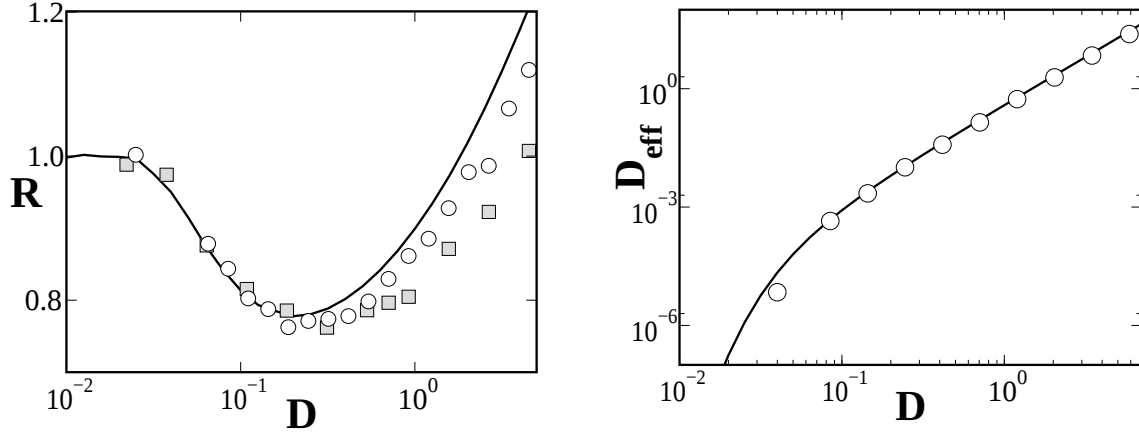


Figure 3.12.: Left: relative fluctuations versus noise strength D , with $\gamma = 0.8, b = 0.9$. Approximation (solid line) compared to simulations with $\epsilon = 10^{-3}$ (squares) and $\epsilon = 10^{-4}$ (circles). Right: Diffusion coefficient of the spike count versus noise strength D , with $\gamma = 0.8, b = 0.9$. Approximation (solid line) compared to simulations with $\epsilon = 10^{-4}$ (circles).

D_{eff} does not occur we may infer that the FN model exhibits only the weak form of coherence resonance if the fixed point is not close to the separatrix.

As another example we consider $\gamma = 1.5, b = 0.6$ corresponding to the position of the y null cline in Fig. 3.6. Here, the fixed point is rather close to the minimum of the x null cline. For comparison we show also the dependence of the rate on D in Fig. 3.13 (l.h.s.).

Like in the previous case the coefficient of variation attains a minimum as a function of noise (Fig. 3.13, r.h.s.). This minimum is much deeper than before ($R \geq 0.2$). The deviations of the theory from the simulation data at finite ϵ are slightly stronger than previously in particular for weak noise intensity. Likewise for the rate, the deviations of theory from the simulation results are most pronounced for small D . Note that we have in this case also verified the analytics by results of simulations at $\epsilon = 0$. The minima in R shift by increasing ϵ again to larger noise intensity. In contrast to the case discussed above the CV attains for finite ϵ a somewhat larger minimal value.

For a fixed point close to threshold the diffusion coefficient of the spike count attains a local minimum, too. Like for the CV the effect is most pronounced in the theory, i.e., for $\epsilon = 0$. While the depth of the minimum varies with ϵ this is apparently not the case for the height of the local maximum at weak noise intensity. The minimum in D_{eff} occurs at smaller value of the noise strength than the CV does. This can be understood like in the previous chapter by the relation of the diffusion coefficient to CV and rate (see the side remark on p. 50).

The occurrence of the minimum in the diffusion coefficient of the spike count is a manifestation of a strong coherence resonance. Spike trains $x(t)$ at three different noise values for the above parameters were shown in the introduction (Fig. 1.1) illustrating

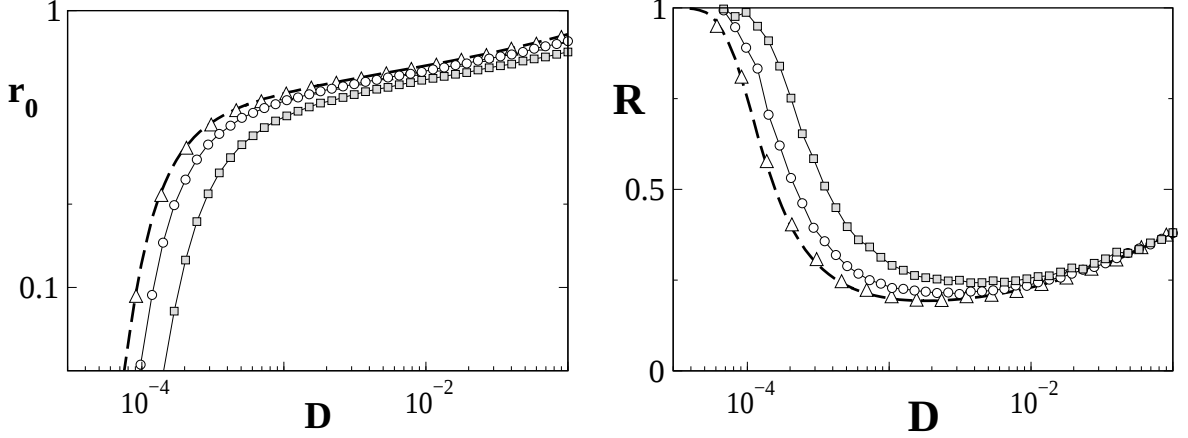


Figure 3.13.: Stationary spike rate (left) and coefficient of variation (right) versus noise intensity D at $\gamma = 1.5, b = 0.6$. Approximation (dashed line) compared to simulations with $\epsilon = 10^{-3}$ (squares), $\epsilon = 10^{-4}$ (circles) and $\epsilon = 0$ (triangles).

the enhanced regularity at optimal noise. It is worth mentioning that the minimum is obtained for a fixed point that is close but not extremely close to the separatrix as opposed to the LIF model where such a minimum was observed only for a fixed point (the potential minimum at $v = \mu$) very close to the “separatrix” (i.e., the threshold $v = v_T$). This is apparently due to the fact that in the FN model also the firing time is taken into account. Another reason could be the strong nonlinearity of the potentials $V_{l,r}(y)$ compared to the simple parabolic potential in the LIF model.

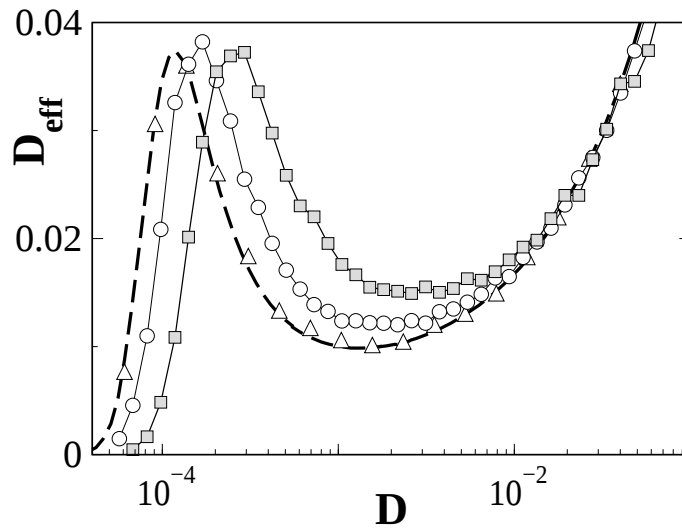


Figure 3.14.: Diffusion coefficient of the spike count versus noise intensity D $\gamma = 1.5, b = 0.6$. Approximation (dashed line) compared to simulations with $\epsilon = 10^{-3}$ (squares), $\epsilon = 10^{-4}$ (circles) and $\epsilon = 0$ (triangles).

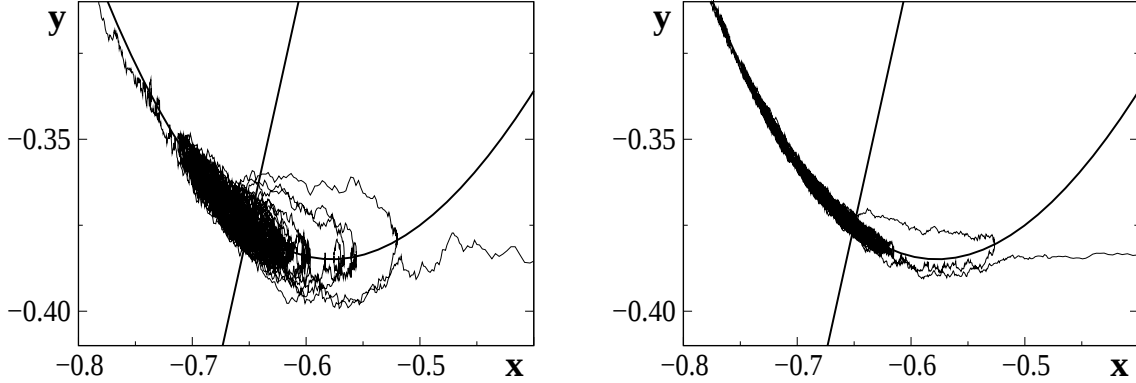


Figure 3.15.: Typical passages of the state point through the fixed point towards the separatrix for $D = 5 \times 10^{-4}$ with $\epsilon = 0.01$ (l.h.s.) and $\epsilon = 0.001$ (r.h.s.). Only a small region around the fixed point given by the intersection of the null clines (smooth solid lines) are shown. Remaining parameters: $\gamma = 1.5, b = 0.6$.

To understand the deviations we have found in the simulations at finite ϵ and small D look at Fig. 3.15. Here trajectories of the state point are shown for one passage from the left to the right branch. At finite ϵ the separatrix line is still below the x null cline. The distance between the lines will be zero for $\epsilon = 0$ and grow with increasing ϵ . Therefore at $\epsilon > 0$, trajectories may reach the line $y = y_-$ without being “absorbed”. Instead, they will perform a noise-induced subthreshold oscillation like illustrated in Fig. 3.15 (recall that the region between the lines gave in the deterministic case the initial points for subthreshold pulses). Incidentally, this may happen also if the state point overcomes the separatrix but gets a negative “kick” by fluctuations that drives it back onto the left branch. In terms of our approximation this means that the boundary y_- is not an entirely absorbing boundary and second that its effective value will be below the minimum of the x null cline, i.e., $y_- \rightarrow \tilde{y}_-(\epsilon)$. A lower boundary implies a slightly increased barrier height for the escape from the left branch. The increased barrier has dramatic consequences at weak noise where the rate depends exponentially on its height. This is what diminishes the rate at small D . At larger noise the dependence on the barrier height is weaker and therefore, the approximation for $\epsilon = 0$ is closer to the simulation results.

Instead of looking at the rate, one may also consider the ratio of activation and excursion time. According to the above line of reasoning it is evident that with growing ϵ the activation time rather than the excursion time is increased and hence their ratio increases as well. Coherence resonance can be observed if both this ratio and the standard deviation of the excursion time are small (cf. eq. (1.7) and the surrounding discussion in the introduction). An increase of the ratio at finite ϵ can be thus compensated by an increase of the noise intensity which strongly decreases the ratio. Doing so we increase the jitter of the excursion time as well and the process is not as regular as for $\epsilon = 0$. Consequently, the minima in R and D_{eff} are shallower and appear at larger

noise intensity.

We have focused at the excitable regime of the FN model. Can the coherence resonance effect also be expected in one of the other dynamical regimes? First of all, one may certainly exclude that this resonance appears in the oscillatory regime since the limit cycle motion is perfectly regular for $D = 0$, hence, the regularity cannot be further enhanced by noise. On the other hand, such an enhancement seems to be possible in the bistable regime for the following reasons. Under the presumption that the two fixed points are close to the minimum and maximum of the cubic null cline, the motion of the state point will be regular due to the long times of quasi deterministic relaxations into the fixed points. At an appropriate noise intensity the escape to the absorbing boundaries will be fast and the mentioned relaxation times will possess a small jitter. In the limits of vanishing and large noise we obtain again Poisson and purely noise dominated processes, respectively. Hence, the regularity is optimized at finite noise intensity. In particular for a symmetric bistable system ($b = 0$, i.e., $\langle T_l \rangle = \langle T_r \rangle$ and $\langle \Delta T_l^2 \rangle = \langle \Delta T_r^2 \rangle$) we obtain for CV and D_{eff} .

$$R = \frac{\sqrt{\langle \Delta T_l^2 \rangle + \langle \Delta T_r^2 \rangle}}{\langle T_l \rangle + \langle T_r \rangle} = \frac{1}{\sqrt{2}} \frac{\sqrt{\langle \Delta T_l^2 \rangle}}{\langle T_l \rangle} = \frac{1}{\sqrt{2}} R_l$$

and

$$D_{\text{eff}} = \frac{\langle \Delta T_l^2 \rangle + \langle \Delta T_r^2 \rangle}{(\langle T_l \rangle + \langle T_r \rangle)^3} = \frac{1}{4} D_{\text{eff},l}$$

Here we have expressed these functions by CV and diffusion coefficient when the interspike interval consists only of the passage time on one branch. But this is obviously identical to the characteristics of the LIF model (though with nonlinear leakage). Hence, since the LIF model in the noise coded firing regime exhibits strong coherence resonance (see previous chapter) the bistable FN model may do as well. This will be also demonstrated by spectral measures in the next section.

To conclude we have studied the FitzHugh-Nagumo model with cubic nonlinearity driven by white Gaussian noise in the recovery variable. For a perfect time scale separation of fast voltage and slow recovery variable the system was shown to separate into two one-dimensional subsystems that exchange probability by currents. In this limit, marginal probability densities, spike rate, coefficient of variation and diffusion coefficient of the spike count could be exactly determined by analytical expressions. It was demonstrated that these formulae may serve as an approximation for small but finite time scale separation. The deviations between the theory and some results of numerical simulations could be also explained. Most importantly, the approximation describes well the phenomenon of coherence resonance in the FN model. For a fixed point close to the separatrix the model exhibits minima in the coefficient of variation and the diffusion coefficient versus noise intensity indicating a strong coherence resonance (Pikovsky and Kurths, 1997). For a fixed point with a larger distance to the

separatrix the minimum in the diffusion coefficient vanishes, however, the coefficient of variation still displays a minimal value versus noise strength. In this case only a weak CR effect is obtained. The FN model similarly to the LIF model shows therefore a gradual enhancement of the CR effect if the parameters are changed such that the system comes closer to the bifurcation point.

3.2. Piecewise linear FitzHugh-Nagumo model and two-state approximation

In order to make further analytical progress we may reduce the effective potentials $U_{l,r}$ to parabolic ones. This corresponds to a FN model with piecewise instead of a cubic null cline as verified in the following. For this simplified system we shall consider not only the excitable regime but also the oscillatory and bistable regimes of the FN model. The usage of a piecewise linear function in the FN model was introduced by McKean (1970) and later also utilized in the spatial extended system (Rinzel and Keller, 1973). Since the FN model is just “the model of a model” (Murray, 1993), namely by itself a simplification of the Hodgkin-Huxley dynamics it is rather a matter of taste whether one uses a cubic or a different N-shaped function. Remarkably, Abbott and Kepler (1990) pointed out that the usage of a piecewise linear function may be even the better approximation to the Hodgkin-Huxley model than the cubic null cline that appears in the classic FN model.

A further reduction of the model to a two-state system was first carried out by Abbott (1990) who studied deterministic networks of such two-state elements. Abbott (1990) considered the case that these elements are in an oscillatory modus where the neuronal dynamics is similar to a relaxation oscillator. We will consider a similar reduction but for the stochastic system and for all regimes of the FitzHugh-Nagumo model.

3.2.1. Derivation of the two-state dynamics

We consider the FN model with a piecewise linear null cline in the fast voltage variable. To be consistent with our work in Lindner and Schimansky-Geier (2000) we will rename voltage and recovery variable by v and u , respectively and also refer to the noise intensity by Q instead of D . All other parameters remain unchanged. The dynamics of the FN model thus reads

$$\begin{aligned}\epsilon \dot{v} &= F(v) - u + s \\ \dot{u} &= \gamma v - u + b + \sqrt{2Q}\xi(t)\end{aligned}\tag{3.36}$$

where the function $F(v)$ is given by

$$F(v) = \begin{cases} -1 - v & , \quad v \leq -1/2 \\ v & , \quad -1/2 < v < 1/2 \\ +1 - v & , \quad v \geq 1/2 \end{cases} \quad (3.37)$$

As before the constant parameter s may be lumped into b and is therefore set to zero without loss of generality. Like in the previous section we consider the limit

$$\epsilon \rightarrow 0.$$

The absorbing boundaries are now at $u_{\pm} = \pm 1/2$. The inverse of $F(v)$ is simply a linear function on the left and right branch

$$v_{l,r} = -u \mp 1 \quad (3.38)$$

and the stochastic differential equations that govern the slow motion on the branches read

$$\dot{u} = -(1 + \gamma)u + b \mp \gamma + \sqrt{2Q}\xi(t) \quad (3.39)$$

where the upper and lower sign results for the left and right branch, respectively. Of course, we may now write down the stationary solution of the corresponding Fokker-Planck equations using the solution for the cubic FN model and replacing only the potentials U_l and U_r by the respective parabolic potentials. In view of the calculations we will perform in chapter 6 it is, however, convenient to somewhat simplify the system. The prefactor of the first term on the right hand side can be eliminated by a new time

$$\tilde{t} = (1 + \gamma)t. \quad (3.40)$$

Furthermore, we may eliminate the constant terms and turn the coordinate system on one branch such that the absorbing boundary is on both branches on the left hand side. This requires different variables for the slow variable on the left and right branch.

$$x = u - \frac{b - \gamma}{1 + \gamma} \quad y = -u + \frac{b + \gamma}{1 + \gamma} \quad (3.41)$$

The new Langevin equations for the two branches are now very simple

$$\begin{aligned} \dot{x} &= -x + \sqrt{2D}\xi(t) \\ \dot{y} &= -y + \sqrt{2D}\xi(t) \end{aligned} \quad (3.42)$$

where the rescaled noise intensity is given by $D = Q/(1 + \gamma)$. Whether the dynamics is bistable, excitable, or oscillatory depends now solely on the absorbing boundaries and

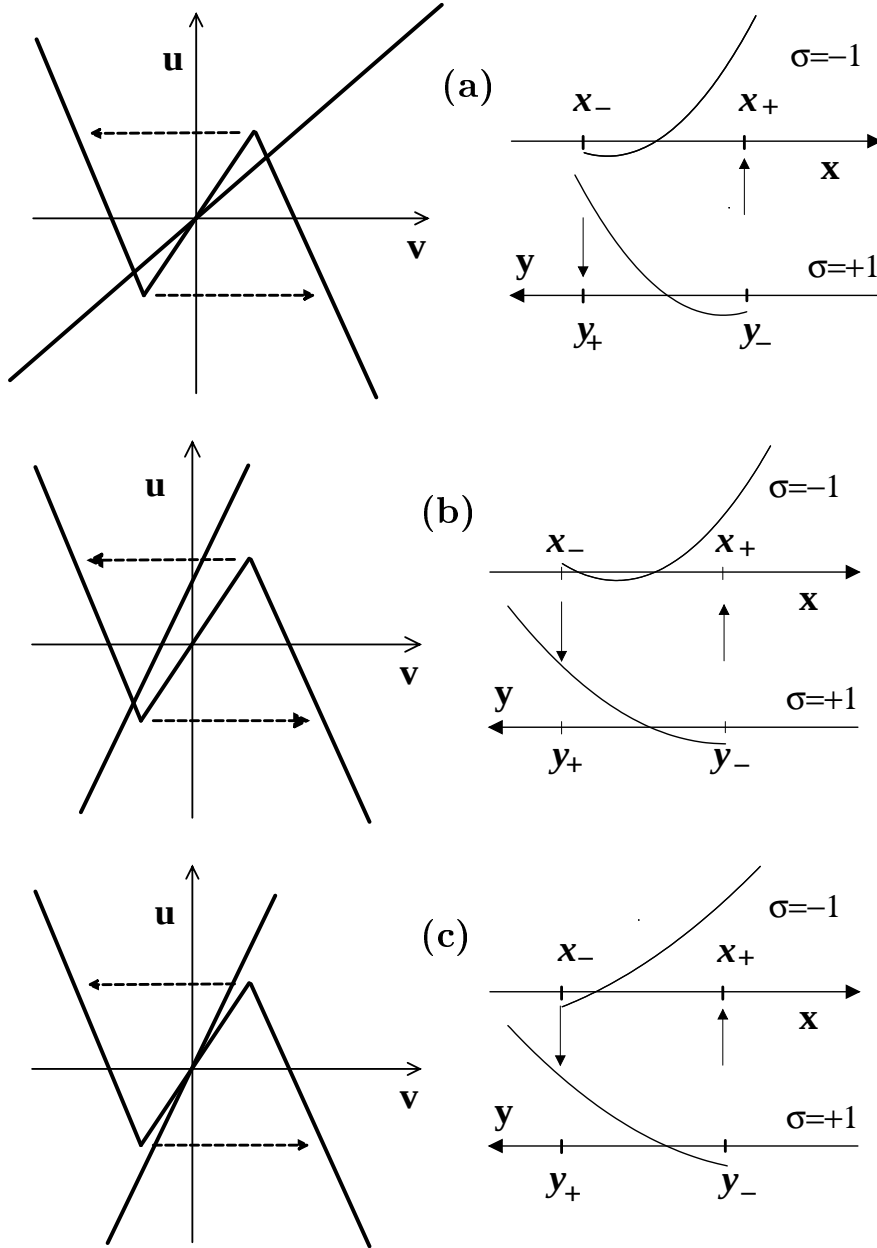


Figure 3.16.: Reduction of the two-dimensional dynamics to a two-state system. Possible transitions are indicated by arrows. (a) The bistable dynamics is mapped to a system with two stable states. (b) One stable fixed point (excitable regime) leads to one stable and one unstable state. (c) the limit cycle dynamics corresponds to a system without any stable state.

reset points. These were given in the old variable u by $\pm 1/2$, in the new variables they read

$$\begin{aligned} x_- &= -\frac{1}{2} - \frac{b - \gamma}{1 + \gamma} \\ x_+ &= \frac{1}{2} - \frac{b - \gamma}{1 + \gamma} \\ y_- &= -\frac{1}{2} + \frac{b + \gamma}{1 + \gamma} \\ y_+ &= \frac{1}{2} + \frac{b + \gamma}{1 + \gamma} \end{aligned} \quad (3.43)$$

The mapping from the two-dimensional dynamics to the two one dimensional dynamics is illustrated in Fig. 3.16. On the left hand side, the null clines are shown according to the different regimes of the FN model. On the right hand side the schemes similar to that in Fig. 3.7 illustrate the dynamical situation on each branch by a sketch of the effective potentials that are now purely parabolic

$$U(x) = \frac{x^2}{2}, \quad U(y) = \frac{y^2}{2}. \quad (3.44)$$

The similarity to the LIF model is now even stronger than for the approximation of the cubic FN model. Since we have chosen coordinates x and y such that the potential minimum is always at zero the presence or absence of a minimum depends on the sign of the absorbing boundary. In other words, for $x_- < 0$ and $y_- < 0$ a potential minimum is present on the left and right branch, respectively, otherwise not.

In the bistable case, both dynamics are governed by potentials with minimum and hence both states are stable and can be left only by the assistance of noise. In the excitable regime as previously exemplified only one of the branches or states is stable, the other (the right branch or firing state) is left even in the absence of noise. Eventually, the third possibility is that both dynamics are unstable corresponding to the oscillatory regime of the FN model.

We will use the following parameter sets to study the three different regimes.

regime	γ	b	$\rightarrow$	x_-	y_-	x_+	y_+
bistable	2/3	0	$\rightarrow$	-0.1	-0.1	0.9	0.9
excitable	1	2/5	$\rightarrow$	-0.2	0.2	0.8	1.2
oscillatory	7/3	0	$\rightarrow$	0.2	0.2	1.2	1.2

Note that we have chosen the parameters such that in the excitable and bistable regimes the potential minima are close to the absorbing boundaries. In both cases, the long times of relaxation of the state point into the minima may introduce a certain regularity of the motion of the state point. In the bistable regime, the excursion time

is the sum of these long relaxation times whereas the activation time also consists of two times, namely the escape times from the potential minima on the left and right branches. Furthermore, the reset and absorption points in the bistable and oscillatory cases are symmetric ($x_+ = y_+$, $x_- = y_-$) due to our choice $b = 0$.

The voltage variable v is within the approximation $\epsilon = 0$ determined by the value of the slow variable and - more importantly - by the branch that is currently occupied by the state point. Since we are only interested whether the neuron is in the firing state or in a silent state (including relative refractory state) we may reduce the consideration to a discrete variable describing the left branch by $\sigma = -1$ (rest state) and the right branch by $\sigma = +1$ (firing state), i.e.

$$\sigma(t) = \text{sgn}(v(t)). \quad (3.45)$$

These states are also indicated in Fig. 3.16. The process $\sigma(t)$ corresponds to a two-state filtering of the process $v(t)$ often applied in studies on stochastic resonance in order to eliminate the irrelevant intrawell dynamics (Gammaitoni et al., 1998).

We may thus look upon the right column of Fig. 3.16 as different regimes of a two-state model. This model is more general than those described by a simple Master equation (van Kampen, 1992) since the waiting times in each state can obey a variety of different statistics depending on the choice of reset and absorption points as well as on the noise intensity. Furthermore, the two-state model can be regarded as a formal extension of the Schmitt trigger driven by colored noise (see introduction, p. 16). The latter is obtained for $x_- = y_- = -y_+ = -x_+$ and was analytically treated by Melnikov (1993). The more general boundary and reset points in our model require only small modifications of Melnikov's theory. However, since the calculation is also close to this carried out for the leaky integrate-and-fire model we will exclusively refer to the previous chapter.

3.2.2. Fokker-Planck equation, stationary solution and spike rate

The FPE for the two one-dimensional dynamics read

$$\begin{aligned} \partial_t P_x(x, t) &= \partial_x(x + D\partial_x)P_x(x, t) \\ \partial_t P_y(y, t) &= \partial_y(y + D\partial_y)P_y(y, t). \end{aligned} \quad (3.46)$$

Similar to the system in the previous chapter we take account of in and out going currents by appropriate boundary and jump conditions. For the density on the left branch ($\sigma = -1$) one obtains

$$P_x(x_-, t) = 0, \quad (3.47)$$

$$[P_x(x, t)]_{x_+} = 0, \quad (3.48)$$

$$\left[\frac{\partial P_x(x, t)}{\partial x} \right]_{x_+} = - \left. \frac{\partial P_y(y, t)}{\partial y} \right|_{y_-}, \quad (3.49)$$

$$\lim_{x \rightarrow \infty} P_x(x, t) = 0 \quad (3.50)$$

and on the right branch

$$P_y(y_-, t) = 0, \quad (3.51)$$

$$[P_y(y, t)]_{y_+} = 0, \quad (3.52)$$

$$\left[\frac{\partial P_y(y, t)}{\partial y} \right]_{y_+} = - \left. \frac{\partial P_x(x, t)}{\partial x} \right|_{x_-}, \quad (3.53)$$

$$\lim_{y \rightarrow \infty} P_y(y, t) = 0. \quad (3.54)$$

Two differences become apparent by comparing with eq. (2.26) -(2.29). Since probability that leaves one state is injected into the other state, the systems are coupled by the flow of probability like in case of the cubic FN model. Second, since the orientation of boundary and reset points is inverted compared to the LIF model some of the signs in the boundary and jump conditions change.

The stationary densities and the spike rate are found in exactly the same way as before. The densities read

$$P_x^0(x) = \frac{r_0}{D} e^{-x^2/2D} \int_{x_-}^x dz e^{z^2/2D} \Theta(z - x_+), \quad (3.55)$$

$$P_y^0(y) = \frac{r_0}{D} e^{-y^2/2D} \int_{y_-}^y dz e^{z^2/2D} \Theta(z - y_+) \quad (3.56)$$

One sees that the density is (apart from the orientation of the coordinate system) proportional to the stationary density in the leaky integrate-and-fire model with the corresponding boundaries $x_+ = v_R - \mu$ and $x_- = v_T - \mu$. The rate r_0 is again determined by the conservation of probability that yields

$$r_0 = \left(\int_{x_-/\sqrt{2D}}^{x_+/\sqrt{2D}} dz e^{z^2} \operatorname{erfc}(z) + \int_{y_-/\sqrt{2D}}^{y_+/\sqrt{2D}} dz e^{z^2} \operatorname{erfc}(z) \right)^{-1} / \sqrt{\pi}. \quad (3.57)$$

The probability $p(\sigma = \pm 1)$ of the state $\sigma = \pm 1$ is given by the integral of $P_{y,x}^0$ over the valid range of the respective coordinate. It is straightforward to show that

$$p(\sigma = -1) = \int_{x_-}^{\infty} dx P_x^0(x) = r_0 \langle T_l \rangle, \quad p(\sigma = 1) = \int_{y_-}^{\infty} dy P_y^0(y) = r_0 \langle T_r \rangle \quad (3.58)$$

where $\langle T_{l,r} \rangle$ are the first passage times from x_-, y_- to x_+, y_+ , respectively. By means of the probabilities, mean and variance of σ are given by

$$\langle \sigma \rangle = r_0 \langle T_r - T_l \rangle, \quad \langle \Delta \sigma^2 \rangle = 4p(\sigma = 1)p(\sigma = -1) = 4r_0^2 \langle T_l \rangle \langle T_r \rangle \quad (3.59)$$

Besides these functions one may easily find expressions for the coefficient of variation and the diffusion coefficient of the spike count. However, the probability density as well as the function R and D_{eff} are basically not different from that found for the LIF and cubic FN models. We therefore abstain from an explicit discussion of them.

More interesting is the fact that we may calculate the power spectrum of the FN model, at least for two-state filtered voltage, i.e., for our approximation of $v(t)$ by $\sigma(t)$.

3.2.3. Power spectrum and noise-induced oscillations

The time intervals that the state point spends on each branch are statistically independent of each other. For this case, the spectrum of the two-state process can be calculated by a formula due to Stratonovich (1967).

$$\begin{aligned} S(\omega) &= \int_{-\infty}^{\infty} d\tau \langle (\sigma(t) - \langle \sigma \rangle)(\sigma(t + \tau) - \langle \sigma \rangle) \rangle e^{i\omega\tau} \\ &= \frac{8r_0}{\omega^2} \Re \left(\frac{(1 - \varrho_l(\omega))(1 - \varrho_r(\omega))}{1 - \varrho_l(\omega)\varrho_r(\omega)} \right). \end{aligned} \quad (3.60)$$

where $\Re(\cdot)$ denotes the real part of a complex function. At $\omega = 0$ one can make use of the expansion of the characteristic functions for small frequency. This leads to (Stratonovich, 1967)

$$S(\omega = 0) = 4 \frac{\langle T_l \rangle^2 \langle \Delta T_r^2 \rangle + \langle T_r \rangle^2 \langle \Delta T_l^2 \rangle}{(\langle T_l \rangle + \langle T_r \rangle)^3}. \quad (3.61)$$

The characteristic functions $\varrho_{l,r}(\omega)$ are the same as for the LIF model with vanishing absolute refractory period ($\tau = 0$) and threshold and reset voltages x_-, x_+ and y_-, y_+ , respectively³. Inserting into eq. (3.60) and some further simplifications yield

$$S(\omega) = \frac{8r_0}{\omega^2} \Re \left(\frac{[\mathcal{D}_{i\omega}(\frac{x_-}{\sqrt{D}}) - e^{\Delta x} \mathcal{D}_{i\omega}(\frac{x_+}{\sqrt{D}})][\mathcal{D}_{i\omega}(\frac{y_-}{\sqrt{D}}) - e^{\Delta y} \mathcal{D}_{i\omega}(\frac{y_+}{\sqrt{D}})]}{\mathcal{D}_{i\omega}(\frac{x_-}{\sqrt{D}})\mathcal{D}_{i\omega}(\frac{y_-}{\sqrt{D}}) - e^{\Delta x} e^{\Delta y} \mathcal{D}_{i\omega}(\frac{x_+}{\sqrt{D}})\mathcal{D}_{i\omega}(\frac{y_+}{\sqrt{D}})} \right) \quad (3.62)$$

with

$$\Delta x = \frac{x_+^2 - x_-^2}{4D}, \quad \Delta y = \frac{y_+^2 - y_-^2}{4D}.$$

³As mentioned above, the orientation of the variables x and y is different to the voltage variable of the conventional LIF model.

Some properties of the spectrum can be explored without usage of the parabolic cylinder functions $\mathcal{D}_{i\omega}(z)$. First of all, the integral over the spectrum is given by the variance of the process (eq. (3.59)) multiplied by 2π .

$$\int_{-\infty}^{\infty} d\omega S(\omega) = 2\pi\langle\Delta\sigma^2\rangle = 8\pi r_0^2\langle T_l\rangle\langle T_r\rangle = 8\pi \frac{\langle T_l\rangle\langle T_r\rangle}{(\langle T_l\rangle + \langle T_r\rangle)^2}. \quad (3.63)$$

The finite variance indicates that the spectrum is restricted to a frequency band and cannot saturate like the spectrum of a δ spike train. In addition, one may infer from eq. (3.63) what happens with the area under the spectral function if the noise intensity goes to zero.

1. The integrated spectrum approaches zero if $\langle T_l\rangle/(\langle T_l\rangle + \langle T_r\rangle)$ or $\langle T_r\rangle/(\langle T_l\rangle + \langle T_r\rangle)$ vanishes, i.e., in the excitable or asymmetric bistable regime.
2. It approaches a finite value in the asymmetric oscillatory regime since the intervals tend to constants in this case.
3. It is constant ($\int d\omega S(\omega) = 2\pi$) regardless of the value of the noise intensity for symmetric systems (bistable or oscillatory regime with $b = 0$, i.e., $x_- = y_-$, $x_+ = y_+$).

Furthermore, also the spectrum at zero frequency given by eq. (3.61) deserves a closer inspection since it determines the *intensity* of the process $\sigma(t)$. To be precise,

$$D_\sigma = \int_0^\infty d\tau \langle (\sigma(t) - \langle\sigma\rangle)(\sigma(t+\tau) - \langle\sigma\rangle) \rangle = S(\omega = 0)/2. \quad (3.64)$$

Now, in the following cases the intensity becomes a more simple expression

1. In the excitable regime at weak noise intensity D we expect that the variance of the firing time vanishes while the time spent in the silent state is large and obeys nearly a Poisson statistics, i.e.

$$\langle T_r \rangle \approx \text{const}, \quad \langle \Delta T_r^2 \rangle \approx 0, \quad \langle T_l \rangle \gg \langle T_r \rangle, \quad \langle \Delta T_l^2 \rangle \sim \langle T_l \rangle^2$$

With these relations one obtains

$$S(\omega = 0) \approx 4\langle T_r \rangle^2 \frac{\langle \Delta T_l^2 \rangle}{(\langle T_l \rangle + \langle T_r \rangle)^3} \approx 4\langle T_r \rangle^2 R^2 r_0. \quad (3.65)$$

Apart from the prefactor (almost constant) this coincides with that from the LIF model.

3. The stochastic FitzHugh-Nagumo model and coherence resonance

2. The symmetric case ($b = 0$, i.e., $x_- = y_-$, $x_+ = y_+$) either in the bistable or in the oscillatory regime. Here, we have

$$\langle T_l \rangle = \langle T_r \rangle = \langle T \rangle / 2, \quad \langle \Delta T_l^2 \rangle = \langle \Delta T_r^2 \rangle = \langle \Delta T^2 \rangle / 2$$

and, consequently,

$$S(\omega = 0) = \frac{\langle \Delta T^2 \rangle}{\langle T \rangle} = \frac{R^2}{r_0}. \quad (3.66)$$

In the weak noise limit the spectrum at $\omega = 0$ drops to zero in the oscillatory case (since $r_0 \rightarrow \text{const}$, $R \rightarrow 0$ for $D \rightarrow 0$) whereas it tends to infinity in the bistable case (because $r_0 \rightarrow 0$, $R \rightarrow 2^{-1/2}$ for $D \rightarrow 0$). The former limit is also expected for an asymmetric oscillatory system since the variances in eq. (3.61) vanish while the mean intervals remain finite.

The spectrum given by eq. (3.62) represents an approximation to the spectrum of the voltage variable $v(t)$. Like in the previous chapter, we may also consider the spectrum of the spike train. In case of the two-state variable $\sigma(t)$ the latter is given as a sum of δ spikes at the transition times for which

$$\sigma(t_i) = -1 \rightarrow \sigma(t_i + 0) = +1, \quad (3.67)$$

i.e., the transitions from silent to firing state. Note that the inverse transitions ($+1 \rightarrow -1$) are ignored. Now, the intervals between subsequent firings are independent realizations of the sum $T_l + T_r$ the characteristic function of which reads

$$\varrho_{l+r}(\omega) = \varrho_l(\omega) \varrho_r(\omega) \quad (3.68)$$

since the times T_l, T_r are likewise independent of each other. Inserting this function into the spectrum formula for a renewal process (eq. (2.63)) yields⁴

$$S_{\text{spiketrain}}(\omega) = r_0 \frac{\left| \mathcal{D}_{i\omega}(\frac{x_-}{\sqrt{D}}) \mathcal{D}_{i\omega}(\frac{y_-}{\sqrt{D}}) \right|^2 - e^{2\Delta x} e^{2\Delta y} \left| \mathcal{D}_{i\omega}(\frac{x_+}{\sqrt{D}}) \mathcal{D}_{i\omega}(\frac{y_+}{\sqrt{D}}) \right|^2}{\left| \mathcal{D}_{i\omega}(\frac{x_-}{\sqrt{D}}) \mathcal{D}_{i\omega}(\frac{y_-}{\sqrt{D}}) - e^{\Delta x} e^{\Delta y} \mathcal{D}_{i\omega}(\frac{x_+}{\sqrt{D}}) \mathcal{D}_{i\omega}(\frac{y_+}{\sqrt{D}}) \right|^2}. \quad (3.69)$$

This formula may be of practical use if only spiking times are known from an experiment but not the time series of the voltage. However, here we do not consider the spectrum given by eq. (3.69) for the following reason. The derivative $\dot{\sigma}(t)$ of the two-state process forms also a train of δ spikes, though with alternating positive and negative sign. The information content of this process is obviously the same like that of the two-state process. The spikes with positive sign are identical to those of the above defined spike train while the negative spikes carry information about the transitions from firing to

⁴Like in eq. (3.62) we omit the zero frequency spike that is due to the non-vanishing mean value of the output.

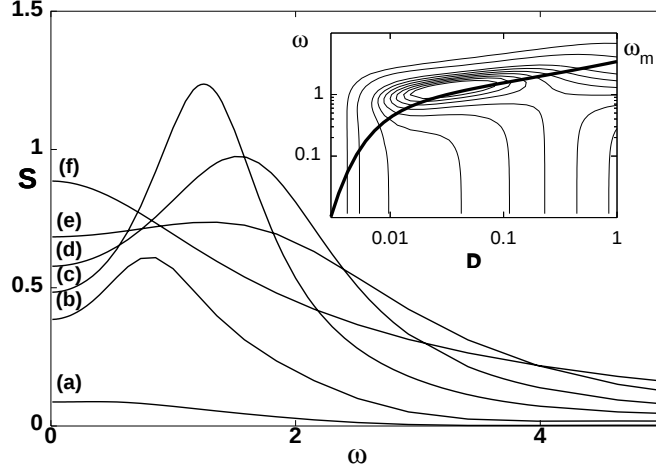


Figure 3.17.: Output spectrum of the excitable system versus frequency and different noise levels (a)-(f): $D = 0.004, 0.009, 0.033, 0.094, 0.207, 0.769$. Inset: Contour plot of spectral density versus D and ω compared with the mean frequency $\omega_m(D)$ (thick line) from eq. (3.70).

silent state. The latter is neglected in the spectrum of the positive spikes eq. (3.69) what is justified if the system is excitable and possesses only a short firing time. However, the error can be serious if the system is bistable and thus both transitions are of equal importance. Hence, in general, the two-state process carry more information on the dynamical properties of the system than the spike train and the corresponding spectrum do.

Although the low and high frequency limits of the two-state spectrum differ in general from those of the spike train spectrum the two measures share one feature as it will become apparent in the following. A pronounced regular oscillation is manifested by spectral maxima in both cases. Once more, we will compare the noise induced eigenfrequency at which the maximum of the two-state spectrum is observed with the mean frequency determined by the stationary spike rate

$$\omega_m = 2\pi r_0. \quad (3.70)$$

Let us first explore the spectrum in the excitable case ($x_- < 0, y_- > 0$, Fig. 3.17). It starts at small noise intensity at a low level for all frequencies. The intensity of the process vanishes for decreasing noise. For increasing noise a peak appears shifting first to larger then back to lower frequencies where it vanishes for large noise intensity. The peak height as a function of D goes through a maximum. This is again a manifestation of coherence resonance. Comparison of the contour lines of the spectral density with the mean frequency ω_m from eq.(3.70) shows that -within the relevant parameter range- the induced eigenfrequency is larger than the mean frequency. If the system is “easier excitable”, i.e., if $x_- \rightarrow 0$ also relevant contributions to higher harmonics are obtained,

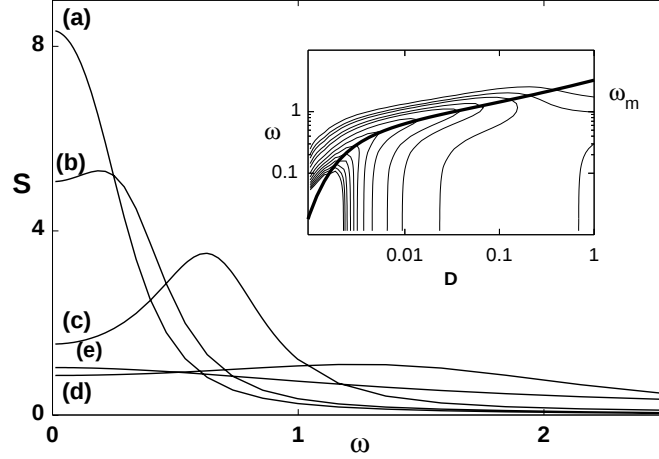


Figure 3.18.: Output spectrum of the bistable system versus frequency for different noise levels (a)-(e): $D = 0.0024, 0.0031, 0.0089, 0.1226, 1.0$. Inset: Contour plot of spectral density versus D and ω compared with the mean frequency $\omega_m(D)$ (thick line) from eq. (3.70).

and the spectrum looks fairly similar to the one of the oscillatory system for small noise.

For the bistable case of a symmetric Schmitt trigger ($x_+ = y_+ = -x_- = -y_-$) treated by Melnikov this spectrum exhibits a Lorentz-like shape for arbitrary noise strength (not shown). There is no maximum at a finite frequency. In contrast, for the above mentioned bistable case of long lasting relaxation at small barriers for both states i.e. $x_+ > |x_-|$ and $y_+ > |y_-|$, the output spectrum displays for an intermediate noise strength a peak at finite frequency (Fig. 3.18), indicating a regular behavior. This is an example for *coherence resonance* in a bistable system caused by large quasi-deterministic times of relaxation in both states. Consequently, it is a result of the

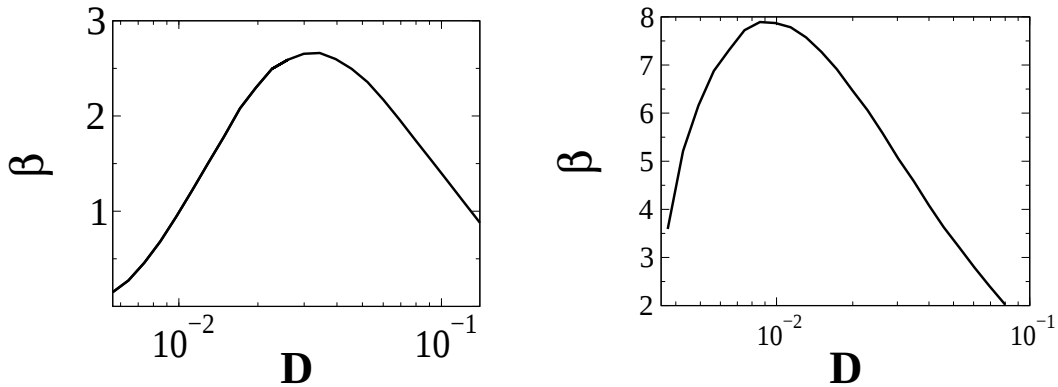


Figure 3.19.: Degree of coherence for excitable (left) and bistable case (right) with $a = 1.2$.

non-potential character of the FN model. The noise-induced eigenfrequency, i.e., the position of the peak is close to the mean frequency of the system given by eq. (3.70) (cf. contour plot in Fig. 3.18). Of course, the height and width of the observed peak can be improved by decreasing the distances of the minima to the absorbing boundaries $|x_-|$ and $|y_-|$.

The dependence of the peak on noise intensity in the excitable and bistable regimes can be described by a signal-to-noise ratio appropriate for autonomous dynamics (Gang et al., 1993), also called the degree of coherence. The signal is quantified by the peak height $S(\omega_{max})$ while the output noise is described by the so called quality factor that is the width at which the spectrum decays to a certain fraction $1/a$ (with $a > 1$) of the maximal value divided by the frequency ω_{max}

$$\beta = \frac{S(\omega_{max})}{\Delta\omega/\omega_{max}} \quad (3.71)$$

with

$$\Delta\omega = \omega_1 - \omega_2, \quad S(\omega_1) = S(\omega_2) = S(\omega_{max})/a, \quad \omega_1 < \omega_{max} < \omega_2$$

Here, we choose $a = 1.2$, however, the value of a has no impact on the principal dependence of β on D . In Fig. 3.19 one can see that in both the excitable and bistable case β passes through a maximum as a function of noise. Its absolute value is even larger in the bistable than in the excitable case. Reasons for this difference are the larger intensity in the former case leading to generally higher peaks but also the fact that with the parameters chosen, the minima in the bistable case are closer to threshold ($x_- = y_- = -0.1$) than the single minimum is in the excitable case ($x_- = -0.2$).

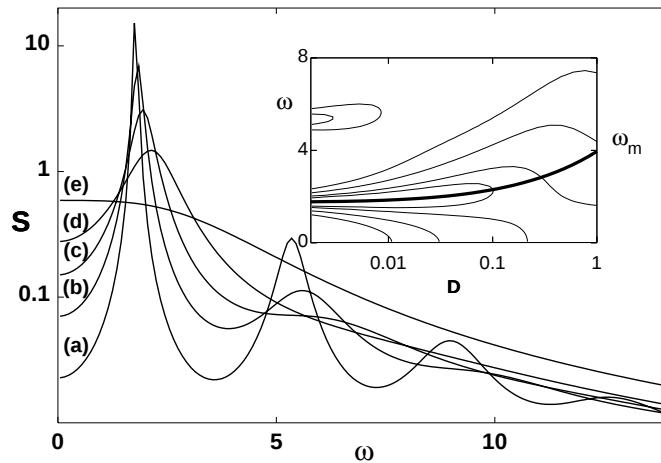


Figure 3.20.: Output spectrum of the oscillatory system versus frequency for different noise levels (a)-(e): $D = 0.0018, 0.00684, 0.0195, 0.0558, 0.35$. Inset: Contour plot of spectral density versus D and ω compared with the mean frequency $\omega_m(D)$ (thick line) from eq. (3.70).

The spectrum for the symmetric oscillatory case ($x_- = y_- > 0, y_+ = x_+$) is shown in Fig. 3.20 as a function of frequency and for different noise strength. Note, that the spectral density is scaled logarithmically. For low noise intensity we obtain high peaks close to the (deterministic) fundamental frequency $\omega_0 = \pi / \ln(x_+/x_-)$ and its (odd) harmonics. The mean frequency (cf. the contour plot in Fig. 3.20) does not vanish for $D \rightarrow 0$ like in bistable or excitable systems but tends to ω_0 . With growing noise the peaks are shifted towards higher frequencies, an effect which has been found numerically in Gang et al. (1993), then peaks at higher harmonics vanish. Finally, also the peak close to the fundamental frequency disappears and a Lorentz-like shape of the spectrum is observed for large noise strength. It is obvious that in the oscillatory case β decreases only as a function of noise and therefore we do not show this curve.

3.3. Summary

In conclusion, in the limit of a perfect time scale separation we have calculated marginal densities, spike rate, coefficient of variation and diffusion of the spike count for the classic FitzHugh-Nagumo model with white noise driving in the slow variable. While with a fixed point far from threshold separatrix only weak coherence resonance was found in the model a fixed point close to separatrix yields the strong resonance known from the literature (Pikovsky and Kurths, 1997). Furthermore, for a piecewise linear version of the FN model we were able to find an approximate formula for the power spectrum of the voltage variable. This power spectrum exhibits peaks at finite frequency in both the excitable and bistable regime if noise intensity is moderate. The coherence resonance found in the spectrum could be quantified by a signal-to-noise ratio that passes through a maximum as a function of noise. The impact of this noise induced eigenfrequency on the transmission of a periodic signal will be one of the issues in chapter 6.

4. Coherent motion in a tilted periodic potential

There are many examples of stochastic dynamics which can be described by the Brownian motion in a tilted washboard potential ranging from the mathematical pendulum with dissipation and noise (Risken, 1984) to superionic conduction (Fulde et al., 1975). The qualitative asymptotic behavior of the system is well known. Expressed in terms of real Brownian motion, particles in a tilted washboard subject to friction and noise will diffuse and drift in the direction of the bias. The determination of mean velocity and effective diffusion coefficient, however, was a challenging task for decades and can be performed in the general damped case only by simulations or by a numerical solution of the Fokker-Planck equation (Risken, 1984).

The *overdamped* limit case of this model in turn can be treated analytically to a great extend. Already in 1958, Stratonovich (1958, 1967) derived a closed expression for the stationary mean velocity and gave also an approximative expression for the effective diffusion coefficient. During the 1970's, an exact expression for the diffusion coefficient could be calculated for the special case of vanishing bias (Festa and d'Agliano, 1978; Guyer, 1980). Another approximation for a *finite* bias has been proposed recently by Costantini and Marchesoni (1999).

Stratonovich's approach to the diffusion coefficient holds true for a weak tilting of the potential and small noise intensity. In this case the particle jumps rarely from one potential minimum to the right or left ones whereby one of the directions is preferred due to the bias. Stratonovich assumed in this regime that the process can be modeled by a biased random walk. Thus, the diffusion coefficient is determined by the rate from the minimum to the left and right potential barriers (maxima of the potential). This Ansatz neglects the relaxation time from barrier to the minimum that becomes relevant for stronger tilt. It fails completely for a so called supercritical tilt for which minima and maxima of the potential vanish since in this case the process cannot be described by a Poissonian hopping process anymore. In the case of a very strong tilt, however, the situation is simplified again since the potential shape can be ignored and the diffusion coefficient coincides with that of free diffusion.

The transport of particles is characterized by an average motion in direction of the bias and the counteracting spreading effect due to the presence of noise. While the drift may be desired the dispersion is an unwanted but - especially in case of a subcritical bias -

inevitable side effect. Coherent transport refers to the case of large mean velocity at fairly small diffusion. It can be best quantified by the non-dimensional Péclet number, i.e., a proper ratio of velocity and effective diffusion coefficient. Clearly, the transport is most coherent when this number is maximum.

In this chapter we address a situation where the minima and maxima of the effective potential are still present (subcritical tilt) but the tilt is sufficiently strong that the relaxation time scale has to be taken into account. We will restrict ourselves to the overdamped case and derive exact expressions for the diffusion coefficient and the Péclet number. It will be shown that a strong relaxation time scale can lead to a coherent (regular) transport of particles when the noise strength is optimally chosen. This becomes manifest by a maximum of the Péclet number with respect to the noise intensity. We will illustrate the meaning of this maximum in terms of the time dependent probability density of the particles¹.

Further, for specific potential shapes another quality of coherence appears. If the potential is flat and possesses small sharp maxima the effective diffusion coefficient itself attains a local minimum as a function of the noise intensity.

It will emerge that there is a close relation to coherence resonance studied in the previous chapter. This is not surprising. Especially for a biased cosine potential, the overdamped limit of the equations was frequently used as an approximative description for a phase or phase differences of autonomous or driven stochastic oscillators, respectively (Adler equation). Thus, the effective diffusion coefficient can be identified with the phase diffusion coefficient or with the diffusion coefficient of the number of excitations/oscillations. Further, the enhanced regularity of the oscillations in case of CR possesses its counterpart in a coherent transport of particles in a periodic potential or - in terms of the mentioned phase description - in a coherent increase of the phase or number of oscillations. In spite of these similarities, we note that in contrast to an autonomous excitable system the periodic potential allows the possibility of *back jumps* of the phase.

4.1. Model and quantities of interest

Consider the overdamped motion of a Brownian particle in a potential $U(x)$ with period L subject to a tilting force F and a white Gaussian noise

$$\dot{x} = -\frac{d}{dx}(U(x) - Fx) + \sqrt{2D}\xi(t). \quad (4.1)$$

Here, the friction coefficient γ has been omitted what can be easily realized by rescaling of the force term and noise intensity D . For real particles the latter is related to temperature and friction according to the Einstein relation $D = k_B T / \gamma$. The force in

¹This as well as the numerical validation of our theoretical results has been performed by Dr. Marcin Kostur (Berlin, Katowice, Maine) using a finite-element method.

(4.1) can be written as the derivative of the *effective* potential $V(x) = U(x) - Fx$. If $U(x)$ displays minima and maxima there exists obviously a critical tilt F_c where the corresponding minima and maxima vanish for $V(x)$.

The corresponding probability density for eq. (4.1) obeys the Fokker-Planck equation

$$\partial_t P(x, t) = \partial_x (V'(x) + D\partial_x) P(x, t) = -\partial_x J(x, t) \quad (4.2)$$

where $J(x, t)$ denotes the probability current.

An ensemble represented by $P(x, t)$ started at the sharp value x_0 moves in the direction of the bias and spreads at the same time over several periods of the potential (cf. Fig. 4.1).

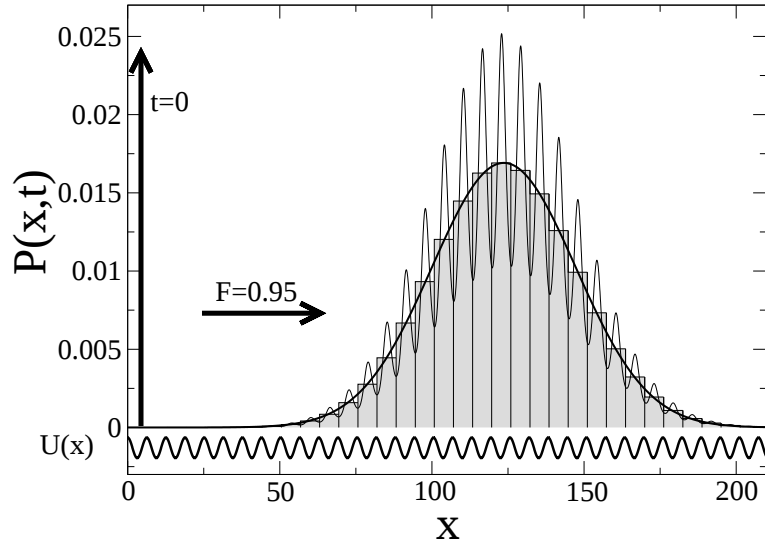


Figure 4.1.: Evolution of the density $P(x, t)$ (thin line) for the potential $U(x) = \cos(x)$, $F = 0.95$ and $D = 2.05$. The density started at $x_0 = 4.4$ (arrow) is calculated by a numerical solution of eq. (4.2). Additionally shown: the coarse grained density (histogram) and a fit of $P(x, t)$ to a Gaussian function (thick line) which coincides in line thickness with a filtered version of $P(x, t)$ (not shown). The potential $U(x)$ is drawn at the bottom for comparison.

For large times, the drift is characterized by the mean stationary velocity

$$v = \langle \dot{x} \rangle = \lim_{t \rightarrow \infty} \frac{\langle x(t) - x(0) \rangle}{t} \quad (4.3)$$

while the dispersion is quantified by the effective diffusion coefficient

$$D_{\text{eff}} = \frac{1}{2} \lim_{t \rightarrow \infty} \frac{\langle \Delta x(t)^2 \rangle}{t} = \frac{1}{2} \lim_{t \rightarrow \infty} \frac{\langle [x(t) - \langle x(t) \rangle]^2 \rangle}{t}. \quad (4.4)$$

The density itself tends asymptotically to

$$P_{\text{as}}(x, t) = P_0(x) \frac{\exp[-(x - vt)^2 / 4D_{\text{eff}}t]}{\sqrt{4\pi D_{\text{eff}}t}}. \quad (4.5)$$

4. Coherent motion in a tilted periodic potential

Here, P_0 refers to the stationary (necessarily periodic) solution of eq. (4.2) (Risken, 1984) with the special normalization $\int_0^L dx P_0(x) = L$. Clearly, this function is responsible for the local structure (local minima and maxima) whereas the Gaussian part represents the coarse grained density (thick solid line in Fig. 4.1). The asymptotic mean and variance of the true density $P_{as}(x, t)$ coincide with those of the Gaussian factor as we have tacitly assumed in eq. (4.5).

We show this for the variance using the mean value theorem $\int_a^b dx f(x)g(x) = f(x_k) \int_a^b dx g(x)$ with $a \leq x_k \leq b$

$$\begin{aligned} \langle \Delta x^2 \rangle &= \int_{-\infty}^{\infty} dx (x - vt)^2 P_{as}(x, t) = \sum_{k=-\infty}^{\infty} \int_{kL}^{(k+1)L} dx (x - vt)^2 \frac{e^{-\frac{(x-vt)^2}{4D_{\text{eff}}t}}}{\sqrt{4\pi D_{\text{eff}}t}} P_0(x) \\ &= \sum_{k=-\infty}^{\infty} (x_k - vt)^2 \frac{e^{-\frac{(x_k-vt)^2}{4D_{\text{eff}}t}}}{\sqrt{4\pi D_{\text{eff}}t}} \int_{kL}^{(k+1)L} dx P_0(x) = 4D_{\text{eff}}t \sum_{k=-\infty}^{\infty} \frac{y_k^2}{\sqrt{\pi}} e^{-y_k^2} \frac{L}{\sqrt{4D_{\text{eff}}t}} \end{aligned}$$

The width of the interval from which the points y_k are taken is obviously $\Delta y = \frac{L}{\sqrt{4D_{\text{eff}}t}}$, thus, we have $\sum_{k=-\infty}^{\infty} \frac{y_k^2}{\sqrt{\pi}} e^{-y_k^2} \Delta y \xrightarrow{t \rightarrow \infty} \int_{-\infty}^{\infty} dy \frac{y^2}{\sqrt{\pi}} e^{-y^2} = \frac{1}{2}$ and obtain asymptotically $\langle (x - vt)^2 \rangle \rightarrow 2D_{\text{eff}}t$ as asserted.

The Gaussian function can be numerically extracted from $P(x, t)$ in different ways (cf. Fig. 4.1). One may fit $P(x, t)$ to a Gaussian function, filter the density (Fourier transformation, cutting off the high frequencies and perform the back transformation) or carry out a direct coarse graining by $\tilde{P}(\tilde{x}, t) = \int_{\tilde{x}-L/2}^{\tilde{x}+L/2} dx P(x, t)/L$ with $\tilde{x} = x_0 + kL, k \in \mathbb{Z}$. All three methods yield a satisfying agreement. For the data in Fig. 4.1, the fitted and filtered functions coincide within line thickness while the histogram obtained from the coarse graining seems to be the discrete counterpart to these functions.

It might be desired that particles started at a sharp value should reach a certain region without much spreading. An optimal transport in this sense is realized at large velocity and small diffusion and will result in a large Péclet number

$$Pe = \frac{vL}{D_{\text{eff}}}. \quad (4.6)$$

This non-dimensional ratio was frequently used in convection problems (Landau and Lifschitz, 1971) and also recently applied to the transport problem in ratchet potentials (Freund and Schimansky-Geier, 1999).

Beside the trivial case of vanishing potential $U(x) \equiv 0$ (then $v = F$, $D_{\text{eff}} = D$), the usual approach to the diffusion problem posed by eq. (4.4) is to extract the diffusion coefficient from the time dependent solution of the Fokker-Planck equation (4.2). This works, e.g. in case of piecewise constant potential $U(x)$ (Risken, 1984), however, for a general periodic potential the time dependent solution is not available. Another way is the usage of a generalized fluctuation-dissipation relation (Risken, 1984), however,

this applies only in case of equilibrium systems, i.e., for vanishing tilt ($F = 0$) and results for a system with finite bias in an only approximate formula (Costantini and Marchesoni, 1999).

Our approach utilizes the fact that the diffusion is entirely determined by the local properties of the system due to the periodicity of the potential. This allows a mapping onto a discrete process yielding the coarse grained density the asymptotic variance of which can be easily calculated.

4.2. Calculation of diffusion coefficient and Péclet number

The process described by eq. (4.1) is physically equivalent to the motion of a particle in an infinite ordered set of segments of the effective potential $V(x)$ as sketched in Fig. 4.2. The spatial overlap between subsequent segments is given by one period L while the length of a single segment is $2L$. Whenever the particle reaches the left or right boundary it is absorbed and reinjected in the respective neighboring segment. These jump events have no physical meaning since coordinates and potential forces at absorption and injection points coincide. The probability in the n -th segment $P_n(x, t)$ obeys a FPE like (4.2) with absorbing boundary conditions and with an additional source of probability corresponding to the particle injection in the middle of the segment (similar to the approximation for the FitzHugh-Nagumo system in chapter 3). The true density $P(x, t)$ from eq. (4.2) results by summing up these densities $P_n(x, t)$. The seemingly complicated mapping onto the system of segments allows a rough discrete determination of the particle's position in terms of the segment n_t . Choosing the boundaries of the segments so that $x = 0$ (starting point) is in the middle of the segment with $n = 0$, we can approximate $x(t) \approx Ln_t$ with an uncertainty $\Delta x = \pm L$ at any time t . In the asymptotic limit $t \rightarrow \infty$

$$\langle x(t) \rangle = L \langle n_t \rangle, \quad \langle \Delta x(t)^2 \rangle = L^2 \langle \Delta n_t^2 \rangle \quad (4.7)$$

holds true.

Writing $x(t) = L(n_t + \alpha_t)$ with $\alpha_t \in (-1, 1) \forall t$ we obtain $\langle x(t)^2 - \langle x(t) \rangle^2 \rangle = L^2(\langle \Delta n_t^2 \rangle + 2(\langle n_t \alpha_t \rangle - \langle n_t \rangle \langle \alpha_t \rangle) + (\langle \alpha_t^2 \rangle - \langle \alpha_t \rangle^2))$. In the long time limit the first term grows in proportion to t while the second term vanishes since n_t and α_t can be assumed as uncorrelated for $t \rightarrow \infty$. The last term in turn is limited to one. Asymptotically, we thus recover the second equation in (4.7).

Moreover, it can be shown that the discrete probability density $p_n(t) = \int dx P_n(x, t)$ for the variable n_t tends asymptotically to a Gaussian density coinciding with that from eq. (4.5) by virtue of eq. (4.7).

Turning now to the properties of the process n_t we note that it consists of a sequence of jumps with random increments $W_i \in \{-1, 1\}$ at likewise random time instants t_i ,

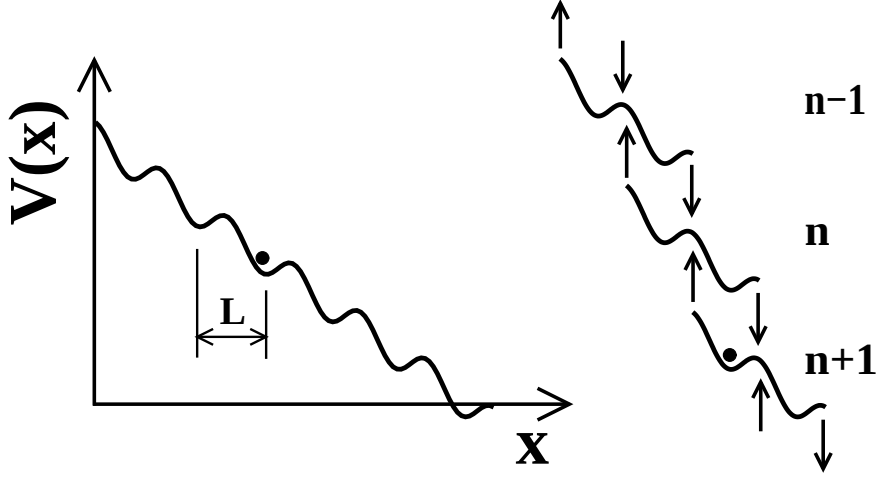


Figure 4.2.: The motion of the particle (circle) in the tilted periodic potential $V(x)$ (left) is equivalent to that one in an infinite number of segments of the potential (right) with length $2L$. The arrows indicate transitions from one segment to the other.

i.e.,

$$n_t = \sum_{i=1}^{N_t} W_i. \quad (4.8)$$

where N_t denotes the total number of events. Compare also Fig. 4.3 (r.h.s.) for an example trajectory. Since each realization of an escape event from one segment is independent of all other (forgoing or subsequent) realizations, the escape times $T_i = t_i - t_{i-1}$ and increments W_i are independent of all other escape times and increments, respectively. The only nontrivial relation is a potential statistical dependence of W_i on the foregoing escape time T_i . Under these conditions, the total number of events N_t forms a renewal process (Cox, 1962) while n_t in turn is a so called cumulative process (Cox, 1962).

A closer inspection of the escape time statistics reveals that also W_i and T_i are *uncorrelated*. This can be seen as follows (cf. Fig. 4.3, l.h.s.). After an injection of the particle in the middle of a segment at $T = 0$ all probability is concentrated there. If no reinjection is considered the modulus of the out currents of probability at the absorbing boundaries $J_-(T)$ and $J_+(T)$ are related to the conditional escape time densities $\rho_-(T)$ and $\rho_+(T)$ to the left and right boundary, respectively, by (Gardiner, 1985)

$$J_{\pm}(T) = p_{\pm} \rho_{\pm}(T). \quad (4.9)$$

Here, p_- and p_+ denote the total probability to escape via the left and right boundary, respectively. Now, the crucial point is that these currents share the same time dependence, i.e., they differ only by the prefactors p_- and p_+ . Consequently, the densities

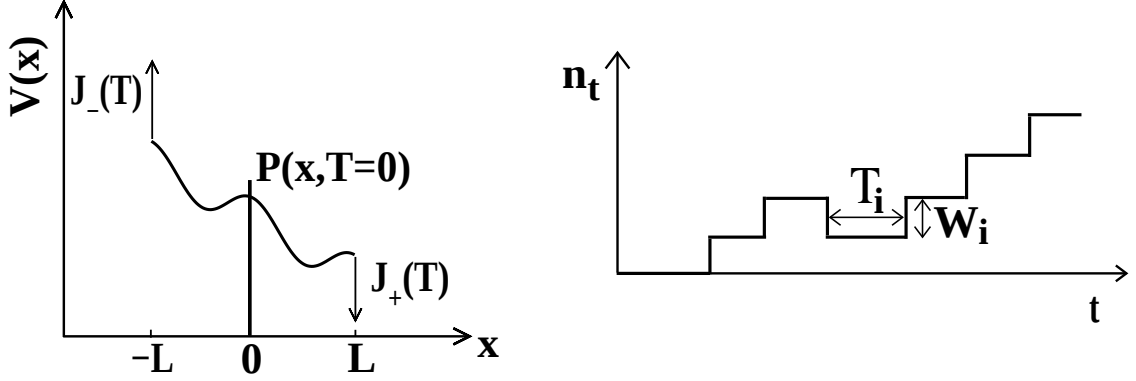


Figure 4.3.: Left: The problem of escape from a single well. The initial condition $P(x, T = 0) = \delta(x)$ is indicated by a line. $J_-(T)$, $J_+(T)$ denote out currents of probability. Right: a sample trajectory of the process n_t . The random increments $W_i \in \{-1, 1\}$ and the intervals T_i correspond to independent realizations of the escape problem sketched at the l.h.s.

$\rho_{\pm}$ are *exactly equal* $\rho(T) = \rho_-(T) \equiv \rho_+(T)$ - a surprising property of the system ² that can be proven as follows.

Consider the escape problem illustrated in Fig. 4.3 (l.h.s.) with the initial condition $P(x, 0) = \delta(x)$ and the boundary conditions

$$P(-L, t) = P(L, t) = 0. \quad (4.10)$$

The absolute values of the out currents read

$$J_+(t) = J(L, t) = -D \left. \frac{\partial P(x, t)}{\partial x} \right|_{x=L}, \quad J_-(t) = -J(-L, t) = D \left. \frac{\partial P(x, t)}{\partial x} \right|_{x=-L}. \quad (4.11)$$

The special Laplace transformation $p(x, \lambda) = \exp[(V(x) - V(0))/2D] \int_0^\infty dt e^{-\lambda t} P(x, t)$ applied to eq. (4.2) leads to

$$\hat{L}p = Dp''(x, \lambda) - \left(\frac{(V'(x))^2}{4D} - \frac{V''(x)}{2} + \lambda \right) p(x, \lambda) = -\delta(x) \quad (4.12)$$

where the prime denotes the derivative with respect to x . The (conventional) Laplace transforms of $J_-(t)$ and $J_+(t)$ in terms of $p(x, \lambda)$ are given by

$$j_+(\lambda) = -De^{\frac{FL}{2D}} \left. \frac{\partial p(x, \lambda)}{\partial x} \right|_{x=L}, \quad j_-(\lambda) = De^{-\frac{FL}{2D}} \left. \frac{\partial p(x, \lambda)}{\partial x} \right|_{x=-L}. \quad (4.13)$$

It is well known that an equation like (4.12) can be treated by means of homogeneous solutions in $[-L, 0]$ and $[0, L]$ which have to be connected according to

$$[p(x, \lambda)]_0 = 0 \quad (4.14)$$

²Naively, one might expect, for instance a longer mean time for the escape to the left than to the right in Fig. 4.3, l.h.s.

4. Coherent motion in a tilted periodic potential

and

$$[p'(x, \lambda)]_0 = -\frac{1}{D}. \quad (4.15)$$

Provided that $\psi_1(x), \psi_2(x)$ and $\phi_1(x), \phi_2(x)$ (omitting the second argument λ) are such independent solutions of the homogeneous problem in $[-L, 0]$ and $[0, L]$, respectively

$$\begin{aligned} \hat{L}\psi_{1,2}(x) &= 0, & -L < x < 0 \\ \hat{L}\phi_{1,2}(x) &= 0, & 0 < x < L \end{aligned} \quad (4.16)$$

then we may assume

$$\phi_1(x) = \psi_1(x - L) \text{ and } \phi_2(x) = \psi_2(x - L) \quad (4.17)$$

because of the periodicity of the force field in (4.12).

The Ansatz

$$p(x, \lambda) = \begin{cases} c_1\psi_1 + c_2\psi_2, & -L < x < 0 \\ d_1\phi_1 + d_2\phi_2, & 0 < x < L \end{cases} \quad (4.18)$$

leads by (4.10, 4.14, 4.17) to

$$\begin{aligned} c_1 &= -\frac{\psi_2(-L)/D}{\psi_2'(-L)\psi_1(0) - \psi_2(-L)\psi_1'(0) + \psi_1(-L)\psi_2'(0) - \psi_1'(-L)\psi_2(0)}, \quad c_2 = -c_1 \frac{\psi_1(-L)}{\psi_2(-L)}, \\ d_1 &= \frac{\psi_2(0)/D}{\psi_2'(-L)\psi_1(0) - \psi_2(-L)\psi_1'(0) + \psi_1(-L)\psi_2'(0) - \psi_1'(-L)\psi_2(0)}, \quad d_2 = -d_1 \frac{\psi_1(0)}{\psi_2(0)}. \end{aligned} \quad (4.19)$$

For the ratio of the currents one obtains by (4.13)

$$\frac{j_+}{j_-} = \frac{\psi_1'(0)\psi_2(0) - \psi_1(0)\psi_2'(0)}{\psi_1'(-L)\psi_2(-L) - \psi_1(-L)\psi_2'(-L)} e^{\frac{FL}{D}}. \quad (4.20)$$

The expression $\psi_1'(x)\psi_2(x) - \psi_1(x)\psi_2'(x)$ which occurs at different argument in the fraction does not depend on the argument x . This can be shown by taking the derivative with respect to x and employing (4.16). Hence, we have for arbitrary λ

$$\frac{j_+(\lambda)}{j_-(\lambda)} = e^{\frac{FL}{D}} \quad (4.21)$$

that is, the ratio p_+/p_- . Obviously, the time dependent currents possess the same ratio. From this fact one can conclude the equivalence of the conditional escape time distributions $\rho_+ = J_+/p_+$ and $\rho_- = J_-/p_-$.

Since the escape time statistics is the same for left ($W = -1$) and right ($W = 1$) jumps no correlations occur between the increment and the foregoing escape time.

For the cumulative process n_t with *independent increments*, the asymptotic mean and variance can be expressed (Cox, 1962) by mean and variance of the increment W and by those of the escape time, henceforth denoted by $\langle T \rangle = \int_0^\infty dT T \rho(T)$ and $\langle \Delta T^2 \rangle = \int_0^\infty dT (T - \langle T \rangle)^2 \rho(T)$.

$$\begin{aligned} \langle n_t \rangle &= \langle W \rangle \frac{t}{\langle T \rangle} \\ \langle \Delta n_t^2 \rangle &= \langle \Delta W^2 \rangle \frac{t}{\langle T \rangle} + \langle W \rangle^2 \frac{t \langle \Delta T^2 \rangle}{\langle T \rangle^3} \end{aligned} \quad (4.22)$$

4.2. Calculation of diffusion coefficient and Péclet number

By definition, the probabilities of $W = -1$ and $W = +1$ are equal to p_- and p_+ , respectively. For mean and variance one easily verifies

$$\langle W \rangle = p_+ - p_- , \quad \langle \Delta W^2 \rangle = 4p_+p_- . \quad (4.23)$$

Using eqs. (4.3), (4.4), (4.7), (4.22) and (4.23), yields the stationary mean velocity

$$v = L \frac{p_+ - p_-}{\langle T \rangle} \quad (4.24)$$

and the effective diffusion coefficient

$$D_{\text{eff}} = \frac{L^2}{2} \left(\frac{1}{\langle T \rangle} + \frac{(p_+ - p_-)^2}{\langle T \rangle^3} (\langle \Delta T^2 \rangle - \langle T \rangle^2) \right) . \quad (4.25)$$

According to eq. (4.6) the Péclet number reads

$$Pe = 2 \frac{p_+ - p_-}{1 - (1 - \frac{\langle \Delta T^2 \rangle}{\langle T \rangle^2})(p_+ - p_-)^2} . \quad (4.26)$$

In all formulae, p_- and p_+ denote the total probability to escape from the segment via the left and right boundary, respectively which are given by (Gardiner, 1985)

$$p_+ = 1 - p_- = \frac{1}{1 + e^{-\frac{FL}{D}}} . \quad (4.27)$$

The central moments of the escape time density $\rho(T)$ can be calculated by standard formulae (see e.g. Gardiner (1985)). Assuming without loss of generality that the middle of the segment is at $x = 0$ and the boundaries are at $\pm L$ yields

$$\langle T \rangle = \frac{1}{D(1 + e^{-\frac{FL}{D}})} \int_0^L dx \int_{x-L}^x dy \frac{\Phi(x)}{\Phi(y)} , \quad (4.28)$$

$$\langle \Delta T^2 \rangle = \frac{1}{D(1 + e^{-\frac{FL}{D}})} \int_0^L dx \int_{x-L}^x dy \frac{\Phi(x)}{\Phi(y)} (2T_1(y) - \langle T \rangle) \quad (4.29)$$

where $\Phi(x) = \exp[V(x)/D]$ and $T_1(x)$ is given by

$$T_1(x) = \frac{\left(\int_{-L}^x dy \Phi(y) \right) \int_x^L dy \int_{-L}^y dz \frac{\Phi(y)}{\Phi(z)} - \left(\int_x^L dy \Phi(y) \right) \int_{-L}^x dy \int_{-L}^y dz \frac{\Phi(y)}{\Phi(z)}}{D \int_{-L}^L dy \Phi(y)} . \quad (4.30)$$

We stress that the relations (4.24), (4.25) and (4.26) are exact for any shape of the periodic potential. The quadratures (4.28) and (4.29) have to be evaluated numerically

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in general.

Let us now discuss some limiting cases assuming $F \geq 0$ without loss of generality. For an *unbiased* potential ($F = 0$, i.e., $p_+ = p_-$) the diffusion coefficient reduces to

$$D_{\text{eff}}(F = 0) = \frac{L^2}{2\langle T \rangle} \quad (4.31)$$

while velocity and Péclet number vanish, trivially.

On the other hand, according to Stratonovich's random walk assumption in case of a weak tilt, one may approximate $\langle \Delta T^2 \rangle = \langle T \rangle^2$ (Poissonian escape time intervals). This results in the same expression for the diffusion coefficient like (4.31) and in the approximate Péclet number

$$Pe(F \ll F_c) \approx 2(p_+ - p_-) = 2 \tanh(FL/2D). \quad (4.32)$$

the absolute value of which is a decreasing function of the noise intensity D .

Third, for a strong tilt and not too large noise intensity one may assume that only escapes in direction of the bias occur ($p_+ = 1, p_- = 0$), i.e. n_t is approximated by a renewal process. This leads to

$$D_{\text{eff}}(F \sim F_c) \approx \frac{L^2 \langle \Delta T^2 \rangle}{2\langle T \rangle^3} \quad (4.33)$$

and to the Péclet number

$$Pe(F \sim F_c) \approx \frac{2\langle T \rangle^2}{\langle \Delta T^2 \rangle}. \quad (4.34)$$

The latter formulae are certainly wrong for large noise, they capture, however, the phenomenon of coherent transport occurring at small up to moderate noise intensity. We would like to point out a remarkable property for systems with symmetric potential $U(x) = U(-x)$. In this case, all calculated quantities do not change for the inverse potential $-U(x)$, for instance

$$U(x) = U(-x) \implies D_{\text{eff}}[U(x)] = D_{\text{eff}}[-U(x)] \quad (4.35)$$

and likewise for v and Pe . This can be proven by manipulations of the resulting quadrature formulae for v and D_{eff} . A short proof is possible using formulae by Reimann and coworkers and will be given within the next section.

Relation (4.35) is not surprising for a cosine potential, since the inverse potential is again a cosine with an irrelevant phase shift in x . However, for a symmetric, flat potential with small and sharp barriers, identical characteristics will be found for the inverse potential that possesses “valleys” instead of barriers. We will give an example for this non-obvious result in section 4.5.

4.3. Alternative approach by Reimann and coworkers

The discretization by segments of length $2L$ is not the only valid choice. Reimann et al. (2001) have implicitly used a mapping onto a set of infinitely long segments. They obtained the same result for the effective diffusion coefficient like in the present work and, furthermore, provided an elegant simplification of the quadratures. From our point of view the differences between the approaches which we are going to outline now are nevertheless interesting enough.

In accordance with Reimann et al. (2001), the velocity and effective diffusion coefficient for $F \geq 0$ are given by

$$v = \frac{L}{\langle T_{0 \rightarrow L} \rangle} \quad , \quad D_{\text{eff}} = \frac{L^2}{2} \frac{\langle \Delta T_{0 \rightarrow L}^2 \rangle}{\langle T_{0 \rightarrow L} \rangle^3} \quad (4.36)$$

here, $\langle T_{0 \rightarrow L} \rangle$ denotes the mean of the first passage time from 0 to L with absorbing boundary at $-\infty$ and L while $\langle \Delta T_{0 \rightarrow L}^2 \rangle$ is the variance of this time. The expressions can be further simplified (Reimann et al., 2001) to

$$\begin{aligned} v &= \frac{L(1 - e^{-LF/D})}{\int_0^L dx I_{\pm}(x)} \quad , \\ D_{\text{eff}} &= DL^2 \frac{\int_0^L dx I_+(x) I_-^2(x)}{\left[\int_0^L dx I_{\pm}(x) \right]^3} = DL^2 \frac{\int_0^L dx I_-(x) I_+^2(x)}{\left[\int_0^L dx I_{\pm}(x) \right]^3} \end{aligned} \quad (4.37)$$

where “ $\pm$ ” indicates that one may use either “ $+$ ” or “ $-$ ”. I_+ and I_- are given by

$$I_+ := \frac{1}{D} e^{V(x)/D} \int_{x-L}^x dy e^{-V(y)/D} \quad , \quad I_- := \frac{1}{D} e^{-V(x)/D} \int_x^{x+L} dy e^{V(y)/D}. \quad (4.38)$$

Eq. (4.37) is not just a much shorter expression than ours but is also expressed in terms of only *two* instead of *four* quadratures - a great advantage for the numerical evaluation, in particular, at small noise intensity D .

The formulae (4.36) hold asymptotically for a renewal process corresponding to the discrete mapping depicted in Fig. 4.4 (l.h.s.) since apparently only forward jumps are considered.

Seemingly, the Ansatz should fail in particular at large noise and small bias since the density $p(n)$ is distorted in direction of the bias (obviously, starting an ensemble of particles in the segment with $n = 0$ won't yield any contributions for $n < 0$). Furthermore, it is not obvious which segment number belongs to a certain interval of x . However, formula (4.36) emerges to be correct and is equivalent to our result (4.25).

In order to proof this equivalence we derive and employ a relation between the Laplace transforms of the escape time densities corresponding to finite and infinite segment. The renewal event in the above discretization is the escape out of the single *infinite* segment starting in a distance of one period from the absorbing right boundary (Fig. 4.4, middle). It can be expressed by the

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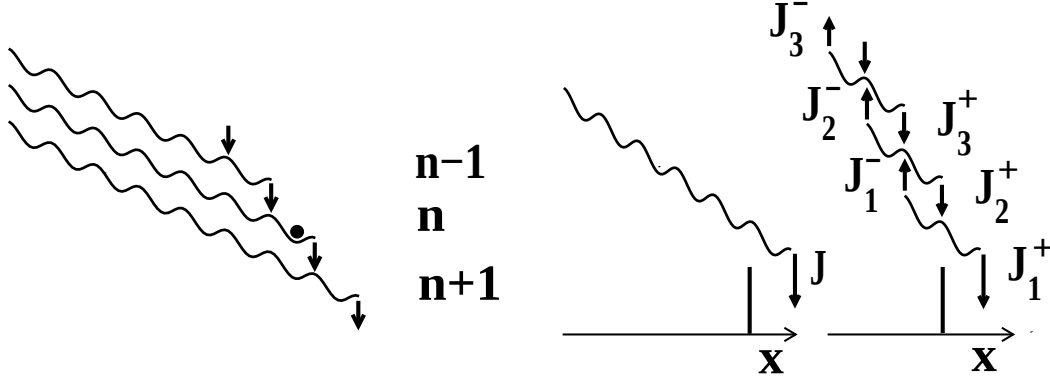


Figure 4.4.: Left: Renewal process resulting in eqs. (4.36). Right: An ensemble of particles indicated by the thick lines is started at $T = 0$, $x = 0$ and absorbed at $x = L$. $j(T), j_i^\pm(T)$ with $i = 1, 2, 3 \dots$ are the absolute values of the respective probability currents. Note that the numbering of the segments is vice versa to that in Fig. 4.2 for technical reasons.

escape via the corresponding right boundary in an *infinite* number of *finite* segments (Fig. 4.4, r.h.s.). The escape time density out of the infinite segment is given by the current $J(T_{0 \rightarrow L})$ which is equal to $J_1^+(\tau = T_{0 \rightarrow L})$ (Fig. 4.4) since both discrete descriptions apply to the same physical situation. The current $J_1^+(\tau)$ can be expressed by two contributions. One is due to the initial condition and equal to the current out of one single segment in the absence of any influx ($p_+ \rho(\tau)$). The other is due to the current J_2^+ resulting from the probability which leaves the first segment via the left boundary. An infinitesimal probability dP arriving by $J_2^+(\tau')$ at time τ' and $x = 0$ causes a probability current $p_+ dP \rho(\tau - \tau')$. Thus, we obtain

$$J(T_{0 \rightarrow L}) = J_1^+(\tau = T_{0 \rightarrow L}) = \left(p_+ \rho(\tau) + p_+ \int_0^\tau d\tau' J_2^+(\tau') \rho(\tau - \tau') \right) \Big|_{\tau=T_{0 \rightarrow L}}. \quad (4.39)$$

In the same way one obtains for an arbitrary segment with $n > 1$

$$J_n^+(\tau) = \int_0^\tau d\tau' [p_+ J_{n+1}^+(\tau') + p_- J_{n-1}^+(\tau')] \rho(\tau - \tau') \quad (4.40)$$

where we have additionally used the relation $J_n^-(\tau) = J_n^+(\tau) p_- / p_+$ derived in the previous section.

Let $j(\lambda), j_n(\lambda)$ and $\varrho(\lambda)$ be the Laplace transforms of $J(T_{0 \rightarrow L}), J_n^+(\tau)$ and $\rho(\tau)$, respectively. Then, eqs. (4.39) and (4.40) lead to a one-sided recurrence relation

$$p_+ \varrho j_{n+1} - j_n + p_- \varrho j_{n-1} = 0, \quad n \geq 1, \quad j_0 \equiv p_+ / p_- \quad (4.41)$$

the solution of which is given by a periodic continued fraction that can be further simplified (Risken, 1984) to

$$j(\lambda) = j_1(\lambda) = \frac{2p_+ \varrho(\lambda)}{1 + \sqrt{1 - 4p_+ p_- \varrho(\lambda)^2}}. \quad (4.42)$$

From this relation between the escape time densities the relations between the central moments $\langle T_{0 \rightarrow L} \rangle$, $\langle \Delta T_{0 \rightarrow L}^2 \rangle$ and $\langle T \rangle$, $\langle \Delta T^2 \rangle$ are readily obtained by the first two derivatives of $\ln(j(\lambda))$

yielding

$$\langle T_{0 \rightarrow L} \rangle = \frac{\langle T \rangle}{p_+ - p_-}, \quad (4.43)$$

$$\langle \Delta T_{0 \rightarrow L}^2 \rangle = \frac{\langle \Delta T^2 \rangle}{p_+ - p_-} + \frac{4p_+ p_- \langle T \rangle}{(p_+ - p_-)^2}. \quad (4.44)$$

For the diffusion constant $D_{\text{eff}} = L^2 \langle \Delta T_{0 \rightarrow L}^2 \rangle / (2 \langle T_{0 \rightarrow L} \rangle^3)$ according to eq. (4.36) one recovers our result eq. (4.25). Hence, the equivalence of both approaches is proved.

Why do the two approaches yield the same velocity and effective diffusion coefficient? In order to answer this question consider the discretization illustrated in Fig. 4.5. Here, the system is mapped to the motion in a set of segments of three period length which is a kind of compromise between the two mappings.

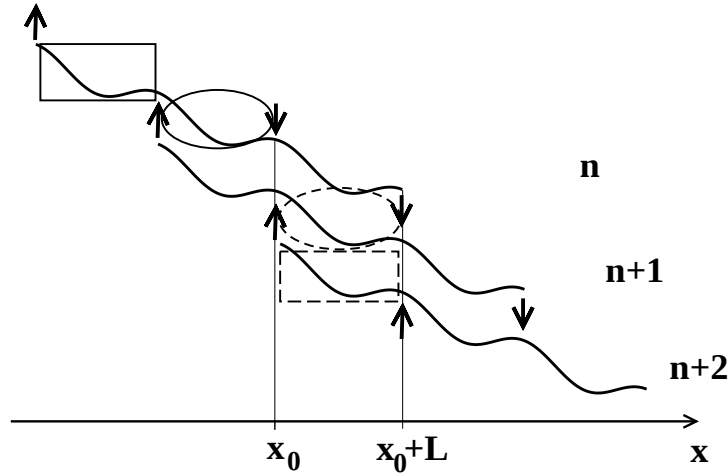


Figure 4.5.: A discretization consisting of segments of length $3L$.

For large times, the true density $P(x, t)$ exhibits a quasi periodicity over a finite number of periods.

Consider the relative change of the coarse grained density $f(x) \equiv \exp[-(x - vt)^2 / 4D_{\text{eff}}t]$

$$f'(x)/f(x) = -(x - vt)/2D_{\text{eff}}t$$

the absolute value of which grows with increasing distance from the mean value $x = vt$. If we go not further than a multiple of the dispersion $x_{\pm} = vt \pm k\sqrt{2D_{\text{eff}}t}$ (for instance, $k = 3$ implies that less than 0.3 % of the probability lay beyond the interval (x_-, x_+)) we find

$$f'(x_{\pm})/f(x_{\pm}) = \mp k\sqrt{2D_{\text{eff}}t}/2D_{\text{eff}}t \xrightarrow{t \rightarrow \infty} 0$$

Since the relative change of the Gaussian factor becomes arbitrarily small, a spatial variation of the density for finite intervals does only occur due to the periodic stationary solution in eq. (4.5).

The probability $P_n(x, t)$ is not periodic with respect to x , obviously, the rightmost period contains “more probability” than each of the other two periods of the segment

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due to the finite bias. The periodicity of $P(x, t)$, however, makes it plausible to assume $P_n(x, t) \approx P_{n+1}(x + L, t)$ that becomes exact for $t \rightarrow \infty$.

Let us assume that the probability belonging to state n represents (approximately) all probability contained by the interval $[x_0, x_0 + L]$, i.e. the rightmost period of the segment. Of course, this probability is actually given by the sum of the probabilities (a) within the corresponding part of state n (b) that of state $n + 1$ indicated by the dashed ellipse (c) that of state $n + 2$ indicated by the dashed box. The latter two contributions are under the above assumptions equal to the remaining probability of state n , indicated by solid box and ellipse, respectively. Hence, the state n represents indeed all probability within $[x_0, x_0 + L]$ and the mapping becomes exact for $t \rightarrow \infty$. In principle, the same line of reasoning applies in case of segments longer than three periods. Additionally, for given F and D the probability outflux to the left becomes negligible for a certain length mL , thus as matter of fact, there is no difference of this case to the discretization with infinitely long segments.

Finally, a fairly short proof for the relation (4.35) can be given by means of formulae (4.37) and (4.38).

First, we show two properties of $I_{\pm}$ provided that $U(x) = U(-x)$ holds true.

(a) periodicity: $I_+(x + L) = I_+(x)$

$$\begin{aligned} I_+(x + L) &= \frac{1}{D} e^{V(x+L)/D} \int_x^{x+L} dy e^{-V(y)/D} \stackrel{(\tilde{y}=y-L)}{=} \frac{1}{D} e^{-FL/D} e^{V(x)/D} \int_{x-L}^x d\tilde{y} e^{-V(\tilde{y}+L)/D}, \\ &= \frac{1}{D} e^{-FL/D} e^{V(x)/D} e^{FL/D} \int_{x-L}^x d\tilde{y} e^{-V(\tilde{y})/D} = I_+(x) \end{aligned}$$

and analog for $I_-(x)$

(b) Considering $I_{\pm}$ as functionals $I_{\pm} = I_{\pm}[U, x]$ it holds $I_+[-U, -x] = I_-[U, x]$

$$\begin{aligned} I_+[-U, -x] &= \frac{1}{D} e^{(Fx - U(-x))/D} \int_{-x-L}^{-x} dy e^{(U(y) + Fy)/D} \\ &\stackrel{(\tilde{y}=-y)}{=} -\frac{1}{D} e^{(Fx - U(x))/D} \int_{x+L}^x d\tilde{y} e^{(U(-\tilde{y}) - F\tilde{y})/D} \\ &= \frac{1}{D} e^{-V(x)/D} \int_x^{x+L} dy e^{V(y)/D} = I_-[U, x]. \end{aligned}$$

Using **(a)** and **(b)** it follows for the integrals appearing in eqs. (4.37)

$$\int_0^L dx I_+[U, x] \stackrel{(b)}{=} \int_0^L dx I_-[-U, -x] = \int_{-L}^0 d\tilde{x} I_-[-U, \tilde{x}]$$

$$\stackrel{(a)}{=} \int_0^L dx I_-[-U, x] = \int_0^L dx I_+[-U, x]$$

and

$$\begin{aligned} \int_0^L dx I_+[U, x] I_-^2[U, x] &\stackrel{(b)}{=} \int_0^L dx I_-[-U, -x] I_+^2[-U, -x] = \int_{-L}^0 d\tilde{x} I_-[-U, \tilde{x}] I_+^2[-U, \tilde{x}] \\ &\stackrel{(a)}{=} \int_0^L dx I_-[-U, x] I_+^2[-U, x] = \int_0^L dx I_+[-U, x] I_-^2[-U, x] \end{aligned}$$

where in the respective last step the equivalence implied by formulae 4.37 was utilized. Since the only dependence of v , D_{eff} and Pe on the potential is due to the above integrals one may conclude that those quantities are independent of the sign of $U(x)$.

4.4. Optimal transport in a cosine potential

Consider the archetypical cosine Potential $U(x) = \cos(x)$. The critical tilt at which the minima and maxima of the effective potential vanish is given by $F_c = 1$. For a strong but subcritical tilt $F = 0.95$ (see Fig. 4.6), velocity and effective diffusion coefficient are increasing functions of the noise intensity (cf. Fig. 4.7). The Péclet number, however, attains a maximum at a moderate value of D indicating an optimal transport in this case. These findings are confirmed by results of a numerical solution of the FPE (4.2).

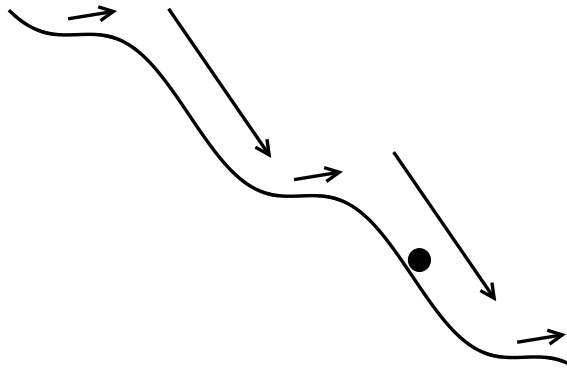


Figure 4.6.: Coherent motion of the particle (filled circle) at strong bias ($F = 0.95$) and moderate noise intensity. The arrows indicate the most likely processes: relaxation from the left barrier to the minimum (long arrow) and escape via the right maximum (short arrow).

At the optimal noise intensity, the particle motion is mainly determined by two processes (illustrated in Fig. 4.6): the noise driven escape from the potential minimum via the right potential barrier followed by a relaxation into the next minimum. Like

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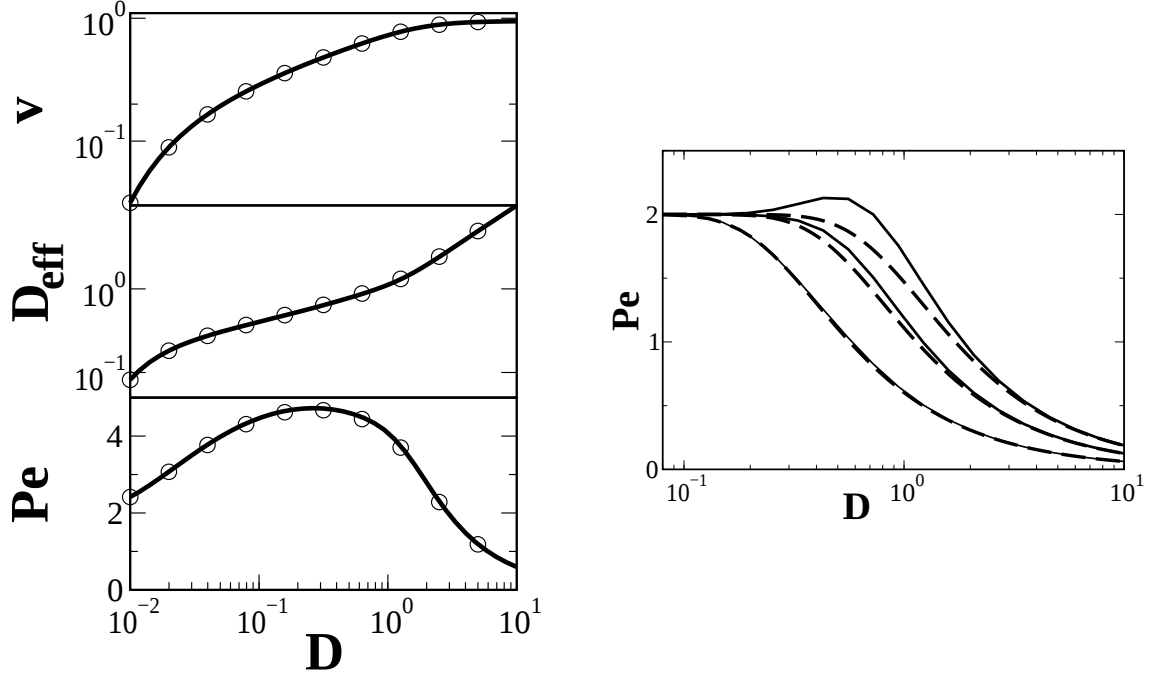


Figure 4.7.: Left: Velocity, diffusion coefficient, and Péclet number according to eqs. (4.24),(4.25),(4.26) versus noise intensity for $F = 0.95$. Circles indicate results from a numerical solution of (4.2). Right: Péclet number for different tilting forces $F = 0.1, 0.2, 0.3$ (from bottom to top). Theory according to eq. (4.26) (solid) compared with 'biased-random-walk' approximation eq. (4.32) (dashed).

in the leaky integrate-and-fire or excitable FitzHugh-Nagumo models, the relaxation time depends only weakly on the noise strength and possesses a small variance. The non-negligible presence of this quasi deterministic time leads to a certain regularity of the particle motion and accounts for the maximum of the Péclet number. This is in close analogy to the increased regularity of the spike train generated by an excitable system in case of coherence resonance (see also below).

A weaker maximum of Pe is also observed at smaller tilt. Fig. 4.7 (r.h.s) shows the Péclet number for $F = 0.1, 0.2, 0.3$ compared to the random walk approximation (4.32). The latter is sufficient for $F = 0.1$ as well as for small and large noise intensity at arbitrary tilt. It fails, however, to reproduce the nonmonotonous dependence on noise strength that arises numerically for $F > 0.24$.

The coherent transport can be illustrated in the following way. At three different noise intensities $D_1 < D_2 < D_3$ (with $D_2 = D_{\text{max}}$ resulting in the maximal Péclet number) an ensemble of particles is started at fixed position x_0 . The Fokker-Planck equation is integrated until the mean of the respective density reaches a given marker x_e . This will, of course, take different times Δt_i for the three different noise intensities. For the

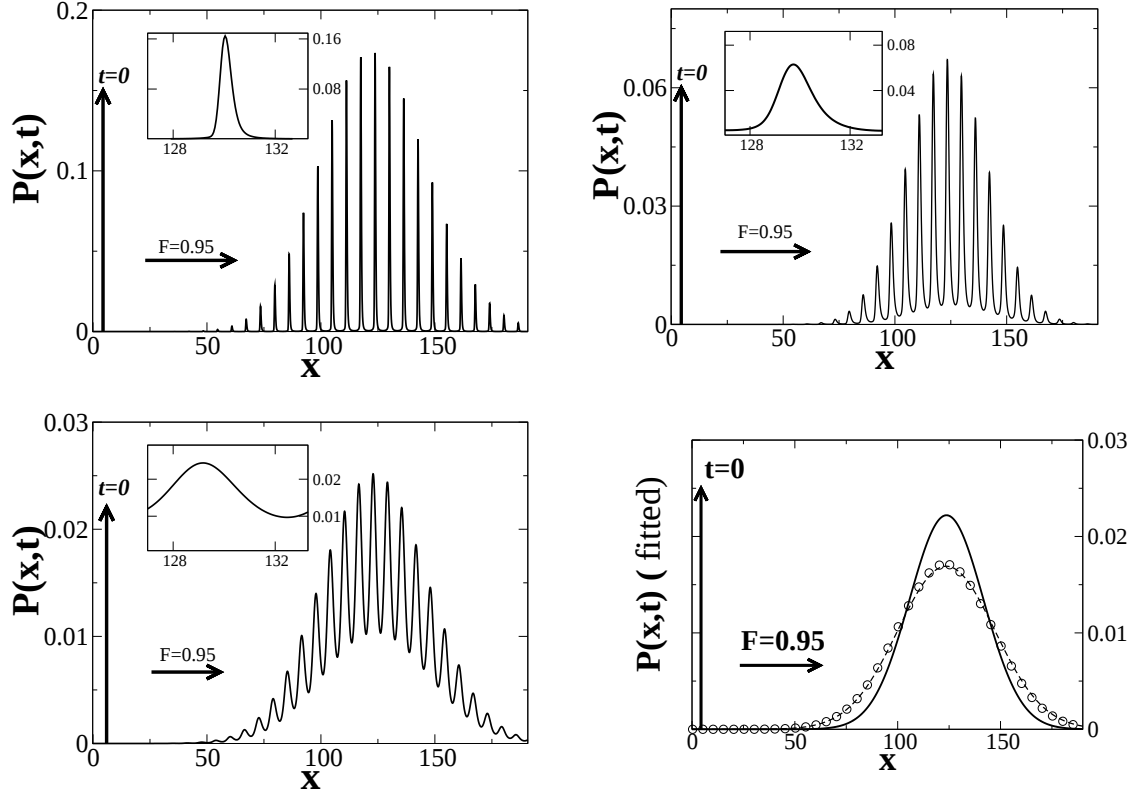


Figure 4.8.: Probability densities for $F = 0.95$ and three different noise levels $D_1 = 0.015$, $D_2 = 0.25$ and $D_3 = 2.05$ at $t \approx 1919, 275$ and 139 , respectively. D_1, D_3 are chosen such that $Pe(D_1) = Pe(D_3)$ and D_2 is the optimal value from Fig. 4.7. Densities obtained by numerical solution of the FPE (4.2) with $P(x, t = 0) = \delta(x - 4.4)$ (arrow) for D_1 (top left), D_2 (top right) and D_3 (bottom left). The insets show the densities for one period. Bottom right: Gaussian fits to these densities, D_1 (circles), D_2 (solid), D_3 (dashed).

variances of the densities $\langle \Delta x_i^2 \rangle$ one obtains

$$\langle \Delta x_i^2 \rangle = 2D_{\text{eff}} \Delta t_i = 2 \frac{Lv_i \Delta t_i}{Pe_i} = 2 \frac{L(x_e - x_0)}{Pe_i}, \quad i = 1, 2, 3. \quad (4.45)$$

Thus one may conclude that the density at greatest Péclet number will have the smallest variance. This can be verified numerically for the densities depicted in Fig. 4.8 and is clearly seen when the densities are fitted to Gaussian functions (Fig. 4.8, bottom right). For a given subcritical tilt, the ordered transport of particles from x_0 to x_e is thus apparently optimized at finite noise strength.

4.5. Enhanced transport coherence due to a particular potential shape

The optimal transport discussed in the previous section became manifest by a maximum of the Péclet number with respect to the noise intensity. An even stronger coherence of the particle motion emerges for specific potential shapes with a long relaxation period and a short lasting escape event. Such shape can be realized, for instance by the potential

$$U(x) = \frac{\Delta}{\varepsilon} e^{\varepsilon(\cos(x) - 1)}. \quad (4.46)$$

For large ε the potential is flat apart from periodically occurring small barriers (cf. Fig. 4.9, r.h.s., top) the height of which can be scaled by the parameter Δ . If Δ is negative (cf. Fig. 4.9, r.h.s., black dashed line), the potential exhibits small valleys instead of barriers. For the opposite limit $\varepsilon \rightarrow 0$ and fixed $\Delta = 1$ in turn, one recovers the cosine potential.

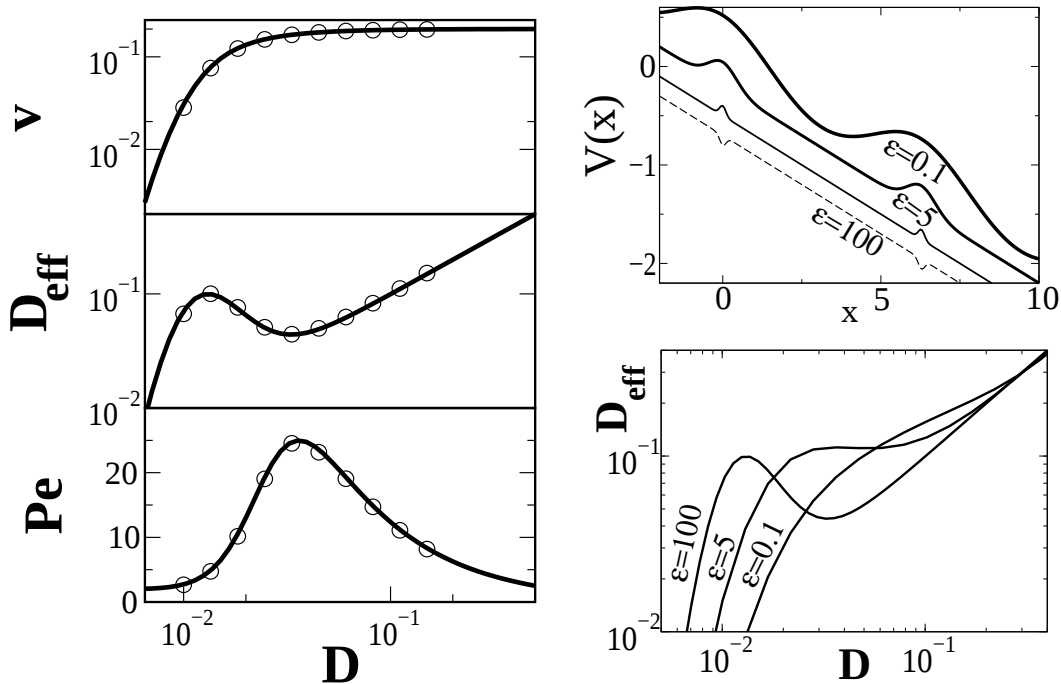


Figure 4.9.: Left: Velocity, diffusion coefficient and Péclet number for the potential eq. (4.46) according to eqs. (4.24), (4.25), (4.26) versus noise intensity D . Circles indicate results from the numerical solution of the FPE (4.2). Parameters: $\Delta = 10$, $\varepsilon = 100$, $F = 0.2$. Right top: The potentials for decreasing values of $\varepsilon = 100, 5, 0.1$ with $\Delta = 10, 0.1, 0.01$, respectively. Right bottom: The effective diffusion coefficient versus noise intensity for the potentials plotted above. The minimum of D^{eff} vanishes at $\varepsilon \approx 5$.

Besides the maximum in the Péclet number, we find for large ε a pronounced minimum in the effective diffusion coefficient at almost the same noise level (see Fig. 4.9, l.h.s.). This remarkable result (increasing noise decreases diffusion) relies on the large ratio of relaxation to escape time for the specific potential ($\varepsilon = 100$) at optimal noise intensity. Since the potential tends to a cosine for $\varepsilon \rightarrow 0$, we expect the minimum to vanish for decreasing ε . This is shown in Fig. 4.9 (r.h.s., bottom) for the potentials depicted in Fig. 4.9 (r.h.s., top). Here, the parameter Δ was tuned such that the potential barriers to the right and left are the same for all potentials.

Because the potential (4.46) possesses spatial symmetry we find according to relation (4.35) the same functions if $\Delta \rightarrow -\Delta$, i.e., the same velocity, diffusion coefficient and Péclet number for the potentials drawn as black solid and dashed lines in Fig. 4.9 (r.h.s., top).

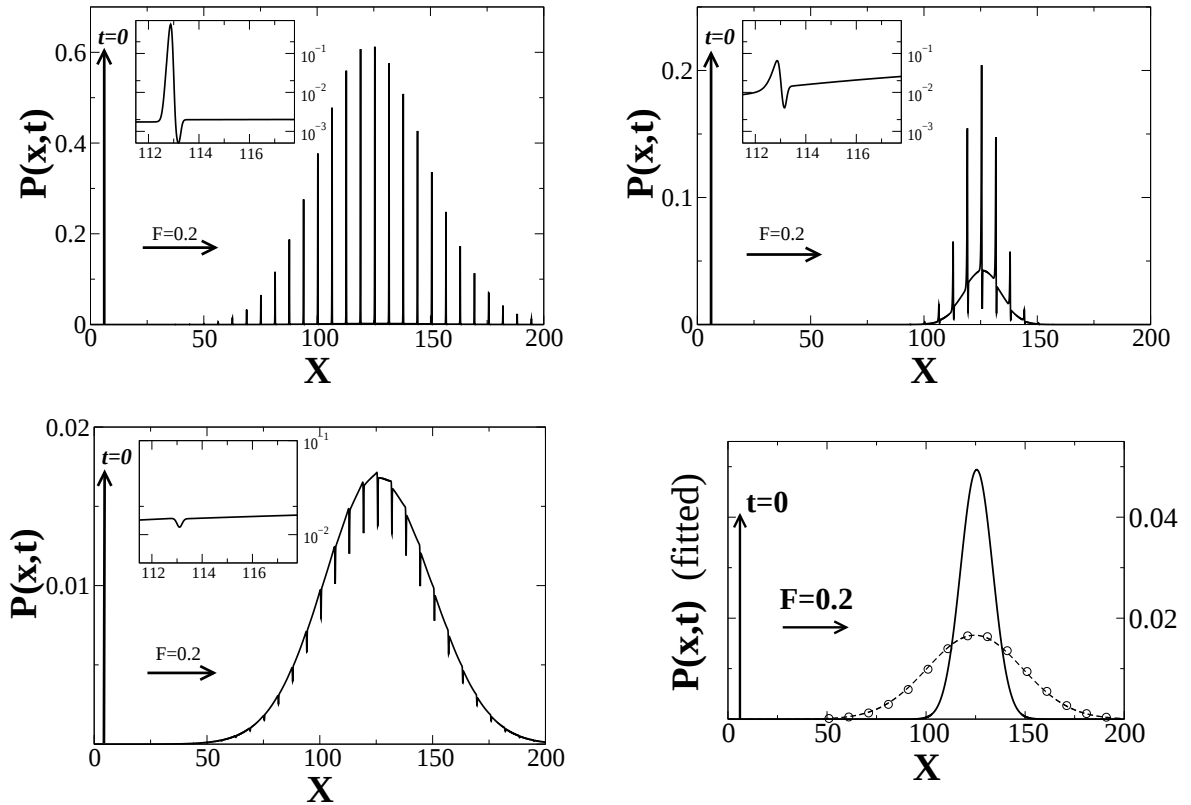


Figure 4.10.: Probability densities for $F = 0.2$ and three different noise levels $D_1 = 0.01$, $D_2 = 0.033$, $D_3 = 0.472$ at $t \approx 4540, 691$ and 625 , respectively. D_1, D_3 are chosen such that $Pe(D_1) = Pe(D_3)$ and D_2 is the optimal value from Fig. 4.9. Densities were obtained by numerical solution of the FPE (4.2) with $P(x, t = 0) = \delta(x - 6.1)$ (arrow), D_1 (top left) D_2 (top right) and D_3 (bottom left). The insets show the logarithm of the densities for one period. Bottom right: Gaussian fits to these densities, D_1 (dashed), D_2 (solid), D_3 (circles).

In contrast to the cosine potential, the velocity at the optimal noise intensity is almost saturated ($v \approx F$). Furthermore, the maximal value of Pe exceeds the maximal Pe of a one-sided random walk (i.e., the small noise limit with $Pe = 2$) by one order of magnitude. Consequently, a much more pronounced coherence is expected for the same 'experiment' like in the previous section. Indeed, the numerical results in Fig. 4.10 reveal a larger difference in the dispersions at small, large and optimal noise intensity. In addition, the difference in the times to reach the marker x_e is small for optimal and large noise. Hence, for the special potential the *most coherent diffusive* transport at optimal noise intensity is only slightly slower than the *fastest diffusive* transport at large D .

The minimum of the diffusion coefficient implies trivially a minimum of the dispersion for the optimal noise intensity when a fixed time instead of a fixed distance is considered.

4.6. Relation to coherence resonance in excitable systems

The effect of optimal transport is strongly related to the coherence resonance (CR) that was the subject of the previous chapters. This can be seen as follows. One measure of coherence resonance we have employed in the previous chapters is the coefficient of variation, i.e., the relative standard deviation R of the time interval between subsequent excitations

$$R = \frac{\sqrt{\langle \Delta T^2 \rangle}}{\langle T \rangle}. \quad (4.47)$$

Furthermore, we have used the diffusion coefficient of the numbers of excitations to quantify the coherence resonance.

$$D_{\text{eff}} = \frac{1}{2} \frac{\langle \Delta T^2 \rangle}{\langle T \rangle^3}. \quad (4.48)$$

As a manifestation of CR, both quantities become minimal for a moderate noise intensity, indicating that the excitation sequence (which was in the previous chapters the spike train) is closest to a regular periodic one. Now, in case of the motion in a periodic potential it is not straightforward to decide what kind of excitations should be considered since there are jumps to the left and to the right. If, however, for a given positive bias F we count only the jumps by one period to the right, i.e. we consider the passages like in Reimann et al. (2001) and section 4.3 (cf. in particular Fig. 4.4, l.h.s.) the above quantities are precisely defined as the CV of the jump times to the right and as the diffusion coefficient of the number of jumps to the right. It is readily

shown that the CV is simply related to the Péclet number.

$$Pe = \frac{vL}{D_{\text{eff}}} = 2 \frac{\langle T_{0 \rightarrow L} \rangle^2}{\langle \Delta T_{0 \rightarrow L}^2 \rangle} = \frac{2}{R^2}. \quad (4.49)$$

where we have used eq. (4.6) and the equivalence of the two expressions for mean velocity and diffusion coefficient eq. (4.24), eq. (4.25) and eq. (4.36).

First, it is clearly seen that Pe becomes maximum when R is minimal. A (possibly weak) coherence resonance of the above defined passage time hence implies an optimal transport of particles and vice versa. Furthermore, a minimum in the effective diffusion coefficient as a function of noise can be as well interpreted as a minimum in the diffusion coefficient of the number of excitations. In other words, such a minimum implies a strong coherence resonance of the jump event sequence.

The tilted washboard potential were proposed as a phase dynamics for the FitzHugh-Nagumo model by Kurrer and Schulten (1995). In the previous section we have seen that the original FN model with fixed point close to the separatrix line (high excitability) exhibits a strong CR effect manifested by the minimum in the spike count diffusion coefficient. For low excitability that was not the case and CR was only weakly present and manifested by a shallow minimum in the CV. For a periodic potential in turn a minimum in the diffusion coefficient was obtained in case of a flat potential with small sharp barriers but apparently not for the archetypic cosine potential used by Kurrer and Schulten (1995). One may infer that at least for the case of high excitability in the FN model the cosine potential is not suitable but has to be replaced by a potential with many higher harmonics similar to our example above. It should be clear that the approximation of the phase dynamics by means of a cosine potential is nevertheless justified for the FN model with low excitability since in this case the CR effect is limited to a minimum (maximum) in the CV (Pe).

4.7. Summary

We have calculated the effective diffusion coefficient and Péclet number for an overdamped Brownian particle in a tilted periodic potential of arbitrary shape. For a strong but subcritical bias a coherent motion of particles at a finite noise level was found manifested by a maximum of the Péclet number as a function of D . This was verified by numerical solutions of the Fokker-Planck equation for the cosine potential with tilt. For another shape of the potential consisting of flat parts and small sharp barriers a higher coherence could be achieved at finite noise. In this case, the effective diffusion coefficient exhibited a local minimum as a function of noise intensity. The effect of coherent motion was related to the coherence resonance effect in excitable systems revealing that a coherence resonance of the jump times in direction of the applied bias implies a coherent motion of particles and vice versa. Finally, from the results of the previous chapters we could draw the conclusion that a phase dynamics

4. *Coherent motion in a tilted periodic potential*

of the FitzHugh-Nagumo model is not in all cases well approximated by the motion in a cosine potential but rather in a potential with many higher harmonics.

5. Signal transmission by leaky integrate-and-fire neurons

As it was shown in the introduction, there is evidence for two kinds of signals that are processed by higher order sensory or cortical neurons. In this chapter, the response of a leaky integrate-and-fire neuron to these signals will be studied. To be exact, we will investigate the LIF model driven by a time dependent base current and fluctuations of time dependent intensity

$$\dot{v} = -v + \mu + \varepsilon_\alpha \cos(\omega_s t + \varphi) + \sqrt{2[D + \varepsilon_\beta \cos(\omega_s t + \varphi)]}\xi(t). \quad (5.1)$$

In addition to the input eq. (1.38), we have included an arbitrary initial phase φ . The spike generation scheme is the same as in eq. (2.2) (including a finite absolute refractory period τ) except, of course, for the presence of the signals in the stochastic differential equation.

What happens in response to a weak periodic modulation is the following:

- The probability density of the voltage $P(v, t)$ and the instantaneous firing rate $r(t)$ are explicitly time dependent. In the asymptotic limit, we expect

$$r(t) = r_0 + A \cos(\omega_s t + \varphi - \phi)$$

where $A \ll r_0$ and ϕ are amplitude and phase shift of the response, respectively.

- The spectral density exhibits δ peaks at the driving frequency. The spectral background will be that of the unperturbed system ($\varepsilon_\alpha = \varepsilon_\beta = 0$).
- The interspike interval density is not unimodal like in the absence of signals but multimodal with peaks close to the driving period and its multiples. Subsequent intervals are correlated by the signal phase, hence, we do *not* deal with a renewal process anymore.

Here, we will focus on the first two points and explore the differences between the spectral responses to additive and noise coded signals, respectively. Of particular interest is a possible stochastic resonance for both kinds of signals with respect to the background noise intensity. Moreover, we address the role of coherence resonance for

the neuronal signal transmission. Before we come to the calculation and discussion of the response, we give a review of some special cases of the model that have been (mostly numerically) treated in the literature.

Temporally modulated noise as neuronal input is a rather new topic - the only somewhat related studies to our knowledge are those by Feng and Titozzi (2000), Brunel (2000) and Pawelzik (2000). Feng and Titozzi (2000) investigated correlated Poissonian spike trains with modulated rates that are the input to a single neuron. They found numerically an enhancement of signal transmission for optimal (finite) correlations between the input spike trains. Brunel (2000) considered a sparsely connected network of LIF neurons and explored analytically the stability of the autonomous dynamics of the network. In this work, the time dependent noise intensity of the input to the single neuron resulted from the network itself. For the FitzHugh-Nagumo model an additive aperiodic signal and a signal or output correlated noise modulation was considered by Chow et al. (1998). They observed an enhancement of stochastic resonance with respect to the additive signal through noise modulation. An explicit distinction between additive and noise coded signals as well as a comparison of the responses of a neuronal system was not made and addressed in those works. Most related to these questions is the work by Pawelzik (2000) who has investigated the response of a *neuronal ensemble* to a step like change in either the base current or the noise intensity. The latter “signal” resulted in an instantaneous jump of the spike rate (averaged over the ensemble). This indicates the possibility of a finite high frequency transmission - a feature that will be studied in detail in this chapter.

Beyond neuron models, stochastic resonance in a bistable system with time dependent noise has been investigated by Dykman et al. (1992, 1993) and Gammaitoni et al. (1994). A spectral SR effect was found only if the system was asymmetric. Additionally, in contrast to our dynamics eq. (5.1), the signal amplitude in Dykman et al. (1992, 1993); Gammaitoni et al. (1994); Chow et al. (1998) was scaled with the constant part of the noise strength. In our notation that would mean that $D(t) = D(1 + \varepsilon_\beta \cos(\omega_s t))$ and imply that the background intensity is not taken into account.

Much more has been done in studying the response to a pure additive signal (Bulsara et al., 1996; Stemmler, 1996; Lánský, 1997; Plesser and Tanaka, 1997; Plesser and Geisel, 1999b; Shimokawa et al., 1999b,a,c). In the beginning, researchers focused on the case where the signal phase is reset to a constant value Φ every time the neuron fires a spike and made attempts to approximate the interspike interval density under this assumption (Bulsara et al., 1996) or to determine it by elaborated numerical methods (Plesser and Tanaka, 1997; Shimokawa et al., 1999b). To be more precise, one simulates the dynamics, starting at $t = 0$

$$\dot{v}(t) = -v + \mu + \varepsilon \cos(\omega_s t + \Phi) + \xi(t). \quad (5.2)$$

until the voltage reaches the threshold at $t = t_1$ and resets not just $v = v_T$ but also $t = 0$. We thus obtain directly by repeating the procedure the interspike intervals t_i .

The spiking times are then given by the sums of a certain number of subsequent intervals t_i . This approach has the advantage that the process is still renewal (subsequent interspike intervals are independent). The reset of the signal phase may correspond in some approximation to a so called endogenous stimulation (Lánský, 1997), i.e., the signal originates in the neuron itself and, hence, if voltage reaches threshold the signal generated by the neuron may be influenced.

Using the above scheme (eq. (5.2)), Bulsara et al. (1996) found a multimodal shape of the interspike interval density with peaks at the driving period and its multiples. Furthermore, they could show that stochastic resonance occurs due to time scale matching: the peak height in the density is maximized whenever the driving period matches the internal period of the neuron (the latter given by the mode of the density in absence of a periodic stimulus). This can be achieved by tuning the signal period or by changing the noise strength, i.e., the internal period.

Spectral quantities also show stochastic resonance (Plesser and Tanaka, 1997; Shimokawa et al., 1999b,a), however, in a recent work Plesser and Geisel (2001) claim that stochastic resonance vanishes in the reset model when a more realistic noise-adapted signal phase is used.

The more biological realistic and interesting case is certainly the external (exogenous) stimulation, i.e., the signal is *not* influenced by the dynamics of the neuron and thus the signal phase is *not* reset after the generation of an action potential. Then, in general, the renewal property is destroyed. The firing is more likely for certain signal phases and since the end point of an interspike interval I_i having the phase $\Phi_{i,end}$ is the start point for the next interval I_{i+1} , i.e. $\Phi_{i+1,start} = \Phi_{i,end}$, there will be a correlation of subsequent intervals due to the signal phase.

The case of an exogenous subthreshold additive signal has been treated with a numeric Markov chain method by Plesser and Geisel (1999b); Plesser (1999) and Shimokawa et al. (1999b,a). The main result for the interspike interval density is basically the same as for the model with reset: time scale matching, though not a perfect one is also observed if the signal phase is not reset and the signal amplitude is not too strong. The spectral response in turn, clearly exhibited stochastic resonance.

In Plesser and Geisel (1999b), another interesting property was discovered, namely, that for certain values of the base current μ the spectral signal-to-noise ratio can be also maximized by tuning the driving frequency. This is in contrast to the conventional bistable system where the spectral response always decreases with growing driving frequency.

For a weak additive signal without phase reset an analytical expression for the instantaneous firing rate $r(t)$ was very recently published by Brunel et al. (2001) and independently by the author and his supervisor (Lindner and Schimansky-Geier, 2001). Here, we derive this result and demonstrate how spectral quantities can be obtained from $r(t)$ and the knowledge of the background spectrum. We will show that the nonmonotonous dependence of the spectral response on the driving frequency found numerically by Plesser relies on the presence of coherence resonance in the system.

The resonance is hence a classical resonance with respect to the noise induced eigenfrequency exhibited by the system at moderate noise intensity.

Furthermore, we will calculate an exact expression for the firing rate in response to a weak noise coded signal and derive the spectral characteristics. We will discuss and compare the transmission features for additive and noise coded signals both in the noise-activated and in the deterministic firing regime. It will emerge that the response to the noise coded signal is rather strong and exhibits also stochastic resonance. Additionally, high frequent noise coded signals are transmitted with a finite amplitude, in other words, the response does not show a lowpass filtering for high frequent signals as it is typical for the neural transmission of additive signals.

Besides the spectral response of a single neuron, we will also briefly consider the response of an ensemble. Here, the modulation of the firing rate can be directly observed in the mean activity. In particular, the transmission of high frequent noise coded signals seems to be more relevant in neuronal ensembles or populations and may explain the fast signal transmission found, e.g., in the visual system (Thorpe et al., 1996).

The only approximation that we will use is that of small amplitudes of the signals. With regard to one of our main questions, namely, as to whether the neuronal transmission benefits from stochastic resonance, the limit of small amplitudes is natural since generally stochastic resonance is useful only for the amplification of weak signals and larger amplitudes deteriorate the effect.

5.1. Analytical treatment

As mentioned, we consider only the linear response to weak signals. In this case, the linear Ansatz for the probability density

$$P(v, t) = P_0(v) + \varepsilon_\alpha P_\alpha(v, t) + \varepsilon_\beta P_\beta(v, t) \quad (5.3)$$

with $P_0(v)$ being the stationary solution (2.43) reveals that the responses to additive and noise coded signals can be separately studied.

This becomes evident by splitting the Fokker-Planck operator in time dependent and independent parts

$$\hat{L} = \hat{L}_0 + \varepsilon_\alpha \hat{L}_\alpha + \varepsilon_\beta \hat{L}_\beta \quad (5.4)$$

with

$$\hat{L}_0 = \partial_v(v - \mu + D\partial_v), \quad \hat{L}_\alpha = -\cos(\omega_s t + \varphi)\partial_v, \quad \hat{L}_\beta = \cos(\omega_s t + \varphi)\partial_v^2. \quad (5.5)$$

The Ansatz (5.3) leads to

$$\begin{aligned} \partial_t P(v, t) &= \hat{L}P(v, t) \\ \varepsilon_\alpha \partial_t P_\alpha + \varepsilon_\beta \partial_t P_\beta &\approx \varepsilon_\alpha (\hat{L}_\alpha P_0 + \hat{L}_0 P_\alpha) + \varepsilon_\beta (\hat{L}_\beta P_0 + \hat{L}_0 P_\beta) \end{aligned} \quad (5.6)$$

where we have neglected terms of higher than first order at the r.h.s. A similar line of reasoning applies for the boundary conditions. Since ε_α and ε_β are small but arbitrary one may set one of them equal zero and calculate the time dependent part of the density in response to either the additive or the noise coded signal.

In the following we will determine the *asymptotic* density and response (firing rate), i.e., we neglect transients. This assumption seems to be justified, since the membrane voltage is expected to be within the usual range and also a neuronal ensemble should be not far from the stationary state. The asymptotic density in response to a small signal won't deviate much from this steady state solution. Therefore, the relaxation will be rather fast - this is also found in numerical simulations where the system is started in the steady state and the signal is switched on at a later instant.

5.1.1. Linear response to the additive signal

In the following ε_β is set to zero. It is convenient to change the variable

$$x(t) = v - \mu + \varepsilon_\alpha (Ae^{-i\omega_s t} + c.c.), \quad A = \frac{e^{-i\varphi}}{2i\omega_s - 2} \quad (5.7)$$

where *c.c.* denotes here and in the following the complex conjugated of the last terms within the respective brackets. This yields a Langevin equation without periodic forcing

$$\dot{x} = -x + \sqrt{2D}\xi(t) \quad (5.8)$$

but with time dependent threshold and reset points

$$\begin{aligned} x_t(t) &= x_- + \varepsilon_\alpha (Ae^{-i\omega_s t} + A^*e^{i\omega_s t}), & x_- &:= v_T - \mu, \\ x_r(t) &= x_+ + \varepsilon_\alpha (Ae^{-i\omega_s t} + A^*e^{i\omega_s t}), & x_+ &:= v_R - \mu. \end{aligned} \quad (5.9)$$

Using the first equation in (5.7) as an Ansatz we obtain the Langevin equation

$$\begin{aligned} \dot{x} &= \dot{v} - \varepsilon_\alpha \omega_s (Aie^{-i\omega_s t} + c.c.) \\ &= -v + \mu + \frac{\varepsilon_\alpha}{2} (e^{-i\omega_s t} e^{-i\varphi} + c.c.) - \varepsilon_\alpha \omega_s (Aie^{-i\omega_s t} + c.c.) + \sqrt{2D}\xi(t) \\ &= -x + \varepsilon_\alpha (Ae^{-i\omega_s t} + c.c.) + \frac{\varepsilon_\alpha}{2} (e^{-i\omega_s t} e^{-i\varphi} + c.c.) - \varepsilon_\alpha \omega_s (Aie^{-i\omega_s t} + c.c.) + \sqrt{2D}\xi(t) \\ &= -x + \sqrt{2D}\xi(t) + \varepsilon_\alpha \left(e^{-i\omega_s t} \left(A - Ai\omega_s + \frac{e^{-i\varphi}}{2} \right) + c.c. \right). \end{aligned}$$

In order to arrive at eq. (5.8), the last term must vanish and we get the above expression for A . It is evident that this transformation is not offhand possible for any potential since by the used Ansatz we get higher harmonics if the force (here, simply x) is nonlinear.

The corresponding Fokker-Planck equation for (5.8) reads

$$\partial_t P(x, t) = \partial_x (x + D\partial_x) P(x, t) = -\partial_x J(x, t). \quad (5.10)$$

Regarding the boundary and jump conditions for the density $P(x, t)$, we may adopt those from chapter 2 with the important difference that threshold and reset points are now time dependent.

$$P(x_t(t), t) = 0, \quad (5.11)$$

$$[P(x, t)]_{x_r(t)} = 0, \quad (5.12)$$

$$\left[\frac{\partial P(x, t)}{\partial x} \right]_{x_r(t)} = \frac{\partial P(x, t - \tau)}{\partial x} \Big|_{x_t(t - \tau)}, \quad (5.13)$$

$$\lim_{x \rightarrow -\infty} P(x, t) = 0. \quad (5.14)$$

Like in chapter 2, the instantaneous firing rate as the quantity of prior interest is given by

$$r(t) = J(x_t, t) = -D \frac{\partial P(x, t)}{\partial x} \Big|_{x_t(t)}. \quad (5.15)$$

Thus, once $P(x, t)$ is known the rate can be determined from this equation. One limit case can be estimated easily. If the frequency tends to zero (adiabatic limit), we expect $P(x, t)$ to be the stationary density at a “static” signal $\varepsilon_\alpha \cos(\omega_s t)$. This implies that for a weak signal the rate is

$$r_0(\mu + \varepsilon_\alpha \cos(\omega_s t)) \approx r_0(\mu) + \frac{dr_0}{d\mu} \varepsilon_\alpha \cos(\omega_s t) \quad (5.16)$$

and hence directly proportional to the signal (no phase shift). Furthermore, the relative amplitude of the response equals the derivative of the rate (i.e., the transfer function) with respect to the base current μ (Stemmler, 1996; Chialvo et al., 1997; Longtin, 2000).

For the general nonadiabatic case we make a linear Ansatz for the asymptotic density

$$P(x, t) = P_0(x) + \varepsilon_\alpha \left(A e^{-i\omega_s t} p(x) + c.c. \right) e^{(x_+^2 - x^2)/(4D)}. \quad (5.17)$$

Inserting this function into the FPE (5.10) yields the ordinary differential equation

$$Dp''(x) - \left(\frac{x^2}{4D} - i\omega_s - \frac{1}{2} \right) p(x) = 0 \quad (5.18)$$

and the complex conjugated of this equation, respectively. One solution of this equation is known from chapter 2

$$\psi(x) = U \left(-i\omega_s - \frac{1}{2}, -\frac{x}{\sqrt{D}} \right) = \mathcal{D}_{i\omega_s} \left(-\frac{x}{\sqrt{D}} \right). \quad (5.19)$$

In order to determine $p(x)$, we expand the boundary conditions (5.11), (5.12), (5.13) to linear order in ε_α . This yields

$$p_- = \frac{r_0}{De^\Delta}, \quad (5.20)$$

$$[p]_+ = \frac{r_0}{D}, \quad (5.21)$$

$$[p']_+ - e^\Delta e^{i\omega_s \tau} p'_- = \frac{r_0}{2D^2} (e^{i\omega_s \tau} x_- - x_+). \quad (5.22)$$

Here, we have used $\Delta = (x_+^2 - x_-^2)/4D$.

We explicitly derive eqs.(5.20,5.21,5.22).

Expanding (5.11) yields

$$\begin{aligned} P(x_- + \varepsilon_\alpha(Ae^{-i\omega_s t} + c.c.), t) &\approx P(x_-, t) + \varepsilon_\alpha(Ae^{-i\omega_s t} + c.c.) P'(x, t)|_- \approx 0 \\ &\approx P_{0-} + \varepsilon_\alpha \{Ae^{-i\omega_s t}(p_- e^\Delta + P'_{0-}) + c.c.\}. \end{aligned}$$

Since $P_{0-} = 0$ (absorbing boundary condition for the stationary density) we can infer that

$$p_- = -P'_{0-}/e^\Delta. \quad (5.23)$$

A similar expansion of (5.12)

$$\begin{aligned} [P(x, t)]_{x_+ + \varepsilon_\alpha(Ae^{-i\omega_s t} + c.c.)} &\approx [P(x, t)]_+ + \varepsilon_\alpha(Ae^{-i\omega_s t} + c.c.)[P'(x, t)]_+ \approx 0 \\ &\approx [P_0]_+ + \varepsilon_\alpha \{Ae^{-i\omega_s t}([p]_+ + [P'_0]_+) + c.c.\}. \end{aligned}$$

yields because of $[P_0]_+ = 0$

$$[p]_+ = -[P'_0]_+. \quad (5.24)$$

Furthermore, we have to find the derivative at x_- and the jump of the derivative x_+ .

$$\begin{aligned} P'(x, t - \tau)|_{x_- + \varepsilon_\alpha(Ae^{-i\omega_s(t-\tau)} + c.c.)} &\approx P'(x, t - \tau)|_- + \varepsilon_\alpha(Ae^{-i\omega_s(t-\tau)} + c.c.) P''(x, t - \tau)|_- \\ &\approx P'_{0-} + \varepsilon_\alpha \left\{ Ae^{-i\omega_s(t-\tau)} \left(P''_{0-} + e^\Delta(p'_- - \frac{x_-}{2D}p_-) \right) + c.c. \right\} \end{aligned}$$

and

$$\begin{aligned} [P'(x, t)]_{x_+ + \varepsilon_\alpha(Ae^{-i\omega_s t} + c.c.)} &\approx [P'(x, t)]_+ + \varepsilon_\alpha(Ae^{-i\omega_s t} + c.c.) [P''(x, t)]_+ \\ &\approx [P'_0]_+ + \varepsilon_\alpha \left\{ Ae^{-i\omega_s t} \left([P''_0]_+ + [p']_+ - \frac{x_+}{2D}[p_+] \right) + c.c. \right\}. \end{aligned}$$

Using eq. (5.13) one obtains

$$P'_{0-} - [P'_0]_+ = \varepsilon_\alpha \left\{ Ae^{-i\omega_s t} \left([P''_0]_+ + [p']_+ - \frac{x_+}{2D}[p_+] - e^{i\omega_s \tau} (P''_{0-} + e^\Delta p'_- - e^\Delta \frac{x_-}{2D}p_-) \right) + c.c. \right\}. \quad (5.25)$$

Regarding the derivatives at x_- , x_+ we recall their relations to the stationary current and steady state firing rate, respectively

$$[P'_0]_+ = P'_{0-} = -\frac{J_0}{D} = -\frac{r_0}{D}. \quad (5.26)$$

For the higher derivatives, one may utilize the stationary FPE

$$(xP_0)' + DP_0'' = 0 \rightarrow P_0'' = -\frac{P_0 + xP_0'}{D}.$$

Hence, we obtain

$$P''_{0-} = \frac{x_- r_0}{D^2}, \quad [P''_0]_+ = \frac{x_+ r_0}{D^2}. \quad (5.27)$$

Inserting the derivatives into eqs. (5.23), (5.24), (5.25) results, after some simplifications in the above boundary conditions.

Additionally, condition (5.14) leads to $\lim_{x \rightarrow -\infty} p(x) = 0$. This is fulfilled if $p(x)$ for $x \rightarrow -\infty$ becomes proportional to $\psi(x)$ which possesses the asymptotic behavior

5. Signal transmission by leaky integrate-and-fire neurons

$\psi(x) \sim \exp[-x^2/4D]$ (see appendix A). Including the boundary conditions (5.20) and (5.21), we find

$$p(x) = \begin{cases} \left(\frac{r_0}{De^\Delta \psi_-} - \frac{r_0}{D\psi_+} + kY_+ \right) \psi(x) & , \quad x < x_+ \\ \frac{r_0}{De^\Delta} \frac{\psi(x)}{\psi_-} + kY(x)\psi_+ & , \quad x_+ < x < x_- \end{cases} \quad (5.28)$$

where $Y(x) = \psi(x)\psi_{2-} - \psi_- \psi_2(x)$ with $Y_- = 0, Y'_- = 1$ (see chapter 2). The constant k can be determined by eq. (5.22) yielding

$$k = \frac{r_0/D}{\psi_- - e^\Delta e^{i\omega_s \tau} \psi_+} \left(\frac{\psi'_-}{\psi_-} e^{i\omega_s \tau} - \frac{\psi'_+}{\psi_+} - \frac{x_+ - e^{i\omega_s \tau} x_-}{2D} \right). \quad (5.29)$$

Using eq. (5.28) the derivatives read

$$p'_- = \frac{r_0}{De^\Delta} \frac{\psi'_-}{\psi_-} + k\psi_+$$

and

$$\begin{aligned} [p']_+ &= \frac{r_0}{De^\Delta} \frac{\psi'_+}{\psi_-} + kY'_+ \psi_+ + \frac{r_0}{D} \frac{\psi'_+}{\psi_+} - \frac{r_0}{De^\Delta} \frac{\psi'_+}{\psi_-} - kY_+ \psi'_+ \\ &= \frac{r_0}{D} \frac{\psi'_+}{\psi_+} + k(Y'_+ \psi_+ - Y_+ \psi'_+) \\ &= \frac{r_0}{D} \frac{\psi'_+}{\psi_+} + k \left(\underline{\psi'_+ \psi_{2-} \psi_+} - \psi_- \psi'_{2+} \psi_+ - \underline{\psi_+ \psi_{2-} \psi'_+} + \psi_- \psi_{2+} \psi'_+ \right) \\ &= \frac{r_0}{D} \frac{\psi'_+}{\psi_+} + k\psi_- \end{aligned}$$

where the underlined terms cancel each other and we have again utilized the relation $\psi'(x)\psi_2(x) - \psi(x)\psi'_2(x) = 1$. After inserting these expressions in (5.22) and solving with respect to k one obtains the asserted formula.

Since $p(x)$ is now fully determined we can calculate the instantaneous firing rate by eq. (5.15).

Details:

$$\begin{aligned} r(t) &= J(x_t(t), t) = -D \frac{\partial P}{\partial x} \Big|_{x_- + \varepsilon_\alpha (Ae^{-i\omega_s t} + c.c.)} \\ &\approx -D \left(P'_0 + \varepsilon_\alpha \left\{ Ae^{-i\omega_s t} (P''_0 + e^\Delta p'_- - e^\Delta \frac{x_- p_-}{2D}) + c.c. \right\} \right) \\ &= r_0 - \varepsilon_\alpha D \left(Ae^{-i\omega_s t} (e^\Delta p'_- + \frac{x_-}{2D^2} r_0) + c.c. \right) \\ &= r_0 + \frac{\varepsilon_\alpha}{2} (\alpha e^{-i\omega_s t - i\varphi} + c.c.) = r_0 + \varepsilon_\alpha |\alpha| \cos(\omega_s t + \varphi - \phi_\alpha). \end{aligned}$$

ϕ_α is the complex phase of the response function α which can be further simplified by means of eq. (5.7) and some of the previous equations.

$$\begin{aligned}\alpha &= -2DAe^{i\varphi}(e^\Delta p'_- + \frac{x_-}{2D^2}r_0) \\ &= \frac{-D}{i\omega_s - 1} \left(\frac{r_0}{D} \frac{\psi'_-}{\psi_-} + k\psi_+ e^\Delta + \frac{x_-}{2D^2}r_0 \right) \\ &= -\frac{r_0}{i\omega_s - 1} \frac{\psi'_- + \frac{x_-}{2D}\psi_- - e^\Delta(\psi'_+ + \frac{x_+}{2D}\psi_+)}{\psi_- - e^\Delta e^{i\omega_s \tau} \psi_+}.\end{aligned}$$

Now we make use of the recurrence relation (A.5) which for $\psi(x) = \mathcal{D}_{i\omega_s}(-x/\sqrt{D})$ takes on the form

$$\psi'(x) + \frac{x}{2D}\psi(x) = -\frac{i\omega_s}{\sqrt{D}}\mathcal{D}_{i\omega_s-1}\left(-\frac{x}{\sqrt{D}}\right)$$

Finally, one has to replace $x_\pm = v_{R,T} - \mu$.

We find thus a compact expression for the asymptotic linear response of the LIF neuron to an additive signal (Lindner and Schimansky-Geier, 2001)

$$r(t) = r_0 + \varepsilon_\alpha |\alpha| \cos(\omega_s t + \varphi - \phi_\alpha) \quad (5.30)$$

with the linear response function and the phase shift given by

$$\alpha = \frac{r_0 i\omega_s / \sqrt{D}}{i\omega_s - 1} \frac{\mathcal{D}_{i\omega_s-1}\left(\frac{\mu-v_T}{\sqrt{D}}\right) - e^\Delta \mathcal{D}_{i\omega_s-1}\left(\frac{\mu-v_R}{\sqrt{D}}\right)}{\mathcal{D}_{i\omega_s}\left(\frac{\mu-v_T}{\sqrt{D}}\right) - e^\Delta e^{i\omega_s \tau} \mathcal{D}_{i\omega_s}\left(\frac{\mu-v_R}{\sqrt{D}}\right)} \quad (5.31)$$

$$\phi_\alpha = \arg(\alpha), \quad \Delta = \frac{v_R^2 - v_T^2 + 2\mu(v_T - v_R)}{4D}.$$

The solution given by (5.31) can be for most parameter values readily evaluated. Some limiting cases will be shown in the discussion of our results.

We would like to point out that our result for the relative amplitude α coincides for the special case of $\tau = 0$ with a result that has been recently obtained by Brunel et al. (2001).

In Brunel et al. (2001), the LIF model is considered in the following form

$$\tau_m \dot{V} = V_{rest} - V + I_0 + I_1 \cos(\omega t) + \sqrt{\tau_m} \sigma \xi(t)$$

with threshold and reset value V_{th} and V_{reset} , respectively, and a vanishing refractory period ($\tau = 0$). To eliminate the membrane time constant τ_m , we choose the new non-dimensional time $\tilde{t} = t/\tau_m$. This yields the dynamics (5.1) with the parameters

$$\mu = V_{rest} + I_0, \quad D = \sigma^2/2, \quad \varepsilon_\alpha = I_1, \quad \omega_s = \omega \tau_m.$$

Brunel et al. (2001) write for the instantaneous firing rate¹

$$r(t) = R_0 + R_1(\omega) \cos[\omega t + \Phi(\omega)].$$

¹Here as in the following we change slightly the notation from (Brunel et al., 2001) to prevent confusion with ours.

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Here, $R_0 = r_0/\tau_m$ with r_0 given by eq. (2.44) stands for the stationary rate (spikes per unit time that is now τ_m). In linear response used here as well as in (Brunel et al., 2001) $R_1(\omega)$ and $\Phi(\omega)$ should be related to our measures as follows

$$R_1(\omega) = \varepsilon_\alpha |\alpha(\omega\tau_m, \tau = 0)|/\tau_m, \quad \Phi(\omega) = -\varphi(\omega\tau_m, \tau = 0)$$

(recall that the rate refers to the unit time which was originally τ_m). Consequently, we have to show that

$$R_1 e^{i\Phi} = \varepsilon_\alpha \alpha^*(\omega\tau_m, \tau = 0)/\tau_m \quad (5.32)$$

is consistent with the result from Brunel et al. (2001)

$$R_1 e^{i\Phi} = \frac{R_0 I_1}{\sigma(1 + i\omega\tau_m)} \frac{\frac{\partial U_s}{\partial y}(y_t, \omega) - \frac{\partial U_s}{\partial y}(y_r, \omega)}{U_s(y_t, \omega) - U_s(y_r, \omega)} \quad (5.33)$$

with

$$y_t = (V_t - I_0 - V_{rest})/\sigma = (v_T - \mu)/\sqrt{2D}, \quad y_r = (V_{reset} - I_0 - V_{rest})/\sigma = (v_R - \mu)/\sqrt{2D}$$

and the function $U_s(y, \omega)$ given by a sum of two of Kummer's functions

$$U_s(y, \omega) = \frac{e^{y^2}}{\Gamma[(1 + i\omega\tau_m)/2]} M\left(\frac{1 - i\omega\tau_m}{2}, \frac{1}{2}, -y^2\right) + \frac{2ye^{y^2}}{\Gamma[i\omega\tau_m/2]} M\left(1 - \frac{i\omega\tau_m}{2}, \frac{3}{2}, -y^2\right).$$

Utilizing the relation of the parabolic cylinder functions to Kummer's function (appendix, eq. (A.6)), the Kummer transformation (Abramowitz and Stegun, 1970) $M(a, b, z) = e^z M(b - a, b, -z)$, and the recurrence relation for the parabolic cylinder function (appendix, eq. (A.5)), we may express the function $U_s(y, \omega)$ and its derivative in the following way

$$U_s(y, \omega) = \frac{2^{i\omega\tau_m/2}}{\sqrt{\pi}} e^{y^2/2} \mathcal{D}_{-i\omega\tau_m}(-\sqrt{2}y), \quad \frac{\partial U_s(y, \omega)}{\partial y} = \frac{2^{i\omega\tau_m/2}}{\sqrt{\pi}} e^{y^2/2} \sqrt{2} i\omega\tau_m \mathcal{D}_{-i\omega\tau_m-1}(-\sqrt{2}y). \quad (5.34)$$

Inserting these expressions in (5.33) and using our notation yields

$$\begin{aligned} R_1 e^\Phi &= \varepsilon_\alpha \frac{(r_0/\tau_m) i(-\omega_s)/\sqrt{D} \mathcal{D}_{-i\omega\tau_m-1}(\frac{\mu-v_T}{\sqrt{D}}) - e^\Delta \mathcal{D}_{-i\omega\tau_m-1}(\frac{\mu-v_R}{\sqrt{D}})}{i(-\omega_s) - 1 \mathcal{D}_{-i\omega\tau_m}(\frac{\mu-v_T}{\sqrt{D}}) - e^\Delta \mathcal{D}_{-i\omega\tau_m}(\frac{\mu-v_R}{\sqrt{D}})} \\ &= \varepsilon_\alpha \alpha(-\omega\tau_m, \tau = 0)/\tau_m = \varepsilon_\alpha \alpha^*(\omega\tau_m, \tau = 0)/\tau_m \end{aligned}$$

like asserted.

5.1.2. Linear response to the noise coded signal

Here, we set $\varepsilon_\alpha = 0$. A transformation of the noise coded signal to time dependent boundaries is apparently not possible, nevertheless, we eliminate the base current by the new coordinate $x = v - \mu$, i.e., we deal with the Langevin equation

$$\dot{x} = -x + \sqrt{2(D + \varepsilon_\beta \cos(\omega_s t + \varphi))} \xi(t) \quad (5.35)$$

with threshold and reset points $x_\mp = v_{T,R} - \mu$. The corresponding Fokker-Planck equation is given by

$$\partial_t P(x, t) = \partial_x \left(x + (D + \varepsilon_\beta \cos(\omega_s t + \varphi)) \partial_x \right) P(x, t). \quad (5.36)$$

The boundary conditions read

$$P(x_-, t) = 0, \quad (5.37)$$

$$[P(x, t)]_+ = 0, \quad (5.38)$$

$$\left(1 + \frac{\varepsilon_\beta}{D}(Ae^{-i\omega_s t} + c.c.)\right) \left[\frac{\partial P(x, t)}{\partial x} \right]_+ = \left(1 + \frac{\varepsilon_\beta}{D}(Ae^{-i\omega_s(t-\tau)} + c.c.)\right) \frac{\partial P(x, t-\tau)}{\partial x} \Big|_-, \quad (5.39)$$

$$\lim_{x \rightarrow -\infty} P(x, t) = 0 \quad (5.40)$$

where we have used $A := \exp[-i\varphi]/2$. Note that the prefactors in eq. (5.39) follow from the time dependent noise strength that enters the equality of in and outfluxes at x_+ and x_- , respectively.

Again, we make a linear Ansatz for the asymptotic probability density

$$P(x, t) = P_0(x) + \frac{\varepsilon_\beta}{D} (Ae^{-i\omega_s t} q(x) + c.c.) e^{-x^2/(4D)} \quad (5.41)$$

that leads to the ordinary inhomogeneous differential equation

$$\hat{L}_\beta q = Dq''(x) - \left(\frac{x^2}{4D} - i\omega_s - \frac{1}{2} \right) q(x) = -De^{\frac{x^2}{4D}} P_0''(x). \quad (5.42)$$

The boundary conditions for $q(x)$ obtained from (5.37), (5.38) and (5.39) read

$$q_- = 0, \quad (5.43)$$

$$[q]_+ = 0, \quad (5.44)$$

$$e^{i\omega_s \tau} e^{-x_-^2/(4D)} q'_- - e^{-x_+^2/(4D)} [q']_+ = \frac{r_0}{D} (e^{i\omega_s \tau} - 1). \quad (5.45)$$

The first two conditions are evident, while for the third one we disregard nonlinear terms in ε_β

$$\begin{aligned} & \left(1 + \frac{\varepsilon_\beta}{D}(Ae^{-i\omega_s t} e^{i\omega_s \tau} + c.c.)\right) \left(P'_0(x) + \frac{\varepsilon_\beta}{D}(Ae^{-i\omega_s t} e^{i\omega_s \tau} (q(x) e^{-x^2/(4D)})' + c.c.) \right) \Big|_- \approx \\ & \approx \left(1 + \frac{\varepsilon_\beta}{D}(Ae^{-i\omega_s t} + c.c.)\right) \left[P'_0(x) + \frac{\varepsilon_\beta}{D}(Ae^{-i\omega_s t} (q(x) e^{-x^2/(4D)})' + c.c.) \right]_+, \end{aligned}$$

$$\begin{aligned} & \underline{P'_{0-}} + \frac{\varepsilon_\beta}{D} (Ae^{-i\omega_s(t-\tau)} \left\{ P'_{0-} + (q e^{-x^2/(4D)})' \right\} \Big|_- + c.c.) \approx \\ & \underline{[P'_0]_+} + \frac{\varepsilon_\beta}{D} (Ae^{-i\omega_s t} \left\{ [P'_0]_+ + [(q e^{-x^2/(4D)})']_+ \right\} + c.c.). \end{aligned}$$

With $P'_{0-} = [P'_0]_+ = -r_0/D$ the underlined terms cancel. Using conditions (5.43) and (5.44) we obtain (5.45).

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The inhomogeneous equation (5.42) can be treated by means of the Green's function $g(x, y)$ that is the solution of $\hat{L}_\beta g(x, y) = -\delta(x - y)$. One readily verifies that

$$g(x, y) = -\frac{1}{D\psi_-} \begin{cases} Y(y)\psi(x) & , \quad x < y \\ Y(x)\psi(y) & , \quad y < x < x_- \end{cases} \quad (5.46)$$

where $\psi(x)$ and $Y(x)$ are the auxiliary functions from the previous section. The solution for $q(x)$ reads

$$\begin{aligned} q(x) &= D \int_{-\infty}^{x_-} dy g(x, y) e^{y^2/(4D)} P_0''(y) + k \begin{cases} Y_+\psi(x) & , \quad x < x_+ \\ Y(x)\psi_+ & , \quad x_+ < x < x_- \end{cases} \\ &= -\frac{\psi(x)}{\psi_-} \int_x^{x_-} dy Y(y) P_0''(y) e^{y^2/(4D)} - \frac{Y(x)}{\psi_-} \int_{-\infty}^x dy \psi(y) P_0''(y) e^{y^2/(4D)} \\ &\quad + k \begin{cases} Y_+\psi(x) & , \quad x < x_+ \\ Y(x)\psi_+ & , \quad x_+ < x < x_- \end{cases} \end{aligned} \quad (5.47)$$

In the first line, the first term takes account of the inhomogeneity² while the second term satisfies the homogeneous equation with a potential jump condition at x_+ .

It is straightforward that the first boundary condition is satisfied independent of the choice of k (recall that $Y_- = 0$). This holds true also for the second condition.

The limit in eq. (5.44) has to be taken with care since $P_0''(y)$ contains a δ function due to the discontinuity of P_0' at x_+ , i.e., $P_0''(x) = [P_0']_+ \delta(x - x_+) + \dots$ where the dots indicate a rest without singularity.

$$\begin{aligned} [q]_+ &= \lim_{\epsilon \rightarrow 0} \left\{ -\frac{\psi_+}{\psi_-} \left(\int_{x_++\epsilon}^{x_-} dy \dots - \int_{x_+-\epsilon}^{x_-} dy \dots \right) - \frac{Y_+}{\psi_-} \left(\int_{-\infty}^{x_++\epsilon} dy \dots - \int_{-\infty}^{x_+-\epsilon} dy \dots \right) \right\} \\ &= \lim_{\epsilon \rightarrow 0} \left\{ \frac{\psi_+}{\psi_-} \int_{x_+-\epsilon}^{x_++\epsilon} dy Y e^{y^2/(4D)} ([P_0']_+ \delta(x - x_+) + \dots) - \frac{Y_+}{\psi_-} \int_{x_+-\epsilon}^{x_++\epsilon} dy \psi e^{y^2/(4D)} ([P_0']_+ \delta(x - x_+) + \dots) \right\} \\ &= \frac{r_0}{\psi_- D} e^{x_+^2/(4D)} (Y_+ \psi_+ - \psi_+ Y_+) = 0. \end{aligned}$$

The third condition (5.45) determines the constant k . The derivative at the absorbing boundary is given by

$$q'_- = k\psi_+ - \frac{1}{\psi_-} \int_{-\infty}^{x_-} dy \psi(y) e^{y^2/(4D)} P_0''(y) \quad (5.48)$$

²Clearly, $\hat{L}_\beta \int dy g(x, y) f(y) = \int dy \delta(x - y) f(y) = f(x)$.

where we have again employed $Y_- = 0$ and $Y'_- = 1$.
The jump of the derivative at x_+ reads

$$[q']_+ = k\psi_- + \frac{r_0}{D}e^{x_+^2/(4D)}. \quad (5.49)$$

Here, one must use the same trick as above

$$\begin{aligned} [q']_+ &= \lim_{\epsilon \rightarrow 0} \left\{ k(Y'_+\psi_+ - Y_+\psi'_+) + \frac{\psi'_+}{\psi_-} \int_{x_+-\epsilon}^{x_++\epsilon} Y(y)e^{y^2/(4D)} P_0''(y) + \frac{\psi_+}{\psi_-} e^{x_+^2/(4D)} Y_+ \underline{[P_0'']_+} - \right. \\ &\quad \left. \frac{Y'_+}{\psi_-} \int_{x_+-\epsilon}^{x_++\epsilon} \psi(y)e^{y^2/(4D)} P_0''(y) - \frac{Y_+}{\psi_-} e^{x_+^2/(4D)} \psi_+ \underline{[P_0'']_+} \right\} \\ &= \lim_{\epsilon \rightarrow 0} \left\{ k\psi_- - \frac{\psi'_+}{\psi_-} \int_{x_+-\epsilon}^{x_++\epsilon} Y(y)e^{y^2/(4D)} \frac{r_0}{D} \delta(y-x_+) + \frac{Y'_+}{\psi_-} \int_{x_+-\epsilon}^{x_++\epsilon} \psi(y)e^{y^2/(4D)} \frac{r_0}{D} \delta(y-x_+) \right\} \end{aligned}$$

where the underlined terms cancel each other. Now we have

$$[q']_+ = k\psi_- + \frac{r_0 e^{x_+^2/(4D)}}{D\psi_-} (Y'_+\psi_+ - Y_+\psi'_+)$$

from which one obtains (5.49)

Inserting these expressions into eq. (5.45) yields

$$k = \frac{-e^{i\omega_s\tau}}{\psi_- - e^{\Delta} e^{i\omega_s\tau} \psi_+} \left(\frac{r_0}{D} e^{x_+^2/(4D)} + \frac{e^{\Delta}}{\psi_-} \int_{-\infty}^{x_-} dy \psi(y) e^{y^2/(4D)} P_0''(y) \right) \quad (5.50)$$

Thus, the derivative at x_- takes on the form

$$q'_- = -\frac{1}{\psi_- - e^{\Delta} e^{i\omega_s\tau} \psi_+} \left(\frac{r_0}{D} e^{x_+^2/(4D)} e^{i\omega_s\tau} \psi_+ + \int_{-\infty}^{x_-} dy \psi(y) e^{y^2/(4D)} P_0''(y) \right). \quad (5.51)$$

Now, we are able to determine the instantaneous firing rate by

$$\begin{aligned} r(t) &= -D \left(1 + \frac{\varepsilon_\beta}{D} (Ae^{-i\omega_s t} + c.c.) \right) \frac{\partial P(x, t)}{\partial x} \Big|_- \\ &= r_0 - \varepsilon_\beta \left\{ Ae^{-i\omega_s t} \left(q'_- e^{-x_-^2/(4D)} - \frac{r_0}{D} \right) + c.c. \right\} \\ &= r_0 + \varepsilon_\beta |\beta| \cos(\omega_s t + \varphi - \phi_\beta) \quad , \quad \phi_\beta = \arg(\beta). \end{aligned} \quad (5.52)$$

The function β

$$\beta = \frac{r_0}{D} + \frac{e^{-x_-^2/(4D)}}{\psi_- - e^{\Delta} e^{i\omega_s\tau} \psi_+} \left(\frac{r_0}{D} e^{x_+^2/(4D)} e^{i\omega_s\tau} \psi_+ + \int_{-\infty}^{x_-} dy \psi(y) e^{y^2/(4D)} P_0''(y) \right) \quad (5.53)$$

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can be further simplified ³.

First, we introduce for the sake of brevity the auxiliary functions $\Phi(x) = \mathcal{D}_{i\omega_s-1}(-x/\sqrt{D})$, $\Upsilon(x) = \mathcal{D}_{i\omega_s-2}(-x/\sqrt{D})$ and $\tilde{P}_0(x) = P_0(x) \exp[x^2/4D]$ which possess the following properties

$$\left(\psi(x)e^{\frac{x^2}{4D}}\right)' = -\frac{i\omega_s}{\sqrt{D}} \left(\Phi(x)e^{\frac{x^2}{4D}}\right), \quad \left(\Phi(x)e^{\frac{x^2}{4D}}\right)' = -\frac{i\omega_s-1}{\sqrt{D}} \left(\Upsilon(x)e^{\frac{x^2}{4D}}\right)$$

that follow by reapplying the recurrence relation (A.5) and

$$D\tilde{P}_0''(x) - \left(\frac{x^2}{4D} - \frac{1}{2}\right)\tilde{P}_0(x) = 0$$

which can be verified by inserting in the stationary FPE (2.25). Additionally, we remark that for the special parabolic cylinder function $\Upsilon(x)$ we can write

$$D\Upsilon''(x) - \left(\frac{x^2}{4D} - i\omega_s + \frac{3}{2}\right)\Upsilon(x) = 0 \quad \rightarrow \quad \Upsilon = \frac{1}{2-i\omega_s} \left(D\Upsilon''(x) - \left(\frac{x^2}{4D} - \frac{1}{2}\right)\Upsilon(x)\right).$$

The integral in (5.53) can be performed by parts if one again takes care of the singularity at x_+ .

$$\begin{aligned} & \int_{-\infty}^{x_-} dy \psi(y) e^{y^2/(4D)} P_0''(y) \lim_{\epsilon \rightarrow 0} \left\{ \int_{-\infty}^{x_+-\epsilon} dy \cdots + \int_{x_+-\epsilon}^{x_++\epsilon} dy \cdots + \int_{x_++\epsilon}^{x_-} dy \cdots \right\} = \\ & = \lim_{\epsilon \rightarrow 0} \left\{ \psi e^{y^2/(4D)} P_0' \Big|_{-\infty}^{x_+-\epsilon} + \psi_+ e^{x_+^2/(4D)} [P_0']_+ + \psi e^{y^2/(4D)} P_0' \Big|_{x_++\epsilon}^{x_-} - \int_{-\infty}^{x_-} dy (\psi e^{y^2/(4D)})' P_0'(y) \right\} \\ & = e^{x_+^2/(4D)} \psi_+ ([P_0']_+ - [P_0']_-) + e^{x_-^2/(4D)} \psi_- P_0' + \frac{i\omega_s}{\sqrt{D}} \int_{-\infty}^{x_-} dy \Phi e^{y^2/(4D)} P_0' \\ & = -\frac{r_0}{D} e^{x_-^2/(4D)} \psi_- + \frac{i\omega_s}{\sqrt{D}} \left(e^{y^2/(4D)} \Phi P_0' \Big|_{-\infty}^{x_-} - \int_{-\infty}^{x_-} dy (\Phi e^{y^2/(4D)})' P_0' \right) \\ & = -\frac{r_0}{D} e^{x_-^2/(4D)} \psi_- + \frac{i\omega_s(i\omega_s-1)}{D} \int_{-\infty}^{x_-} dy \Upsilon \tilde{P}_0. \end{aligned}$$

In the last but one line we have used that $P_0(x)$ vanishes at the absorbing boundary while $P_0(x)$ as well as $\Phi(x)$ tends to zero for $x \rightarrow -\infty$. The integral within the last line can be treated using the above relations for $\tilde{P}_0$ and Υ .

$$\int_{-\infty}^{x_-} dy \Upsilon(y) \tilde{P}_0(y) = \frac{1}{2-i\omega_s} \left(D \int_{-\infty}^{x_-} dy \Upsilon'' \tilde{P}_0 - \int_{-\infty}^{x_-} dy \left(y^2/(4D) - \frac{1}{2} \right) \Upsilon \tilde{P}_0 \right). \quad (5.54)$$

The first term can be once integrated by parts

$$D \int_{-\infty}^{x_-} dy \Upsilon'' \tilde{P}_0 = D \Upsilon' \tilde{P}_0 \Big|_{-\infty}^{x_-} - D \int_{-\infty}^{x_-} dy \Upsilon' \tilde{P}_0'$$

³The following calculation seems to be somewhat long winded. The reader is invited to find a shorter way (email to benji@physik.hu-berlin.de).

$$= -D \lim_{\epsilon \rightarrow 0} \left\{ \int_{-\infty}^{x_+ - \epsilon} dy \Upsilon' \tilde{P}'_0 + \int_{x_+ + \epsilon}^{x_-} dy \Upsilon' \tilde{P}'_0 \right\}.$$

In the last line, the point x_+ was excluded. This does not change the integral since both $\Upsilon'(x)$ and $P'_0(x)$ do not contain singularities.

A second integration by parts yields

$$\begin{aligned} D \int_{-\infty}^{x_-} dy \Upsilon'' \tilde{P}_0 &= -D \lim_{\epsilon \rightarrow 0} \left\{ \Upsilon \tilde{P}'_0 \Big|_{-\infty}^{x_+ - \epsilon} + \Upsilon \tilde{P}'_0 \Big|_{x_+ + \epsilon}^{x_-} - \int_{-\infty}^{x_+ - \epsilon} dy \Upsilon \tilde{P}_0'' - \int_{x_+ + \epsilon}^{x_-} dy \Upsilon \tilde{P}_0'' \right\} \\ &= \int_{-\infty}^{x_-} dy \Upsilon \left(y^2/(4D) - \frac{1}{2} \right) \tilde{P}_0 + D([\tilde{P}'_0]_+ \Upsilon_+ - \tilde{P}'_{0-} \Upsilon_-). \end{aligned}$$

One sees that the integral cancels the second one in eq. (5.54). Thus, for β we obtain

$$\begin{aligned} \beta &= \frac{r_0}{D} \left\{ 1 + \frac{e^{-x_-^2/(4D)}}{\psi_- - e^{\Delta} e^{i\omega_s \tau} \psi_+} \left(e^{i\omega_s \tau} e^{x_+^2/(4D)} \psi_+ - e^{x_-^2/(4D)} \psi_- + \right. \right. \\ &\quad \left. \left. + \frac{i\omega_s(i\omega_s - 1)}{2 - i\omega_s} (e^{x_-^2/(4D)} \Upsilon_- - e^{x_+^2/(4D)} \Upsilon_+) \right) \right\} = \frac{r_0}{D} \frac{i\omega_s(i\omega_s - 1)}{2 - i\omega_s} \frac{\Upsilon_- - e^{\Delta} \Upsilon_+}{\psi_- - e^{\Delta} e^{i\omega_s \tau} \psi_+}. \end{aligned}$$

Finally, one has to replace all abbreviations used in the calculation.

The firing rate in response to a weak noise coded signal is thus given by

$$r(t) = r_0 + \varepsilon_\beta |\beta| \cos(\omega_s t + \varphi - \phi_\beta), \quad \phi_\beta = \arg(\beta) \quad (5.55)$$

where the linear response function is given by (Lindner and Schimansky-Geier, 2001)

$$\beta = \frac{r_0 i\omega_s(i\omega_s - 1)}{D(2 - i\omega_s)} \frac{\mathcal{D}_{i\omega_s - 2}(\frac{\mu - v_T}{\sqrt{D}}) - e^{\Delta} \mathcal{D}_{i\omega_s - 2}(\frac{\mu - v_R}{\sqrt{D}})}{\mathcal{D}_{i\omega_s}(\frac{\mu - v_T}{\sqrt{D}}) - e^{\Delta} e^{i\omega_s \tau} \mathcal{D}_{i\omega_s}(\frac{\mu - v_R}{\sqrt{D}})}, \quad (5.56)$$

$$\Delta = \frac{v_R^2 - v_T^2 + 2\mu(v_T - v_R)}{4D}.$$

5.2. The spectral response

Having found the instantaneous firing rate of the LIF neuron, i.e., its time dependent mean output $\langle \sigma(t) \rangle$

$$\langle \sigma(t) \rangle = r(t) = r_0 + \varepsilon_\alpha |\alpha| \cos(\omega_s t - \phi_\alpha + \varphi) + \varepsilon_\beta |\beta| \cos(\omega_s t - \phi_\beta + \varphi) \quad (5.57)$$

we may characterize the signal transmission by means of the relative amplitudes $|\alpha|$ and $|\beta|$. However, given a single spike train measured in experiment is may be complicated to estimate the *instantaneous* rate but rather simple to compute its

power spectrum and to quantify the signal transmission by measures derived from the spectrum. One of these quantities will turn out as simply related to the relative amplitudes and therefore $|\alpha|$ and $|\beta|$ are not explicitly discussed in the following. First, we show the general relations between time dependent rate and spectral measures. Then we separately consider the response to a pure additive or noise coded signal, respectively. By this distinction we would like to gain insights into the similarities and differences of the transmission features for these signals. Afterwards we will also discuss the case that both signals are present (mixed response).

5.2.1. Spectral measures and their relation to the firing rate

The power spectrum in presence of a periodically modulated mean value (excluding the peak at zero frequency) reads

$$\begin{aligned} S(\omega) &= \int_{-\infty}^{\infty} d(t-t') \langle \langle (\sigma(t) - r_0)(\sigma(t') - r_0) \rangle \rangle_{\varphi} e^{-i\omega(t-t')} \\ &= \lim_{T \rightarrow \infty} \frac{\langle \langle |\tilde{\sigma}(\omega)|^2 \rangle \rangle_{\varphi}}{T}, \quad \tilde{\sigma}(\omega) = \int_0^T dt e^{i\omega t} (\sigma(t) - r_0). \end{aligned} \quad (5.58)$$

Besides the usual average over the noise (ensemble average) one must perform the average over the initial phase, too, corresponding to a randomized initial time in experiment (McNamara and Wiesenfeld, 1989).

The time dependent mean value causes δ peaks at the driving frequency and its higher harmonics which are superimposed on a continuous background spectrum. The weak signal assumption implies that **1)** peaks at higher harmonics can be neglected and **2)** the background spectrum can be approximated by the spectrum of the unperturbed dynamics ($\varepsilon_{\alpha} = \varepsilon_{\beta} = 0$, eq. (2.77)). The peak at the fundamental frequency is obtained by replacing the random spectrum by its mean in eq. (5.58)

$$\lim_{T \rightarrow \infty} \frac{\langle \langle |\tilde{\sigma}(\omega)|^2 \rangle \rangle_{\varphi}}{T}. \quad (5.59)$$

By virtue of eq. (5.57) this can be readily calculated. Thus the full spectrum reads

$$S(\omega) = S_{bg}(\omega) + \frac{\pi}{2} \left(\varepsilon_{\alpha}^2 |\alpha|^2 + \varepsilon_{\beta}^2 |\beta|^2 + 2\varepsilon_{\alpha}\varepsilon_{\beta} |\alpha||\beta| \cos(\phi_{\alpha} - \phi_{\beta}) \right) [\delta(\omega - \omega_s) + \delta(\omega + \omega_s)]. \quad (5.60)$$

Besides the relative amplitudes, the difference between the *phase lags of the output* $\phi_{\alpha}, \phi_{\beta}$ determine the output signal strength as well. This is evident also from eq. (5.57) since the sum of two cosine functions with the same frequency yields again a cosine with an amplitude that depends on the phase lag.

If one of the amplitudes $\varepsilon_\alpha, \varepsilon_\beta$ is zero, then, the output signal power depends linearly on the intensity of the remaining input signal. To quantify the responses to a pure additive or pure noise coded signal, we will use measures that are scaled by this intensity. The first of these measures is the spectral power amplification (SPA) given as the ratio of output and input signal intensity

$$\eta_\alpha = |\alpha|^2, \quad \eta_\beta = |\beta|^2. \quad (5.61)$$

for additive and noise coded signal, respectively. Since the amplification is equal to the square of the respective relative amplitude we know that resonances found in the SPA will be also present in $|\alpha|$ or $|\beta|$, respectively. Therefore, we will show and discuss only the SPA.

Furthermore, we use a signal-to-noise ratio that is also scaled by the signal intensity and is thus given as the ratio of spectral amplification and the background spectrum eq. (2.77) at ω_s

$$\text{SNR}_\alpha = \frac{|\alpha|^2}{S_{bg}(\omega_s)} \quad \text{SNR}_\beta = \frac{|\beta|^2}{S_{bg}(\omega_s)}. \quad (5.62)$$

As an additional measure we will also consider the spectral power amplification divided by the high frequency limit of the power spectrum

$$\eta_\alpha/r_0 = \frac{|\alpha|^2}{r_0}, \quad \eta_\beta/r_0 = \frac{|\beta|^2}{r_0} \quad (5.63)$$

which corresponds to a different definition of the signal-to-noise ratio more common in the neurobiological community (Stemmler, 1996; Shimokawa et al., 1999a; Plesser and Geisel, 1999b). For the pooled output of a large neuronal ensemble, this ratio is proportional to the conventional SNR since in this case the output spiking tends to a Poisson process with flat background spectrum (see Shimokawa et al. (1999c) and section 5.3).

So far, we have dealt with an ensemble of infinitely long spike trains. However, any experiment on real neurons and every computer simulation of a neuronal model will be restricted to a finite measuring time. Then, only a spectral histogram $S_{his}(\omega_i)$ of finite height with a frequency bin $\Delta\omega = 2\pi/T$ can be computed (see, for example, Fig. 5.1).

For sufficiently large time this histogram averaged over many realizations tends to a discrete version of the background spectrum - independent of T . On the other hand, for the frequency bin containing ω_s the spectrum will increase in proportion to T . We obtain (without taking the limit $T \rightarrow \infty$ in eq. (5.58))

$$\begin{aligned} S_{his}(\omega_i = \omega_s) &\approx S_{bg}(\omega_s) + (\varepsilon_\alpha^2 |\alpha|^2 + \varepsilon_\beta^2 |\beta|^2 + 2\varepsilon_\alpha \varepsilon_\beta |\alpha| |\beta| \cos(\phi_\alpha - \phi_\beta)) \frac{T}{4} \\ &\approx S_{bg}(\omega_s) + (\varepsilon_\alpha^2 |\alpha|^2 + \varepsilon_\beta^2 |\beta|^2 + 2\varepsilon_\alpha \varepsilon_\beta |\alpha| |\beta| \cos(\phi_\alpha - \phi_\beta)) \frac{\pi}{2\Delta\omega} \end{aligned} \quad (5.64)$$

where ω_i is the center frequency of the respective bin. From eq. (5.64) we may either predict the height of the histogram peak or estimate the theoretical measures, e.g. the SPA. In the

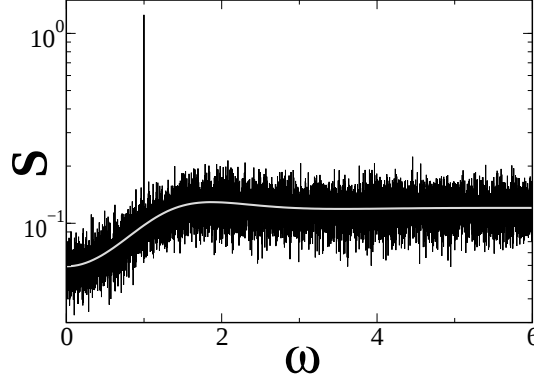


Figure 5.1.: Power spectrum (histogram) averaged over 30 realizations for the LIF model driven by an additive signal ($\varepsilon_\alpha = 0.02, \omega_s = 1$) at $\mu = 0.8$ and $D = 0.015$. The peak at $\omega = 1$ depends on the simulation time that was here $T = 10^4$. The background spectrum is well approximated by the spectrum in the absence of a signal (grey line, eq. (2.77) from chapter 2).

subsequent sections we will validate some important analytical results by simulation data that were obtained as follows: Power spectra like that depicted in Fig. 5.1 were computed from a spike train of length T generated by the periodically driven LIF model. The latter was integrated with a simple Euler procedure at time step Δt for a range of voltages not too close to threshold. In the vicinity of the threshold the numerics is very sensitive to the time step (Plesser, 1999). Therefore, in the region $(v_T - 0.05, v_T)$ the time step was decreased $\Delta t \rightarrow \Delta t/100$ yielding a satisfying agreement for the exactly known quantities like mean interspike interval, coefficient of variation and power spectra in the absence of a periodic signal. The initial time was randomly drawn from the interval $(0, 2\pi/\omega_s)$ corresponding to a random initial phase. Using the height of the peak at the driving frequency ω_s and an estimate of the background spectrum obtained by averaging over 20 points in the vicinity of ω_s , the intensity of the signal correlated output was computed. The procedure was repeated N times to estimate an error for the spectral power amplification.

In the following section we address the spectral response to a pure additive or noise coded signal by means of the introduced spectral amplifications η_α, η_β and the two kinds of signal-to-noise ratio $\text{SNR}_{\alpha,\beta}$ and $\eta_{\alpha,\beta}/r_0$. Important parameters of the signal transmission are noise strength, driving frequencies and the base current μ . Variations of the absolute refractory period, threshold and reset voltage are not considered, we set

$$\tau = 0.1, v_T = 1 \text{ and } v_R = 0$$

throughout the remainder of the chapter. Plotting the spectral response quantities versus ω_s and/or D will reveal whether the transmission is characterized by stochastic resonance and / or a preference for a certain frequency band. This will certainly depend on the base current since this parameter determines the firing regime (noise-activated or oscillatory) as well as the presence or absence of a noise-induced eigenfrequency. For this reason we will consider the spectral response for different values of the base

current. With our choice of the reset point $v_T = 1$ this means in the following

$$\begin{aligned} \mu < 1 & \quad \text{noise-activated firing regime} \\ \mu > 1 & \quad \text{deterministic (oscillatory) firing regime} \end{aligned}$$

analog to the discussion in chapter 2.

5.2.2. Spectral response to the additive signal

Before we turn to the discussion of particular parameter sets, we give formulae for two simple limits, the adiabatic and the high frequency case.

In the adiabatic limit (i.e., for a static signal) our results can be simplified to

$$\eta_\alpha(\omega_s = 0) = \left(\frac{dr_0}{d\mu} \right)^2, \quad (5.65)$$

$$\frac{\eta_\alpha}{r_0}(\omega_s = 0) = \frac{1}{r_0} \left(\frac{dr_0}{d\mu} \right)^2, \quad (5.66)$$

$$\text{SNR}_\alpha(\omega_s = 0) = \frac{1}{2D_{\text{eff}}} \left(\frac{dr_0}{d\mu} \right)^2 = \frac{1}{R^2 r_0} \left(\frac{dr_0}{d\mu} \right)^2 \quad (5.67)$$

where R denotes the coefficient of variation (CV) in the absence of a signal (see chapter 2). These relations can be derived from eq. (5.31) using eq. (A.22) and eq. (A.23) from the appendix, a small frequency expansion of the characteristic function and the low frequency limit of the background spectrum given by eq. (2.79).

It is worth mentioning that eq. (5.65) holds true in general for all systems that are entirely determined by a transfer function $r_0(\mu)$ (Chialvo et al., 1997). Like in non-dynamical threshold devices at arbitrary driving frequencies, the stochastic resonance in the LIF model driven by a very slow signal is solely based on the fact that the sensitivity of the rate to a change in base current is maximized at a moderate noise intensity. Both, eq. (5.65) and eq. (5.66), were derived by Stemmler (1996) who considered the LIF model with static signal. Stemmler (1996) additionally gave a lower bound for the Fisher information of the spike train

$$J_{\text{LB}} = \frac{1}{\sigma_N^2} \left(\frac{d\mu_N}{d\mu} \right)^2 \quad (5.68)$$

(μ_N, σ_N^2 - mean and variance of the spike count within $(0, T)$) and derived under the assumption that the spike train generated by the LIF neuron is a Poissonian one

$$J_{\text{LB}} \sim \text{SNR}_\alpha. \quad (5.69)$$

Now, recall that for sufficiently large time window T (such that the definition of a SNR makes sense) we have $\sigma_N^2 = 2D_{\text{eff}}T$ and $\mu_N = r_0T$ and hence by virtue of eq. (5.67) we find

$$J_{\text{LB}} = \text{SNR}_\alpha T \quad (5.70)$$

without the Poisson approximation of the spike train presumed by Stemmler (1996). In the case of high driving frequency, one may employ the respective asymptotics of the cylinder functions to derive

$$\alpha \rightarrow r_0 e^{i\pi/4} / \sqrt{D\omega_s} \quad (5.71)$$

and hence the spectral measures approach

$$\eta_\alpha \approx \frac{r_0^2}{D\omega_s}, \quad (5.72)$$

$$\frac{\eta_\alpha}{r_0} \approx \text{SNR}_\alpha \approx \frac{r_0}{D\omega_s}. \quad (5.73)$$

This means that in general the response is decreased with frequency. The LIF neuron operates as a lowpass filter for high frequent additive signals irrespective of the dynamical regime.

It is also possible to carry out a weak noise approximation of the response amplitudes at finite frequency using the asymptotics of the parabolic cylinder functions eqs. (A.10), (A.11), (A.13), (A.14) given in the appendix. In contrast to the above formulae for low and high driving frequency, the resulting expressions for weak D and finite ω_s are rather involved and depend also crucially on the dynamical regime considered, i.e., on the value of μ , therefore, we abstain from discussing them.

Our discussion of the response at arbitrary frequency and noise intensity starts with the simpler limit cases of small and large base current ($\mu = 0.5$ and $\mu = 1.2$), respectively. This means either transmission in the noise activated regime where a stochastic resonance effect is expected to occur (Plesser and Geisel, 1999b; Shimokawa et al., 1999a) and Shimokawa et al. (1999c) or an oscillatory regime where large resonances at small or zero noise appear (Knight, 1972b). Then we explore the subthreshold regime at large base current. We will use $\mu = 0.8$ and $\mu = 0.95$, i.e., the same values that were used in our study of coherence resonance, chapter 2.

Noise activated firing regime with low refractoriness (additive signal)

$\mu = 0.5$, Fig. 5.2 (left column)

We show η_α , SNR_α and η_α/r_0 as functions of noise and driving frequency. According to the numerical findings in Plesser and Geisel (1999b), Shimokawa et al. (1999b) and Shimokawa et al. (1999c) we expect stochastic resonance which indeed becomes manifest for all quantities by maxima versus D for arbitrary but fixed frequency. The spectral amplification drops very slowly for large increasing noise. In fact, the decrease is for a certain range of μ (in particular for $\mu = 0.5$) only due to the presence of a finite

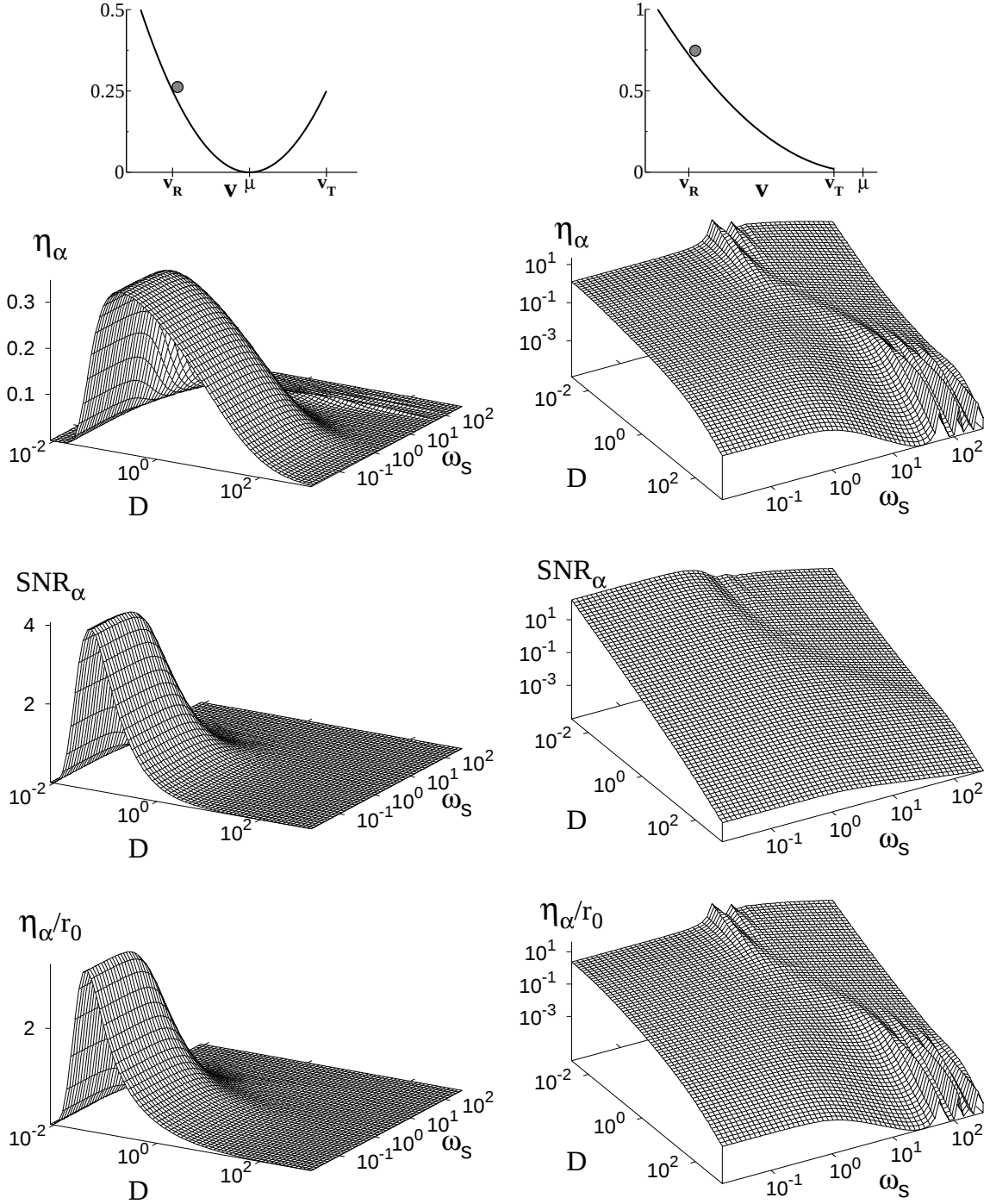


Figure 5.2.: Spectral amplification, conventional signal-to-noise ratio and ratio of SPA to mean rate for the additive signal versus noise strength and driving frequency. Left column: $\mu = 0.5$ (noise-activated firing regime). Right column: $\mu = 1.2$ (deterministic firing regime). The upper two panels illustrate the respective potential for the voltage $(v - \mu)^2/2$.

absolute refractory period in the system (Stemmler, 1996). The maxima of SNR_α and η_α/r_0 appear at somewhat smaller D values than that of η_α . This is due to the fact that the background spectrum (denominator in SNR_α) and the rate r_0 grow with increasing noise strength. In other words, for a fixed frequency we find a maximal η_α and hence a strong signal output at D_{max} but also strong fluctuations.

Note that this is different from a bistable dynamics where at low frequency the background spectrum may *decrease* for increasing noise and hence the SNR attains its maximum at *larger* noise intensity than the SPA does (McNamara and Wiesenfeld, 1989).

The adiabatic limits eq. (5.65), eq. (5.67) and eq. (5.66) correspond to the limiting curves reached for $\omega_s \rightarrow 0$. These curves exhibit stochastic resonance as well. Regarding the two different SNRs, note that in the low frequency limit the difference is determined by the coefficient of variation which is for $\mu = 0.5$ and small to moderate noise between 0.8 and 1. Therefore, SNR_α is only slightly above η_α/r_0 and hence, may be approximated by the latter expression (Stemmler, 1996). It will turn out that the case of small base current is the only limit where this approximation is reasonable.

Going to the nonadiabatic regime we find that for $\mu = 0.5$ increasing driving frequency leads to a drop in all characteristics. For small relative refractory period, that is in the absence of a noise induced eigenfrequency and coherence resonance the optimal transmission is observed at $\omega_s = 0$. The maximum of the amplification η_α shifts slightly to larger values of the noise strength. For large frequency the drop in the response becomes proportional to $1/\omega_s$ (eq. (5.72)). To stress this again: high frequent additive signals are not efficiently transmitted by the white noise driven LIF neuron. Note, however, that by considering also synaptic filtering (i.e., colored instead of white noise) the range of transmitted frequencies may be extended (see (Brunel et al., 2001), but also our remarks in section 5.3).

A third limit worth to consider is that of strong noise. As seen in the upper panel, an unusual resonance effect appears in the spectral amplification for large D and high frequencies of the order $2\pi/\tau$. Here, the system possesses resonances due to the absolute refractory period. In chapter 2 we have seen that the system exhibits in the large noise limit an eigenfrequency close to $2\pi/\tau$. Although the peaks at this frequency and its higher harmonics can become considerably strong, the resonances are weak compared to the response at low up to moderate noise. The reason for this behavior is simple: at large noise the influence of the signal on the dynamics is rather weak - it does not modulate the absolute refractory state but only slightly the voltage dynamics that is very fast. Therefore in the limit of $D \rightarrow \infty$, only the refractory period remains and the resonances vanish. In the SNR_α the resonances do not occur at all since here the maxima of amplification and background cancel each other. In contrary, the resonances are in principle present in the ratio η_α/r_0 since the denominator does not depend on ω_s . However, they are hardly visible since dividing by r_0 singles out the region of low to moderate D and suppresses the function in the high noise region.

In result we have found that stochastic resonance occurs for an additive signal in the noise activated firing regime. The maximal response is obtained in the finite adiabatic limit which shows SR as well.

Deterministic firing regime (additive signal)

$\mu = 1.2$, Fig. 5.2 (right column)

Here, we show SPA, SNR_α and η_α/r_0 in a logarithmic scale. This emphasizes the pronounced resonances that can be found at small and large noise intensity.

The peaks at small D correspond to a matching of signal period and the very regular mean interspike interval as it was discussed for the first time by Knight (1972b). The same author also found in a simplified version of the noisy LIF model the reduction of the resonances for increasing D which becomes apparent also in the upper and lower panel. We notice that the SPA saturates for $D \rightarrow 0$ except for the frequency $2\pi/r_0(0)$ (with the deterministic eigenfrequency $r_0(D)$ given by eq. (2.46)) and its higher harmonics where it diverges. One might wonder why apart from the plain divergences in this limit a smooth curve results. Recall, however, that the system is not entirely deterministic since we average any realization over the initial phase. While the ratio η_α/r_0 shows in principle the same features at small D like the amplification, the SNR_α does not show any resonances but only a decrease of the response at high frequency. In this respect the two ratios differ significantly and an approximation of SNR_α by η_α/r_0 as was possible for small μ seems to be undue.

At large D resonances occur again due to the absolute refractory period and are essentially the same like for $\mu < 1$. As mentioned in chapter 2, the influence of the value of μ at large D is rather weak.

All data shown in Fig. 5.2 (right column) demonstrate that in general, stochastic resonance is absent in the oscillatory regime. However, for certain driving frequencies a SR like effect may be observed. If the driving frequency is slightly above the deterministic eigenfrequency of the system, additional noise may improve the signal transmission as illustrated in Fig. 5.3. Here, also numerical simulations are shown that confirm the theoretical prediction. For $\mu > v_T$, the noise does not assist a barrier crossing process but increases both the eigenfrequency (compare the increase of the firing rate with increasing noise discussed in chapter 2) and the variability of the interspike interval. Hence, the neuronal firing may more often match the “too short” driving period. The fact that a similar resonance cannot be found for $\omega_s < \omega_0$ indicates that the increase in the rate (the decrease of the interspike interval) with growing noise is essential for this kind of noise enhanced signal transmission.

Additionally, we note that for small D we find numerically a strong nonlinearity in the spectral response even at small signal amplitude. In contrast to the noise activated firing regime, the spectrum possesses already in the absence of a signal large peaks. For very small D , combinatorial frequencies occur (cf. Fig. 5.3, l.h.s.) due to nonlinear mixing between the signal and background peaks. Consequently, also the background spectrum is considerably reduced and does not coincide with the spectrum of the un-

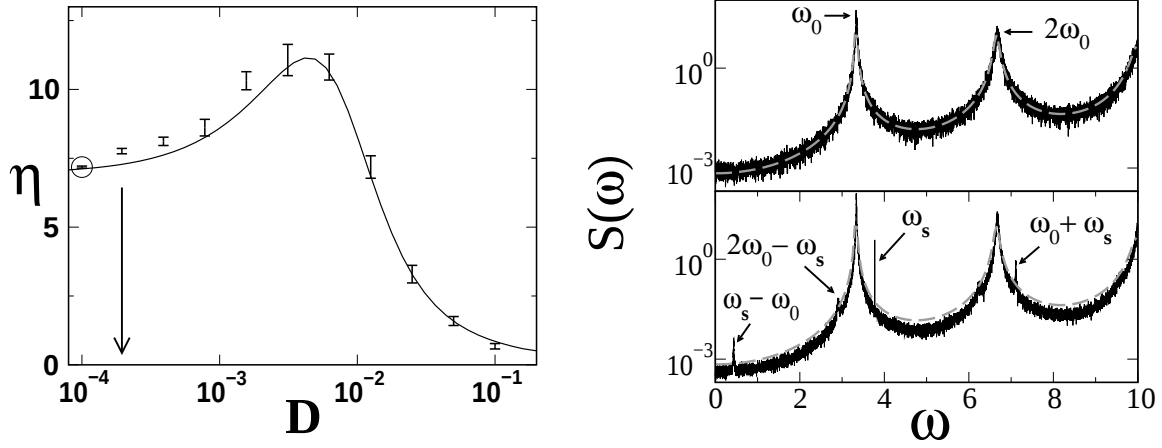


Figure 5.3.: Stochastic resonance like effect for the additive signal in the deterministic firing regime and deviations from linear response theory. Left: spectral amplification for an additive signal versus noise strength for $\mu = 1.2$ and $\omega_s = 3.77$. Theory (solid line) compared to results of simulations. The arrow indicates the value of D corresponding to the power spectra at the r.h.s. The encircled error bar is a result for $D = 0$ (position with respect to D axis is meaningless). Parameters: $\varepsilon_\alpha = 0.02$, $T = 5000$, $N = 200$ and $\Delta t = 10^{-5} - 10^{-2}$. Right: averaged power spectrum for $D = 1.95 \times 10^{-4}$ and $N = 20$, $T = 5000$ with $\varepsilon_\alpha = 0$ (no signal, top) and $\varepsilon_\alpha = 0.02$ (bottom). Grey dashed line is theory eq. 2.77, $\omega_0 = 2\pi r_0(D = 0)$ is the eigenfrequency of the system. Furthermore, combination frequencies (sidebands) are also indicated.

perturbed system ($\varepsilon_\alpha = 0$) anymore. The nonlinearity is certainly responsible for the small deviations of the simulation results from theory seen for small D in Fig. 5.3. We stress that this effect is an exception. For all other cases that were or will be discussed, the background spectrum $S_{bg}(\omega)$ is well approximated by our analytical result eq. (2.77) if the signal strength is sufficiently weak.

In conclusion, in the oscillatory regime the neuronal transmission shows resonances for small and large noise strength with respect to the deterministic eigenfrequency and that due to the absolute refractory period, respectively. A stochastic resonance like effect may be observed if the signal frequency exceeds slightly the deterministic eigenfrequency.

Noise activated firing regime with strong refractoriness (additive signal)

$\mu = 0.8$ and $\mu = 0.95$, Fig. 5.2 (left and right column, respectively)

In general, the dependence on D is qualitatively the same like for $\mu = 0.5$. Stochastic resonance manifests itself in all spectral measures by maxima versus noise intensity at arbitrary but fixed frequency. Since the barrier $(\mu - 1)^2/2$ is considerably decreased the periodic response and the SNR are much stronger. For the same reason, the maximum of the SPA versus D occur at smaller values of the noise intensity than in case

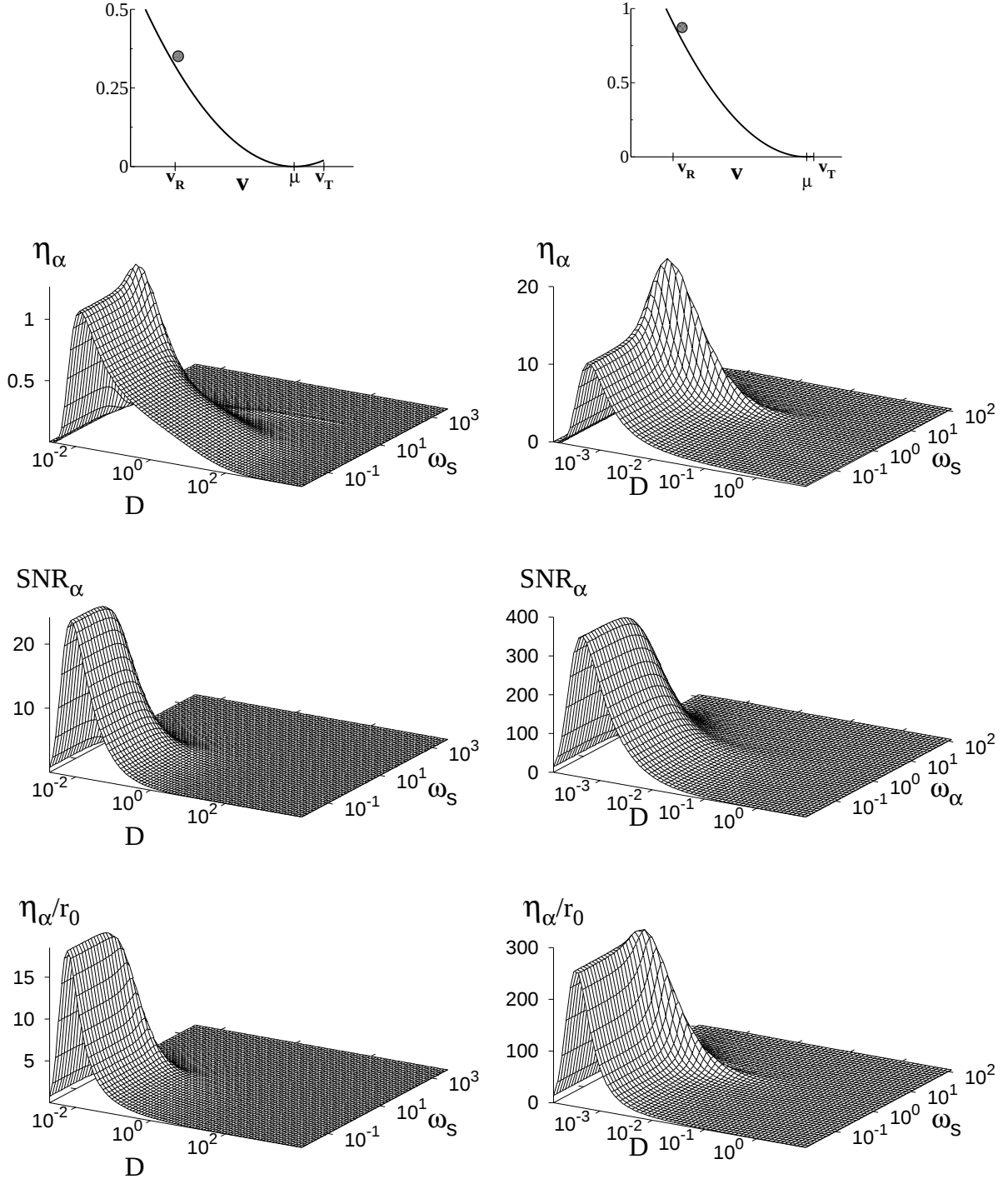


Figure 5.4.: Spectral amplification, conventional signal-to-noise ratio and ratio of SPA to mean rate for the additive signal versus noise strength and driving frequency. Left column: $\mu = 0.8$. Right column: $\mu = 0.95$ (both noise-activated firing regime). The upper two panels illustrate the respective potential for the voltage $(v - \mu)^2/2$.

of $\mu = 0.5$.

The novel and most important feature is the occurrence of a maximum with respect to the driving frequency for a finite range of moderate noise intensities. In fact, the response quantified by η_α (upper panel) exhibits an overall maximum versus both D (conventional stochastic resonance) and driving frequency. This stochastic double resonance (Plesser and Geisel, 1999b; Plesser, 1999) is more pronounced for $\mu = 0.95$ than for $\mu = 0.8$.

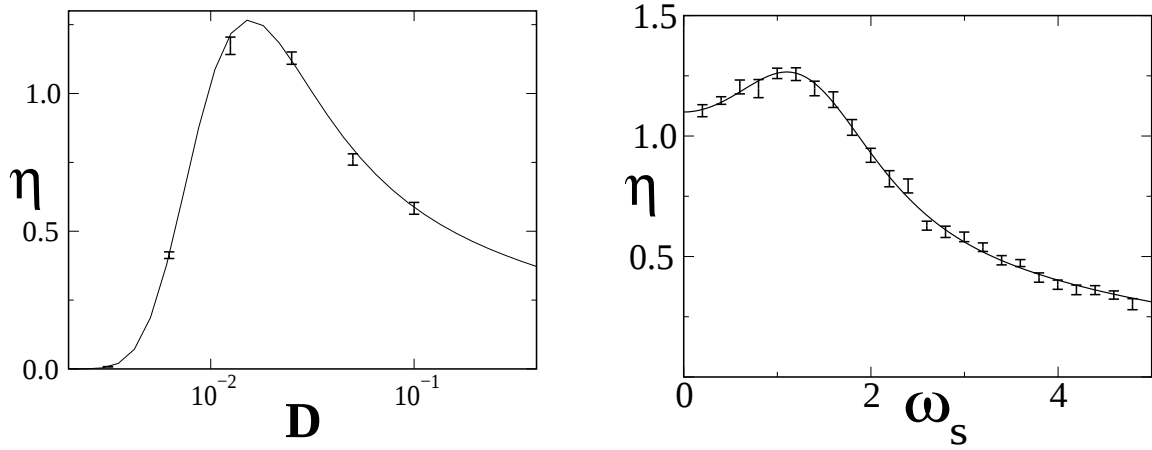


Figure 5.5.: Spectral amplification in response to the additive signal versus noise strength (left) for $\omega_s = 1.12$ and driving frequency for $D = 0.015$ (right), respectively, for $\mu = 0.8$. Theory (solid line) compared to results of simulations. Parameters: $\varepsilon_\alpha = 0.02$, $T = 10^4$, $N = 300$ and $\Delta t = 10^{-5} - 10^{-2}$.

In Fig. 5.5 we compare the prediction for the spectral amplification with results of a numerical simulation for $\mu = 0.8$. Here, noise strength or frequency are varied with the other parameter fixed such that the overall maximum of Fig. 5.4 (upper right panel) is included in the curves. For the amplitude $\varepsilon_\alpha = 0.02$ used in the simulations, the agreement between theory and simulation results is excellent. The numerics confirm clearly the stochastic resonance effect as well as the nonmonotonous dependence of the response on the driving frequency. Larger signal amplitudes reveal the same qualitative behavior as long as the stimulation is subthreshold. The amplification decreases slightly with growing amplitude, in particular for small D and ω_s . This kind of saturation effect is also known to occur in bistable systems (Jung, 1993).

What is the reason for the nonmonotonous dependence on the driving frequency? As we have seen in chapter 2, a large but subcritical base current ($\mu < 1$, $1 - \mu \ll 1$) leads in conjunction with an appropriate (moderate) noise intensity to coherence resonance, i.e., to the occurrence of a noise-induced eigenfrequency being manifest by a pronounced hump in the power spectral density $S(\omega)$. If we drive the system by a signal close to this eigenfrequency we may expect a resonance similar to that in the deterministic firing

regime. In contrast to the latter, here the maximal resonance does not occur for $D \rightarrow 0$ (where the neuron is silent) but at finite noise intensity due to coherence resonance. Note that the overall maximum of η_α occurs at smaller values than the coherence resonance described in chapter 2. At $\mu = 0.95$ for instance we find an optimal SPA at $D \approx 0.001$ while the measure β from chapter 2 is maximal at $D = 0.005$. While the ω_s dependence of the output can be understood by the CR effect, the noise dependence is apparently not influenced by the presence of a noise induced eigenfrequency. This emphasizes that both effects are due to different physical mechanisms: Coherence resonance occurs as a (relative) variance reduction of the interspike interval in absence of a signal. Stochastic resonance in turn appears as an optimal sensitivity of the neuron to periodic stimulation.

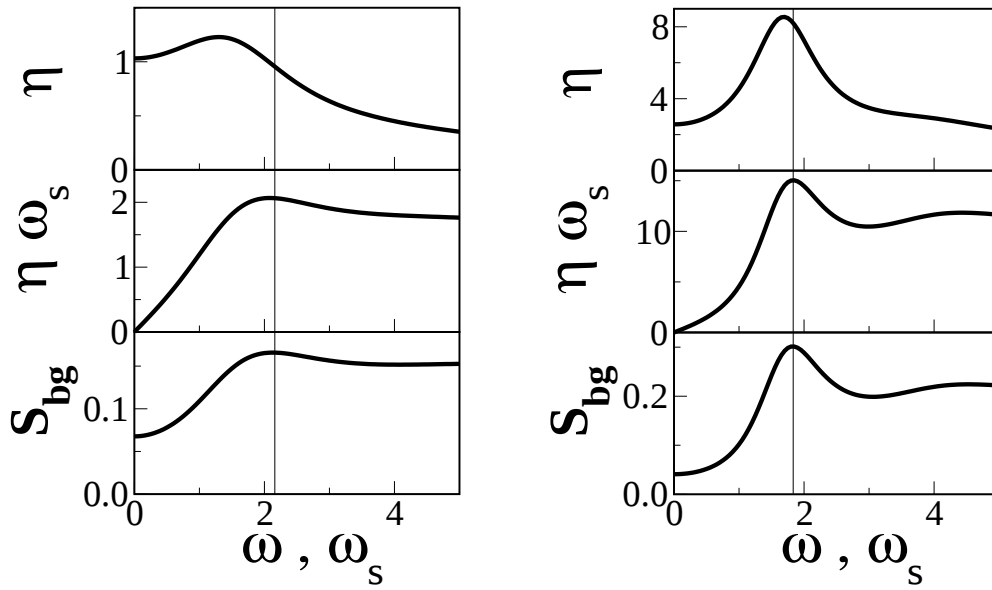


Figure 5.6.: Spectral power amplification η_α , auxiliary function $\eta_\alpha \cdot \omega_s$ and background spectrum (i.e., the spectrum in absence of a signal) versus frequency / driving frequency. Left: $\mu = 0.8, D = 0.02$. Right: $\mu = 0.95, D = 0.005$. Noise intensities were chosen such that the CR effect is most pronounced. Vertical lines indicate the maximum of the spectrum.

If we plot amplification and background spectrum in the same frequency range, the resonance and the spectral hump should occur at the same position (Fig. 5.6). This is not fully exact especially for $\mu = 0.8$ at which the CR effect is not very pronounced. The resonance frequency is smaller than the “hump frequency” and this seems to be so due to the low pass filtering. Multiplying the amplification by ω_s removes (qualitatively) the low pass behavior and for the resulting function the maximum is indeed much closer to the noise induced eigenfrequency. Note that the closer we come to $\mu = 1$ the less important the low pass induced shift of the resonance frequency becomes. Hence,

the observed maximum versus ω_s is nothing but a resonance with the noise induced eigenfrequency. In other words, if the signal's period matches the period of the coherent oscillations an enlarged spectral response can be expected.

This conclusion is also confirmed by SNR_α - it does not show a maximum with respect to ω_s . As can be also inferred 'by eye' from Fig. 5.6, the maximum in the resonance curve is canceled by the spectral maximum (the hump) due to the noise-induced regular oscillation. This does not hold in principle for the ratio η_α/r_0 . Here, the spectral amplification is divided by the high frequency limit of the power spectrum (i.e., by r_0) and not by a ω_s dependent curve. Consequently, this ratio also exhibits maxima versus frequency for a certain range of noise intensities. For $\mu = 0.95$, even the overall maximum versus D and ω_s appears at finite values. For $\mu = 0.8$ this is not the case because dividing the SPA by r_0 raises too much the parameter region of small D where the CR effect and hence also a nonmonotonous dependence of η_α on ω_s is absent. Note, however, that Plesser and Geisel (1999b); Plesser (1999) found numerically a larger range of μ values for which an overall maximum of η_α/r_0 is observed. This relies probably on the nonlinear response of the system for large amplitudes used by these authors.

The distance between potential minimum and threshold is $1 - \mu$. Since we can look upon the additive signal as a periodic modulation of the boundary by ε_α the amplitude at which a low frequent stimulus gets suprathreshold is $\varepsilon_\alpha = 1 - \mu$. In Fig. 5.5 results are presented for $\mu = 0.8$ and $\varepsilon_\alpha = 0.02$, i.e., the used stimulation is subthreshold and corresponds to a change of the distance by 10%. Large amplitudes used by Plesser (1999) where in the range (0.08,0.24), i.e., from large subthreshold (40%) to weak suprathreshold (120%).

The corrections to linear response result essentially in a reduction of the amplification at low noise - this is what also becomes evident in computer simulations. Therefore, at large signal amplitude, η_α/r_0 attains its overall maximum at larger noise intensity where a nonmonotonous dependence of the SPA on ω_s is present.

In result, the response to a weak signal in the noise activated firing regime with a strong relative refractory period is characterized by stochastic resonance and by a nonmonotonous dependence on the driving frequency. The origin of the latter is obviously the noise-induced eigenfrequency of the neuron, i.e., the regular oscillations due to coherence resonance introduce a preferred driving frequency for the neuronal response.

5.2.3. Spectral response to the noise coded signal

Like for the additive signal, the limiting cases of either vanishing or infinite frequencies lead to considerably simplified expressions for the spectral response quantities of the noise coded signal.

In the adiabatic case (i.e., static noise coded signal) one may easily derive the following relations using the expressions for the cylinder functions eq. (A.22) and eq. (A.24) and the low frequency limit of the background spectrum (eq. (2.79)) in eq. (5.56) and the expressions for the SPA and the SNRs, respectively.

$$\eta_\beta(\omega_s = 0) = \left(\frac{dr_0}{dD} \right)^2, \quad (5.74)$$

$$\frac{\eta_\beta}{r_0}(\omega_s = 0) = \frac{1}{r_0} \left(\frac{dr_0}{dD} \right)^2, \quad (5.75)$$

$$\text{SNR}_\beta(\omega_s = 0) = \frac{1}{2D_{\text{eff}}} \left(\frac{dr_0}{dD} \right)^2 = \frac{1}{R^2 r_0} \left(\frac{dr_0}{dD} \right)^2. \quad (5.76)$$

Alternatively, the response function β can be obtained from the static (quasi stationary) rate by expansion in a Taylor series with respect to a small (and adiabatically slow) change in noise strength. Hence, as in the additive case, the adiabatic response to a noise coded signal is determined by the sensitivity of the stationary firing rate to a change in a parameter, here, the noise intensity D .

For very high frequencies, the density $P(v, t)$ is not influenced by the signal and will be therefore coincide with the stationary density. However, this does not hold for the instantaneous firing rate since the rate is given by the product of the derivative of the density at threshold and the instantaneous noise intensity $[D + \varepsilon_\beta \cos(\omega_s t + \varphi)]$. If the density is stationary, the rate becomes thus directly proportional to the noise coded signal

$$r(t) \rightarrow [D + \varepsilon_\beta \cos(\omega_s t + \varphi)] \frac{r_0}{D} \quad \text{for} \quad \omega_s \rightarrow \infty \quad (5.77)$$

which allows the conclusion that $\beta \rightarrow r_0/D$ in this limit. In other words, in both the noise-activated and deterministic firing regimes, we expect to find a *finite high frequency transmission* with a response amplitude given by the ratio of stationary spike rate to overall noise intensity. In addition, it is apparent from eq. (5.77) that the phase shift ϕ_β must vanish in the very same limit.

The simple relation $\beta = r_0/D$ can also be derived from the full solution eq. (5.56) using eq. (A.18) and eq. (A.20) from the appendix. Exploiting furthermore the high frequency limit of the background spectrum eq. (2.78) we obtain

$$\eta_\beta(\omega_s \rightarrow \infty) \approx \frac{r_0^2}{D^2}, \quad (5.78)$$

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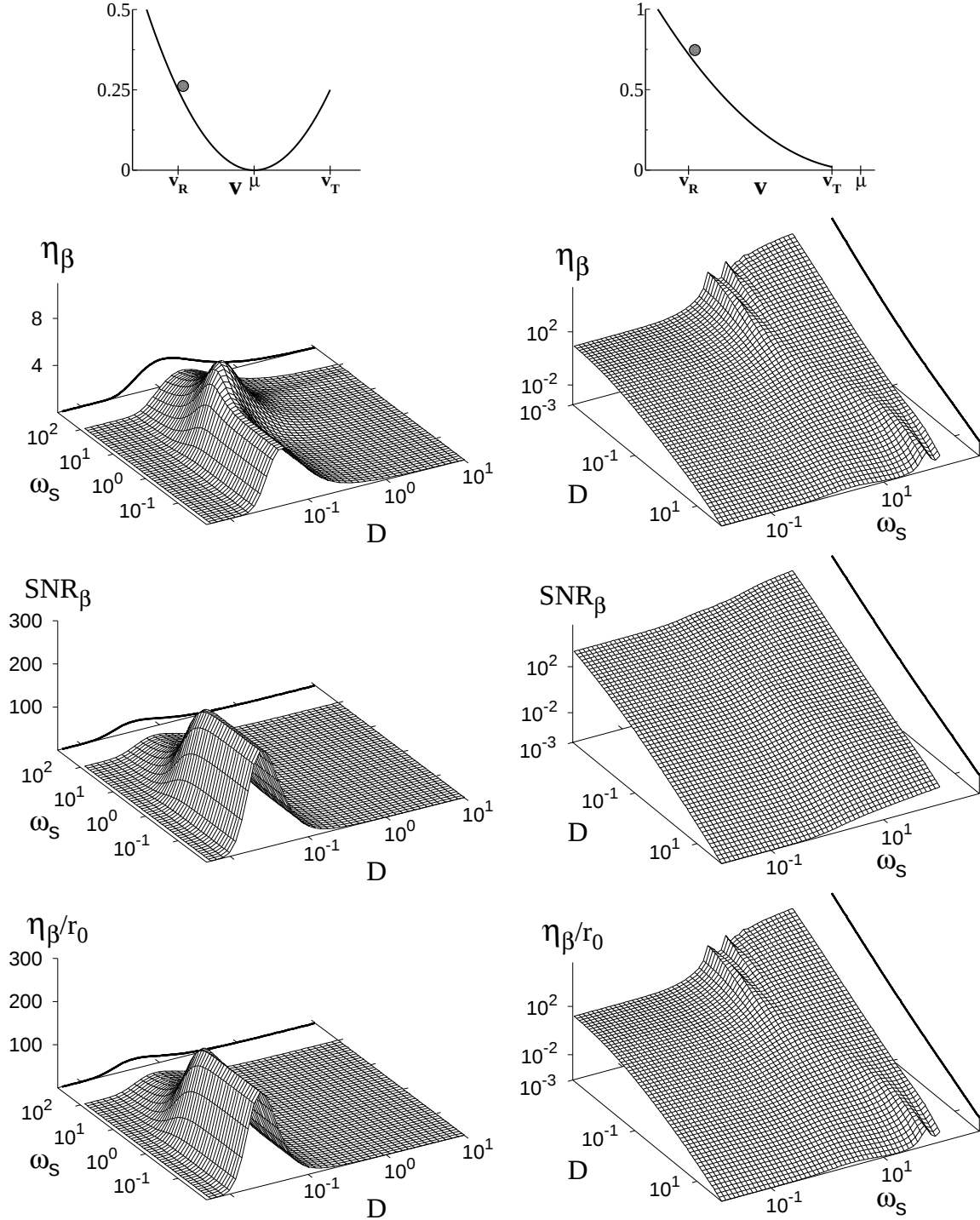


Figure 5.7.: Spectral amplification, conventional signal-to-noise ratio and ratio of SPA to mean rate for the noise coded signal versus noise strength and driving frequency. Left column: $\mu = 0.5$ (noise-activated firing regime). Right column: $\mu = 1.2$ (deterministic firing regime). The upper two panels illustrate the respective potential for the voltage $(v - \mu)^2/2$.

$$\frac{\eta_\beta(\omega_s \rightarrow \infty)}{r_0} \approx \text{SNR}_\beta(\omega_s \rightarrow \infty) \approx \frac{r_0}{D^2}. \quad (5.79)$$

According to the definition of the second signal-to-noise ratio, the two SNRs are equal in the high frequency limit.

Now, we discuss the spectral transmission at arbitrary frequency for the same values of μ like in the previous section.

Noise activated firing regime with a small relative refractory period (noise coded signal)

$\mu = 0.5$ - Fig. 5.7 (left column)

The first important feature is a stochastic resonance effect for the noise coded signal with respect to the effective noise intensity D . All spectral response characteristics exhibit maxima versus D at a fixed ω_s . Like in case of an additive signal, the respective maximum shifts to larger values if the frequency is increased. Also, we find again that SNR_β and η_β/r_0 peak at smaller noise strength than the relative amplitude and the spectral amplification. To understand the SR effect consider the two limits $D \rightarrow 0$ and $D \rightarrow \infty$. At small noise, the stationary spike rate is very low. The output signal results from a modulation of this stationary rate and, therefore, it will be also weak. On the other hand, if D is large, the stationary rate is close to saturation and an additional (absolutely) small modulation of it does not make an impact on the escape to threshold. The maximum of the periodic response and hence SR for noise coded signals is thus a compromise between a sufficiently large firing rate and a sufficient impact of a noise modulation on the firing rate. This is clearly seen in the adiabatic limit (eq. (5.74), eq. (5.75) and eq. (5.76)) where the sensitivity to a change in noise strength is quantified by the derivative of the rate with respect to this parameter. The maximum in the derivative itself is a consequence of the sigmoidal shape of the rate dependence on D .

The second feature apparent for all response measures is the finite high frequency limit as predicted by eq. (5.78) and eq. (5.79) (thick lines at $\omega_s \approx 10^3$). In contrast to additive signals where we have found a lowpass filtering, a noise coded signal of arbitrary high frequency leads to a spectral peak with finite height. Mathematically, the finite amplitude relies on the fact that the instantaneous firing rate is directly proportional to the instantaneous noise intensity, i.e., to the noise coded signal. In other words, the effect is based on the presence of a threshold and noise in the system. From these mathematical facts we may infer that physically the fast dynamical variables that lead to an (only approximate) threshold condition as well as the kind of input (a large sum of spike trains with small positive and negative amplitudes) are responsible for the finite high frequency transmission.

The zero phase shift mentioned above implies that the finite response at large frequencies is accompanied by a vanishing delay. This is as well as the finite response amplitude simply due to the proportionality relation between instantaneous rate and time dependent noise strength.

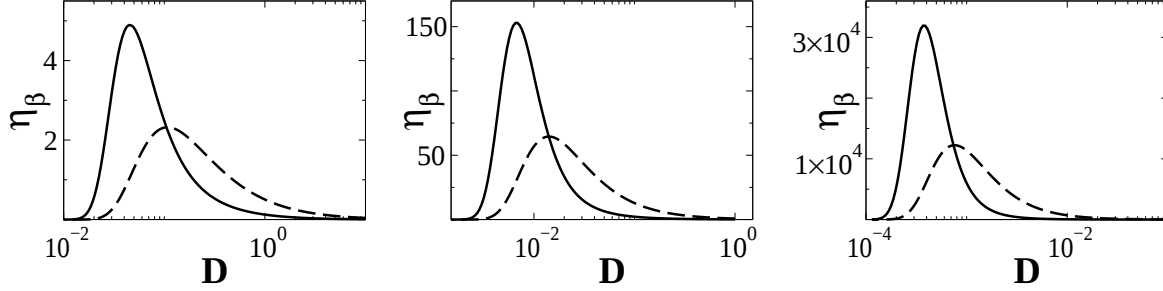


Figure 5.8.: Spectral power amplification η_β for the noise coded signal at zero (solid line) and infinite (dashed line) driving frequency versus noise intensity. From left to right: $\mu = 0.5, 0.8$ and 0.95 .

Either the adiabatic and high frequency limit show stochastic resonance in all spectral measures. This is in detail shown in Fig. 5.8. Apparently, the high frequency limit becomes maximal at a larger noise strength than the adiabatic response. Furthermore, the former maximum is smaller. The ratio of the noise intensities that maximize the limiting curves is virtually independent of the base current as long as this parameter is below the critical value. The difference between the maxima increases slightly with μ .

In contrast to the additive signal with $\mu = 0.5$ (Fig. 5.2) there is an overall maximum with respect to noise strength and driving frequency. Actually, a weak peak is already present for $\mu = 0$ and $\tau = 0$ (not shown). Therefore, the maximum is not only due to the refractory period although more pronounced if refractoriness is involved. Furthermore, if the coherence resonance effect is very pronounced (long relative refractory period) it seems to dominate the frequency dependence and the enhanced response appears to be a resonance with the noise-induced eigenfrequency like for the additive signal (see below). The weak nonmonotonous dependence on driving frequency in case of vanishing refractoriness is one of the open problems of this thesis.

In result, for small μ the system shows stochastic resonance with respect to the effective noise intensity D and a finite spectral response at large frequencies which displays SR, too. A weak nonmonotonous dependence on the signal frequency is observed at moderate noise intensity.

Noise coded signal in the deterministic firing regime

$\mu = 1.2$ Fig. 5.7 (right column)

Here, we obtain again the resonances similar to those discussed for the additive signal. Recall that the amplitude of the noise coded signal has to be smaller than the constant noise intensity D . This implies (incidentally, also for the other cases considered) that the data shown have only a meaning for D values above ε_β . For a low noise level obeying this condition the modulation of noise intensity leads to a higher or lower probability of firing in positive or negative half periods of the signal. If the period of

this modulation coincides with the rather regular interspike interval in absence of a signal a resonance can be expected like in case of additive driving. Once more, we find that this resonance does not appear in SNR_β while the ratio η_β displays it for the very same reasons given in the previous section.

It can be verified by a small D expansion that the derivative of the rate r_0 with respect to the noise strength, i.e., the adiabatic limit of β becomes constant for $D \rightarrow 0$. This is different for high frequencies. It is evident from eq. (5.78) that if r_0 tends to a finite value for $D \rightarrow 0$ the spectral power amplification must diverge like D^{-2} . Note, however, that the apparent huge effect at small noise is limited by the above mentioned fact that the signal amplitude has to be smaller than D . In fact the spectral peak will be proportional to $\varepsilon_\beta^2 \eta_\beta$ and this means the peak intensity cannot exceed $\pi r_0^2/2$. In addition, this upper limit is clearly beyond the validity of the linear response theory we have applied.

For large noise, the typical resonances due to the absolute refractory period, though weaker than in the additive case, can be found. Furthermore, we would like just to mention that although stochastic resonance for the noise coded signal is in general absent in the deterministic firing regime an equivalent effect like for an additive signal (Fig. 5.3) can be found: if the driving frequency is slightly above the deterministic eigenfrequency, an enhancement of the SPA by finite noise is encountered.

To summarize, the LIF model driven by a noise coded signal in the oscillatory regime displays resonances at small and large D . Additionally, the system performs an efficient high frequency transmission in this case.

Noise activated firing regime at a strong relative refractory period (noise coded signal)

$\mu = 0.8$ and $\mu = 0.95$ - Fig. 5.9 (left and right column, respectively)

For large but subcritical base current, we obtain a much stronger spectral response like in case of the additive signal. Stochastic resonance and high frequency transmission are still present like for $\mu = 0.5$. The nonmonotonous dependence of the amplification on ω_s is more sharpened such that for $\mu = 0.95$ even the ratio η_β/r_0 attains an overall maximum at finite frequency. Thus, also for noise coded signals the relative refractory period, i.e., the coherence resonance effect results in a resonance like behavior if the system is periodically driven by this frequency.

This is also verified in Fig. 5.10 by the comparison of background spectrum and amplification analog to that for the additive signal in Fig. 5.6. Obviously, the maxima of background and amplification do not fully match but are rather close to each other. For $\mu = 0.95$ a second peak versus frequency becomes manifest which corresponds to the first harmonic of the noise induced eigenfrequency. This second maximum of η_β is remarkably large. For larger noise intensity it can become even larger than the first maximum.

The main features of the response to a pure noise coded signal are once more illustrated in Fig. 5.11: stochastic resonance, resonance with respect to the noise induced eigenfre-

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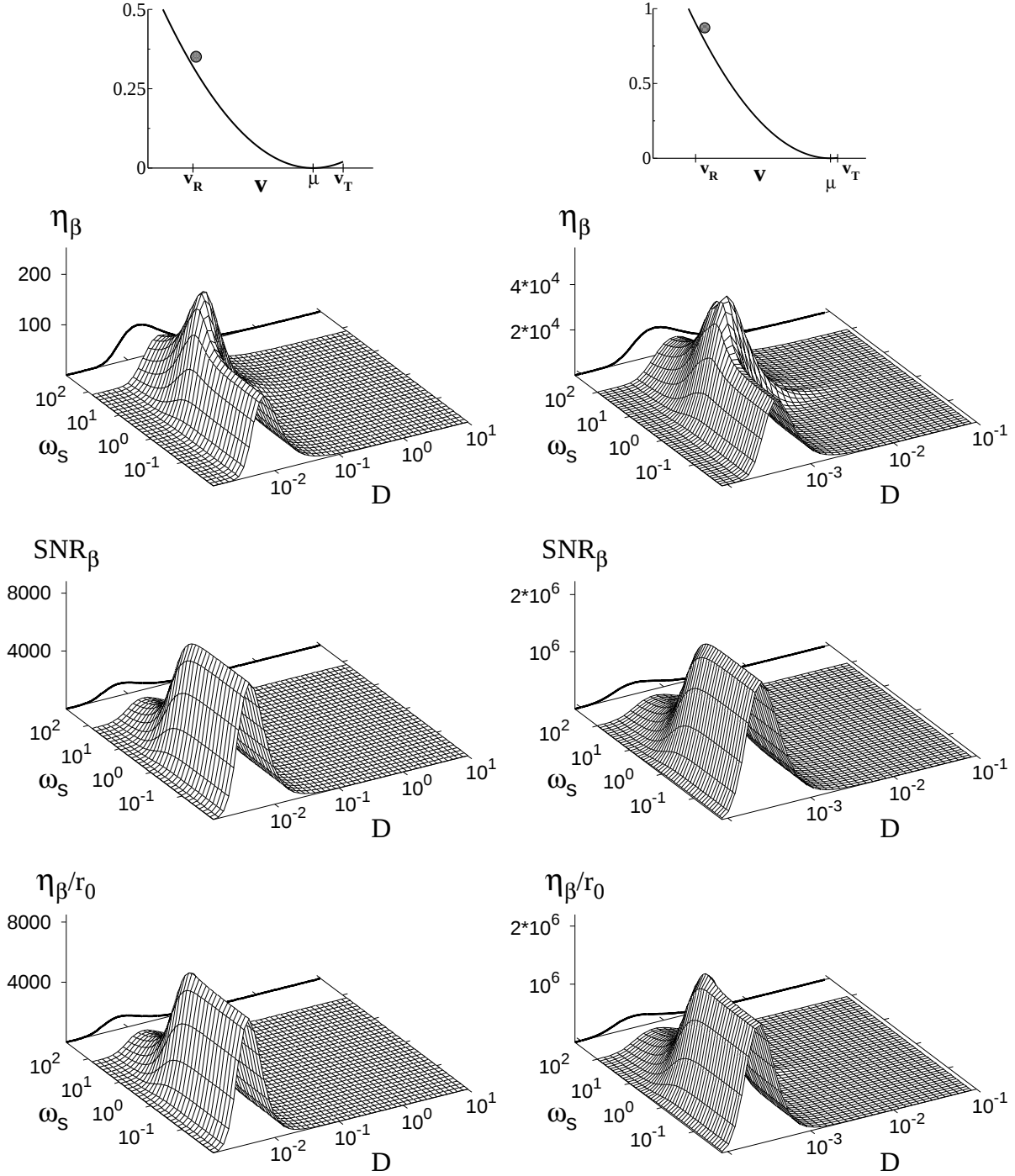


Figure 5.9.: Spectral amplification, conventional signal-to-noise ratio and ratio of SPA to mean rate for the noise coded signal versus noise strength and driving frequency. Left column: $\mu = 0.8$. Right column: $\mu = 0.95$ (both noise-activated firing regime). The upper two panels illustrate the respective potential for the voltage $(v - \mu)^2/2$.

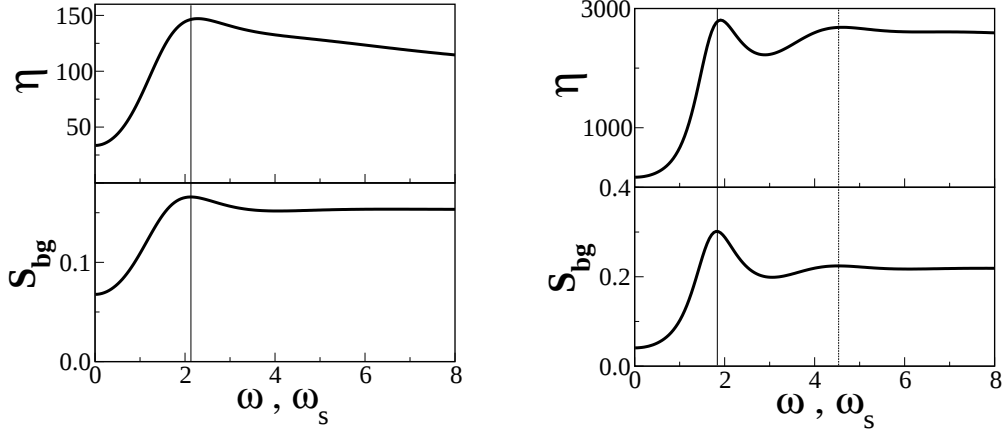


Figure 5.10.: Spectral power amplification η_β and background spectrum for a noise coded signal versus frequency / driving frequency. Left: $\mu = 0.8, D = 0.02$. Right: $\mu = 0.95, D = 0.005$. Noise intensities were chosen such that the CR effect is most pronounced. Vertical lines indicate the maximum (or maxima) of the spectrum.

quency and the finite high frequency limit. We compare for $\mu = 0.8$ the amplification (including its overall maximum) with data from numerical simulations. As in case of the additive signal, the spectral amplification is well described by the theory. Note that

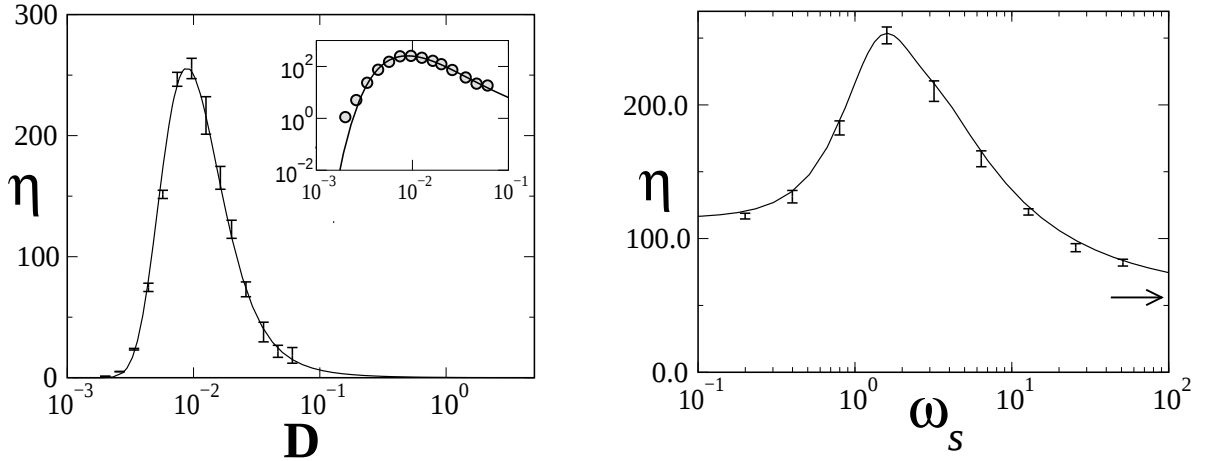


Figure 5.11.: Spectral amplification in the response to a noise coded signal versus noise strength (left, with a log-log plot of the same function in the inset) and driving frequency (right), respectively, for $\mu = 0.8$. The arrow in the right panel indicates the theoretical high frequency limit of η_β . Theory (solid line) compared to results of simulations (error bars and circles). Parameters l.h.s.: $\varepsilon_\beta = 0.002$, $\omega_s = 1.46$, $T = 4 \times 10^3$, $N = 100$. Parameters r.h.s.: $\varepsilon_\beta = 0.0015$, $D = 0.0098$, $T = 8 \times 10^3$, $N = 200$. In both simulations $\Delta t = 10^{-5} - 10^{-2}$.

the frequency in Fig. 5.11 (right panel) was varied over several orders of magnitude and also the high frequency response is thus clearly verified (for further numerical evidence see section 5.3). As mentioned above, a finite amplitude ε_β imposes a restriction on the range of D values ($D \geq \varepsilon_\beta$). The leftmost point in the inset of Fig. 5.5 (left panel) is in fact for $D = \varepsilon_\beta$. It is the only point that shows an appreciable deviation from theory. This is not astonishing because for this value linear response theory must fail. In conclusion, we have shown that the stochastic resonance effect is strongly pronounced for noise coded signals. A large refractory period sharpens the resonance with respect to the signal frequency - the resonance frequency is close the noise induced eigenfrequency. A higher harmonics in the spectrum results in a second maximum of the amplification versus driving frequency. The response quantified by the spectral amplification is considerably larger than in the case of additive signals. This is also important for the high frequency transmission. Although it is for moderate noise smaller than the adiabatic response its size exceeds the additive signal still by orders of magnitude.

5.2.4. The mixed response and the phase shift

We have seen that the response to the noise coded signal is for most parameter values stronger than to the additive signal in the sense that if the non-dimensional amplitudes $\varepsilon_\alpha, \varepsilon_\beta$ are of the same order of magnitude the resulting output intensities will significantly differ. Therefore, the mixed response will be clearly dominated by the noise coded signal. An exception is the strong noise limit, where the response amplitude of the additive signal decreases only slowly, but this regime seems to be of minor biological relevance. What happens if the output intensities due to either signals are

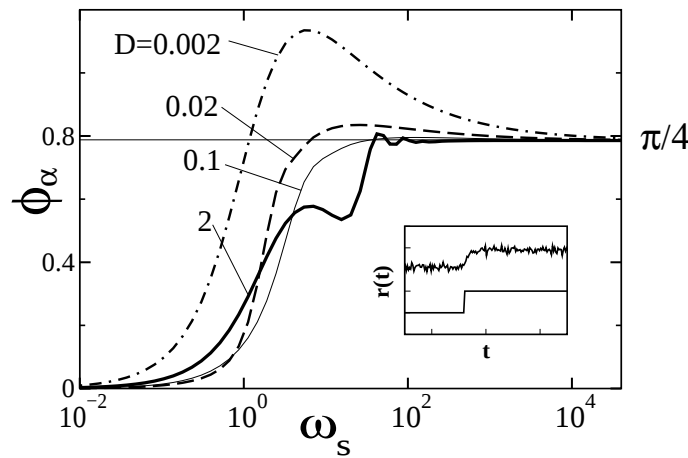


Figure 5.12.: Phase shift to the additive signal versus driving frequency for $\mu = 0.8$. Inset: the response of the activity to a step like signal (thick) in the base current $\mu \rightarrow \mu + \varepsilon$ at $D = 0.1$ and $\varepsilon = 0.05$.

comparable in magnitude? Not only for this reason it is interesting to look at the phase shifts that we have ignored so far. Restricting ourselves to the base current $\mu = 0.8$ (noise activated firing regime) we shall discuss the two phase shifts ϕ_α, ϕ_β and show the output intensity given implicitly by eq. (5.60) for a particular set of amplitudes. In case of an *additive signal* (Fig. 5.12) the positive phase shift illustrates primarily the delay of the neuronal response. This delay is only zero in the adiabatic limit for obvious reasons. For increasing frequency it passes through a maximum - most pronounced if the noise intensity is low - and saturates at $\pi/4$. The latter limit is related to the response behavior at small times which is in leading order $\sim \sqrt{\Delta t}$. Regarding the maximum of the phase shift, we notice that it appears in general at considerably larger frequency than the maximum of the relative amplitude $|\alpha|$ or the SPA η_α , i.e., the subsequent *decrease* of the phase shift does not possess much importance since for these frequencies the response amplitude is rather weak. At large noise strength the phase shift displays several local minima and maxima. This behavior is related to the resonances due to the trivial eigenfrequency $2\pi/\tau$ caused by the absolute refractory period.

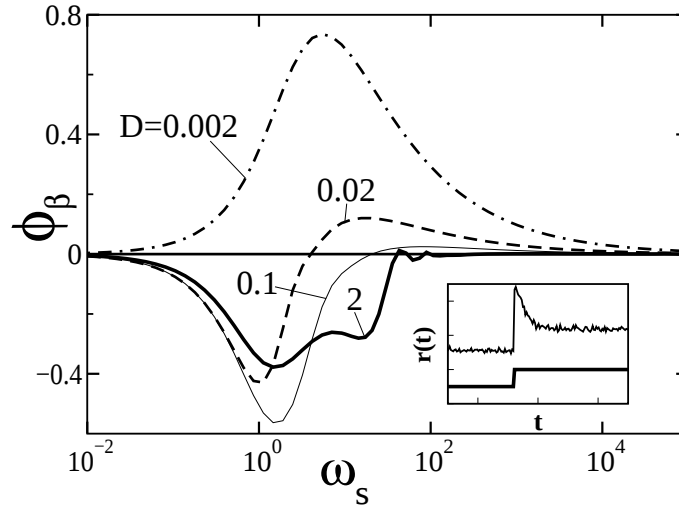


Figure 5.13.: Phase shift to the noise coded signal versus driving frequency for $\mu = 0.8$. Inset: the response of the activity to a step like signal (thick) in the noise intensity $D \rightarrow D + \varepsilon$ at $D = 0.1$ and $\varepsilon = 0.05$.

For a *noise coded signal*, the phase shift looks quite different. It is not surprising that it tends to zero for $\omega_s \rightarrow 0$ which is again the adiabatic limit, however, it vanishes as well for infinite driving frequency. This can be understood by the asymptotic behavior of β that tends to the (real valued) function r_0/D as was shown above. We stress once more that besides the finite relative amplitude at high frequencies the response to a noise coded signal exhibits also a vanishing delay manifested by the zero phase shift.

Another somewhat surprising feature concerns the sign of the phase for moderate to large noise intensity and low to moderate frequency. Here the phase shift is *negative*. This implies that the output signal precedes the input signal which seems to contradict causality. Note, however, that we deal here with an asymptotic solution, i.e., the neuron is adapted to the (somewhat poor) cosine signal and knows so to say “what comes next”.

Thus, the causality principle is rescued, but what is the reason for the negative sign of ϕ_β ? To answer this question look at a simpler problem studied by Pawelzik (2000), namely, the response of the rate to a step like increase of the noise intensity depicted in the inset of Fig. 5.13. The rate was in this case determined by a numerical solution for an ensemble of neurons. As it is clearly seen, the proportionality of the rate to the instantaneous noise strength causes an instantaneous response to the step like change $D \rightarrow D + \varepsilon$. This jump is followed by a slow adaption towards the new stationary rate $r(D + \varepsilon)$ which is here *smaller* than the switch value $r_0(D + \varepsilon)/D$. This implies that a *positive* signal (the increase in noise strength) causes an instantaneous increase (no phase shift) and a delayed *decrease* of the response, i.e., a response in *anti phase* to the signal. For a continuous signal we have thus a negative phase shift with respect to the input signal provided that $r_0(D)[D + \varepsilon]/D \gg r(D + \varepsilon)$. The latter condition is not fulfilled for very small noise what explains the positive phase shift in this case (dashed-dotted line in Fig. 5.13) but holds true for moderate to large noise intensity.

The same features are, of course, absent in the response to a step like increase in the base current (inset of Fig. 5.12). Here, just a delayed response and adaption towards the new stationary rate is obtained.

On comparing Fig. 5.12 and Fig. 5.13 we see that the difference $\phi_\alpha - \phi_\beta$ does not exceed $\pi/2$ and is mostly smaller than $\pi/4$. It follows from eq. (5.60) that the output is larger

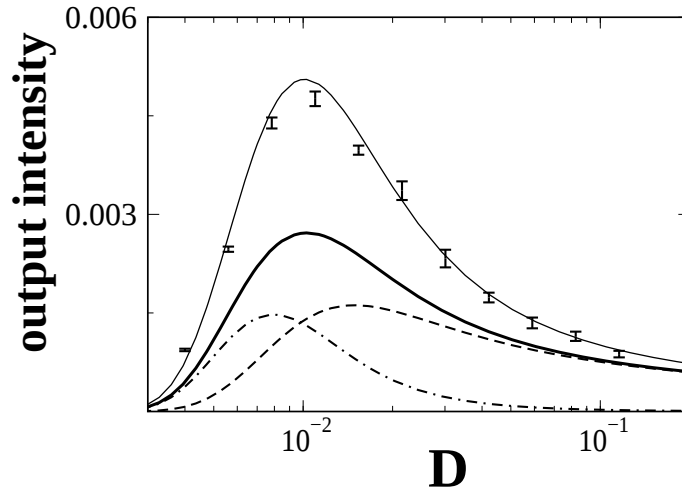


Figure 5.14.: Output signal intensity in presence of additive and noise coded signal versus noise intensity for $\mu = 0.8, \varepsilon_\alpha = 0.02857, \varepsilon_\beta = 0.002$ and $\omega_s = 1$. Theory (thin solid line) compared to results of a numerical simulation (error bars) with $N = 200, T = 2000, \Delta t = 10^{-5} - 10^{-2}$. Additionally shown: response to the noise coded (dot-dashed line) or additive signal (dashed line). The thick line indicates the sum of the single responses.

than the mere sum of the outputs in response to the single signals. Here, we use as a measure of stochastic resonance the output signal intensity defined by

$$\text{output} = \lim_{\Delta\omega \rightarrow 0} \int_{\omega_s - \Delta\omega/2}^{\omega_s + \Delta\omega/2} d\omega S(\omega). \quad (5.80)$$

In the numerical simulation we have to subtract the background from the peak height at the driving frequency and to multiply by the frequency bin. The output intensity will depend on the signal amplitudes. For the data shown in Fig. 5.14 the amplitudes were tuned such that the maximal single responses to the signals were roughly the same.

As we have pointed out above, the response to noise coded signal is maximized at smaller D than that to the additive signal. If both signals are present we observe thus a maximum of the response in between these two values. The mere sum of the two intensities (thick line) is only about one half of the actual output (thin line) - the presence of both signals leads to an enhanced stochastic resonance effect. This important result is also confirmed by the numerical simulations.

The dependence on driving frequency is interesting as well. As we have discussed above, the peak of the SPA for the additive signal occurs before the noise-induced eigenfrequency due to the low pass behavior of the response. This does not hold for the noise coded signal and, therefore, we expect a maximum in between the eigenfrequency and

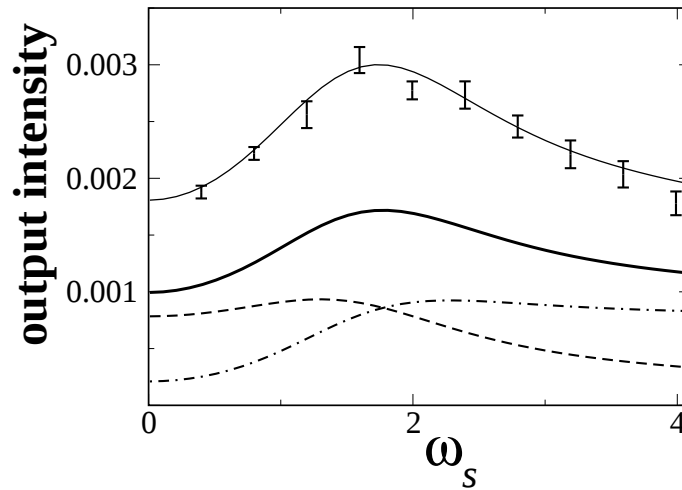


Figure 5.15.: Output signal intensity in presence of additive and noise coded signal versus driving frequency for $\mu = 0.8, \varepsilon_\alpha = 0.022, \varepsilon_\beta = 0.002, D = 0.02$. Theory for a fixed zero phase shift between the input signals (thin solid line) compared to results of a numerical simulation (error bars) with $N = 200, T = 2000, \Delta t = 10^{-5} - 10^{-2}$. Additionally shown: response to only the noise coded (dot-dashed line) or additive signal (dashed line), only. The thick line indicates the sum of the single responses.

the frequency at which η_α is maximized. This is confirmed by the numerics (Fig. 5.15). Again we find that the output (thin line) is considerably larger than that the mere sum of the single response intensities (thick line). It can be seen as well that if both signals are present, the nonmonotonous behavior with respect to the driving frequency is more pronounced. Hence, even if the coherence resonance effect is not extremely distinctive, the noise-induced eigenfrequency may lead to a strong resonance effect in the response.

5.2.5. Stochastic resonance with respect to background activity

We have demonstrated stochastic resonance in the noise-activated firing regime of the LIF model for both kinds of signals as well as for the mixed response. The resonance became manifest as a maximum with respect to the overall noise intensity D . Does this result imply SR with respect to the background activity of the neural network quantified by D_{bg} ? To answer this question we recall our definitions of the effective parameters made in the introduction

$$\mu = \mu_{\text{bg}} + a, \quad D = D_{\text{bg}} + b, \quad \varepsilon_\alpha = a\varepsilon, \quad \varepsilon_\beta = b\varepsilon. \quad (5.81)$$

Although the parameters a and b were introduced as scaling factors in the numbers of excitatory and inhibitory neurons, we mentioned that these parameters scale generally the strength of the input ensemble's impact on the target neuron determined by the number of input neurons, the single neurons rate, and the synaptic amplitudes.

The first precondition for SR at arbitrary driving frequency is a base current smaller than threshold, i.e., both parameters μ_{bg} and a should be small or at least one of them should be negative (excess of inhibitory synapses) to compensate a large value of the other one. Furthermore, assume that we have found a maximum in SPA or SNR with respect to D at $D = D_{\text{max}}$ in one of the spectral measures for one kind of signal. Then, if the parameter b is larger than this value, that is, $b > D_{\text{max}}$ additional noise from the neuronal background deteriorates the transmission performance. This is different for a small value of b obeying $b < D_{\text{max}}$ where for $D_{\text{bg}} = 0$ the signal transmission is suboptimal. In this case, background fluctuations, i.e., the activity of incoherently firing neurons enhances the performance significantly.

We have seen that for a finite frequency the optimal noise intensity is always larger than in the adiabatic case. Therefore, the simpler expressions given by eq. (5.65), eq. (5.66), eq. (5.67) and eq. (5.74), eq. (5.75), eq. (5.76) may be used in order to estimate an upper bound for b below of which stochastic resonance is expected for additive and noise coded signals, respectively.

In conclusion, stochastic resonance with respect to the background activity is observed for an ensemble input with weak impact on the dynamics of the target neuron. This is consistent with the notion that stochastic resonance in the majority of cases is relevant for the detection of weak signals, only.

5.3. The response of a neuronal ensemble and some remarks on the high frequency limit of transmission

One might be tempted to think that the finite high frequency response to noise coded signals implies a *fast* signal transmission. However, the high frequent modulation of the firing rate seems to be useless for this purpose since the *temporal mean* of the rate is low to moderate and that means there is only a little chance to observe even one spike within the small signal period.

One solution of this dilemma is an ensemble average (“neurons in parallel”). So, we come back to the model proposed in the introduction: instead of a single neuron we consider a whole ensemble of neurons that obey an equation like eq. (5.1). One may assume that the noise sources are independent if two neurons share only a small negligible number of common connections to the input ensemble. This is, of course, a crude approximation as well as the assumption is that the neurons within the ensemble are not connected at all. However, some elaborated models of neural circuits are in fact based on the picture we have in mind, namely, an ensemble that drives another ensemble. More generally, one considers a whole chain of such unidirectionally driven ensembles known as synfire chains (Abeles, 1991). Neglecting the internal connections is in this case justified since the main excitation originates in the driving ensemble (the “sending node” in the language of Abeles (1991)).

The advantage of neglecting all correlations in the input is that we can immediately adopt the results for the single neuron since the spike trains generated by the ensemble neurons will be entirely independent. The pooled output of the ensemble forms a point process, the rate of which is simply given by the single neuron’s rate $r(t)$ times the number of neurons N

$$R(t) = Nr(t). \quad (5.82)$$

In the context of neuronal populations that consist in general of *connected and non-identical neurons* the quantity $R(t)/N$ is also referred to as mean (or global) activity (see, e.g. Spiridon and Gerstner, 1999) and will be different from the instantaneous rate of the single neuron. Note that the term ‘ensemble’ does not imply that all neurons are either excitatory or inhibitory - we may have a mixture of both. This, however, is not reflected in the activity.

As a matter of fact, for large N the point process generated by the ensemble will be a *Poisson process* with time dependent rate $R(t)$ (Cox, 1962; Shimokawa et al., 1999c) what can be seen as follows.

Consider an interval $(t, t + \Delta t)$ with sufficiently small Δt . Each of the N neurons contributes at most one spike to this interval with probability $r(t)\Delta t$ and this contribution is independent of the others. For large N , we will have a still large number $Nr(t)\Delta t$ of points independently distributed over the interval, i.e., we have locally in time a Poisson process. At the same time, for $N \rightarrow \infty$, the correlations between successive firing times of a single neuron as well as the

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statistics of the corresponding interval lose importance because the interval is split into many independent subintervals.

The background spectrum for the activity is thus given by that of a Poisson process with rate $Nr(t)$, i.e., $S_{bg} = Nr_0$ in this case. For the signal-to-noise ratio one finds $N\eta^2/r_0$ for the spatially averaged rate (Neiman et al., 1997b) as well as for the total output spike train (Shimokawa et al., 1999c).

Using this property we may estimate a relative error of the mean activity measured by the number of spikes n in a sufficiently small time bin $\Delta t \ll 2\pi/\omega_s$

$$s = \pm \frac{\sqrt{\langle \Delta n^2 / (N\Delta t)^2 \rangle}}{\langle n / (N\Delta t) \rangle} = \pm \frac{\sqrt{\langle n / (N\Delta t)^2 \rangle}}{r(t)} = \pm \frac{\sqrt{r(t) / (N\Delta t)}}{r(t)} = \pm \frac{1}{\sqrt{r(t)N\Delta t}}. \quad (5.83)$$

The uncertainty thus depends on the number of neurons, the firing rate and the time bin. That allows the following conclusions

- Since $\Delta t \ll 2\pi/\omega_s$ a given ensemble size N sets a limit to the frequency band signals of which can be transmitted.
- The low noise parameter region is not appropriate for high frequency transmission since the rate $r(t) \sim r_0$ is weak and a huge number of neurons are needed to reduce the error.
- Signal amplitudes should be sufficiently large to result in a significant change in the activity. This is necessary since the relative error for a *weak change* in the rate is considerably larger than the error s of the rate itself.

The latter fact seems to exclude the applicability of linear response theory. Fortunately, at moderate to large noise strength D (second conclusion) the theory works quantitatively rather well and describes accurately relative changes of r_0 up 50%.

The activity in response to either an additive or a noise coded signal is depicted in Fig. 5.16. Different features that were discussed above are now directly observable. For instance, the negative phase shift for the noise coded signal becomes manifest by the fact that the response intersects the r_0 line before the signal does (cf. upper left panel). This phase shift vanishes for higher frequencies, while that due to the additive signal increases with ω_s . Furthermore, although the signal amplitude of the noise coded signal is considerably smaller than the additive signal, the former results in a larger response amplitude. The most important issue is the high frequency transmission ($\omega_s = 200$, right panel). While the modulation due to the additive signal is hardly to see in the simulation results, the response amplitude due to the noise coded signal remains finite. Note that at the rather large noise intensity we have used, the data are almost perfectly described by the linear response theory (response amplitude and phase shift) though the signal amplitudes were not small.

There are several limitations for the high frequency transmission set by the ensemble

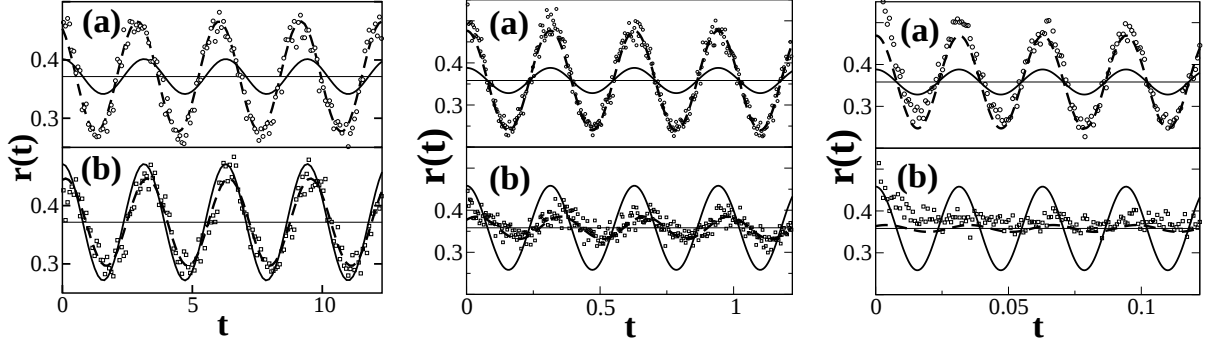


Figure 5.16.: Mean activity of a neuronal ensemble for $\omega_s = 2, 20, 200$ (from left to right) at $\mu = 0.8, D = 0.1$. Upper and lower panels are the responses to a pure noise coded or additive signal with $\varepsilon_\beta = 0.03$ or $\varepsilon_\alpha = 0.1$, respectively. For comparison we show the theory according to eq. (5.31) and eq. (5.56) (dashed lines) and the signal raised by the constant rate (solid lines), i.e., $r_0 + \varepsilon_{\alpha,\beta} \cos(\omega_{\alpha,\beta} t)$. The number of neurons were $N = 20.000$ for the data in the left panel, while in the other two we used $N = 2 \times 10^6$.

size but also due to over simplifications in the LIF model.

First of all, to obtain the “clean” data in Fig. 5.16 that permitted a comparison to the theory also at high frequency, we had to use a quite large ensemble of $N = 2 \times 10^6$. This seems to be a lot for the simple purpose of a fast signal transmission. For still larger frequencies even more neurons would be necessary. Neuronal populations as a chain link in neuronal processing pathways are usually considered to be of the order of magnitude $N \sim 10^2 - 10^5$. How far we can get using an ensemble of “only” 50.000 neurons is shown in Fig. 5.17.

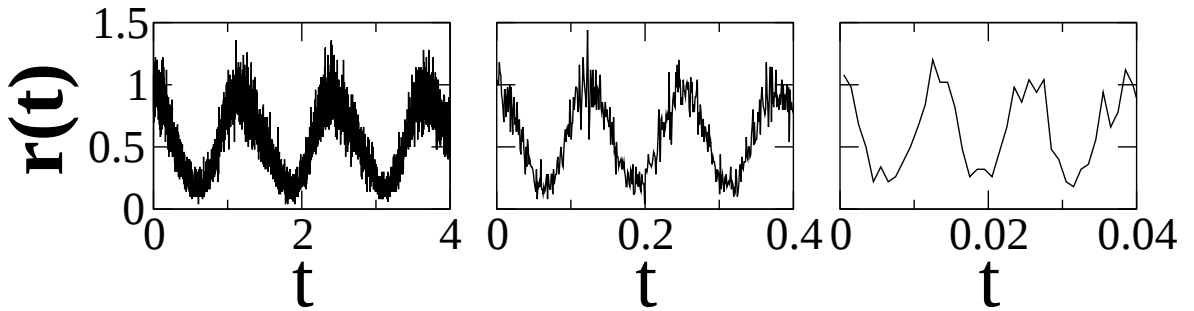


Figure 5.17.: Mean activity of a neuronal ensemble at $\mu = 0.8, D = 0.3$ and a time window of $\Delta t = 0.001$. Responses to a pure noise coded signal with $\varepsilon_\beta = 0.2$ and $\omega_s = 5, 50, 500$ (from left to right).

Here, we have used a purely noise coded signal at larger noise strength and signal amplitude to reduce the relative error. The mean frequency is $r_0 \approx 0.55$ and thus the highest frequency ($\omega_s = 500$) is more than two orders of magnitude larger than the

eigenfrequency $2\pi r_0$. Also in this case one sees that a postsynaptic neuron may get a “rough idea” of the signal. An extension of the frequency band by two orders of magnitude, i.e.,

$$0 < \omega_s < 10^3 r_0 \quad (5.84)$$

seems thus to be possible without using unreasonable huge ensembles.

The second restriction is more serious. The finite amplitude of $\beta(\omega_s \rightarrow \infty)$ relies mathematically on the threshold condition of the LIF model. This approximate condition replaces the dynamics of certain fast variables in more realistic neuronal systems like the FitzHugh-Nagumo or Hodgkin-Huxley model. A separation of time scales by two to three orders of magnitude in those models seems to be realistic. For frequencies up to those corresponding to these time scales, i.e., up to three orders of magnitude above the eigenfrequency of the neuron, it is therefore expected that a noise coded signal is transmitted with a finite amplitude. This is in fact the same frequency range as described by the condition eq. (5.84).

Eventually, the input we have used in our model (a deterministic function of time plus a white noise with time dependent intensity) is also only approximate. In reality, this input is low pass filtered by the synaptic dynamics and thus leads to input currents that are rather described by an Ornstein-Uhlenbeck process with time dependent mean and intensity than by the white noise input we have used. A simple calculation then reveals that the effective amplitudes of the time dependent mean and variance of the OUP process are reduced for high frequencies by a factor $(\omega\tau_s)^{-1}$ and $(\omega\tau_s/2)^{-1}$, respectively, where τ_s is the time constant of the synaptic filter. Apart from the fact that we do not know to what extent a noise coded signal is transmitted if the noise is not white but strongly colored this reduction factor sets a another clear limit to the high frequency transmission. The limit will depend on the ratio of the time scales of the synaptic dynamics τ_s and that of the spike generation (membrane time constant τ_m). Thus, for a fast synaptic dynamics ($\tau_s \ll \tau_m$), the white noise approximation should be valid and also the response reduction by the mentioned prefactor should be negligible for driving frequencies within the range given by eq. (5.84).

A surprising consequence of the consideration of colored noise in the LIF model is that also high frequent *additive* signals may be transmitted with a larger amplitude. This was shown by Brunel et al. (2001) who have found an analytical expression for the high frequency transmission amplitude. Note, however, that they took not account of the mentioned reduction factor but considered a cosine signal with frequency independent amplitude and a colored (“filtered”) noise as the input to the LIF model.

In result we have shown that the high frequent transmission of noise coded signals through neuronal ensembles is possible for an extended frequency range if the following conditions are met 1) a sufficient ensemble size 2) a well established time scale separation for the reset mechanism of the single neuron within the ensemble and 3) a fast synaptic dynamics. Besides the fact that we have neglected all connections between the neurons as well as correlations in the input, these restrictions are rather

strong. Thus extensions of the presented model will certainly be needed for a deeper understanding of the role of noise coded signals for the neuronal communication.

5.4. Summary

We have studied the response of the LIF model to periodic modulation of the base current (additive signal) and noise intensity (noise coded signal) in the noise-activated as well as in the deterministic firing regime. All results were obtained analytically and confirmed by numerical simulations of the model.

In the noise-activated regime the transmission of weak signals can be enhanced by a proper amount of noise resulting from uncorrelated stimulation by the neuronal background. For large but subthreshold base current the response can be further enhanced by tuning of the driving frequency. In contrast to SR in the classic bistable system, measures like the spectral power amplification display an overall maximum at finite noise intensity as well as at finite driving frequency. We have shown that the non-monotonous dependence of the response on driving frequency is a classic resonance with respect to the noise-induced eigenfrequency that appears in a finite range of noise intensities due to coherence resonance.

In the deterministic firing regime a SR like effect was observed. If the driving frequency exceeds slightly the deterministic eigenfrequency the spectral response (power amplification) was maximized at finite background noise for both kinds of signals. However, this enhancement by noise relies on a different mechanism than SR in the noise activated firing regime: fluctuations increase mean and variability of the interspike interval such that it can be better adapted to the “too small” driving period.

Noise coded signals lead to a strong neuronal response, most importantly, the periodic modulation of the firing rate displays a finite high frequency limit without delay between output and input signal. This is in marked contrast to the additive signal that is effectively lowpass filtered at high frequencies. The effect found can be used for a *fast* signal transmission by population coding: a neuronal ensemble driven by a noise coded signal shows an instantaneous change in the mean activity (spatially averaged firing rate), i.e., the mean activity is proportional to the signal. Taking account of the range of validity of the LIF model we concluded that the range of frequencies transmitted by single neuron or ensemble may be under certain restrictions extended by two orders of magnitude of the spontaneous (stationary) firing rate. This might have relevance for signal transmission in the auditory system as well as for the fast signal transmission through the visual cortex.

6. The stochastic FitzHugh-Nagumo model driven by a periodic signal

In the context of stochastic resonance (SR) in biological systems the FN model introduced in chapter 3 is certainly the most often used model in theory. Starting with papers by Longtin (1993) and Wiesenfeld et al. (1994) it has been applied to model multimodal interspike interval histograms (stochastic phase locking) as well as stochastic resonance features as found in real neurons (Douglass et al., 1993; Levin and Miller, 1996; Nozaki et al., 1999). The model was also used for theoretical studies of aperiodic stochastic resonance (noise enhanced transmission of non-periodic signals, see Collins et al., 1995a; Chialvo et al., 1997; Capurro et al., 1998) and of stochastic resonance in neuronal ensembles (SR “without tuning” Collins et al., 1995b; Chialvo et al., 1997). Analytical attempts were restricted to the parameter region of weak noise and adiabatically slow signals employing essentially one-dimensional Kramers rate theory to the escape from fixed point to threshold separatrix. These simple theories neglect the relative refractory period and consequently also of the coherence resonance effect that might have its own impact to the signal transmission as we have seen in the previous chapter. Indeed, Massanés and Vicente (1999) found numerically a resonance with respect to the noise induced eigenfrequency. Besides the stochastic resonance manifesting itself by the existence of an optimal noise intensity there is also an optimal frequency for the response to a subthreshold signal. In other words, due to coherence resonance, the FN model may act as a resonator for additive signals like the LIF model.

In this chapter we explore these and other features by means of the two state approximation to the FN model that takes account of the relative refractory period and coherence resonance and holds true for arbitrary driving frequencies and noise intensities. To be precise, we will calculate the linear response of the two state dynamics to an additive periodic signal. In the previous chapter we gave a detailed discussion and comparison of additive and noise coded signals by means of different spectral measures. Here we restrict ourselves to the case of additive signals and will use the spectral amplification to quantify the response.

For general behavior of the model under the influence of periodic stimulation holds the same as for the LIF model (cf. page 119). In so far, both models reproduce essential features of experimental findings. The difference is - to stress this once more - that in the FN model a finite firing state is modeled, that is as well incorporated in the

two-state approximation.

We start with the inclusion of a periodic signal in the piecewise linear FN model and how it modifies the two state dynamics. Then we give brief view on the analytical treatment that is very close to one of the calculations in the previous chapter. Eventually, we discuss the signal amplification by the two state model for the three different regimes (excitable, bistable and oscillatory).

6.1. The piecewise linear FN model driven by a periodic signal and the corresponding two state model

Like for the noisy forcing of the FN model there are also two different approaches for the inclusion of a signal in the FN dynamics. In general, the parameters s and b in the dynamics eq. (3.36) become now time dependent functions, i.e.

$$\begin{aligned}\epsilon \dot{v} &= F(v) - u + s(t) \\ \dot{u} &= \gamma v - u + b(t) + \sqrt{2Q}\xi(t)\end{aligned}\tag{6.1}$$

with $F(v)$ given by eq. (3.37). A weak signal $\varepsilon \tilde{f}(t) = \varepsilon \cos(\Omega_s t + \phi)$ can enter the system (6.1) in different ways, additive in the equation of the recovery variable u (Longtin, 1993; Wiesenfeld et al., 1994; Pei et al., 1995) or in that of the voltage variable v (Longtin and Chialvo, 1998; Massanés and Vicente, 1999), i.e., either

$$\begin{aligned}\text{(I)} \quad & b(t) = b_0 + \varepsilon \tilde{f}(t) \quad , \quad s = 0 \\ \text{or} \quad \text{(II)} \quad & b = b_0 \quad , \quad s(t) = \varepsilon \tilde{f}(t)\end{aligned}\tag{6.2}$$

By means of the simple transformation $\tilde{u} = u - s(t)$ eqs. (6.1) can be recast into

$$\begin{aligned}\epsilon \dot{v} &= F(v) - \tilde{u} \\ \dot{\tilde{u}} &= \gamma v - \tilde{u} + b(t) - s(t) - \dot{s}(t) + \sqrt{2Q}\xi(t)\end{aligned}\tag{6.3}$$

From these equations it becomes apparent that a difference between both driving modes occurs for high frequencies only since in case (II) the effective amplitude of the signal scales with driving frequency Ω_s due to the temporal derivative, whereas in case (I) it does not.

Like in chapter 3 we perform the limit $\epsilon \rightarrow 0$ in eqs. (6.3) and obtain the two state dynamics with periodic forcing in the two equations for the slow variable. By transformations to a new time $t \rightarrow t/(\gamma + 1)$ and new variables x and y like to eq. (3.41) but with inclusion of the signal similar to that in eq. (5.7)

$$x = \tilde{u} - \frac{b_0 - \gamma}{1 + \gamma} - \varepsilon f(t), \quad f(t) = A(\omega_s)e^{-i\omega_s t} + A^*(\omega_s)e^{i\omega_s t}$$

corresponding to left branch and

$$y = -\tilde{u} + \frac{b_0 + \gamma}{1 + \gamma} + \varepsilon f(t)$$

for the right branch, we obtain Langevin equations without periodic forcing

$$\begin{aligned}\dot{x} &= -x + \sqrt{2D}\xi(t) \\ \dot{y} &= -y + \sqrt{2D}\xi(t)\end{aligned}\tag{6.4}$$

Here, rescaled driving frequency $\omega_s = \Omega_s/(1 + \gamma)$ and noise strength $D = Q/(1 + \gamma)$ have been used. By our choice of variables the time dependent force is transformed to a modulation of the boundary and reset points, where the effective amplitude of the signal is modified by the prefactor

$$\begin{aligned}\text{(I)} \quad A_I &= \frac{e^{i\phi/2}}{(1 + \gamma)(1 - i\omega_s)} \\ \text{or} \quad \text{(II)} \quad A_{II} &= -\frac{e^{i\phi}}{2} \frac{1/(1 + \gamma) + i\omega_s}{(1 - i\omega_s)}\end{aligned}\tag{6.5}$$

We note that for $\gamma \geq 0$ the absolute value of this prefactor is less than unity in both cases. The time dependent absorbing boundaries and reset points of the system are given by

$$\begin{aligned}X_-(t) = x_- - \varepsilon f(t) &= -\frac{1}{2} - \frac{b_0 - \gamma}{1 + \gamma} - \varepsilon f(t) \\ X_+(t) = x_+ - \varepsilon f(t) &= \frac{1}{2} - \frac{b_0 - \gamma}{1 + \gamma} - \varepsilon f(t) \\ Y_-(t) = y_- + \varepsilon f(t) &= -\frac{1}{2} + \frac{b_0 + \gamma}{1 + \gamma} + \varepsilon f(t) \\ Y_+(t) = y_+ + \varepsilon f(t) &= \frac{1}{2} + \frac{b_0 + \gamma}{1 + \gamma} + \varepsilon f(t)\end{aligned}\tag{6.6}$$

Here, one may see that the signal shifts the absorbing boundary into different directions. In other words, at a given time the signal enhances transitions from one state to the other and depresses the inverse transition.

Once more, we consider the discrete variable $\sigma(t) = \pm 1$ that indicates which branch is currently occupied. Like in chapter 3 this is justified since we are interested only in that part of the neuronal activity that becomes manifest by action potentials and not in the subthreshold dynamics of the membrane voltage.

For $\gamma = b = 0$ (i.e., $x_- = y_- = -x_+ = -y_+$) the system is bistable and coincides with the model of a stochastic Schmitt trigger to the inverting terminal of which a harmonic signal and Ornstein-Uhlenbeck noise with correlation time one is added.

This case has been treated by Melnikov (1993) and like in case of the power spectrum we have just slightly to modify his calculation to obtain the linear response of our more general model.

We will discuss the analytical results for the same parameter sets like in chapter 3, namely,

regime	γ	b_0	$\rightarrow$	x_-	y_-	x_+	y_+
bistable	2/3	0	$\rightarrow$	-0.1	-0.1	0.9	0.9
excitable	1	2/5	$\rightarrow$	-0.2	0.2	0.8	1.2
oscillatory	7/3	0	$\rightarrow$	0.2	0.2	1.2	1.2

We would like to point out again that for these parameters **1)** bistable and oscillatory dynamics are symmetric while the excitable case is (necessarily) asymmetric **2)** in the excitable and bistable cases the fixed points (potential minima) are close to the thresholds (absorbing boundaries). We recall that due to the latter fact we observed coherence resonance manifested by maxima in the spectrum in either excitable and bistable cases.

The signal will in general modulate the currents via the absorbing boundaries at the branches. A signal can be referred to as weak if it only weakly modulates the stationary current. This is of course applies only *a posteriori*. We will see, however, that as in case of the LIF model the nonlinearity of the response is small as long as we do not change the regime of the model by the signal. In other words, we exclude signals that move the system between different dynamical regimes as for instance a suprathreshold signal in the excitable or bistable case would do. Furthermore, we consider in the following again the asymptotic linear response and neglect transients. This is justified for the very same reasons as pointed out in the previous chapter.

6.2. Linear response of the two-state system

Due to the presence of the signal the mean value $\langle \sigma(t) \rangle$ is expected to oscillate with the signal frequency. In the power spectrum this oscillation becomes manifest by a δ peak the prefactor of which is quantified by the spectral amplification. The latter we would like to know.

First of all, we may calculate the asymptotic probability densities $P_x(x, t)$ and $P_y(y, t)$ according to the Langevin equations (6.4) and reset conditions. These are the solutions of

$$\begin{aligned}
 \partial_t P_x(x, t) &= \partial_x(x + D\partial_x)P_x(x, t) = -\frac{\partial J_x(x, t)}{\partial x} \\
 \partial_t P_y(y, t) &= \partial_y(y + D\partial_y)P_y(y, t) = -\frac{\partial J_y(y, t)}{\partial y}.
 \end{aligned} \tag{6.7}$$

where we have excluded the points $X_+(t)$ and $Y_+(t)$. The densities must obey the following boundary and jump conditions

$$P_x(X_-(t), t) = 0 \quad (6.8)$$

$$[P_x(x, t)]_{X_+(t)} = 0 \quad (6.9)$$

$$\left[\frac{\partial P_x(x, t)}{\partial x} \right]_{X_+(t)} = - \left. \frac{\partial P_y(y, t)}{\partial y} \right|_{Y_-(t)} \quad (6.10)$$

$$\lim_{x \rightarrow \infty} P_x(x, t) = 0, \quad (6.11)$$

$$P_y(Y_-(t), t) = 0, \quad (6.12)$$

$$[P_y(y, t)]_{Y_+(t)} = 0, \quad (6.13)$$

$$\left[\frac{\partial P_y(y, t)}{\partial y} \right]_{Y_+(t)} = - \left. \frac{\partial P_x(x, t)}{\partial x} \right|_{X_-(t)}, \quad (6.14)$$

$$\lim_{y \rightarrow \infty} P_y(y, t) = 0. \quad (6.15)$$

In contrast to the stationary case treated in chapter 3 the absorbing and reset points vary in time. Due to these dependences also the asymptotic probability densities will depend on time, more exact, they will be periodically modulated with the signal frequency. This is reflected by the following Ansatz.

$$P_x(x, t) = P_{x,0}(x) + \varepsilon \left(e^{(\mathbb{F}^2 - x^2)/(4D)} p_x(x) A e^{-i\omega_s t} + c.c. \right) \quad (6.16)$$

$$P_y(y, t) = P_{y,0}(y) + \varepsilon \left(e^{(y_+^2 - y^2)/(4D)} p_y(y) A e^{-i\omega_s t} + c.c. \right) \quad (6.17)$$

Consequently, also the probability currents from state to state will possess a periodic component that influences the mean value $\langle \sigma(t) \rangle$.

$$\langle \sigma(t) \rangle = \int_{X_-(t)}^{\infty} dx P_x(x, t) - \int_{Y_-(t)}^{\infty} dy P_y(y, t) \quad (6.18)$$

(here we have averaged over the possible values $\sigma = \pm 1$ with the total probabilities to be in the respective state). It is readily seen that the difference between the currents yields the temporal derivative of the mean value.

$$\begin{aligned} \langle \dot{\sigma}(t) \rangle &= \int_{X_-(t)}^{\infty} dx \frac{\partial P_x(x, t)}{\partial t} - \int_{Y_-(t)}^{\infty} dy \frac{\partial P_y(y, t)}{\partial t} \\ &= 2(J(X_-(t)) - J(Y_-(t))) =: 2j(t) \end{aligned} \quad (6.19)$$

Note that when integrating the temporal derivatives of the respective density also the influxes at the reset points have to be taken into account (these points were excluded in the FPE's (6.7)) and thus each current enters the derivative twice - as an influx and as an efflux. This accounts for the factor 2 in the above derivation.

Here $j(t)$ is the net current that flows into the firing state or equivalently out of the silent state. Once this function is known, the time dependent mean value is given as the integral over time. The mean value then permits the determination of the SPA. Inserting the functions given by eqs. (6.16) and (6.17) into the FPEs yields the following equations for $p_x(x)$ and $p_y(y)$.

$$Dp_x'' - \left(\frac{x^2}{4D} - i\omega_s - \frac{1}{2}\right)p_x = 0 \quad (6.20)$$

$$Dp_y'' - \left(\frac{y^2}{4D} - i\omega_s - \frac{1}{2}\right)p_y = 0 \quad (6.21)$$

The general solutions for these equations can be written in terms of the parabolic cylinder functions. Here we use the functions

$$\psi_x(x) := \mathcal{D}_{i\omega_s}(x/\sqrt{D}) , \quad Y_x(x) := \psi_x(x)\psi_{x,2}(x_-) - \psi_x(x_-)\psi_{x,2}(x) \quad (6.22)$$

with $\psi_{x,2}(x)$ being another independent solution of eq. (6.20) that is not needed in the final formulae and is scaled such that $Y_x(x)$ possesses the properties

$$Y_{x-} := Y_x(x_-) = 0 , \quad Y'_{x-} := \left. \frac{dY_x}{dx} \right|_{x_-} = 1 \quad (6.23)$$

Completely analog we define

$$\psi_y(y) = \mathcal{D}_{i\omega_s}(y/\sqrt{D}) , \quad Y_y(y) = \psi_y(y)\psi_{y,2}(y_-) - \psi_y(y_-)\psi_{y,2}(y) \quad (6.24)$$

Apart from some inverted signs the calculation of the functions p_x and p_y is almost the same as in the previous chapter. Expanding the boundary and jump conditions eqs. (6.8), (6.9), (6.12), (6.13) and taking into account eqs. (6.11), (6.15) one finds

$$p_x(x) = \begin{cases} k_x Y_x(x)\psi_{x+} + e^{-\Delta x} \frac{r_0}{D} \frac{\psi_x(x)}{\psi_{x-}} & , \quad x_- < x < x_+ \\ \left(k_x Y_{x+} + e^{-\Delta x} \frac{r_0}{D\psi_{x-}} - \frac{r_0}{D\psi_{x+}} \right) \psi_x(x) & , \quad x > x_+ \end{cases} \quad (6.25)$$

and

$$p_y(y) = \begin{cases} k_y Y_y(y)\psi_{y+} - e^{-\Delta y} \frac{r_0}{D} \frac{\psi_y(y)}{\psi_{y-}} & , \quad y_- < y < y_+ \\ \left(k_y Y_{y+} - e^{-\Delta y} \frac{r_0}{D\psi_{y-}} + \frac{r_0}{D\psi_{y+}} \right) \psi_y(y) & , \quad y > y_+ \end{cases} \quad (6.26)$$

where $\Delta x = (x_+^2 - x_-^2)/(4D)$, $\Delta y = (y_+^2 - y_-^2)/(4D)$ and k_x, k_y are constants determined by the remaining conditions eqs. (6.10) and (6.14). Note that the different signs in eq. (6.25) and eq. (6.26) result from the signs by which the signal enters the boundaries and reset points in eq. (6.6).

In order to obtain the derivatives at the boundaries and reset points one has to calculate higher derivatives of the stationary densities at those points analog to the procedure in the previous chapter. Doing so, we find

$$\left. \frac{dP_x(x, t)}{dx} \right|_{X_-(t)} = \frac{r_0}{D} + \varepsilon \left\{ A e^{-i\omega_s t} \left[k_x \psi_{x+} e^{\Delta x} + \frac{r_0}{D} \left(\frac{\psi'_{x-}}{\psi_{x-}} + \frac{x_-}{2D} \right) \right] + c.c. \right\} \quad (6.27)$$

$$\left[\frac{dP_x(x, t)}{dx} \right]_{X_+(t)} = -\frac{r_0}{D} - \varepsilon \left\{ A e^{-i\omega_s t} \left[k_x \psi_{x-} + \frac{r_0}{D} \left(\frac{\psi'_{x+}}{\psi_{x+}} + \frac{x_+}{2D} \right) \right] + c.c. \right\} \quad (6.28)$$

$$\left. \frac{dP_y(y, t)}{dy} \right|_{Y_-(t)} = \frac{r_0}{D} + \varepsilon \left\{ A e^{-i\omega_s t} \left[k_y \psi_{y+} e^{\Delta y} - \frac{r_0}{D} \left(\frac{\psi'_{y-}}{\psi_{y-}} + \frac{y_-}{2D} \right) \right] + c.c. \right\} \quad (6.29)$$

$$\left[\frac{dP_y(y, t)}{dy} \right]_{Y_+(t)} = -\frac{r_0}{D} - \varepsilon \left\{ A e^{-i\omega_s t} \left[k_y \psi_{y-} - \frac{r_0}{D} \left(\frac{\psi'_{y+}}{\psi_{y+}} + \frac{y_+}{2D} \right) \right] + c.c. \right\} \quad (6.30)$$

Using now the remaining conditions one obtains

$$k_x = \frac{r_0}{D} \frac{e^{\Delta y} [\psi_{y+} (\frac{\psi'_{x-}}{\psi_{x-}} + \frac{x_- + y_+}{2D}) + \psi'_{y+}] - \psi_{y-} (\frac{\psi'_{x+}}{\psi_{x+}} + \frac{x_+ + y_-}{2D}) - \psi'_{y-}}{\psi_{x-} \psi_{y-} - e^{\Delta x} e^{\Delta y} \psi_{x+} \psi_{y+}} \quad (6.31)$$

$$k_y = -\frac{r_0}{D} \frac{e^{\Delta x} [\psi_{x+} (\frac{\psi'_{y-}}{\psi_{y-}} + \frac{x_+ + y_-}{2D}) + \psi'_{x+}] - \psi_{x-} (\frac{\psi'_{y+}}{\psi_{y+}} + \frac{x_- + y_+}{2D}) - \psi'_{x-}}{\psi_{x-} \psi_{y-} - e^{\Delta x} e^{\Delta y} \psi_{x+} \psi_{y+}} \quad (6.32)$$

By these expressions the response of the system to the signal thus also that of the probability currents is entirely determined. Applying the recurrence relation eq. (A.5) and some additional manipulations yield the net current into the firing state as follows.

$$\begin{aligned} j(t) = \varepsilon A e^{-i\omega_s t} \frac{i r_0 \omega_s / \sqrt{D}}{e^{\Delta x} e^{\Delta y} \psi_{x+} \psi_{y+} - \psi_{x-} \psi_{y-}} \{ & (e^{\Delta y} \psi_{y+} - \psi_{y-}) (e^{\Delta x} \Phi_{x+} - \Phi_{x-}) + \\ & + (e^{\Delta y} \Phi_{y+} - \Phi_{y-}) (e^{\Delta x} \psi_{x+} - \psi_{x-}) \} + c.c. \end{aligned} \quad (6.33)$$

The functions Φ are given by the following parabolic cylinder functions

$$\Phi_{x\pm} = \mathcal{D}_{i\omega_s - 1} \left(\frac{x_{\pm}}{\sqrt{D}} \right), \quad \Phi_{y\pm} = \mathcal{D}_{i\omega_s - 1} \left(\frac{y_{\pm}}{\sqrt{D}} \right) \quad (6.34)$$

To obtain $\sigma(t)$ one may easily integrate $2j(t)$ with respect to time according to eq. (6.19). The constant of integration is apparently given by the time independent

mean value given by eq. (3.59). We may also express the time dependent mean value by spectral power amplification η and phase shift ϕ .

$$\begin{aligned}\langle \sigma(t) \rangle &= \langle \sigma \rangle_0 + \varepsilon \left[\frac{2r_0 A e^{-i\omega_s t} / \sqrt{D}}{e^{\Delta x} e^{\Delta y} \psi_{x+} \psi_{y+} - \psi_{x-} \psi_{y-}} \left\{ (e^{\Delta y} \psi_{y+} - \psi_{y-}) (e^{\Delta x} \Phi_{x+} - \Phi_{x-}) + \right. \right. \\ &\quad \left. \left. + (e^{\Delta y} \Phi_{y+} - \Phi_{y-}) (e^{\Delta x} \psi_{x+} - \psi_{x-}) \right\} + c.c. \right] \\ &= \langle \sigma \rangle_0 + \varepsilon \sqrt{\eta} \cos(\omega_s t + \phi - \varphi)\end{aligned}\tag{6.35}$$

The amplification can be read off to be

$$\eta = \frac{16r_0^2}{D} \left| A \frac{(e^{\Delta y} \psi_{y+} - \psi_{y-}) (e^{\Delta x} \Phi_{x+} - \Phi_{x-}) + (e^{\Delta y} \Phi_{y+} - \Phi_{y-}) (e^{\Delta x} \psi_{x+} - \psi_{x-})}{e^{\Delta x} e^{\Delta y} \psi_{x+} \psi_{y+} - \psi_{x-} \psi_{y-}} \right|^2\tag{6.36}$$

The phase shift φ in turn is given by the complex phase of the expression within the bars, however, we will not discuss it in the following. The total spectrum is given again by the sum of the δ peak and the background spectrum.

$$S(\omega) = S_{bg}(\omega) + \frac{\varepsilon \pi}{2} \eta [\delta(\omega - \omega_s) + \delta(\omega + \omega_s)]\tag{6.37}$$

Within linear response theory the background spectrum is given by eq. (3.62), i.e., by the spectrum in absence of a signal.

Note that in Lindner and Schimansky-Geier (2000) the amplification factor was incorrectly defined. In this paper, half of the output signal intensity (corresponding to the prefactor of one spectral δ spike) was divided by the square of the signal amplitude, i.e. just by ε^2 . In the correct definition that we use here the amplification is given by the output intensity scaled by the input intensity $\varepsilon^2 \pi$ (corresponding to the total intensity of both peaks). Consequently, also the plots of η that we will show in the following differ by a factor of $\pi/2$ from those presented in Lindner and Schimansky-Geier (2000).

We recall that the factor A appearing in eq. (6.36) has to be either A_I or A_{II} from eq. (6.5) according to the driving mode under consideration. In the following section we compare the response in these modes as well as in all dynamical regimes of the two state model.

6.3. Spectral power amplification of the two state model

Looking at eq. (6.5) it becomes apparent that the amplifications in the two driving modes differ by a frequency dependent factor

$$\frac{\eta_{II}}{\eta_I} = (1 + (1 + \gamma)^2 \omega_s^2).$$

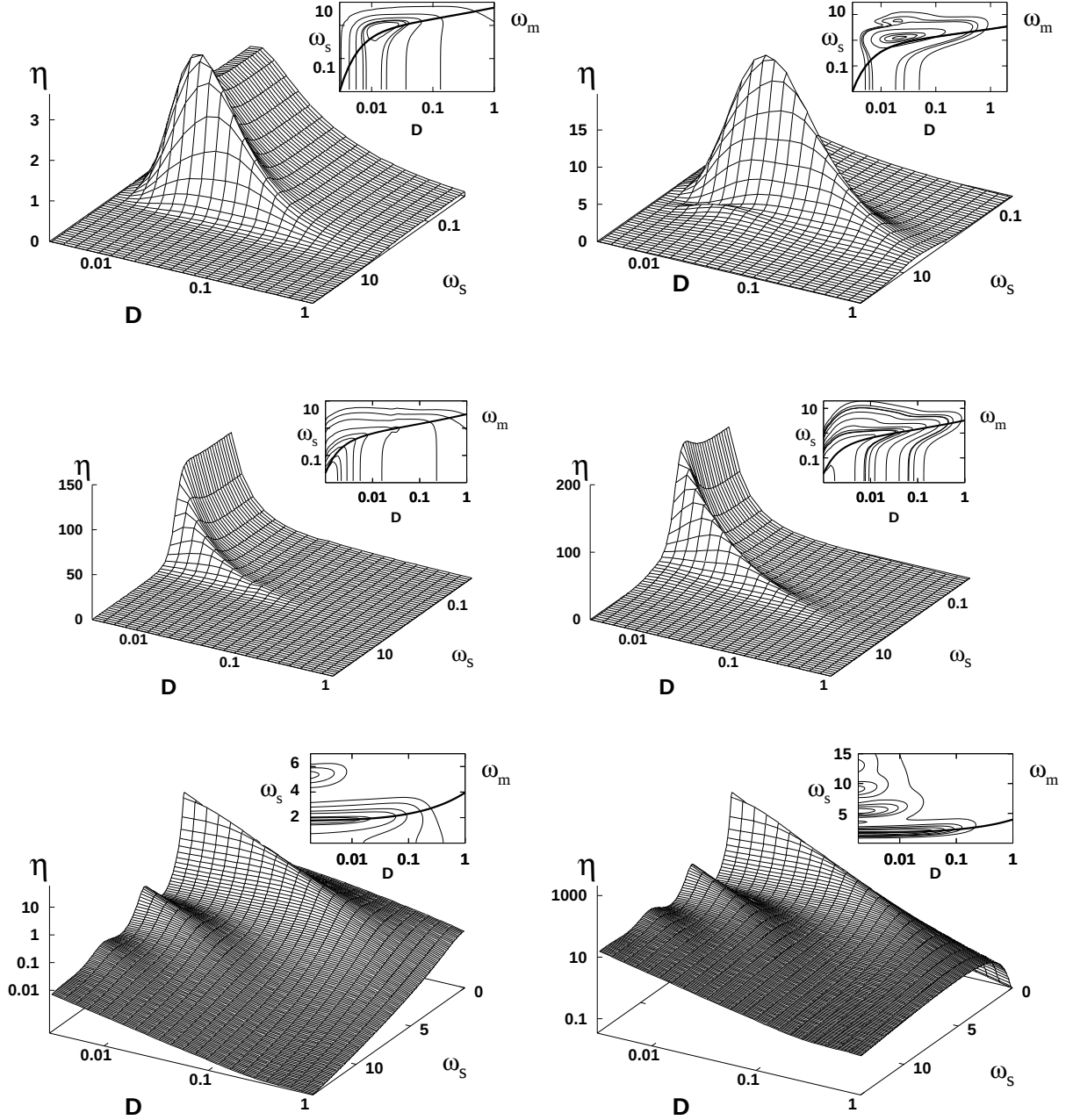


Figure 6.1.: Spectral amplification versus noise intensity and driving frequency for driving mode *I* (left column) and mode *II* (right column). Upper, mid and lower panels are for the excitable, bistable and oscillatory regime of the model, respectively. Shown in the insets: contour lines of the respective amplification compared to the mean frequency that is drawn as a function of the noise intensity.

Since γ is a positive parameter, the response is obviously larger in driving mode (II), in particular for growing frequency. In fact, all resonance phenomena we will discuss in the following are in general more pronounced in this case. This is important because a direct driving of the voltage dynamics is more realistic from the biological point of view.

Let us consider the amplification in the excitable regime. It is shown as a function of noise intensity and driving frequency in the upper panels of Fig. 6.1 for driving mode (I) (left) and (II) (right). First of all, as expected from findings by Wiesenfeld et al. (1994); Longtin (1995b) and others, stochastic resonance becomes manifest by a maximum versus D for arbitrary but fixed driving frequency. Furthermore, for a finite range of moderate noise intensity, there exists a nonmonotonous dependence of the amplification on frequency. This is more pronounced in driving mode (II) (signal on voltage) and results in both modes in an overall maximum of η with respect to noise intensity and driving frequency, very similar to our observations made in the previous chapter for the LIF neuron. Also the rationale behind this effect is obviously the same like explained there. The FN model possesses a noise induced eigenfrequency due to coherence resonance. The nonmonotonous dependence is a classical resonance with respect to this eigenfrequency. Additionally, the resonance with respect to regularity (CR) appears parametrically close to the noise intensity at which stochastic resonance is observed, consequently, the global maximum is attained at finite frequency.

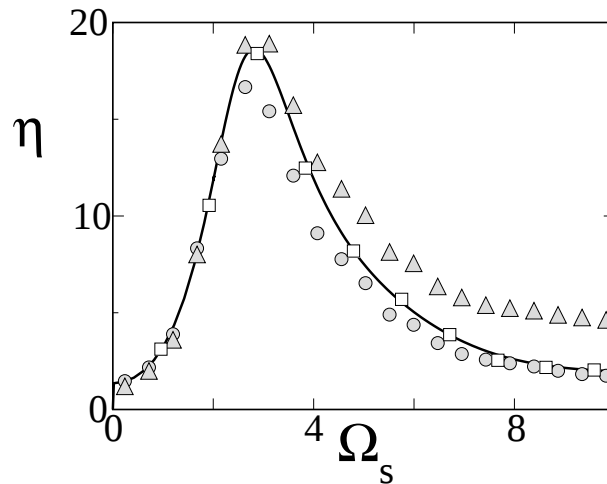


Figure 6.2.: Spectral power amplification for driving mode (II) in the excitable regime versus (original) driving frequency Ω_s . Results from numerical simulations (symbols) of the FN dynamics at finite ϵ compared to theory (solid line). Circles: two-state filtering with $\epsilon = 10^{-3}$. Squares: two-state filtering with $\epsilon = 10^{-4}$. Triangles: the amplification for the voltage variable $v(t)$ at $\epsilon = 10^{-4}$. In all simulation data: $\gamma = 1$, $b_0 = 0.4$, $Q = 0.066$, $\epsilon = 0.065$.

The resonance is once more shown in Fig. 6.2 for the driving mode (*II*) and compared to numerical data from the simulation of the FN dynamics at finite time scale separation ϵ . Note that we show the amplification for the original frequency of the FN model and that also the original parameters have been used. For the spectral amplification of the two state variable $\sigma(t)$ there is an almost perfect agreement for $\epsilon = 10^{-4}$, the resonance is slightly weakened for $\epsilon = 10^{-3}$. If one considers the data for the original continuous voltage variable one finds also an surprisingly good agreement with the theory for low up to moderate frequencies¹. At larger frequencies the response of the voltage is slightly stronger. Note, however, that height and position of the resonance maximum are almost perfectly reproduced by the two-state approximation.

The similarities and differences between the driving modes deserve some additional remarks. First, both responses coincide in the adiabatic limit where the amplification tends to the following expression

$$\eta(\omega_s = 0) = \left(\frac{d\langle\sigma(\varepsilon)\rangle_0}{d\varepsilon} \Big|_{\varepsilon=0} \right)^2 \quad (6.38)$$

where ε is a static negative (positive) change of the absorption and reset points in state $\sigma = -1$ ($\sigma = +1$). This relation holds in general (i.e., also for the oscillatory and bistable dynamics) and may be expressed by quadrature formulae using the relation eq. (3.59). Second, the amplification in driving mode (*II*) grows much stronger with respect to frequency than that in mode (*I*). The reason for this is easily found. In driving mode (*I*) the signal acts directly on the recovery variable. Alternatively, we may say that it acts low pass filtered on the dynamics of the voltage variable and is therefore weaker in effective amplitude for growing frequencies than an unfiltered signal (i.e., driving mode (*II*)) is. Third, due to the stronger response at higher frequencies, the data for driving mode (*II*) show also a second local maximum versus frequency that implies a second local maximum with respect to both noise intensity and driving frequency. In between the two maxima, the dependence of the amplification on D reveals further interesting features (Fig. 6.3). In this range, the spectral amplification possesses a fairly broad maximum versus D (note, in particular, curve *b* in Fig. 6.3 where η is almost constant over one order of magnitude of D). It may have even two maxima (Fig. 6.3, curve labeled by *c*). For a neuron transmitting signals within this frequency band a fine tuning of the noise is not needed, somewhat similar to the effect of stochastic resonance without tuning by ensemble transmission (Collins et al., 1995b). Note, however, that for the frequency range in question the amplification is small compared to the overall maximum and thus it seems to be questionable whether the neuron actually operates in the mentioned frequency range.

¹Actually, within the two-state approximation, we should take account of an correction factor for the effective (negative and positive) amplitudes, i.e. the variance of the voltage in the stationary state (McNamara and Wiesenfeld, 1989). If, on the other hand, the action potential is approximately stereotypical in shape, this correction factor is of minor biological interest.

In the bistable case (Fig. 6.1, mid panels) we observe again stochastic resonance. In both driving modes, η passes at fixed frequency through a maximum as a function of noise. This is actually shown only for frequencies larger than 0.45. Since the system was chosen to be symmetric the overall maximum is not at finite frequency. The maximum with respect to D grows and shifts to smaller noise intensities with decreasing frequency. Regardless of the dynamics and the regularity of the trajectory $\sigma(t)$ in the absence of a signal, the maximal (infinite) amplification is achieved for $\omega_s \rightarrow 0, D \rightarrow 0$. In this trivial limit, the signal introduces in the originally symmetric system an arbitrary small asymmetry for a given half period of the signal. For infinitesimal weak noise, all probability moves to one of the states (that with higher barrier at the absorbing boundary depending on the signal phase). Consequently, the mean value switches between -1 and 1 implying at arbitrary small signal amplitude an infinite amplification.

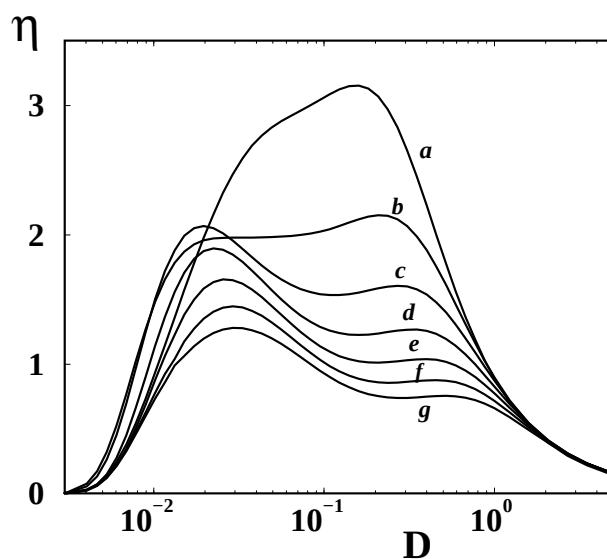


Figure 6.3.: Spectral power amplification in the excitable case and driving mode (II) versus noise intensity at different values of driving frequency (a)-(g): $\omega_s = 4, 5, 6, 7, 8, 9$ and 10.

Although the overall maximum of the amplification is not at finite frequencies like in the excitable case, there exists apparently a nonmonotonous dependence on the driving frequency for a finite range of the noise intensity. This is again due to coherence resonance and is hence due to the non-potential character of the FN model. The effect is not obtained for the parameters of the Schmitt trigger ($x_- = y_- = -x_+ = -y_+$) where a noise-induced eigenfrequency is absent.

Eventually, we consider the symmetric oscillatory case (lower panels in Fig. 6.1). Like for the corresponding regime in the LIF model we obtain at weak noise large peaks

close to the deterministic eigenfrequency of the system that is obviously given by

$$\omega_0 = 2\pi (\ln(x_+/x_-) + \ln(y_+/y_-))^{-1}. \quad (6.39)$$

Peaks are also present at the odd harmonics of this frequency $((2k+1)\omega_0, k = 1, 2, \dots)$. If the driving frequency matches exactly ω_0 or one of its harmonics the amplification diverges in the limit $D \rightarrow 0$ while for a different frequency it reaches a finite value. That is the same behavior like for the amplification of the LIF model in the oscillatory mode. Likewise we find a stochastic resonance for positively detuned driving frequencies (Fig. 6.4) as it was observed in the previous chapter. The reason is the same like there, namely, the decrease in mean and increase in variance of the interspike interval that permits the neuron to (statistically !) adapt the firing times to the “too rapid” input signal.

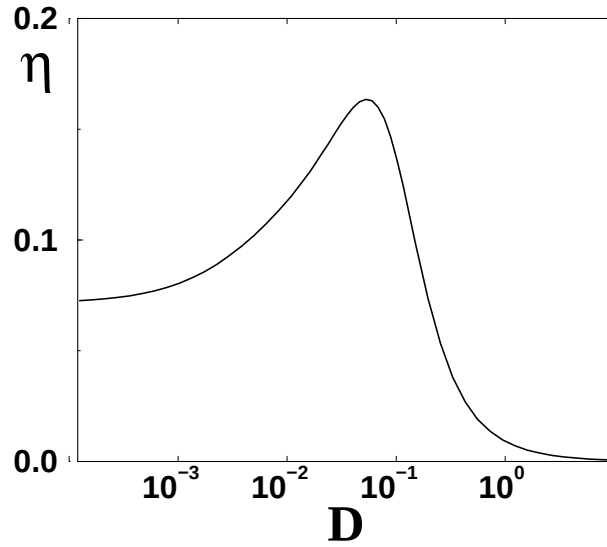


Figure 6.4.: Spectral power amplification for driving mode (I) in the oscillatory case versus noise intensity at $\omega_s = 3.0$ with the deterministic eigenfrequency $\omega_0 \approx 1.79$

The difference between the responses in the two driving modes appears mainly in their amplitudes. As can be read off from the scaling of η in the left and right lower panels, the amplifications differ by almost two order of magnitudes at the eigenfrequency ω_0 due to the fact that it grows with γ . The latter parameter is large in case of an oscillatory dynamics.

6.4. Summary

We have calculated the linear response of a two state model which is the limit case of the stochastic FitzHugh-Nagumo system driven by a periodic signal. Stochastic resonance and a nonmonotonous dependence of the spectral power amplification on the driving frequency were found in either the excitable and bistable regimes of the dynamics. This was shown to be due to the noise induced eigenfrequency at moderate noise and is thus a consequence of coherence resonance exhibited in these cases. A stochastic resonance like effect was also revealed in the oscillatory system for driving frequencies close but above the deterministic eigenfrequency of the system.

7. Conclusions

We have provided a number of analytical results for noise-induced resonance phenomena in simple stochastic systems. Particularly, the insights achieved for neuronal dynamics considered in this work deserve some comments.

Coherence resonance and bandpass filtering

In this thesis we have given theoretical evidence that model neurons like the leaky integrate-and-fire and the FitzHugh-Nagumo systems exhibit the phenomenon of coherence resonance (CR). Is it thus possible to observe CR in real neurons? We are confident that this is indeed the case since suboptimal manifestations of a noise-induced eigenfrequency can be found in spike trains from experiment (Bair et al., 1994). A promising candidate for a potential experiment would be a sensory neuron with low firing rate and small internal noise. A stimulation by a constant input (implying a constant base current) plus a short correlated noise might reveal an optimum of regularity in the spike train at a finite noise intensity. Because of internal noise and neuronal adaption of the firing rate to a constant input it might well be that the effect can never be such pronounced as in the theoretical models where parameters can be fine tuned. However, as we have seen in chapters 5 and 6, even a weak noise-induced eigenfrequency may have strong implications for the transmission of a periodic signal in particular situations (cf. Figs. 5.15 and 6.2).

One may speculate whether the noise-induced preference in signal transmission that is due to coherence resonance may have a functional role in neuronal signal processing. For the simple transmission purpose of signal reproduction in the firing rate, a homogeneous response function with respect to frequency appears to be more natural than the one we have found in case of coherence resonance. Indeed, several authors have argued that a beneficial role of noise could be to reduce large resonances with the internal time scale of the neuron in the deterministic firing regime (Knight, 1972a; Holden, 1976). Partly in opposition to this notion, one may look upon the neuron as a bandpass filter for subthreshold input (Plesser and Geisel, 1999a; Plesser, 1999) with a selectivity for frequencies depending strongly on constant parameters of stimulation like base current and overall noise intensity. The latter can be changed by the neural background, i.e. the neural network may switch the response behavior of the single unit from uniform transmission to a transmission selective for a certain frequency band.

Stochastic resonance and background activity

We have shown that stochastic resonance can be found in all dynamical regimes of the investigated model neurons. While in the oscillatory (deterministic or limit cycle) regimes, the effect occurs only for specific driving frequencies and relies on the increased variability of the interspike interval, the noise enhanced signal transmission is generic in the noise activated (excitable or bistable) regimes of the models. It is observed irrespective of the driving mode (driving in voltage or recovery dynamics, FN model) or the nature of the signal (additive or noise coded signals, LIF model). The only presumption is weakness of the signal amplitude. For sensory neurons the interpretation of this weakness is straightforward: stochastic resonance offers a simple mechanism explaining the astonishing sensitivity found in the sensory systems of many organisms. Also for higher order sensory or cortical neurons the weak signal amplification might be of relevance, possibly with regard to energy consumption. One may hypothesize that, by virtue of stochastic resonance, small signal amplitudes suffice for stable signal transmission since the latter is supported and amplified by background activity - that could mean by a superposition of many independent signals each of which is processed in a similar way in a different region of the neural network.

Noise coded signals - an efficient way neurons talk to each other

Noise may not only induce regularity of spike trains or enhance signal transmission with respect to periodic stimulation. As we have seen in chapter 5 it may also serve as an efficient signal carrier. Noise coded signals of a broad frequency band are conveyed with a strong amplitude. If population coding is involved, this implies a fast signal transmission beyond the limits that are known for additive signals. The presence of noise coded signals does not require a sophisticated setup of signal transmission but appears naturally if the signal is encoded in the firing rate of a population consisting of excitatory and inhibitory neurons. Extended studies of the model should take account of synaptic filtering as well as correlations between the neurons within the input ensemble. Further insights may only be possible looking at real neurons - an experimental study of the transmission features for noise coded signals is highly desirable.

To conclude, we have theoretically demonstrated that noise may influence the neuronal dynamics in three ways, possibly useful for signal transmission and processing: 1) by an increase of regularity of the output spike train 2) by an enhancement of signal transmission with respect to weak signals and 3) as a signal carrier in neuronal communication. The results presented in this thesis provided thus further evidence for a beneficial role of noise in the nervous system.

A. The parabolic cylinder functions

A.1. General properties

The parabolic cylinder functions are defined as the solutions of the following differential equation

$$\frac{d^2y}{dx^2} - (x^2/4 + a)y = 0 \quad (\text{A.1})$$

The standard solutions of eq. (A.1) are denoted by $U(a, x)$ and $V(a, x)$. Throughout the text, we make explicit use of only the first function in a notation that is due to Whittaker, namely

$$U(a, x) = \mathcal{D}_{-a-1/2}(x) \quad (\text{A.2})$$

One readily verifies that if $y(a, x)$ is a solution of eq. (A.1) then $y(a, -x)$ is another (in general, independent) solution of it. In particular, this holds true for the function

$$\mathcal{D}_{-a-1/2}(-x)$$

used within the chapters 2 and 5.

The Wronskian of the two independent solutions $U(a, x)$ and $V(a, x)$ is constant what can be easily shown utilizing eq. (A.1)

$$W\{U, V\} = \frac{dU}{dx}V(x) - U(x)\frac{dV}{dx} = \text{const.} \quad (\text{A.3})$$

There is a useful relation between the two solutions

$$\pi V(a, x) = \Gamma\left(\frac{1}{2} + a\right) (\sin \pi a U(a, x) + U(a, -x)) \quad (\text{A.4})$$

Furthermore, the function $U(a, x)$ obeys the following recurrence relation

$$U'(a, x) + \frac{1}{2}xU(a, x) + \left(a + \frac{1}{2}\right)U(a+1, x) = 0 \quad (\text{A.5})$$

where the prime denotes the derivative with respect to x .

For the numerical evaluation of $U(a, x)$ its relation to the (more common) confluent

hypergeometric function (Kummer's function) can be utilized

$$U(a, \pm x) = \frac{\sqrt{\pi} 2^{-\frac{1}{4}-\frac{1}{2}a} e^{-\frac{1}{4}x^2}}{\Gamma(\frac{3}{4} + \frac{1}{2}a)} M(\frac{1}{2}a + \frac{1}{4}, \frac{1}{2}, \frac{1}{2}x^2) \mp \frac{\sqrt{\pi} 2^{\frac{1}{4}-\frac{1}{2}a} x e^{-\frac{1}{4}x^2}}{\Gamma(\frac{1}{4} + \frac{1}{2}a)} M(\frac{1}{2}a + \frac{3}{4}, \frac{3}{2}, \frac{1}{2}x^2) \quad (\text{A.6})$$

where $M(a, b, z)$ is Kummer's function defined by (Abramowitz and Stegun, 1970, formula (13.1.2))

$$M(a, b, z) = 1 + \frac{az}{b} \frac{(a)_2 z^2}{(b)_2 2!} + \dots + \frac{(a)_n z^n}{(b)_n n!} + \dots$$

$$(a)_n := a(a+1)(a+2) \cdots (a+n-1), (a)_0 = 1$$

The function $M(a, b, z)$ can be obtained for arbitrary complex values of the arguments by computer programs like *Maple* or *Mathematika*.

A.2. Asymptotics and special values

We rewrite some asymptotic expressions for $U(a, z)$ and give also the corresponding expressions for the function $\mathcal{D}_{i\omega-n}(-x/\sqrt{D})$ ($n = 0, 1, 2$) used in the text.

Asymptotics for small D

Small noise intensity D implies that the parabolic cylinder function is taken at a large (positive or negative) real argument z .

For $z \gg 0$ and $|a|$ moderate we have we have

$$U(a, x) \sim e^{-x^2/4} x^{-a-1/2} \left\{ 1 - \frac{(a + \frac{1}{2})(a + \frac{3}{2})}{2x^2} + \frac{(a + \frac{1}{2})(a + \frac{3}{2})(a + \frac{5}{2})(a + \frac{7}{2})}{2 \cdot 4x^4} - \dots \right\} \quad (\text{A.7})$$

$$V(a, x) \sim \sqrt{\frac{2}{\pi}} e^{x^2/4} x^{a-1/2} \left\{ 1 + \frac{(a - \frac{1}{2})(a - \frac{3}{2})}{2x^2} + \frac{(a - \frac{1}{2})(a - \frac{3}{2})(a - \frac{5}{2})(a - \frac{7}{2})}{2 \cdot 4x^4} + \dots \right\} \quad (\text{A.8})$$

The latter relation allows in combination with eq. (A.4) an asymptotic expansion for large *negative* values of z , i.e. for $|z| \gg |\alpha|$ and $z < 0$ we have

$$U(a, x) \sim \frac{\sqrt{2\pi} e^{x^2/4} |x|^{a-1/2}}{\Gamma(1/2 + a)} \left\{ 1 + \frac{(a - \frac{1}{2})(a - \frac{3}{2})}{2x^2} + \frac{(a - \frac{1}{2})(a - \frac{3}{2})(a - \frac{5}{2})(a - \frac{7}{2})}{2 \cdot 4x^4} + \dots \right\} - \sin(\pi a) e^{-x^2/4} |x|^{-a-1/2} \left\{ 1 - \frac{(a + \frac{1}{2})(a + \frac{3}{2})}{2x^2} + \frac{(a + \frac{1}{2})(a + \frac{3}{2})(a + \frac{5}{2})(a + \frac{7}{2})}{2 \cdot 4x^4} - \dots \right\} \quad (\text{A.9})$$

For the special functions with moderate or small value of x

$$\mathcal{D}_{i\omega}(-x/\sqrt{D}), \quad \mathcal{D}_{i\omega-1}(-x/\sqrt{D}), \quad \mathcal{D}_{i\omega-2}(-x/\sqrt{D})$$

we find thus for $D \rightarrow 0$ and $x < 0$ ($z > 0$)

$$\mathcal{D}_{i\omega}(-x/\sqrt{D}) \sim e^{-x^2/(4D)} \left(\frac{-x}{\sqrt{D}} \right)^{i\omega} \left\{ 1 + \frac{i\omega(1-i\omega)}{2x^2} D + \dots \right\} \quad (\text{A.10})$$

$$\mathcal{D}_{i\omega-1}(-x/\sqrt{D}) \sim e^{-x^2/(4D)} \left(\frac{-x}{\sqrt{D}} \right)^{i\omega-1} \left\{ 1 - \frac{(1-i\omega)(2-i\omega)}{2x^2} D + \dots \right\} \quad (\text{A.11})$$

$$\mathcal{D}_{i\omega-2}(-x/\sqrt{D}) \sim e^{-x^2/(4D)} \left(\frac{-x}{\sqrt{D}} \right)^{i\omega-2} \left\{ 1 - \frac{(2-i\omega)(3-i\omega)}{2x^2} D + \dots \right\} \quad (\text{A.12})$$

while for $x > 0$ we have

$$\begin{aligned} \mathcal{D}_{i\omega}(-x/\sqrt{D}) &\sim \frac{\sqrt{2\pi}e^{x^2/(4D)}}{\Gamma(-i\omega)} \left(\frac{x}{\sqrt{D}} \right)^{-i\omega-1} \left\{ 1 + \frac{(1+i\omega)(2+i\omega)}{2x^2} D + \dots \right\} \\ &\quad - \sin(\pi(-i\omega - \frac{1}{2})) e^{-x^2/(4D)} \left(\frac{x}{\sqrt{D}} \right)^{i\omega} \left\{ 1 + \frac{i\omega(1-i\omega)}{2x^2} D + \dots \right\} \end{aligned} \quad (\text{A.13})$$

$$\begin{aligned} \mathcal{D}_{i\omega-1}(-x/\sqrt{D}) &\sim \frac{\sqrt{2\pi}e^{x^2/(4D)}}{\Gamma(1-i\omega)} \left(\frac{x}{\sqrt{D}} \right)^{-i\omega} \left\{ 1 + \frac{i\omega(1+i\omega)}{2x^2} D + \dots \right\} \\ &\quad - \sin(\pi(\frac{1}{2} - i\omega)) e^{-x^2/(4D)} \left(\frac{x}{\sqrt{D}} \right)^{i\omega-1} \left\{ 1 - \frac{(1-i\omega)(2-i\omega)}{2x^2} D + \dots \right\} \end{aligned} \quad (\text{A.14})$$

$$\begin{aligned} \mathcal{D}_{i\omega-2}(-x/\sqrt{D}) &\sim \frac{\sqrt{2\pi}e^{x^2/(4D)}}{\Gamma(2-i\omega)} \left(\frac{x}{\sqrt{D}} \right)^{-i\omega+1} \left\{ 1 - \frac{i\omega(1-i\omega)}{2x^2} D + \dots \right\} \\ &\quad - \sin(\pi(\frac{3}{2} - i\omega)) e^{-x^2/(4D)} \left(\frac{x}{\sqrt{D}} \right)^{i\omega-2} \left\{ 1 - \frac{(2-i\omega)(3-i\omega)}{2x^2} D + \dots \right\} \end{aligned} \quad (\text{A.15})$$

Asymptotics for large frequency

According to (Buchholz, 1953, p. 110) for large values of ω we have

$$\mathcal{D}_a(z) \sim \frac{1}{\sqrt{2}} \exp \left[iz\sqrt{a} + \frac{a}{2}(\ln(a/e) - i\pi) \right] \times \left(\sum_{n=0}^{N-1} i^n (2a)^{-n/2} Q_n(z) + \mathcal{O}(|a|^{-N}) \right) \quad (\text{A.16})$$

where the first three functions $Q_n(z)$ are given by

$$Q_0(z) = 1, \quad Q_1(z) = -\frac{z(z^2 - 6)}{12\sqrt{2}}, \quad Q_2(z) = \frac{z^6 - 12z^4 - 36z^2 + 96}{576} \quad (\text{A.17})$$

A. The parabolic cylinder functions

Taking only into account $Q_0(z)$ (moderate to large noise strength) one obtains

$$\mathcal{D}_{i\omega}\left(-\frac{x}{\sqrt{D}}\right) \sim \frac{1}{\sqrt{2}} \exp \left[-x\sqrt{\frac{\omega}{D}} \cos\left(\frac{3\pi}{4}\right) + \frac{\omega\pi}{4} - i \left(x\sqrt{\frac{\omega}{D}} \sin\left(\frac{3\pi}{4}\right) - \frac{\omega}{2} \ln\left(\frac{\omega}{e}\right) \right) \right] \quad (\text{A.18})$$

The real part of the exponent consists of two parts, the linear term that is independent of x and the square root term that depends on x . We note that the latter is positive for $x > 0$ since

$$\cos\left(\frac{3\pi}{4}\right) = -1/\sqrt{2} < 0.$$

Similar arguments hold asymptotically for the other two functions of interest

$$\mathcal{D}_{i\omega-1}\left(-\frac{x}{\sqrt{D}}\right) \sim \frac{1}{\sqrt{2}} \exp \left[-xi\sqrt{\frac{i\omega-1}{D}} + \frac{i\omega-1}{2} \left(\ln\left(\frac{i\omega-1}{e}\right) - i\pi \right) \right] \quad (\text{A.19})$$

$$\mathcal{D}_{i\omega-2}\left(-\frac{x}{\sqrt{D}}\right) \sim \frac{1}{\sqrt{2}} \exp \left[-xi\sqrt{\frac{i\omega-2}{D}} + \frac{i\omega-2}{2} \left(\ln\left(\frac{i\omega-2}{e}\right) - i\pi \right) \right] \quad (\text{A.20})$$

Vanishing frequency

For values of $a = n + 1/2$ (n - integer) we have the following recurrence relation (Abramowitz and Stegun, 1970, sec. 19.14)

$$U\left(n + \frac{1}{2}, x\right) = e^{x^2/4} Hh_n(x), \quad Hh_n(x) = \int_x^\infty dt Hh_{n-1}(t), \quad Hh_{-1} = e^{-x^2/2} \quad (\text{A.21})$$

By means of this we find

$$\mathcal{D}_0\left(-\frac{x}{\sqrt{D}}\right) = U\left(-\frac{1}{2}, -\frac{x}{\sqrt{D}}\right) = e^{-x^2/(4D)} \quad (\text{A.22})$$

$$\begin{aligned} \mathcal{D}_{-1}\left(-\frac{x}{\sqrt{D}}\right) &= U\left(\frac{1}{2}, -\frac{x}{\sqrt{D}}\right) = e^{x^2/4} \int_{-x/\sqrt{D}}^\infty dt e^{-t^2/2} \\ &= \sqrt{\frac{\pi}{2}} e^{x^2/(4D)} \operatorname{erfc}\left(-\frac{x}{\sqrt{2D}}\right) \end{aligned} \quad (\text{A.23})$$

$$\begin{aligned} \mathcal{D}_{-2}\left(-\frac{x}{\sqrt{D}}\right) &= U\left(\frac{3}{2}, -\frac{x}{\sqrt{D}}\right) = e^{x^2/4} \int_{-x/\sqrt{D}}^\infty dt \sqrt{\frac{\pi}{2}} \operatorname{erfc}(t) = e^{x^2/4} \int_{x/\sqrt{D}}^\infty dt \left(t + \frac{x}{\sqrt{D}}\right) e^{-t^2/2} \\ &= e^{-x^2/(4D)} + x\sqrt{\frac{\pi}{2D}} e^{x^2/(4D)} \operatorname{erfc}\left(-\frac{x}{\sqrt{2D}}\right) \end{aligned} \quad (\text{A.24})$$

where we have used for the last function a relation for repeated integrals of the error function (Abramowitz and Stegun, 1970, cf. eq. (7.2.3)).

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