Impacts of Statistical Feedback on the Flexibility-Accuracy Trade-off in Biological Systems

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Abstract. Biological systems possess the ability to adapt quickly and adequately to both environmental and internal changes. This vital ability cannot be explained in terms of conventional stochastic processes because such processes are characterized by a trade-off between flexibility and accuracy, that is, they either show short transition times (large Kramers escape rates) to broad steady-state distributions or long transition times to sharply peaked distributions. To develop a stochastic theory for systems exhibiting both flexibility and accuracy, we study systems under the impact of white noise multiplied with an accordant statistical measure, here the probability density. This results in negative feedback and circular causality: the more probable a stable state the less it will be affected by noise and, conversely, the less a stable state is affected by noise the more probable it is. Using nonlinear Fokker-Planck equations, steady states are computed via transformations of solutions of the corresponding linear Fokker-Planck equations. Transients reveal rapidly evolving and sharply peaked probability densities and thus mimic systems characterized by both flexibility and accuracy.

Key words: Circular causality, flexibility-accuracy trade-offs, nonlinear Fokker-Planck equations, statistical feedback

1. Introduction

Biological systems are in permanent contact with their environment, exchanging matter, energy and information. Under constant environmental and internal conditions they show stable spatio-temporal patterns. These patterns can be interpreted as attractive stable states in the compound systems formed by the biological systems and their environments. When environmental or internal conditions change, novel attractive states can emerge. Biological systems can benefit from detecting and occupying these states. For example, humans and animals match their gaits to locomotory speeds in order to minimize energy consumption. Consequently, they may switch from one gait to another at particular velocities [37, 50]. Similarly, when performance speed is increased, humans tend to abandon movement patterns requiring a high degree of coordination and show involuntary switches to simpler and more stable coordination patterns. This has been observed, for example, for rhythmic isofrequency finger and wrist movements [8, 9, 29, 41, 42, 53], paced uni-

manual arm movements [54], and polyrhythmic tapping [2, 11, 55]. Furthermore, perceptual patterns of apparent motion change qualitatively when the frequency of stroboscopically presented objects is increased, e.g., [26, 34, 44, 59]. In the regions preceding and following the transition regions, the performed patterns usually exhibit a high degree of accuracy [42, 55]. Similarly, in the pre- and posttransition regions of the apparent motion paradigm humans describe their visual experiences in terms of meaningful perceptual patterns. In sum, there are many instances of qualitative changes in locomotion, coordinated manual movements, and perception under critical task conditions. In these cases, transitions between well-defined (and in this sense accurate) spatio-temporal motoric and perceptual patterns are observed. Therefore, we may say that biological systems and, in particular, human motor control systems, are characterized by both flexibility and accuracy.

Of course, in general, the functional properties of biological systems are subjected to limitations. Many studies have been devoted to examine the limitations of human motor control in tasks requiring a combination of flexibility and accuracy. In the context of goal-directed reaching movements (i.e., movements starting at a ‘home’ position and terminating at a target position), a speed-accuracy trade-off has been identified and, inspired by information theory, a law, known as Fitts’ law [15, 51, 52, 58], has been formulated relating minimal performance time and maximal accuracy. However, before talking about limitations of a particular functional property of a biological system such as the human motor control system, the issue of how this functional property is established in the first place should be clarified. In recognition of this requirement, the present work proposes a possible mechanism leading to a minimization of a trade-off between flexibility and accuracy and thus an understanding of systems showing these properties in combination.

Following the dynamical systems approach and the theory of synergetics [1, 30, 40], we describe biological systems in terms of dynamical systems. Accordingly, the stable behavior of a system obeying a gradient dynamics corresponds to a minimum in a potential. One usually assumes that the most stable behavior under given circumstances is described by the global minimum of the potential (ignoring degenerated states). When circumstances change, a global minimum can become a local minimum and a new global minimum can emerge. In this case, the system may benefit from occupying the state corresponding to the novel global potential minimum, that is, from switching from the local (formerly global) minimum to the global (formerly absent or local) minimum. Therefore, one may ask: How does a system described by a state variable x and a gradient dynamics $\dot{x} = h(x)$ find the global minimum of the corresponding potential $V(x) = -\int^x h(x') dx'$? This is where fluctuations become crucially important. Fluctuations can drive a system away from a local minimum and kick it into the basin of attraction of a global minimum.

In this context, when studying a stochastic process obeying a conventional Langevin equation [57], we realize that fluctuations act as a two-edged sword. On the one hand, if fluctuations dominate the process, the transition time from

a local potential minimum to a global minimum is short (cf. Kramer's escape rate [57, Sec. 5.10], see also [56]) but the stationary distribution is broad. Consequently, deviations of the actual behavior from the optimal behavior (indicated by the global potential minimum) are large and the behavioral accuracy is low. On the other hand, if the impact of fluctuations is small with regard to the potential force, then the stationary distribution is sharply peaked. Unfortunately, this gain in behavioral accuracy is usually achieved at the expense of transition times that tend to be long in this case [57, Sec. 5.10]. In sum, such models only apply to systems suffering from a flexibility-accuracy trade-off. As argued earlier, in biological systems such a trade-off is minimized. In fact, the degree to which biological systems succeed in unifying the conflicting demands of flexibility and accuracy determines their chances of survival in competitive environments. Therefore, the question arises: How can we model biological systems showing a unification of flexibility and accuracy and what kind of underlying mechanisms can support the ability to establish this unification? In what follows, we will address these issues using the notion of self-organization and a fundamental concept of synergetics: circular causality [30, 31].

In many cases, the evolution of biological systems results from the interaction between a collective quantity and the constituents over which this quantity is defined [1, 32, 33, 40]. Such systems typically show self-organization and circular causality. In line with these notions, we consider a stochastic process ξ given by the one-dimensional generalized Langevin equation

$$\begin{aligned} \dot{\xi} &= h(\xi) + \underbrace{\beta g(\mathcal{P}(\xi, t)) \Gamma(t)}_{= \sqrt{Q}} \end{aligned} \quad (1)$$

with a fluctuation strength Q that depends on the value of the corresponding probability density $\mathcal{P}(x, t)$ (i.e., $Q \equiv Q(\mathcal{P})$). The probability density $\mathcal{P}(x, t)$, in turn, can be computed by means of $\mathcal{P}(x, t) = \langle \delta(x - \xi) \rangle_{\xi}$, where $\langle \cdots \rangle_{\xi}$ represents the ensemble average with respect to the random variable ξ . Consequently, Eq. (1) describes a system with circular causality: $\mathcal{P}$ acts on the ξ -dynamics but, at the same time, $\mathcal{P}$ is generated by the stochastic process ξ (note that $\dot{\xi}$ in Eq. (1) denotes the derivative with respect to time t).

As we will show below, depending on the special form of $Q(\mathcal{P})$, one can generate an unsupervised adaptation process which is not subjected to the aforementioned flexibility-accuracy trade-off. In particular, we will show that for monotonically decreasing positive definite functions $g(\mathcal{P})$ large percentages of the realizations of the stochastic process (1) are found close to the global minimum of the potential $V(x) = -\int^x h(x') dx'$. Hence, stationary probability densities with very small variances are created by such processes and transition times are found to be significantly shorter than for conventional Langevin equations without probability dependent noise terms.

Desai and *Zwanzig* interpreted probability dependent coefficients of stochastic evolution equations such as $g(\mathcal{P})$ as collective quantities, which, at the same time,

are produced by the members of statistical ensembles and impinge on these members [12, 17, 25, 60]. Following *Dawson*, the macroscopic state of a system that results from the collective interaction of its constituents, in turn, describes environmental conditions that are experienced by the constituents [10]. *Dawson* referred to this circular causality structure as a feedback control loop. Similarly, *Kuramoto* considered probability dependent coefficients as cluster variables [46, 62] and *Hesse* and *Ramos*, among others, considered them as coefficients depending on empirical probability measures [36]. These cluster variables, as well as the empirical probability measures, may reflect the collective behavior of spatially extended systems (for studies on such systems subjected to multiplicative noise sources see, e.g., *van den Broeck et al.* [66, 67, 68]). More recently, the introduction of a probability dependent Langevin force in a stochastic system has been interpreted as the establishment of a statistical feedback in that a statistical quantity generated by a system is fed back to the system [20, 22, 24, 47]. Therefore, we may say that the dynamics of Eq. (1) entails a circular causality mediated by a statistical collective quantity.

In the context of generalized thermostatics [63], various special cases of the nonlinearity $g(\mathcal{P})$ have been discussed, see [3, 4, 5, 6, 16, 20, 21, 22, 23, 39, 47, 48, 49, 64]. The relationship between transition times and the shape of the finally established distributions, however, was not an objective of these studies. In the present article, we will therefore focus on transient and steady-state properties of Eq. (1) under weak assumptions with regard to the nonlinearity $g(\mathcal{P})$.

2. Stationary solutions

We start out by defining the force h in Eq. (1) as a gradient of a globally attractive potential V

$$h(x) = -\frac{d}{dx}V(x) \quad \text{with} \quad V(x \rightarrow \pm\infty) \rightarrow \infty. \quad (2)$$

As already indicated in Eq. (1), the fluctuation force is composed of two terms, $Q = \beta^2 g^2$ (where β is a positive constant) and $\Gamma(t)$. $\Gamma(t)$ is assumed to be white noise of unit variance ($\langle \Gamma(t) \rangle = 0$ and $\langle \Gamma(t)\Gamma(t') \rangle = \delta(t - t')$ [57]). In general, we consider the case of a non-trivial $\mathcal{P}$ -dependency of the function $g(\mathcal{P}) \in C^\infty$ that should only obey the condition

$$\forall \mathcal{P} : g \geq 0 \wedge \frac{\partial g}{\partial \mathcal{P}} \leq 0. \quad (3)$$

Since $\partial g / \partial \mathcal{P} \leq 0$ holds, we may call the process ξ defined by Eqs. (1-3) a stochastic process with negative feedback [20, 22, 24, 47]. If we compare the case $\partial g / \partial \mathcal{P} < 0$ with $\partial g / \partial \mathcal{P} = 0$, then it is obvious that the latter simply describes the evolution in terms of an ‘ordinary’ Langevin equation. Recall that, for $g \equiv 1$, the stationary probability density reads

$$\mathcal{W}(x) = N_{\mathcal{W}} e^{-2V/\beta^2}, \quad (4)$$

assuming that $\mathcal{W}$ is subjected to natural boundary conditions and that the normalization is given by $1/N_W = \int_{-\infty}^{\infty} \exp\{-2V/\beta^2\}dx$. The position of the maximum of the stationary probability density (4) coincides with the position of the minimum of the potential V (note that we ignore degenerated cases). For $\partial g/\partial \mathcal{P} < 0$, however, the maximum of the probability density corresponds to the minimum of the strength of the fluctuations. In the steady case, ensemble members that are located within a close vicinity of this maximum are less affected by the noise than members at other locations. The resulting aggregation at the global minimum of the potential is, therefore, more pronounced than in the trivial case $g \equiv \text{const}$. This effect can also be viewed in a different way: the nonlinearity $g(\mathcal{P})$ ‘distorts’ the steady probability density $\mathcal{W}$ so that large values are enhanced whereas small values are weakened.

The evolution of the system’s probability density can be calculated by using a nonlinear Fokker-Planck equation [3, 18, 35, 47] that reads

$$\dot{\mathcal{P}}(x, t) = -\frac{\partial}{\partial x} \left[\left\{ h + \beta^2(1 - \varpi) g(\mathcal{P}) \left(\frac{\partial g(\mathcal{P})}{\partial x} \right) - \frac{\beta^2}{2} \frac{\partial}{\partial x} g^2(\mathcal{P}) \right\} \mathcal{P} \right]. \quad (5)$$

The parameter ϖ distinguishes between Ito ($\varpi = 1$) and Stratonovich ($\varpi = 1/2$) calculus [38, 57, 61]. By using natural boundary conditions, $\mathcal{P}(x \rightarrow \pm\infty) = 0$, we directly obtain the corresponding stationary probability density $\mathcal{P}(x, t) \rightarrow \mathcal{P}_0(x)$ via

$$\frac{2}{\beta^2} h = \varpi \frac{\partial}{\partial x} g^2(\mathcal{P}_0) + \frac{g^2(\mathcal{P}_0)}{\mathcal{P}_0} \frac{\partial \mathcal{P}_0}{\partial x}, \quad (6)$$

which, by virtue of Eq. (4), yields the implicit expression

$$N_0 \mathcal{W}(x) = \exp \left\{ \varpi g^2 + \int \frac{g^2}{\mathcal{P}_0} d\mathcal{P}_0 \right\} =: f_{\varpi}(\mathcal{P}_0). \quad (7)$$

The variable N_0 guarantees the normalization of $\mathcal{P}_0$, i.e., $\int \mathcal{P}_0(x) dx = 1$. f_{ϖ} describes the (inverse) distortion of the probability density $\mathcal{P}_0(x)$ for $g \neq 1$ towards $\mathcal{W}(x)$. Assuming that f_{ϖ} is invertible, we can also describe the transformation of $\mathcal{W}$ into $\mathcal{P}_0$ in terms of

$$f_{\varpi}^{-1}(N_0 \mathcal{W}) =: F_{\varpi}(N_0 \mathcal{W}) = \mathcal{P}_0(x). \quad (8)$$

$\mathcal{W}$ can easily be computed using Eq. (4) and the steady probability density $\mathcal{P}_0$ for $\partial g/\partial \mathcal{P}_0 \neq 0$ follows directly from the distortion function $F_{\varpi} = f_{\varpi}^{-1}$. In order to illustrate this procedure, we specify $g(\mathcal{P}) = g_{n,\alpha}$ by means of

$$g_{n,\alpha} = \left(\frac{1}{1 + \alpha \mathcal{P}} \right)^{n/2}, \quad \alpha \geq 0, \quad n = 1, 2, 3, \dots; \quad (9)$$

Figure 1. Inverse distortion $f_{n,\varpi,\alpha}$ vs. $\mathcal{P}_0$ for $n = 1$ (I, II) and $n = 2$ (III, IV): the Ito case ($\varpi = 1$: II, IV) results in stronger distortions than the Stratonovich calculus ($\varpi = 1/2$: I, III); the inset shows the corresponding distortion function $F_{n,\varpi,\alpha}$.

note that for $\alpha \equiv 0$ we have $g_{n,\alpha} = 1$ and the nonlinear Fokker-Planck equation becomes trivial. Inserting Eq. (9) into Eq. (7) the integration yields the inverse distortion functions [13]

$$f_{n,\varpi,\alpha} = \frac{\mathcal{P}_0}{1 + \alpha \mathcal{P}_0} \exp \left\{ \frac{\varpi}{(1 + \alpha \mathcal{P}_0)^n} + \sum_{k=1}^{n-1} \binom{n-1}{k} \frac{(-\alpha \mathcal{P}_0)^k}{k(1 + \alpha \mathcal{P}_0)^k} + C_n \right\}. \quad (10)$$

The constants C_n can take on arbitrary values and can be compensated by the normalization N_0 . Focusing on weak nonlinearities ($n = 1, 2$), we choose $C_1 = 0$, $C_2 = 1$ and obtain

$$\begin{aligned} f_{1,\varpi,\alpha} &= \frac{\mathcal{P}_0}{1 + \alpha \mathcal{P}_0} \exp \left\{ \frac{\varpi}{1 + \alpha \mathcal{P}_0} \right\} \\ f_{2,\varpi,\alpha} &= \frac{\mathcal{P}_0}{1 + \alpha \mathcal{P}_0} \exp \left\{ \frac{\varpi}{(1 + \alpha \mathcal{P}_0)^2} + \frac{1}{1 + \alpha \mathcal{P}_0} \right\}. \end{aligned}$$

In the limit $\mathcal{P}_0 \rightarrow \infty$ the inverse distortions $f_{n=(1,2),\varpi,\alpha}$ converge to a finite value $1/\alpha$. Figure 1 shows all the distortion functions for both the Ito and the Stratonovich case.

A detailed analysis reveals that $f_{2,\varpi=1/2,\alpha}$ (Stratonovich case) is a strictly concave function whereas $f_{2,\varpi=1,\alpha}$ (Ito case) has a maximum at $\mathcal{P}_0 = 1/\alpha$ with a value $1/(2\alpha) \exp\{3/4\} > 1/\alpha$. In addition, at the origin the steepness of $f_{n,\varpi,\alpha}$ reads $\exp\{\varpi + n - 1\}$, which is independent of α but leads to more localized probability densities in the Ito case and in the case of stronger nonlinearities (larger n). All the functions $F_{1,\varpi=1/2,\alpha}$, $F_{1,\varpi=1,\alpha}$, and $F_{2,\varpi=1/2,\alpha}$ have a singularity at $1/\alpha$.

Figure 2. Stationary probability density $\mathcal{P}_0(x)$ of Eq. (5) for a drift h determined by the double-well potential (9). The parameter values are (i) $\sim g \equiv 1$, (ii) $\sim [n=1, \varpi=1]$, and (iii) $\sim [n=2, \varpi=1/2]$; $\alpha=1, \beta=10, k_1=50, k_2=k_3=100$. The inset shows the corresponding potential $V(x)$.

Thus, the normalization constant N_0 must be bounded by $\alpha N_0 < 1/\max\{\mathcal{W}(x)\}$ to map $\mathcal{W}$ onto $\mathcal{P}_0$ [cf. Eq. (8)]. Figure 1 shows that large values are amplified and small values are weakened. Again, the distortion $F_{n,\varpi,\alpha}$ is larger for $n=2$ than for $n=1$ at fixed values of α (compare the functions *II* and *IV* in Figure 1). Note that we only consider the lower branch of $F_{2,1,\alpha}$, i.e., the lower branch of the curve in the inlet of Figure 1 corresponding to graph *IV*. If n is fixed, however, then the distortion increases with α . Close to the singularity $(1/\alpha)$, the derivative of $F_{1,1,\alpha}$ increases drastically for large α and differences of the function values of $\mathcal{W}$ gain importance. This higher sensitivity results in a mapping of all the values except for the maximal one via $F_{1,\varpi,\alpha}$ onto relatively small probability values.

Further analyses of the transformation of $\mathcal{W}$ based on Fokker-Planck equations requires an explicit choice of the deterministic force h or of the potential V , respectively. Here, we consider the potential

$$V(x) = -\frac{k_1}{2}x^2 + \frac{k_2}{3}x^3 + \frac{k_3}{4}x^4 \quad (11)$$

with $k_1 > 0, k_2 > 0$, and $k_3 > 0$, which has a maximum at the origin and both a local and a global minimum (see Figure 2). For a certain fluctuation strength, the probability density $\mathcal{W}$ that corresponds to this potential can be computed with the help of Eq. (4). Aiming at the normalized solution of Eq. (6), we generate a family $\{\mathcal{P}_0(N_0)\}$ of candidates for $\mathcal{P}_0$ by using $F_{n,\varpi,\alpha}$ with various N_0 . Explicitly, we initially estimate N_0 , integrate over $\mathcal{P}_0$, and take the resulting value as new approximation of N_0 . This procedure is repeated iteratively until convergence. Final estimates of the probability densities are given in Figure 2. The undeformed prob-

ability density [$g_{n,\alpha} \equiv 1$, curve (i)] shows a much lower probability at the global minimum of the potential compared to the cases including a nonlinear feedback [curves (ii) and (iii)].

So far, the shape of stationary probability densities has been studied in terms of distortion functions acting on Boltzmann distributions. For some special cases, however, one can also obtain exact solutions for nonlinear Fokker-Planck equations [12, 46, 66]. In particular, a nonlinear Fokker-Planck equation that describes stochastic systems with Bose-Einstein statistics has been proposed [27, 39]. Since for Bose systems the phenomenon of enhanced occupation probabilities of global potential minima is well-known (Bose-Einstein condensation) [7, 43, 69], the corresponding Fokker-Planck equation is likely to represent a special case of the general theory outlined in this section. In fact, a detailed analysis (see Appendix A) shows that this evolution equation can be obtained from Eq. (5) for the Ito case with a nonlinearity g that satisfies the conditions (3).

3. Transient solutions

Besides such analytical studies of the stationary solutions of Eq. (5), one might also be interested in the transient behavior of the Langevin equation (1). To this end, we consider a very weak nonlinearity and choose $n = 1$ in Eq. (9). Note that in this case the convergence of transient solutions to uniquely defined stationary probability densities can be shown by means of Lyapunov's direct method [22, 39]. Furthermore, we used the Euler method [45, 57] to discretize Eq. (1). This discretization scheme is based on the Ito interpretation and reads

$$\xi_{n+1}^r = \xi_n^r + h(\xi_n^r)\tau + \beta g(\mathcal{P}(\xi_n^r, t))\sqrt{\tau}w_n^r, \quad (12)$$

for $r = 1, 2, \dots, N_r$ ensemble members. w_n^r represent Gaussian distributed random values (Box-Muller algorithm) with a unit variance for every realization r . We approximate the probability density $\mathcal{P}$ by the histogram H of the random variable ξ^r given in intervals $[x_j, x_j + \Delta x]$ with $x_j = x_0 + j\Delta x$ and $j = 1, 2, \dots, N_j$. The next-left-neighbor-point $\bar{x}$ of a given value ξ is defined as $\bar{x} := \{x_j : x_j \leq \xi \wedge \xi - x_j = \min\}$ and we obtain

$$H_n = \frac{1}{N_r} \sum_{\Omega} 1, \quad \Omega := \{k : \xi_n^k \in [\bar{x}(\xi), \bar{x}(\xi) + \Delta x]\}; \quad (13)$$

Ω denotes a set of neighbors $\xi_n^{r*} \approx \xi$. The renormalization of H is realized by dividing its value by the spatial discretization length Δx , that is, $\mathcal{P}(x) \approx H(\{\xi^r\})/\Delta x$.

In addition to the force h given by Eq. (11) and $n = 1$, we also fix the noise strength β and focus on the effects of the nonlinearity by manipulating α . Figures 3 and 4 show the numerical solution of the discrete Langevin equation (12) for two different parameter values of α . In the stationary case, the maximum p_m of $\mathcal{P}$ is

Figure 3. Simulation of the discrete Langevin Eq. (12) with g and h given by Eqs. (9) and (11), respectively, and $\alpha = 1$, $\beta = 10$, $\Delta t = 10^{-3}$, $\Delta x = 10^{-2}$, $N_r = 40000$, $k_1 = 50$, $k_2 = k_3 = 100$. Numerical results are plotted at different times t_i . Dashed line in front corresponds to the analytical result, cf. Figure 2 (ii).

Figure 4. Simulation results for $\alpha = 100$ (cf. Figure 3); see text.

located at the global minimum x_m of the potential (11). The numerical simulation for a weak nonlinearity ($\alpha = 1$) is in good agreement with the analytical solution given above (dashed line in Figure 3). An increasing nonlinearity ($\alpha = 100$, Figure 4) results in an increase of the maximum value of the probability density $p_m = \mathcal{P}(x_m)$. Approximately 90% of all subsystems ξ^r are gathered within the interval Δx around $x_m \approx -1.28$. Further, the variance σ^2 decreases enormously. Within the

Figure 5. Maximal probability p_m as function of time t . Stochastic processes with negative statistical feedback ($\alpha = 5$: curve B and $\alpha = 20$: curve C ; $\beta = 10$) show shorter transient parts compared to the reference process without statistical feedback ($\alpha = 0$, $\beta = 3$: curve A).

Figure 6. Variance σ^2 vs. t ; see text and cf. Figure 5.

transient regime, the time-dependent probability density is essentially described by two peaks that correspond to the two minima of the potential. Hence, the evolution can be viewed as rapid and almost discrete jumps of ensemble members between the minima of the potential. The probability of finding one of the members outside close vicinities of the potential minima becomes negligible.

In order to compare the transition times for systems with and without statistical feedback, we adjusted the parameters α and β in such a way that the two posttransition stationary probability densities have approximately either the same peak probability density p_m or the same variance σ^2 . Figures 5 and 6 show the results of these simulations. The graphs *A*, *B*, and *C* were computed from three different processes which will be referred to as *A*-, *B*-, and *C*-processes, respectively. The *A*-process corresponds to the conventional stochastic process given by Eq. (1) with $g = 1$. The *B*- and *C*-processes correspond to processes with statistical feedback. The parameters α and β are chosen such that the posttransition stationary peak probabilities p_m of the *A*- and *B*-processes and the posttransition stationary variances σ^2 of the *A*- and *C*-processes coincide. In comparison to the ‘ordinary’ Langevin equation (curves *A* in Figures 5 and 6), the statistical feedback yields a much quicker relaxation to a steady p_m (Figure 5) whereby stronger nonlinearities again increase the probability at x_m (curve *C* in Figure 5). The variance decreases with increasing α (Figure 6). It relaxes slightly slower compared to smaller α values but reaches its steady value still much quicker than in systems without statistical feedback.

4. Conclusions and outlook

In closing we want to emphasize the great practical importance of the proposed use of noise on the basis of the results obtained in the present study. The aggregation of members of an ensemble in the minimum of an abstract potential representing a deterministic force can be amplified by means of negative statistical feedback. In addition, numerical simulations revealed that the transition times are significantly shorter than those of comparable Langevin equations without statistical feedback. Consequently, a biological system under the impact of negative statistical feedback can detect the position of the minimum value of a potential force with a large probability within a short transient period. In other words, such a system exhibits the ability to generate a punctuated probability density and to respond quickly to changes in both the environment and its internal parameters. Moreover, the form of Eq. (1) does not require any a priori knowledge about the underlying potential. Thus, the system can be considered to be self-organized by means of auto-regulation. Therefore, the algorithm may give new opportunities to describe the stochastic behavior of self-organizing biological systems characterized by both flexibility and accuracy. This also implies that in the present study we have identified a possible mechanism for biological systems to achieve a combination of flexibility and accuracy, namely, negative statistical feedback in combination with self-organization.

The focus in the present study was on the effects of probability-dependent coefficients of Fokker-Planck equations on transition times and the shape of stationary distributions. However, Fokker-Planck equations of this kind can also describe another interesting phenomena: the emergence of multiple stationary distributions,

see, e.g., [10, 12, 28, 46, 68]. We are inclined to say that the three fundamental phenomena, (i) multiplicity of stationary distributions, (ii) shape distortion of stationary distributions, (iii) and increase of mobility, should also occur in systems with multiple stationary distributions and negative statistical feedback. Then, we can further speculate that the vanishing and emergence of eventual multiple stationary distributions will be confounded by the action of negative statistical feedback. That is, critical parameter values may depend on the strength of the feedback control loops (e.g., on the parameter α introduced in Sec. 2). This phenomenon is addressed briefly in Appendix B by means of an illustrative example. A detailed discussion, however, is beyond the scope of the present study.

Appendix A

We consider for $\varpi = 1$ the nonlinearity

$$g_{BE}(\mathcal{P}) = \sqrt{\frac{\ln[1 + \mathcal{P}]}{\mathcal{P}}} , \quad (14)$$

which leads to the Fokker-Planck equation

$$\dot{\mathcal{P}}(x, t) = -\frac{\partial}{\partial x} \left[h(x) \mathcal{P} - \frac{\beta^2}{2} \frac{\partial}{\partial x} \ln[1 + \mathcal{P}] \right] . \quad (15)$$

The stationary probability density of Eq. (15) given by

$$\mathcal{P}_0(x) := \frac{1}{\exp \left\{ \frac{\alpha}{\beta^2} (V(x) - \mu) \right\} - 1} , \quad (16)$$

(where μ is a normalization constant) describes a normalized Bose-Einstein statistics. Therefore, and in line with a proposal by *Uhling* and *Uhlenbeck* formulated as early as 1933 [14, 65], Eq. (15) has recently been proposed as a classical Fokker-Planck description for bosons [27, 39]. Just as in our first example (cf. Eq. (9)), in the limit $\mathcal{P} \rightarrow 0$ the nonlinearity g_{BE} converges to unity (which can be shown by applying l'Hopital's rule to $[g_{BE}]^2$). Moreover, for low density distributions we can approximate the diffusion term of Eq. (15) by $\ln[1 + \mathcal{P}] \approx \mathcal{P} / [1 + 0.5\mathcal{P}]^{-1} + O(\mathcal{P}^3)$. That is, up to terms of the order two, the evolution equation for Bose particles (15) coincides with Eq. (5) for $\varpi = 1$ and $g_{n,\alpha}$ with $n = 1$ and $\alpha = 1/2$. Furthermore, we obtain

$$\frac{\partial}{\partial \mathcal{P}} g_{BE}(\mathcal{P}) = \frac{1}{2\mathcal{P}^2(1 + \mathcal{P})} \sqrt{\frac{\mathcal{P}}{\ln[1 + \mathcal{P}]}} Z(1 + \mathcal{P}) , \quad (17)$$

where $Z(y)$ is defined by $Z(y) := y - 1 - y \ln y$ for $y > 1$ ($\mathcal{P} > 0$) and $Z(1) := 0$. From the well-known inequality $\ln z < z - 1$ for $z > 0$ and $z \neq 1$ it follows that $Z(y) < 0$ for $y > 1$ by substituting z with $1/y$. Consequently, g_{BE} satisfies the

inequalities (3) and Bose systems can be regarded within the Fokker-Planck approach as systems with negative statistical feedback. A salient feature of Bose systems is that their ground states can accommodate large fractions of their particles (Bose-Einstein condensation) [69]. Such a phenomenon does not occur within the Maxwell-Boltzmann statistics. Therefore, this second example illustrates again that negative statistical feedback can increase the occupation probabilities of minimum potential (or minimum energy) levels.

Appendix B

To examine the effect of negative statistical feedback on the emergence of multiple stationary solutions, we may first concentrate on systems that are globally stable, that is, for which the convergence of transient solutions to stationary ones can be shown. In line with an earlier study [19], we therefore may consider a hybrid model arising from a unification of the Desai-Zwanzig model (a benchmark model for systems with multiple stationary distributions) and the model with negative statistical feedback presented in Sec. 2. The corresponding Fokker-Planck equation is given by

$$\frac{\partial}{\partial t} \mathcal{P}(x, t) = \frac{\partial}{\partial x} \left\{ (k_1 x - k_2 x^2 - k_3 x^3 + \epsilon \langle x \rangle) \mathcal{P}(x, t) - \frac{\beta^2}{2} \frac{\partial}{\partial x} \frac{\mathcal{P}}{1 + \alpha \mathcal{P}} \right\} \quad (18)$$

where ϵ describes the strength of a so-called mean field coupling and the nonlinearity in the diffusion term of Eq. (18) corresponds to g defined by Eq. (9) with $n = 1$. For $\epsilon = 0$ the model (18) corresponds to the model discussed in the previous sections (and, in particular, simulated in Sec. 3). For $\alpha = k_2 = 0$, $k_3 = 1$, and $\epsilon \neq 0$, Eq. (18) recovers the Desai-Zwanzig model which shows a single stationary stable distribution for $k_1 < 0$ and two stationary stable distributions for $k_1 > 0$ and β smaller than a critical value β_c [12]. The asymptotic behavior of transition solutions of Eq. (18) can be studied by means of the generalized free energy functional

$$I[\mathcal{P}] = \langle V(x) \rangle_x + \frac{\epsilon}{2} [\langle x \rangle]^2 - \frac{\beta^2}{2} S_{(SFB; \alpha)}[\mathcal{P}]. \quad (19)$$

Here, V is given again by Eq. (11) and the generalized entropy functional $S_{(SFB; \alpha)}$ is defined in [22] according to

$$S_{(SFB; \alpha)}[\mathcal{P}] := - \int \mathcal{P}(z) \ln \left\{ \frac{(1 + \alpha) \mathcal{P}(z)}{1 + \alpha \mathcal{P}(z)} \right\} dz. \quad (20)$$

It can be shown that $I[\mathcal{P}]$ decreases monotonically for transition solutions of the hybrid model (18) and that $I[\mathcal{P}]$ becomes constant for stationary distributions [19], which indicates that transient solutions converge to stationary ones. On account of

this fundamental stability, the hybrid model (18) can be regarded as an appropriate tool for investigating cross-effects between the emergence of multiple stationary probability densities, on the one hand, and phenomena related to negative statistical feedback structures, on the other.

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