Inertia and Prediction in the Response to External Perturbation of Noisy Variables

Nash Rochman

Department of Chemical and Biomolecular Engineering, The Johns Hopkins University

Sean X. Sun

Department of Mechanical Engineering and Biomedical Engineering, The Johns Hopkins University, Baltimore MD 21218

Abstract

For most stochastic dynamical systems, variables which are tightly regulated tend to respond slowly to external changes. This idea is often discussed for applicable systems, within a linear response regime, through the Fluctuation Dissipation Theorem (FDT). In a previous paper, we proposed a phenomenological model for the response of the cell cycle duration distribution to environmental changes which correlated the width of this distribution to response efficiency when FDT was not applicable. Here we emphasize how that model may be used to illustrate this general principle, that the stochasticity of a variable while inversely proportional to stability is often directly proportional to lability. Comparisons are made between this discrete-time model and the simple harmonic oscillator. We then consider a simple continuous dynamical system, the “Active Oscillator”, which illustrates this principle in another fashion.
I. INTRODUCTION

Speed and precision are qualities which often run in opposition to one another. Within stochastically driven systems noisy variables are often a source of systematic instability, negatively impacting predictability while possibly improving adaptability. This phenomenon is well illustrated by the Fluctuation Dissipation Theorem (FDT). In the early 20th century a series of observations\cite{2} regarding thermal noise in conductors lead to the development of FDT relating the stochastic fluctuations of an ensemble at equilibrium around its mean to the relaxation rate of that ensemble when exterior conditions (e.g. temperature) are modulated\cite{1,3}. For example, we may consider a univariate system described by the Hamiltonian $H(x)$ and the corresponding Gibbs measure $P(x) = \exp(-\beta H(x))/\int dx' \exp(-\beta H(x'))$. We perturb the system at time zero such that $H(x, t) = H(x) + f_0 x$ and further restrict the size of this perturbation to satisfy the approximation $\exp(-\beta f_0 x) \approx 1 - \beta f_0 x$. In this case, FDT yields the following result:

$$\langle x(t) \rangle = \langle x(\infty) \rangle + (\langle x(0) \rangle - \langle x(\infty) \rangle) A(t)$$

where $A(t) \equiv \langle (x(t) - \langle x(0) \rangle) (x(0) - \langle x(0) \rangle) \rangle / \langle x(0) x(0) \rangle_{t=0}$ is the autocorrelation function. With this result we find a relationship between the relaxation of the mean of the distribution after the perturbation and the autocorrelation of the system at equilibrium. A shorter correlation at equilibrium (less “memory” in the system) yields a faster rate of response to perturbation. Furthermore, a noisier distribution often generates a shorter correlation function making the connection between speed and precision. While generalizations of FDT have been realized for non-equilibrium systems\cite{5}, not all systems which show a correlation between response dynamics and distribution width are adequately described this way. For a previous problem\cite{4}, we constructed a generalized two-state model transition probability balancing self-similarity and adaptation. Below we revisit this model in a general setting and compare it to two related dynamical systems.

II. MODELING

We consider the following transition rule for moving from state $y$ in the current timestep to state $x$ in the subsequent timestep:
\[ M(y \rightarrow x) = A \exp \left( - (y + x)^2 \right) \exp \left( - \left( \frac{1 - \xi}{\xi} \right) (y - x)^2 \right) \]  

(2)

where \( 0 < \xi < 1 \) and \( A \) is the normalization constant. The first term represents the optimization term, a tendency to move away from the current state towards the “optimal” state (zero) and the second is the inertial term: a tendency to stay in the current state. Rewriting as a single Gaussian function yields:

\[ M(y \rightarrow x) = \sqrt{\frac{1}{\pi \xi}} \exp \left( - (x - y (1 - 2\xi))^2 / \xi \right) \]  

(3)

We can write down the mean of the distribution for the \( n^{th} \) timestep as follows:

\[ \mu_n = \mu + \Pi (\mu_{n-1} - \mu), \quad \Pi \equiv 1 - 2\xi \]  

(4)

and the stationary distribution (\( P^*(y) \) such that \( \int MP^*(y)dy = P^*(x) \)):

\[ P^*(y) = A \exp \left( -4 (1 - \xi) y^2 \right) \]  

(5)

Now we can examine the “relaxation time” defined here to be the number of timesteps it takes for the mean of the distribution to fall within \( e^{-3} \sim 5\% \) of the starting value \( \Delta \):

\[ \left| (1 - 2\xi)^N \Delta \right| = Err = \Delta e^{-3} \]  

(6)

We may scale the error by the initial mean displacement \( \Delta \) to yield:

\[ N = \frac{-3}{\ln (|1 - 2\xi|)} \]  

(7)

where in principle \( N \) must really be the ceiling integer for this value. Similarly, we examine how the standard deviation of the stationary distribution varies with \( \xi \):

\[ \sigma (\xi) = \sqrt{\frac{1}{2 (4 (1 - \xi))}} = \sqrt{\frac{1}{8 (1 - \xi)}} \]  

(8)

We may now look at how the behavior varies across the possible value of \( \xi \):
We find that increasing the weight on the self-similar or inertial term (decreasing $\xi$) while shrinking the spread of the stationary distribution (the “error”) increases the relaxation time. A good compromise is selecting $\xi = 0.5$ where the relaxation time is minimized and the error is still low (1/2). In other words, decreasing the noise in the system, while improving precision, compromises adaptability and the relaxation time.

We may compare the model presented above to the damped harmonic oscillator:

$$\frac{d^2x}{dt^2} + \beta \frac{dx}{dt} + x = 0$$

We will consider the initial conditions $x(0) = 1$ and $\frac{dx}{dt}(0) = 0$ to match our work above and additionally introduce the parameter $\lambda$ which varies from zero to one: $\beta = 2 \left( \frac{\lambda}{1 - \lambda} \right)$. There are three forms for the solutions: overdamped, critically damped, and underdamped corresponding to real distinct, real repeated, and imaginary roots respectively. For each case we have the following solutions. Overdamped:
\[
x(t) = \frac{1}{2}e^{-\beta^2 t}
\left[
\left(1 - \sqrt{\frac{\beta^2}{\beta^2 - 4}}\right) e^{-\frac{1}{2}t\sqrt{\beta^2 - 4}} + \left(1 + \sqrt{\frac{\beta^2}{\beta^2 - 4}}\right) e^{\frac{1}{2}t\sqrt{\beta^2 - 4}}\right]
\]  
(10)

Critically Damped:

\[
x(t) = (1 + t)e^{-t}
\]  
(11)

Underdamped:

\[
x(t) = e^{-\frac{\beta t}{2}} \left[ \cos\left(\frac{\beta t}{2}\sqrt{\beta^2 - 4}t\right) + \sqrt{\frac{\beta^2}{\beta^2 - 4}} \sin\left(\frac{\beta t}{2}\sqrt{\beta^2 - 4}t\right) \right]
\]  
(12)

We will define the relaxation time as the time when all subsequent points in the trajectory fall below the threshold value \(e^{-3}\). There isn’t really an analogous “error” term here since all trajectories (regardless of parameter value) eventually reach the origin; however, we can compare the magnitude of the values at some specified time (i.e. \(|x(1)|\)) for a similar measure. We’ll label time \(s\) and “error” \(\varepsilon\):

Figure 2: Trajectories for all possible values of \(\lambda\). We observe the trend that as the parameter tends to zero the error shrinks but the relaxation time diverges.
We find that the curves qualitatively match those for the discrete-time model and observe the same trend: as the parameter decreases, the error decreases but the relaxation time increases. Below are some representative trajectories from these models for comparison. Parameter values of $\xi = \lambda = \frac{1}{4}, \frac{1}{3}, \frac{1}{2}, \frac{2}{3}$ and $\frac{3}{4}$ are shown:

Figure 3: Comparing individual trajectories for parameter values $\xi = \lambda = \frac{1}{4}, \frac{1}{3}, \frac{1}{2}, \frac{2}{3}$ and $\frac{3}{4}$ for the discrete model and harmonic oscillator.

We would now like to introduce the complementary, “Active Oscillator” toy model. Consider an object with an initial value $x = -\Delta$, zero initial velocity $x' = 0$, and a target position of zero. Next let us define the projected state $x^p(t)$, or the value obtained from a kinematic prediction of the value some time $\tau > 0$ into the future:

$$x^p(t) = x(t) + x'(t)\tau + \frac{1}{2}x''(t){\tau^2}$$  \hspace{1cm} (13)
Let us consider a set of simple rules. The acceleration maintains a value of $\alpha$ until the projected state reaches zero at which time ($t_1$) the acceleration is set to zero. The position then continues to increase until ($t_1 + t_2$) it reaches zero, and the acceleration is set to $-\alpha$. This state is maintained until ($t_1 + t_2 + t_3$) when the velocity reaches zero and the trace either finishes or repeats as discussed below.

First we may scale the variables by the characteristic length scale $\Delta$ and timescale $\sqrt{\frac{2\Delta}{\alpha}}$ for convenience. The projected state reaches zero when:

$$x^p(0) = -1 + \tau^2$$

(14)

When $\tau \geq 1$, we find that the projected state is already positive and the object doesn’t ever move. For $\tau < 1$ we find:

$$x^p(t_1) = 0 = -1 + (\tau + t_1)^2 \Rightarrow t_1 = 1 - \tau$$

(15)

The position reaches zero, $x(t_1 + t) = 0$, when:

$$x(t_1 + t) = -1 + (1 - \tau)^2 + 2(1 - \tau)t = 0 \Rightarrow t_2 = \frac{2\tau - \tau^2}{2(1 - \tau)}$$

(16)

The velocity reaches zero at time $t_1 + t_2 + t_3$, where $t_3 = t_1 = 1 - \tau$. The final position (when the velocity is zero) is given by:

$$X = x(t_1 + t_2 + t_3) = 2(1 - \tau)^2 - (1 - \tau)^2 = (1 - \tau)^2$$

(17)

and the total time it takes to reach this point is:

$$T = t_1 + t_2 + t_3 = 2(1 - \tau) + \frac{2\tau - \tau^2}{2(1 - \tau)}$$

(18)

This may be repeated for smaller values of $\tau$ where $\Delta = X$. The results for the second cycle are (where $X$ is reported positive for convenience) $X = (1 - 2\tau)^2$ and $T = 2(1 - 2\tau) + \frac{2\tau - 3\tau^2}{2(1 - 2\tau)}$ and for the third cycle, $X = (2\tau^2 - 4\tau + 1)^2$ and $T = 2(2\tau^2 - 4\tau + 1) + \frac{4\tau^3 - 7\tau^2 + 2\tau}{2(2\tau^2 - 4\tau + 1)}$. The fourth cycle begins at begins at: $x^p(0) = - (1 - \tau)^2 (1 - 2\tau)^2 (2\tau^2 - 4\tau + 1)^2 + \tau^2 \Rightarrow \tau < 0.18$. The results for the first three cycles are shown below:
Figure 4: The first three cycles for the Active Oscillator corresponding to values of $\tau$ greater than $\sim 0.18$.

The behavior for this system is messier than the previous two; however, within each cycle analogous trends are observed - increasing $\tau$ decreases error and increases relaxation time. The projection length, $\tau$, plays an analogous role to the weight on the self-similar term $\xi$ with large values of $\tau$ corresponding to small values of $\xi$.

III. DISCUSSION

Tightly regulated variables often respond slowly to external changes. We compared two models which display this characteristic stemming from different underlying mechanisms. In the first case, we considered a two-term transition probability in which the second “inertial” term represented a tendency to maintain the current state. The behavior of this system mirrored that of the harmonic oscillator in many ways. When the weight, $\xi$, on the inertial term tended from one half to one, the relaxation time increased and the standard deviation of the resulting distribution increased. While the actual trajectories resemble the under-damped case, the relationship between error and relaxation time is similar to the
overdamped oscillator where $\lambda$ is greater than one half. As $\xi$ tends from one half to one, the standard deviation decreases but the relaxation time still increases resembling the underdamped oscillator where as $\lambda$ tends to zero, the first zero crossing occurs earlier (and the “error” reported above decreases) but the relaxation time diverges. In the second model, we examined another oscillator where the acceleration was partly determined by a kinematic prediction time $\tau$ into the future. The behavior of this model was more complex, but within repeated regions we found that as $\tau$ increases, the relaxation time increases and the error decreases. Both increasing $\tau$ and decreasing $\xi$ tightens a regulatory constraint and doing so makes responses slower but errors smaller.

IV. REFERENCES

[1] Herbert B Callen and Theodore A Welton. Irreversibility and generalized noise. *Physical Review*, 83(1):34, 1951.

[2] John Bertrand Johnson. Thermal agitation of electricity in conductors. *Physical review*, 32(1):97, 1928.

[3] Harry Nyquist. Thermal agitation of electric charge in conductors. *Physical review*, 32(1):110, 1928.

[4] Nash Rochman, Fangwei Si, and Sean X Sun. To grow is not enough: impact of noise on cell environmental response and fitness. *Integrative Biology*, 8(10):1030–1039, 2016.

[5] Gatien Verley, K Mallick, and D Lacoste. Modified fluctuation-dissipation theorem for non-equilibrium steady states and applications to molecular motors. *EPL (Europhysics Letters)*, 93(1):10002, 2011.