Supplementary Notes

Manipulating the edge of instability

Madhusudhan Venkadesan John Guckenheimer
Francisco J. Valero-Cuevas

In this supplementary note, we provide details of the numerical optimization used for finding task-optimal sensory weights. To achieve this, we first mathematically define stability (i.e., the constraints) and the objective function (i.e., the goal) for our model. We then provide an alternate graphical representation of the optimization problem and its results using a 2D 'fitness landscape'.

1 Metrics for stability: "Survival times" and "Success rates"

We first define stability for the noisy, time-delayed model so that it agrees with the experimental notion of stability, namely, a compression was successful so long as it did not slip for a finite period of time. Stability in linear and nonlinear deterministic dynamical systems is a well-defined notion, either in the sense of asymptotic or Lyapunov stability (Doyle et al., 1992; Ogata, 2002; Guckenheimer and Holmes, 1983). For example, defining stability in the local sense (near a specific state of the system) is easily done for a hyperbolic fixed point[1] if the system under consideration is described either by ordinary differential equations (Doyle et al., 1992; Ogata, 2002;

[1]The term hyperbolic refers to the requirement that none of the eigenvalues of the linearization near the fixed point of interest lie on the imaginary axis. In other words, the system can be stable or unstable in different directions, but not marginally stable in any direction.

Guckenheimer and Holmes, 1983) or by delayed differential equations (i.e., systems with time-delay) (Kolmanovskii and Nosov, 1986; Kolmanovskii and Myshkis, 1999; Engelborghs et al., 2000, 2002). However, when there is some source of noise in the dynamic system, stability is often defined in terms of stationary distributions, i.e., using steady-state distributions of time spent in various parts of the phase space of the dynamical system. For some dynamical systems that are modeled using stochastic differential equations, the stationary distribution can be analytically derived using the Fokker-Planck equations (Soize, 1994). However, for most complex dynamical systems, the true distributions are approximated using statistical histograms that are obtained through large ensemble simulations of the given stochastic dynamic system. For example, one could define stability for a noisy system based on distributions of the time spent by trajectories of a stochastic system in different parts of its phase space (Arnold, 1998). Numerically, this could be calculated by simulating large ensembles of the noisy dynamic system and thus obtaining histograms of time spent in different regions (if these distributions converge to stationary distributions). Peaks in the distribution (i.e., "representative" locations) can then be called as "stable" points in the phase space of the dynamical system.

However, in the context of our system, there is an alternate "natural" definition of stability that arises from the task requirement for subjects in the experiments. We called the experimental behavior as "stable" or "successful" if the subjects could prevent the spring from slipping for a finite time period (7s). This definition of "success" in our task naturally lends itself to "be studied in the context of a survival, or first passage, time problem" (Cabrera and Milton, 2004), terms that we define below.

1.1 Definitions of success rate and survival time

The first observation is that if a trajectory (time-series of θ – rotation angle of the spring's endcap; Figure 1, left) leaves the domain of attraction (region enclosed by dashed red curves in Figure 1 on Page 4) and never returns inside it during the 7s period (let us name it T^*), then it almost certainly reached one or the other undesirable stable fixed points (at $\theta \approx$ 0.5rad; solid red curves in Figure 1) and thus, the spring "slipped". So, we can define 'success-rate' (p_{success}) as the probability that the time (t_{exit}) at which the θ trajectory exits the domain of attraction (to never return again) is greater than T^* (the desired duration of the hold phase, namely 7s).

$$t_{\text{exit}} = \min\{T; \text{such that } \theta(t > T) \notin [\theta_0 - \delta\theta, \theta_0 + \delta\theta]\} \tag{1}$$

$$p_{\text{success}} = p(t_{\text{exit}} \geq T^*) \tag{2}$$

where, $\delta\theta$ defines the domain of attraction and p_{success} is the 'success-rate'. The time t_{exit} is called the 'survival time'. Based on approximate estimates (not shown) from experimental data that after training subjects slipped in approximately 20% of the trials, we chose a nominal value of $p^* = 0.8$ for the success-rate to define a "successful compression" in our model. The utilization of p^* in our model will become clear when we define F_s below. For experimental trials, F_s is the maximal sustained load for 7s. Nevertheless, it is important to note that in our simulations we calculate p_{success} by using large ensembles of simulations and calculating the fraction of the ensemble that are 'stable' (p_{success}) in the sense that $t_{\text{exit}} \geq T^*$.

1.2 Definition of F_s in the model

For given sensory weights, the success rate (p_{success}) depends on the value of F_s. Symbolically, $p_{\text{success}} = p_{\text{success}}(F_s)|_{(\omega_1,\omega_2,\omega_3)}$, i.e., for given sensory weights, p_{success} is a well-defined function of F_s. Hence, we can define F_s for a successful compression in our model as the solution to the 'root finding' problem,

$$p_{\text{success}}(F_s)|_{(\omega_1,\omega_2,\omega_3)} = p^* \tag{3}$$

Numerically, we implemented this root finding problem using an adapted version of the Newton-Raphson method. Note that by defining F_s in this manner, it is implicitly (through the definition of p_{success}) an expected value, i.e., a metric of average performance and not single-trial performance. We have thus explained how F_s is defined. We will explain how to calculate sensory weights (i.e., $(\omega_1, \omega_2, \omega_3)$) that maximize F_s in Section 2 below.

1.3 Numerical integration of stochastic delay differential equations

Numerical integration of the one-dimensional stochastic delay differential equation (SDDE) was carried out using a simple Euler integration scheme (Küchler and Platen, 2000). As shown by Küchler and Platen (2000), for the

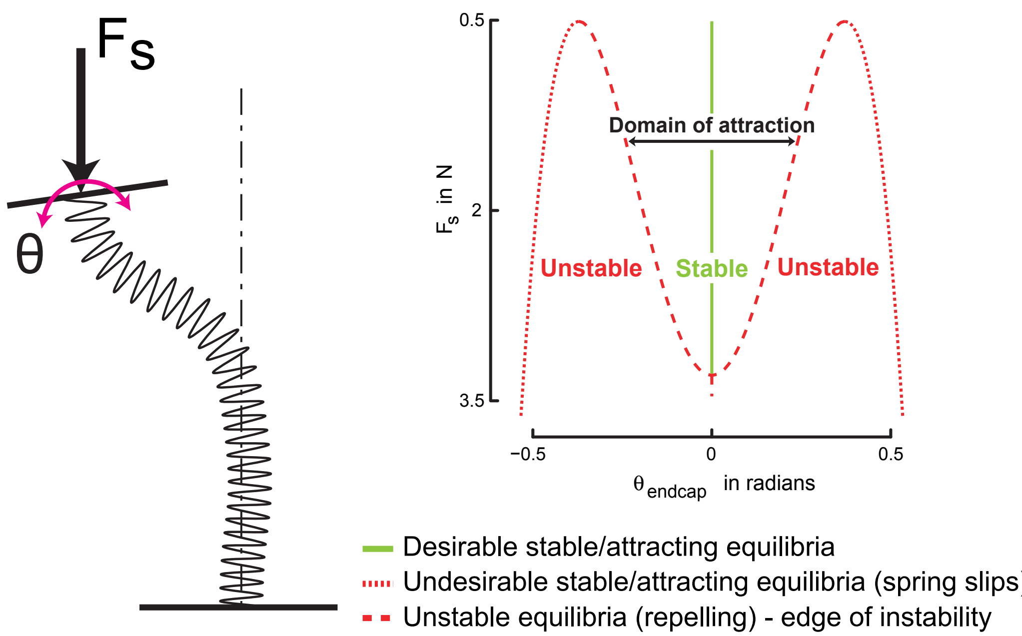

Figure 1: The loci of stable (solid green line) and unstable / undesirable (red dashed / dotted curves) equilibria for the thumb + spring + nervous system's closed loop dynamics without noise or time-delays as the spring is compressed. This figure is a succinct description of the underlying deterministic (no time-delays / noise) dynamics of the subcritical pitchfork bifurcation's normal form equation.

case of additive noise, the Euler integration scheme has a strong order of convergence 1.0. The term 'strong order' just refers to the fact that if the 'true' solution to the SDDE was known for a specific instance of the noisy processes in the system, then, with smaller and smaller time-steps, the numerically integrated solution converges to the true solution. This is different from weakly convergent numerical techniques, where the average of some function of the solution converges to the 'true' value, but each individual solution might itself not converge. We will not say more about numerical techniques for integrating SDDEs since the paper by Küchler and Platen (2000) and the references cited by them provide a good reference for numerical integration of SDDEs.

2 Numerical optimization: sensory weights that maximize F_s

We now outline the numerical optimization procedure used to compute task-optimal sensory weights. There are only three sensory weights that need to be found by our optimization routine that maximizes F_s. Given the additional constraint that the sum of the sensory weights is one, the optimization problem reduces to a 2-parameter optimization problem, namely,

$$\max_{\omega_1,\omega_2,\omega_3} F_s \text{ such that } \sum_{i=1}^{3} \omega_i = 1 \text{ and } p_{\text{success}}(F_s)|_{\omega_1,\omega_2,\omega_3} = 0.8 \qquad (4)$$

This is amenable to a global parameter search. We discretized the plane defined by $\omega_1 + \omega_2 + \omega_3 = 1$ in the positive octant of the space of sensory weights using a fine grid and numerically calculated F_s at each grid point. Thus, we found task-optimal performance and sensory weights for every sensory occlusion condition.

3 Sensory weights that minimize the effects of noise alone

To quantify the impact of time-delays on sensory weighting, we performed simulations using noise-minimizing sensory weights in addition to task-optimal sensory weights (that emerge from the combined effect of noise and time-delays. Any deficit in performance (F_s) and deviation from experimental measurements that arise from using sensory weights that minimize the effects of noise alone can then be attributed to time-delays. The sensory weights that minimize the effect of noise alone are obtained using Bayesian inference for static tasks, i.e.,

$$\omega_i = \frac{1/\sigma_i^2}{\sum_j \left(1/\sigma_j^2\right)} \tag{5}$$

where, σ_i^2 are the variances associated with each sensory channel.

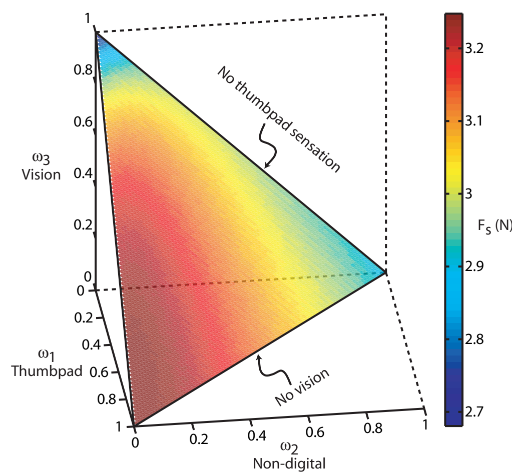

Figure 2: Results of the global optimization using the *65ms simulation*. The edges corresponding to the no vision and no thumbpad sensation conditions are marked in the figure. Note how tactile sensation dominates the landscape when it is available (dark red region). Keep in mind that the vertices of the triangular planar surface of feasible sensory weights are the case when one sensory channel is used exclusively.

4 Fitness landscape representation of simulation results

The results of the global optimization are shown as contour plots for both the *65ms simulation* (Figure 2) and the *100ms simulation* (Figure 3)

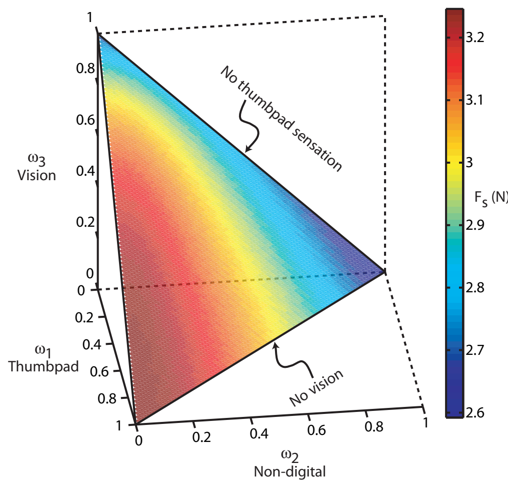

Figure 3: Results of the global optimization using the *100ms simulation*. Note how the peak in F_s for the no thumbpad sensation condition shifts slightly closer to the "vision corner" for the *100ms simulation* compared to the *65ms simulation* (Figure 2).

as an alternate representation of the results presented in the main text to clarify how the task-optimal sensory weights were found. The triangular planar surface in the contour plots are the set of feasible sensory weights, i.e., sensory weights that satisfy both the constraints $\omega_1 + \omega_2 + \omega_3 = 1$ and $\omega_i > 0$ for $i = 1, 2, 3$. The color coding depicts F_s according to the definition given in Equation (3) on Page 3 at each point on the plane.

References

L. Arnold. *Random dynamical systems*. Springer monographs in mathematics. Springer, Berlin ; New York, 1998.

J. L. Cabrera and J. Milton. Stick balancing: On-off intermittency and survival times. *Nonlinear Studies*, 11(3):305–317, 2004.

J. C. Doyle, B. A. Francis, and A. Tannenbaum. *Feedback control theory*. Toronto, New York Macmillan Pub. Co., 1992.

K. Engelborghs, T. Luzyanina, and D. Roose. Numerical bifurcation analysis of delay differential equations. *Journal of Computational and Applied Mathematics*, 125(1-2):265–275, 2000.

K. Engelborghs, T. Luzyanina, and D. Roose. Numerical bifurcation analysis of delay differential equations using dde-biftool. *ACM Transactions on Mathematical Software*, 28(1):1–21, 2002.

J. Guckenheimer and P. Holmes. *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*. Springer, New York, corr. 7th print. edition, 1983.

V. B. Kolmanovskii and A. D. Myshkis. *Introduction to the theory and applications of functional differential equations*. Mathematics and its applications ;; v. 463; Variation: Mathematics and its applications (Kluwer Academic Publishers) ;; v. 463. Boston, Dordrecht, 1999.

V. B. Kolmanovskii and V. R. Nosov. *Stability of functional differential equations*. Mathematics in science and engineering ;; v. 180;. Orlando, London, 1986.

U. Küchler and E. Platen. Strong discrete time approximation of stochastic differential equations with time delay. *Mathematics and Computers in Simulation*, 54(1-3):189–205, 2000.

K. Ogata. *Modern control engineering*. Prentice Hall, Upper Saddle River, NJ, 4th edition, 2002.

C. Soize. *The Fokker-Planck equation for stochastic dynamical systems and its explicit steady state solutions*. Series on advances in mathematics for applied sciences ;; v. 17;. Teaneck, N.J., Singapore, 1994.