Do Fruit Flies Have Free Will?

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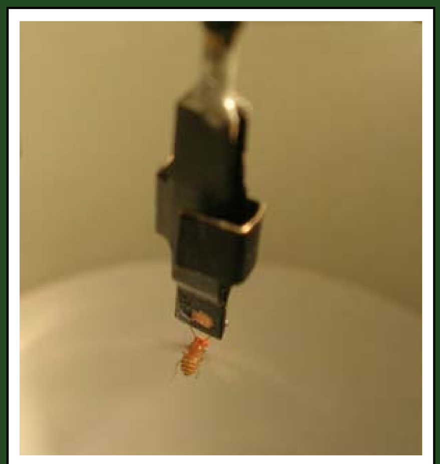


Start: Is there spontaneous behavior?

The concept of causality is so central to the human thought process that Kant concluded it must precede all experience. Science looks for the underlying causes of natural phenomena. According to Laplace, randomness is only a measure of our "ignorance of the different causes involved in the production of events." The neurosciences try to understand the underlying causes for perception, disease, aging or development. Reflecting this view, animals are thought to operate according to laws firmly tying behavioral 'responses' to environmental variables. Once these laws are known, the 'response' of any animal at any time can be predicted from the current environmental situation. In this very successful approach it is often overlooked that animals are not only responding mechanically in a cause and effect (stimulus-response) fashion. Indeed, "even under carefully controlled experimental circumstances, an animal will behave as it damn well pleases".

If animals were but input/output machines which respond to environmental situations in a reproducible manner, identical environments should elicit identical behavior. However, a number of systems from single neurons and synapses to invertebrate and vertebrate animals including humans generate variable output despite no variations in input. This variability is often discounted as extraneous "noise" (Fig. 1). However, our mathematical analyses of behavioral variability suggest that the variability is generated endogenously.

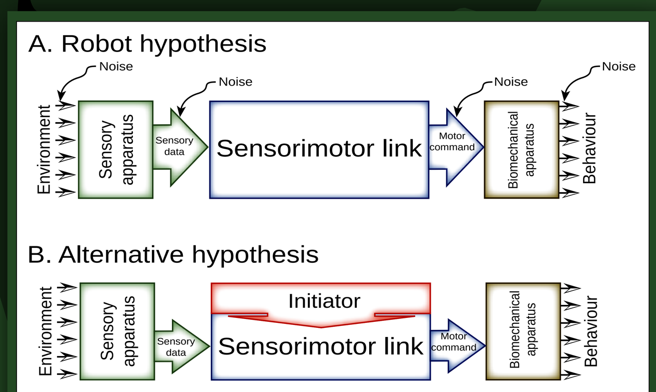
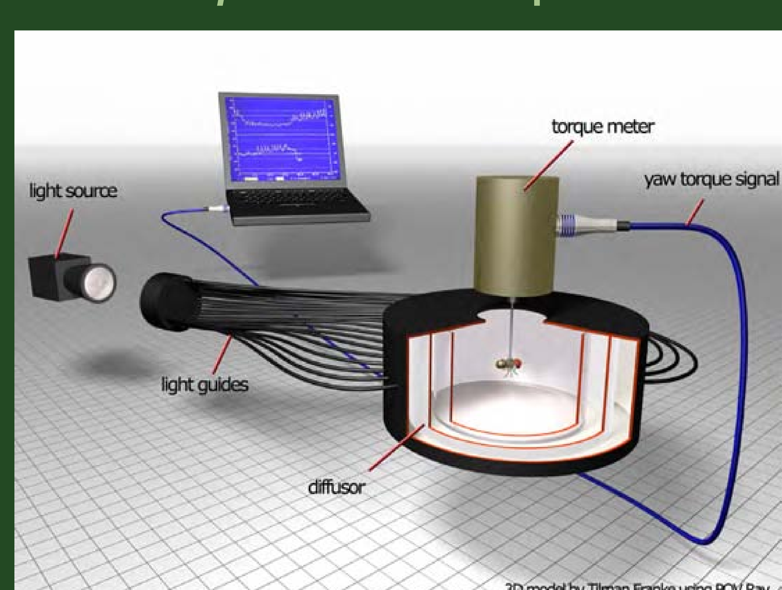


Fig. 1: *Alternative models conceptualizing the open-loop experiment.* A - According to the robot-hypothesis, there is an unambiguous mapping of sensory input to behavioral output. If the behavioral output is not constant in a constant environment, there are a number of possible sources of noise, which would be responsible for the varying output. B - In a competing hypothesis, non-constant output is generated intrinsically by an initiator of behavioral activity. Note that the sources of noise have been omitted in B merely because their contribution is judged to be small, compared to that of the initiator, not because they are thought to be non-existent.

Three groups of flies

The first group ('openloop') flew in a completely featureless white panorama (i.e., without any feedback from the uniform environment - open loop), the second group ('onestripe') flew in an environment that contained a single black stripe in a flight simulator situation that allowed for straight flight in optomotor balance (i.e. the fly could use its yaw torque to control the angular position of the stripe - closed loop) and the third group ('uniform') flew in a uniformly textured environment that was otherwise free of any singularities (i.e., closed loop, the fly could use its yaw torque to control the angular position of the evenly dashed environment).

Drosophila at the torque meter



Torque spike analysis

We chose the temporal sequence of highly stereotyped flight manoeuvres producing short bursts of yaw-torque ('torque spikes', corresponding to body-saccades in free flight) for our analysis (Fig. 2). If the production of torque spikes in a featureless or uniform environment were due to random noise in the *Drosophila* brain or from any uncontrollable input, the time intervals between spikes (inter-spike intervals, ISI) should reflect this stochasticity. In other words, this situation should represent a natural system for generating random numbers.

Spontaneous behavior reveals a fractal order

These results hint at a fractal order rather than random disorder in our data, prompting us to continue with time-series analyses. We first estimated the fractal dimension of the attractor underlying spike production by computing the correlation dimension (Fig. 4a). We then calculated the probability that any randomly shuffled sequence of our ISI data could have produced the same results. The results show clearly that only the recorded sequence of ISIs - and not any random shuffling thereof - can be responsible for the computed correlation dimensions (Fig. 4b).

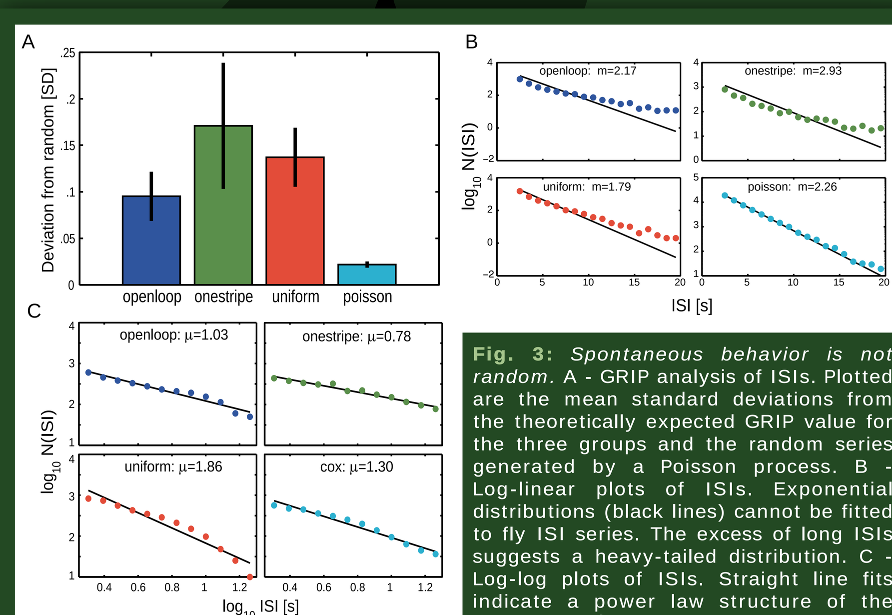


Fig. 3: *Spontaneous behavior is not random.* A - GRIP analysis of ISIs. Plotted are the mean standard deviations from the theoretically expected GRIP value for the three groups and the random series generated by a Poisson process. B - Log-linear plots of ISIs. Exponential distributions (black lines) cannot be fitted to fly ISI series. The excess of long ISIs suggests a heavy-tailed distribution. C - Log-log plots of ISIs. Straight line fits indicate a power law structure of the data. The Lévy exponent μ is calculated from the inclination of the linear fit. A Lévy distribution is defined as 1<μ<3. Smaller values indicate a larger proportion of long ISIs. A Cox Process (cox) reveals a similar power-law structure as the flies.

Spontaneous behavior is not simply random

We adapted a recently developed computational method, Geometric Random Inner Products (GRIP), to quantify the randomness of the ISI sequences. GRIP results from all three groups show that flies are relatively poor random number generators (Fig. 3a). Analyzing the distribution of ISIs, we find heavy-tailed distributions for all fly groups (Fig. 3b). The structure of the data follows a power law and the duration of the *openloop* and *uniform* ISIs decays according to a non-Gaussian Lévy distribution (Fig. 3c).

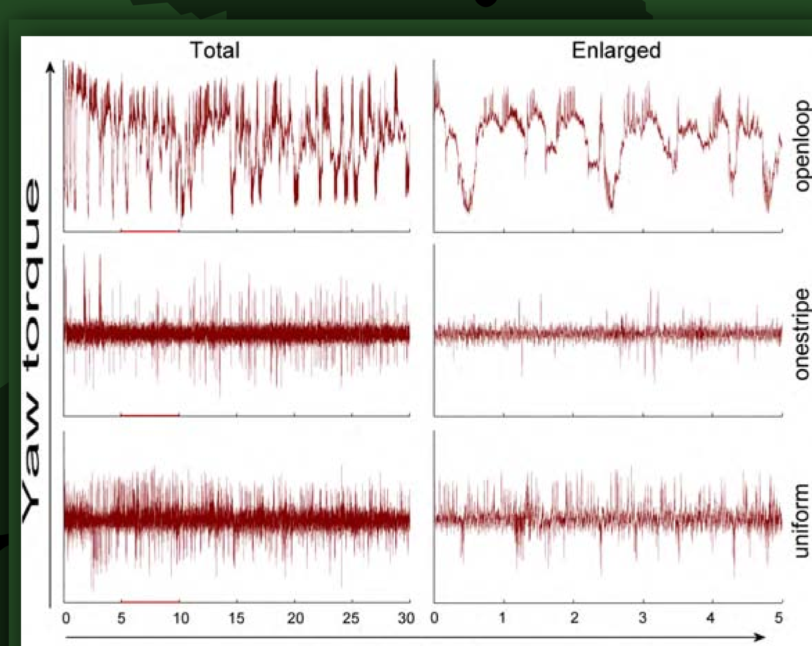


Fig. 2: *Example yaw torque traces.* Left column - total traces. Right column - enlarged section from minutes 5-10 of the total traces. Red lines delineate enlarged sections. Uppermost row is from an animal flying in open loop in a featureless, white panorama (openloop). The middle row is from an animal flying in closed loop in a panorama with a single black stripe (onestripe). The lower row is from an animal flying in closed loop in a uniformly dashed arena (uniform).

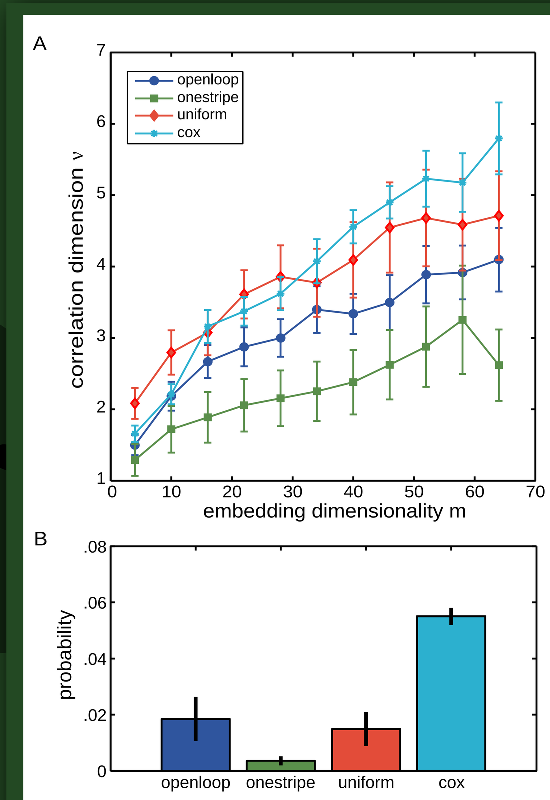


Fig. 4: *Correlation dimension.* A - While the correlation dimension converges on a group-specific value with increasing embedding dimension for fly-generated ISIs (*openloop*, *onestripe*, *uniform*), a number sequence generated randomly by a Cox process (*cox*) diverges. B - Probability to obtain the computed correlation dimensions in A by random shuffling of the original data. While the *cox* group exceeds an alpha value of .05, the three fly groups stay well below that threshold.

Long-range correlations in the behavior imply nonlinearity

There are yet more complex composite stochastic models which can even exhibit a fractal structure. For instance, the so-called "branched Poisson process" (BPP, Fig. 5a) can produce ISI series which show fractal characteristics and cannot be distinguished from fly ISIs by shuffling. This implies that specific ISI durations are determined in part by the timing of other spike(s), and ISI durations fluctuate over time rather than relaxing to a homeostatic steady state. Such a 'memory' can lead to long-range correlations in the data. A sensitive method to detect such correlations is to calculate the root mean square fluctuations in the ISI series (Fig. 5b). We found these correlations in all fly data, but for BPPs, the presence of long-range correlations was dependent on the nonlinearity of the filter function. However, the value for the BPP with the nonlinear filter function is still significantly smaller than the value for the *openloop* group, to which it was fitted, ruling out even BPPs with nonlinear filters as an appropriate model for spontaneous flight behavior in *Drosophila*.

Behavioral indeterminacy

The abundance of nonlinear processes in the brain is per se not a sufficient explanation for the nonlinearity we measured in the fly behavior. Instead, our results imply that not only is the variability in spontaneous fly turning behavior not due to neural noise, but the nonlinear processes controlling the behavior also have to operate at just the right parameters to produce instability. Thus, flies are not simple input/output machines. Rather, our results support the hypothesis that the nonlinear processes underlying spontaneous behavior initiation have evolved to generate behavioral indeterminacy.

Testing for nonlinearity

IThe data now suggest that there may be a dominant nonlinear component in fly ISIs. Nonlinear forecasting comprises a set of established methods from nonlinear time series analysis that involve state space reconstruction with lagged coordinate embeddings. These methods take advantage of the loss of information in nonlinear time series to distinguish them from essentially stochastic (high-dimensional, linear) series. The method of S-maps relies on fitting a series of models (from linear to nonlinear) where the degree of nonlinearity is controlled by a local weighting parameter (θ). Improved out-of-sample forecast skill with increasingly nonlinear models (larger θ) indicates that the underlying dynamics were themselves nonlinear (Fig. 6).

The existence of nonlinear circuits in nervous systems is common knowledge. A critic may argue that any nonlinear signature we find in the fly behavior is merely a reflection of this already well-known property and not indicative of fine-tuned neural control systems. To test this hypothesis, we adapted a virtual agent (automat; Fig. 7), consisting of three nonlinear generators for comparison with our fly raw data (Fig. 6).

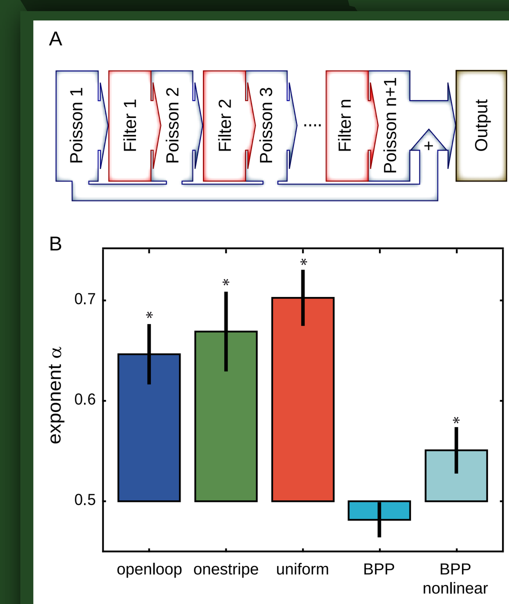


Fig. 5: *Long-range correlations in fly ISIs.* A – The branching Poisson process (BPP) as an example for complex stochastic models. The BPP consists of cascading units of filter functions and Poisson processes. Each unit's filter function receives the events from the Poisson process upstream and drives the rate of the Poisson process associated with it. The (unfiltered) output of all Poisson processes is combined to yield the total output of the model. B - If the slope of the log-log plots of the r.m.s. fluctuation deviates significantly from 0.5, long-range correlations exist in the time series. All three fly groups show a significant deviation from 0.5. The deviation of branched Poisson processes (BPP), however, depends on the nonlinearity of the filter function used to drive the Poisson processes and is significantly smaller than that of fly ISI series. * - significant difference from 0.5.

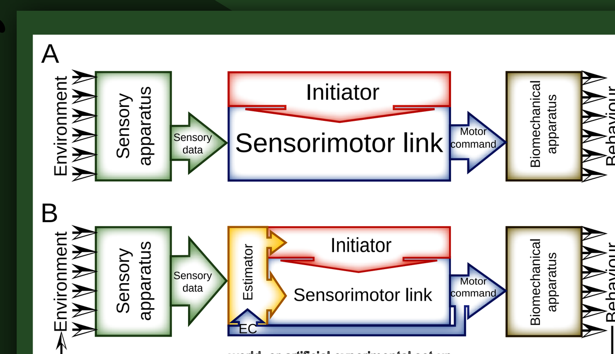


Fig. 9: *Suggested models for open- and closed-loop experiments.* A - Open-loop model as proposed in Fig. 1 (for the *openloop* group). B - Closed-loop model (for the *onestripe* and *uniform* groups). Performance in a situation with a closed reafferent feedback loop is commonly modelled with a state estimator (often approximated by a Bayesian Kalman filter), cross-correlating sensory input with recent motor commands via an efference copy (EC). Such an evaluation is required for efficient behavioral control of incoming sensory data.

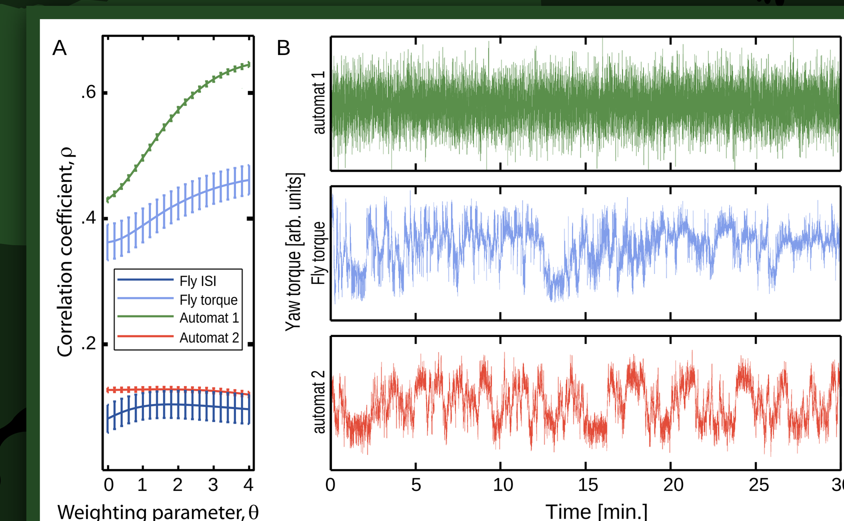


Fig. 6: *Nonlinearity implies instability.* A - S-Map results. Depicted are the averaged results for fly ISIs and raw yaw torque series, together with two automat simulations. The fly ISI series shows a slightly improved forecast skill with increasingly nonlinear S-map solutions (increasing θ). Fly yaw torque series yield both a better overall forecast skill as well as increased nonlinear improvement. The automat simulation can be tuned to produce both linear and nonlinear output. B - Sample raw yaw torque data traces from a real fly and the two versions of the simulated agent depicted in A (automat 1, automat 2).

4 automat properties

1. Similar to how a motor command from the brain would activate motor patterns in the ventral nerve chord, the activator excites the turning oscillators (Fig. 7).
2. The original agent's output has been classified as a Lévy walk.
3. It can be tuned so that its open-loop output shows a similar nonlinear structure as fly turning behavior (Fig. 6a).
4. It can be adjusted such that its output appears to be qualitatively similar to fly open-loop turning behavior (Fig. 6b).

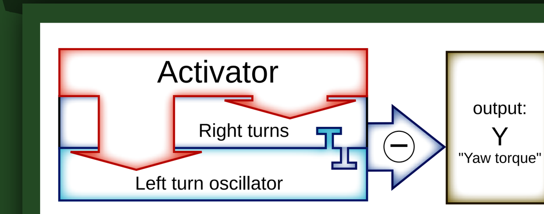


Fig. 7: *Schematic view of the open loop automat.* The activator sends excitatory input to both turn generators. The turn oscillators inhibit each other. The output is the difference signal between the left and right turn oscillator. Each oscillator is described by a logistic map, and the coupling modulates the individual parameters of each map.

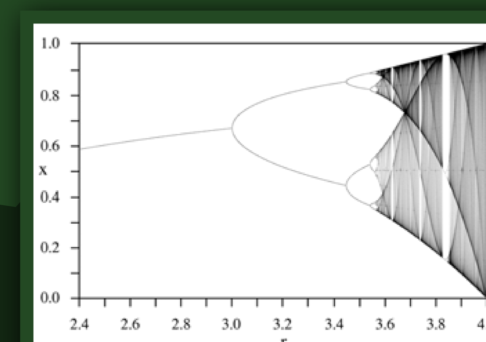


Fig. 8: *Bifurcation Diagram of the Logistic Map.* With r<3 the function converges to one value. This stability is lost wth increasing r. With r between 3 and ~3.45, the population oscillates between two values. Increasing r to ~3.54, the population oscillates between four values, then between 8 values, then 16, 32, etc. Chaos occurs at r of ~3.57. Slight variations in the initial population yield dramatically different results over time.

Linear and nonlinear automat output

If the automat output resembles fly behavior, it does not reveal a nonlinear signature and if it does show the nonlinearity, it doesn't resemble fly behavior (Fig. 6). Indeed, to reveal its nonlinear signature, the automat has to be adjusted such that the nonlinear generators operate under unstable conditions. The failure of this agent to adequately model fly behavior is an example for the rarely appreciated property of nonlinear systems to produce linear output under equilibrium conditions. Only if the processes operate under unstable conditions does the output reveal significant nonlinearity. Neural systems are also known to be able to produce both linear and nonlinear output. This notion is exemplified in the bifurcation diagram of the logistic map, the recursive function used to generate the three oscillators of the automat (Fig. 9).

End: A new type of model

The balance of sensorimotor mapping and superimposed indeterminacy defines the required compromise between unpredictability and meaningful behavior to survive in the physical world. As much as simple taxis, optomotor reflexes or course control require a deterministic sensorimotor program, complex behaviors such as searching or pursuit/evasion contests require fundamental indeterminism. Clearly, entirely deterministic behavior will be exploited and would leave us helpless in unpredictable situations. Our hypothesis predicts that the degree to which an animal behaves deterministically is shaped by evolution and thus depends on the ecological niche to which the animal is adapted. We propose to incorporate the structure of indeterminacy into models of general brain function and to investigate its biological basis.

What would such future models of brain (or robot) function look like? We suggest a model where sensorimotor maps are superimposed by nonlinear variability (Fig. 9a). In addition, a feedback-based state estimator (Fig. 9b) is required for behavioral control in real-world situations. Our data raise the suspicion that future models of the brain may have to incorporate this or a related component for spontaneous behavior initiation, if they strive to be biologically realistic. At the same time, our results provide a basis for speculating about a mechanism for a subjective notion of free will which does not require quantum uncertainty or a violation of causality.

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