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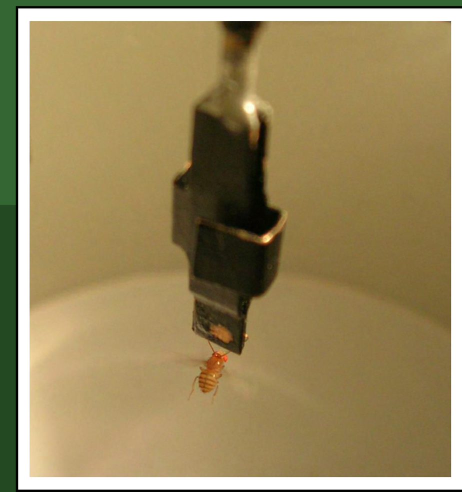

Order in Spontaneous Behavior

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Is there spontaneous behavior?

According to Laplace, randomness is only a measure of our "ignorance of the different causes involved in the production of events." Probably the most fundamental feature of modern scientific inquiry is the ability to predict future events. 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. This basic tenet not only guides basic neurobiological and psychological research but has been the foundation for a great many robotics applications. Contending that less complex brains would be more amenable to this task, the study of invertebrate and in particular fly behavior developed into a prominent focus of attention. However, as the double-slit experiments challenged determinism in physics, a range of behavioral experiments challenged behavioral determinism in the neurosciences. If animals were but input/output machines which respond to environmental situations in a hard-wired, 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 "noise" (Fig. 1).

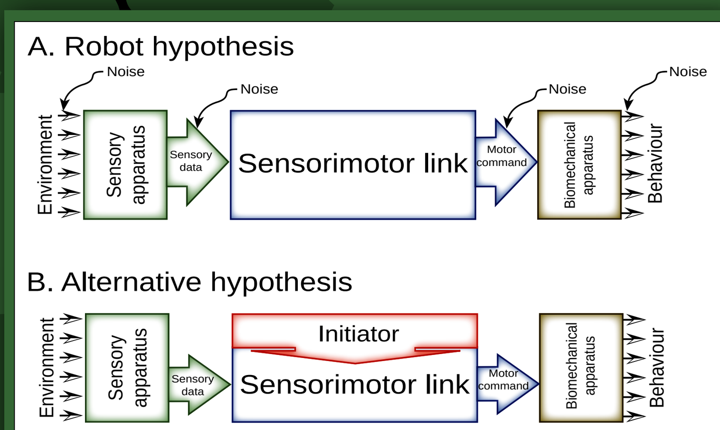
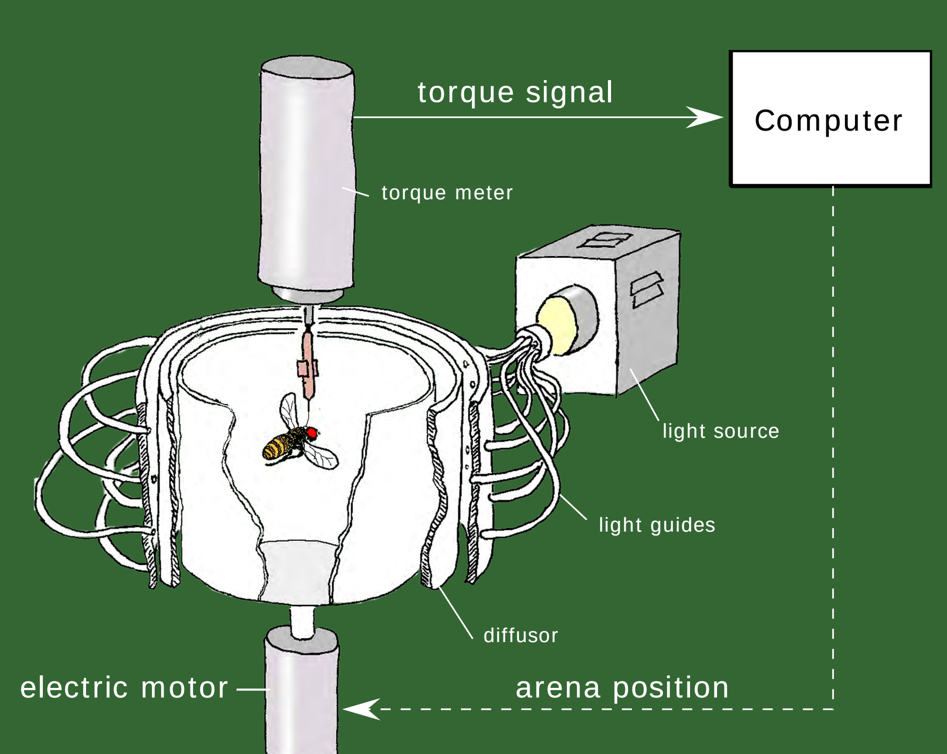


Fig. 1: *Alternative models conceptualizing the open-loop experiment.* A - According to the robot-hypothesis, there is an unambiguous mapping of sensory input to behavioral output. If the behavioral output is not constant in a constant environment, there are a number of possible sources of noise, which 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.

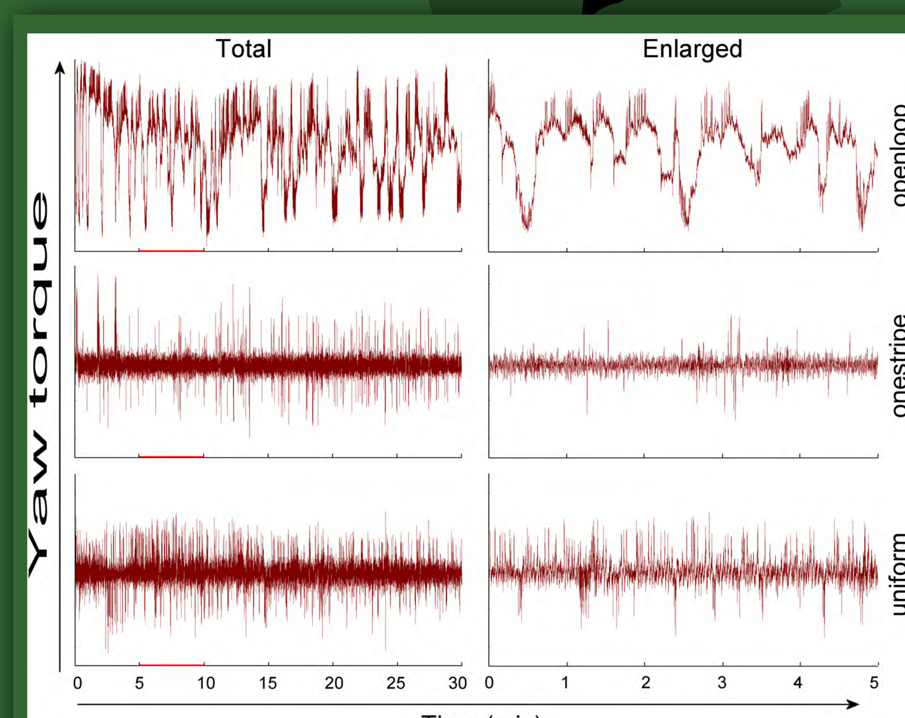


Fig. 2: *Example yaw torque traces.* Left column - total traces. Right column - enlarged section from minutes 5-10 of the total traces. Red lines delineate enlarged sections. Uppermost row is from an animal flying in open loop in a featureless, white panorama (openloop). The middle row is from an animal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

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 found that for the openloop and the onestripe groups, the duration of ISIs decays according to a non-Gaussian Lévy distribution (Fig. 3b).

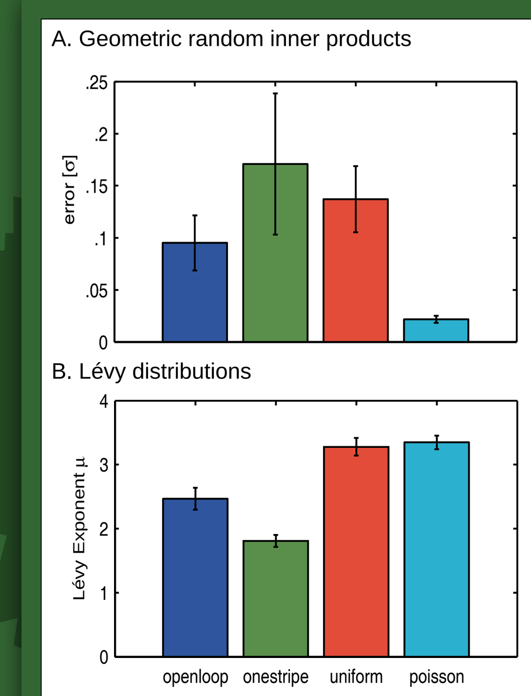


Fig. 3: *Spontaneous behavior is not random.* A - GRIP analysis of ISIs. Plotted are the mean standard deviations from the theoretically expected GRIP value for the three groups and the random series generated by a Poisson process. B - Mean values of the Lévy exponent μ in the three groups of flies. Higher values indicate a lower number of large ISIs and smaller values indicate a larger proportion of long ISIs.

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).

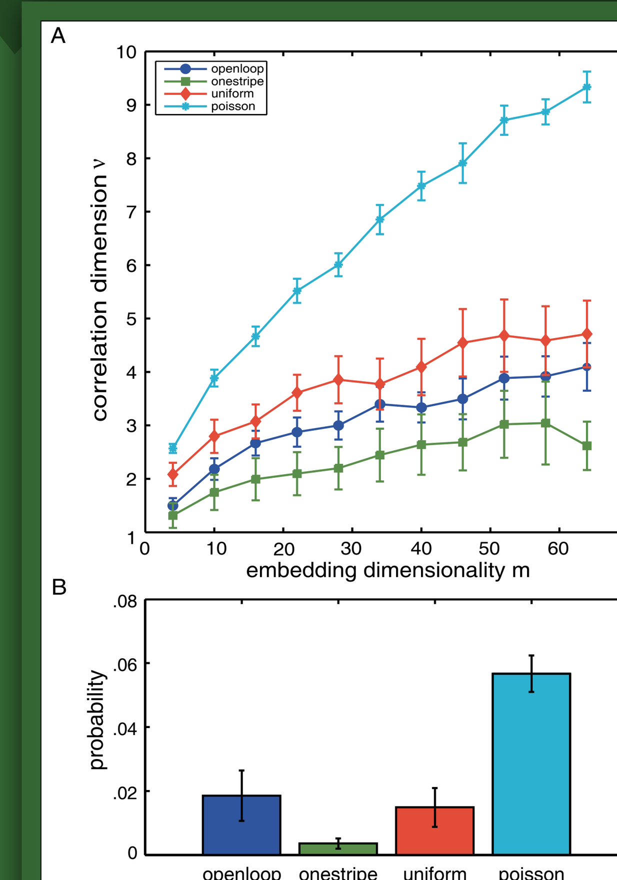


Fig. 4: *Correlation dimension.* A - While the correlation dimension converges on a group-specific value with increasing embedding dimension for fly-generated ISIs (openloop, onestripe, uniform), a number sequence generated randomly by a Poisson process (poisson) diverges. B - Probability to obtain the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

Testing for nonlinearity

Having excluded a random number generator producing spike series reminding of uncorrelated (white) noise, the only possibility that has not been ruled out thus far is correlated (colored) noise. The method best suited to overcome the problems associated with distinguishing linear stochastic processes from nonlinear deterministic ones, is nonlinear forecasting (Fig. 5).

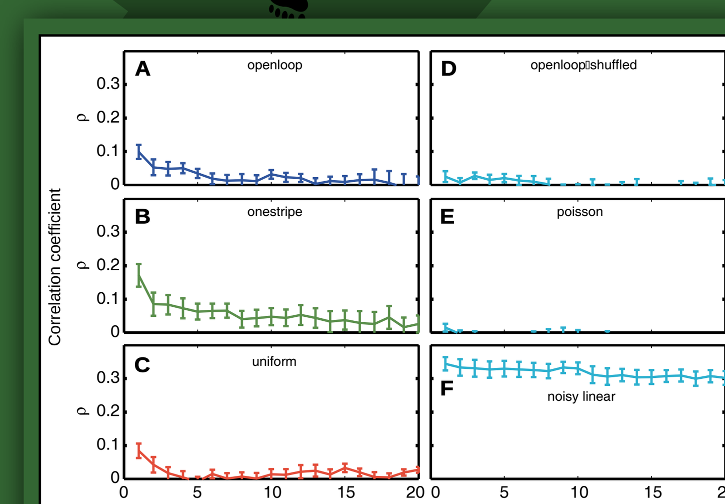
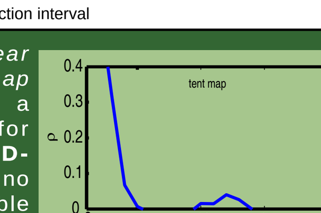
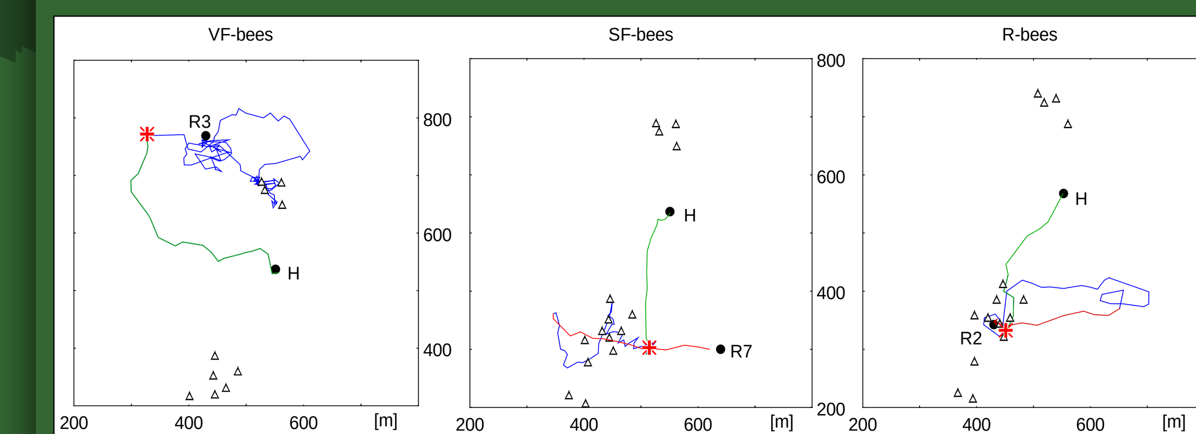


Fig. 5: *Average nonlinear prediction data using the S-map method.* **A-C:** Fly data show a decay in predictability for increasing prediction intervals. **D-F:** The control data either show no predictability or almost stable predictability with increasing prediction intervals.



While the overall predictability of ISI series is low, it is higher than the random series and behaves qualitateively like a non-linear process (inset).

Radar tracking of honeybee search flights



Experimental Groups. Three groups of bees were tested that had the same exploratory memory but differed with respect to route memory: (i) bees trained to a distant (200 m) stationary feeder (SF bees) have extensive route memory; (ii) bees trained to a variable feeder (VF bees) that circled around the hive within a short distance (10 m) lack route memory; and (iii) bees that were recruited (R bees) have ''secondhand'' route information from observing the recruitment dance (9). SF and VF bees were captured at the feeder after sucking to completion and transported in the dark to the release site. R bees were captured at the hive entrance after attending a dancing bee that indicated a feeder 200 m to the east. Because SF and VF bees were satiated before capture, they were motivated to return to the hive. R bees were motivated to search for a new food source but had to fly home quickly because they carried only minimal food supply. A total of 285 radar traces were recorded.
The Structure of Full Flight Paths. Typically, two phases of straight flights, interrupted by one phase of curved flights, can be distinguished (see three examples): an initial straight capture-vector flight (red line) in the compass direction and over the distance of the hive-to-feeder route the bees were pursuing when captured, followed by a curved search flight (blue line) and then by a straight homing flight (green line). We evaluated only the blue search flights. For the evaluation, we generated inter-turn-intervals (ITIs) for all turns larger than 30°.

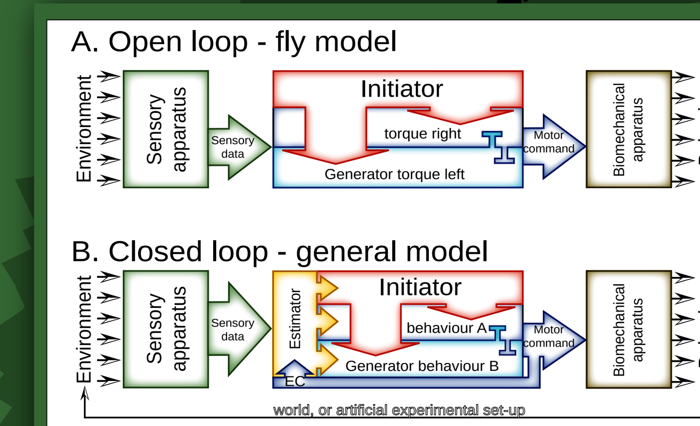


Fig. 6: *Suggested models for open- and closed-loop experiments.* A - Open-loop model. The sensorimotor link consists of three nonlinear oscillators, two mutually inhibiting for left and right torque generation and one initiator. All three generators are always active, with initiator and incoming sensory data modulating the two torque-generators. B - Generalized closed-loop model. 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.

A new type of model

The balance between 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 and course control require a deterministic sensorimotor program, other behaviors 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 centered around a core of three nonlinear oscillators generating spontaneous yaw-torque fluctuations in *Drosophila* (Fig. 6a). In addition, a feedback-based state estimator (Fig. 6b) 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.

Preliminary analysis of honeybee search flights

Encouraged by the fly results, we also started analyzing the structure of search flights from radar-tracked honeybees. Running the data through a similar set of mathematical tools, we were able to detect difference between the three groups, that allow conclusions about the search strategies employed by the bees.

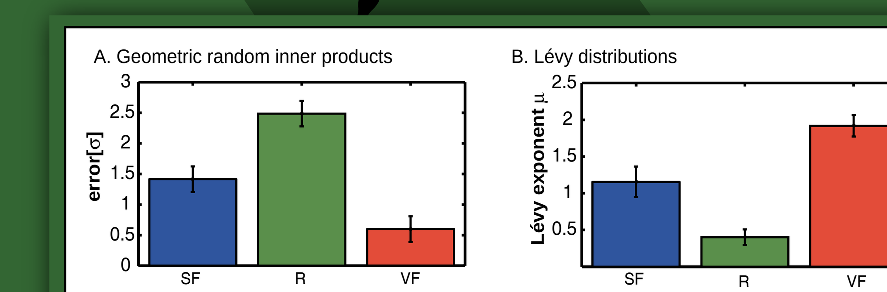


Fig. 7: *GRIP and Lévy analysis as in Fig. 3.* A - GRIP analysis of ITIs. Plotted are the mean standard deviations from the theoretically expected GRIP value for the three bee groups. B - Mean values of the Lévy exponent in the three groups of bees. Higher values indicate a lower number of large ITIs and smaller values indicate a larger proportion of long ITIs.

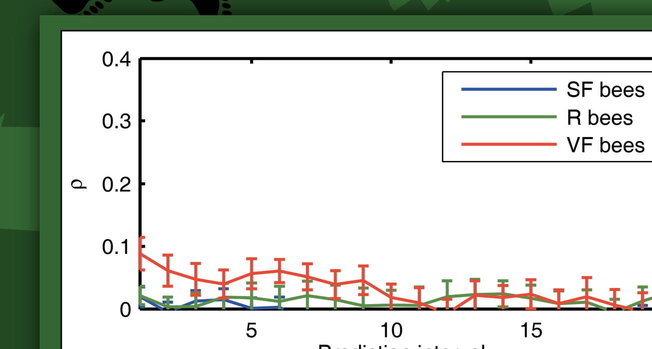


Fig. 8: S-Map procedure on honeybee search flights. Similar to the fly data (Fig. 5), the honeybee search flights show a low predictability that decays to zero with increasing prediction interval.

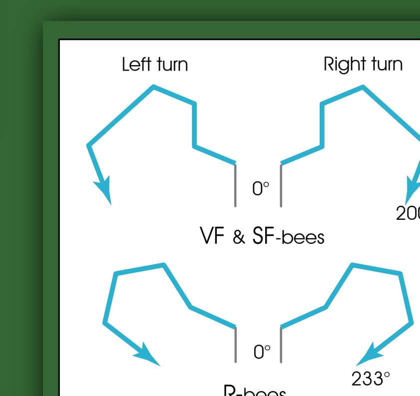


Fig. 9: *Differences in search behavior.* The partial autocorrelation reveals significant differences in the average flight components during the search phase (blue line) for the SF & VF-bees compared to the R-bees. SF & VF-bees show a strong zigzag-component in their right and left curves. R-Bees use a closer turn.

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