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Stochastic resonance and the evolution of *Daphnia* foraging strategy

Nathan D Dees, Sonya Bahar and Frank Moss

Center for Neurodynamics, Department of Physics and Astronomy, University of Missouri at St Louis, St Louis, MO 63121, USA

E-mail: nathan.dees@umsl.edu

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Online at stacks.iop.org/PhysBio/5/044001**Abstract**

Search strategies are currently of great interest, with reports on foraging ranging from albatrosses and spider monkeys to microzooplankton. Here, we investigate the role of noise in optimizing search strategies. We focus on the zooplankton *Daphnia*, which move in successive sequences consisting of a hop, a pause and a turn through an angle. Recent experiments have shown that their turning angle distributions (TADs) and underlying noise intensities are similar across species and age groups, suggesting an evolutionary origin of this internal noise. We explore this hypothesis further with a digital simulation (EVO) based solely on the three central Darwinian themes: inheritability, variability and survivability. Separate simulations utilizing stochastic resonance (SR) indicate that foraging success, and hence fitness, is maximized at an optimum TAD noise intensity, which is represented by the distribution's characteristic width, σ . In both the EVO and SR simulations, foraging success is the criterion, and the results are the predicted characteristic widths of the TADs that maximize success. Our results are twofold: (1) the evolving characteristic widths achieve stasis after many generations; (2) as a hop length parameter is changed, variations in the evolved widths generated by EVO parallel those predicted by SR. These findings provide support for the hypotheses that (1) σ is an evolved quantity and that (2) SR plays a role in evolution.

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Introduction

In its most general form, stochastic resonance (SR) is a process whereby the addition of a random function, or 'noise', can optimize a physical or biological process (Wiesenfeld and Moss 1995). SR has been studied for many years and was discovered in sensory biology well over a decade ago (Douglass *et al* 1993). In nearly all experiments with SR, the noise was added from an external source, such as environmental noise. However, considering the evolution of organisms, if such external noise is, or was, beneficial to sensory systems, one might expect natural selection to have exploited it, as suggested by Jaramillo and Wiesenfeld

(1998). If the advantageous use of noise was subsequently internalized, one might also expect to find neural circuits in the central nervous system specifically designed to make use of SR. Indeed, experimental evidence for such a circuit in the *Drosophila* olfactory system has recently been reported (Shang *et al* 2007). Such circuits, as yet undiscovered elsewhere, may, however, be widespread.

Here, we investigate the nexus between SR and animal foraging behavior, a topic of great recent interest (e.g., Viswanathan *et al* 1996, Bartumeus *et al* 2003, Boyer *et al* 2004, Shlesinger 2006, Buchanan 2008). As a behavior, foraging is subject to noise in the form of a presumably internally-generated variability in an animal's

choice of movements. Animal behavior mediated by internal noise has been reported in two other experiments with *Drosophila* (Maye *et al* 2007, Reynolds and Frye 2007), and more recently in human psychophysics experiments (Emberson *et al* 2007). In our previous experiments, *Daphnia* foraged in a patch with uniformly distributed food, moving in approximately two dimensions. In the absence of directional stimuli (such as visible light or non-uniform food distribution), their turning angle distributions (TADs) $[-\pi$ to $\pi]$, with left-hand and right-hand turns equally probable, were well described by an exponential function (Garcia *et al* 2007), $P(\alpha) = N_o \exp[-|\alpha|/\sigma]$, where α is the turning angle, N_o is the number of angles observed and σ is the noise intensity (characteristic angle or width) of the TAD, the primary quantity measured in the experiment. Since the values of σ were quite similar across five different species, including adults and juveniles of two species, we suggested that the noise intensity is an evolved property (Garcia *et al* 2007). Additional evidence for an evolutionary origin of σ has recently emerged from experiments with single cells of two different species of slime mold searching for a chemical signal in a two-dimensional space. In the absence of directional stimuli, both species exhibited exponential TADs (Liang *et al* 2008) similar to those we observed in *Daphnia* (Garcia *et al* 2007).

To further study the hypothesis that the characteristic widths of TADs are evolved quantities, we have developed a *model-free* simulation, EVO, of natural selection using the simplest and fewest possible assumptions. We compare the results of EVO with simulations of SR similar to those performed by Garcia *et al* (2007) and Dees *et al* (2008) which indicate the values of σ that are optimum for foraging success. These simulations are designed to answer the question: how might the observed exponential TADs and their characteristic widths have arisen?

Methods

EVO simulation

EVO updates an evolving TAD at each generation, commencing with a uniform and uncorrelated distribution of turning angles ranging from $-\pi$ to $+\pi$. This initial distribution represents the ‘primordial noise’, or variability, that is available at the beginning of the natural selection process as originally discussed in detail by Darwin (Gould 2002). Twenty agents forage independently in circular food patches of radius $R = 100$ units. The patches are covered with a uniform grid of $\pi \cdot 10^6$ square cells, 0.1×0.1 units in size. The cells represent food particles to be ‘consumed’ by the agents. Each agent traverses a total distance of 1500 units (simulating a fixed feeding time). The agents can move within or outside the patch, randomly choosing a new turning angle at each hop from the current TAD. All food particles that the agents cross directly while completing their trajectories are removed from the food patch, ‘consumed’, and tabulated. After all agents have completed feeding, the single agent that collected the most food is identified. Only this most successful agent is

allowed to supply information critical to fitness to the next generation of agents. A distribution is created from its choices of turning angles, and a fraction, h , the inheritance of this distribution, is added to the evolving TAD. The next generation of foragers chooses random angles from this modified TAD, and the updating process continues indefinitely.

We emphasize that the ‘inheritance’ consists only of a slight bias in the next generation toward the set of choices made by the most successful feeder in the preceding generation. This does not mean that all members of the next generation will acquire the feeding strategy of the ancestral ‘winner’, as the angles are chosen randomly from the evolving distribution. Indeed, due to the random nature of the simulation, a number of the ‘children’ will perform even *worse* than their gluttonous ancestor.

Daphnia in the wild exhibit so-called *diel vertical migration* (Zaret and Suffern 1976, Ringelberg 1993), avoiding predators by spending the daylight hours near the bottom of a lake or pond (Bollens and Frost 1989) while thin patches of photosynthetic algae (Derenbach *et al* 1979, Lampert 1989, Cowles *et al* 1993, Franks and Jaffe 2001) develop near the surface. At night, *Daphnia* rise to the surface to feed on this algae, and therefore are forced to swim in approximately two-dimensional planes. Also, fractal characterization of three-dimensional *Daphnia pulex* swimming trajectories has shown that their paths are much less vertically complex than pure three-dimensional random walks, and also that they typically travel within 4 cm vertical planes (Uttieri *et al* 2005). We thus justify our two-dimensional approximation in this regard.

In our simulations, the hop length is treated as a fixed parameter. The ratio of hop length to food patch radius is a dimensionless parameter. We hold the radius fixed at 100 units as described above, and perform simulations for three values of the hop length. The results can be compared to experimental studies of *Daphnia* foraging if we take one unit in our simulation as equal to 1 mm, comparable with the average hop length for *D. magna* of 0.95 mm (Dees *et al* 2008). Following this analogy, we can consider the food patches used in our simulations as circles of radius 100 mm. This choice is in agreement with high density food (phytoplankton/prey) patch sizes measured in freshwater (Doubell 2008, personal communication) as well as in marine environments (Doubell *et al* 2006, Franks and Jaffe 2001).

SR simulation

In the SR simulation, agents again forage in food patches as defined in the EVO simulation while traversing a fixed distance (1500 units). Apart from these two constraints, the EVO and SR simulations are completely independent.

At the end of each hop during the SR simulation, an agent chooses a new turning angle at random from a normal distribution (see discussion below) using a predetermined width, σ . Any food particles touched by the agent along its trajectory are removed from the patch and tabulated. Twenty agents feed in this manner for the chosen value of σ . The maximum food gathered by the agents in this population of 20 is then recorded, disregarding extreme outliers (values ≥ 3

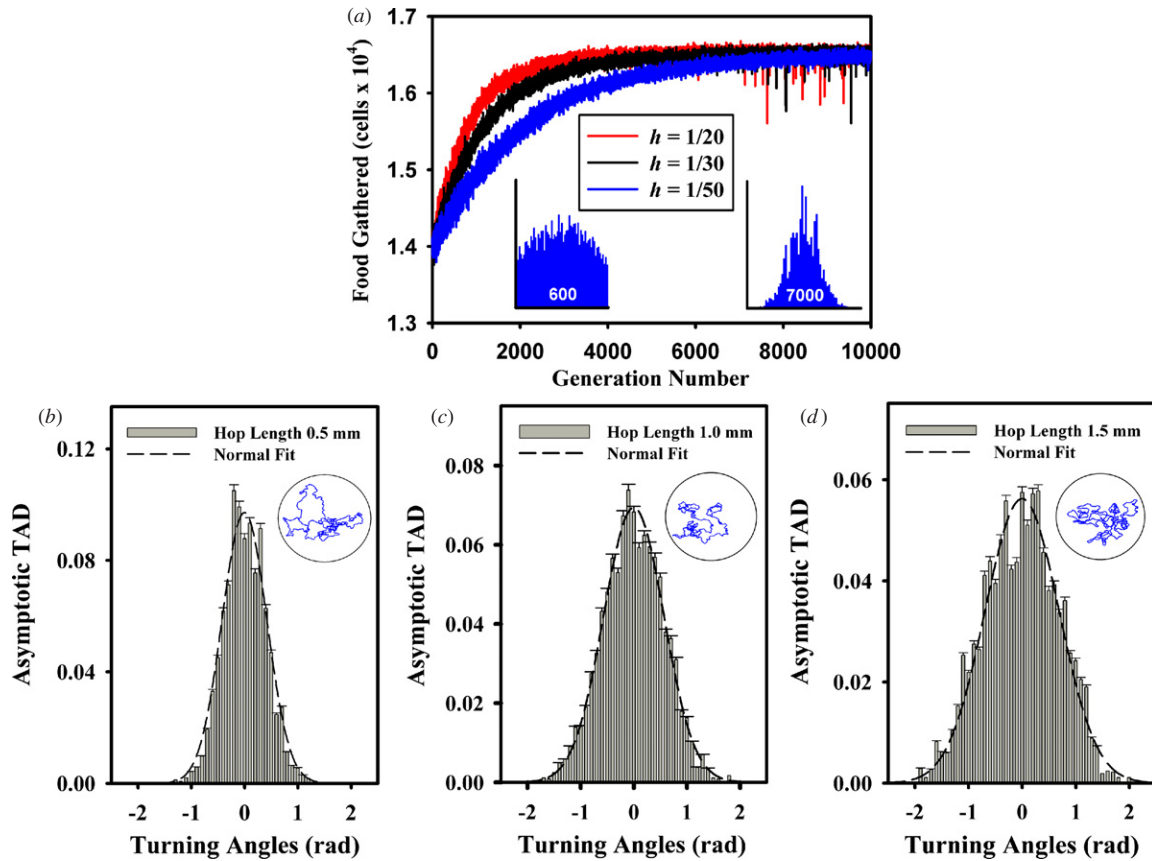


Figure 1. (a) Food gathered by the most successful agent in each generation of the EVO simulation versus generation number for three values of the inheritance parameter h as indicated. Insets show normalized turning angle distributions ($P(\alpha)$ versus α , with α ranging from $-\pi$ to π) for $h = 1/50$ at generation 600 (wide distribution) and generation 7000 (narrow distribution). Asymptotic TADs averaged across ten trials with the hop lengths indicated for $h = 1/50$ are shown in (b)–(d). The dashed lines are fits to the normal distribution with parameters determined by maximum likelihood estimation. The width of each distribution yields a value σ , as listed in table 1. (b) $\sigma = 0.42 \pm 0.01$ rad, (c) $\sigma = 0.57 \pm 0.02$ rad and (d) $\sigma = 0.70 \pm 0.02$ rad. Error bars represent the inheritance, h ($1/50$), multiplied by the bin height, representing the maximum possible inter-generational change in bin height. The insets in (b)–(d) show example trajectories inside circular patches.

Table 1. Asymptotic, optimal and measured values of σ .

Hop length (mm)	Asymptotic noise intensity (EVO) ^a (rad)	Optimal noise intensity (SR) ^b (rad)	Average experimental noise intensity ^c (rad)
0.5	0.42 ± 0.01	0.33 ± 0.06	1.06 ± 0.1
1.0	0.57 ± 0.02	0.50 ± 0.09	
1.5	0.70 ± 0.02	0.61 ± 0.10	

^a Values are the mean and standard deviation of ten trials; $h = 1/50$.

^b Values are the mean and standard deviation of 100 trials.

^c Value is averaged over data from 5 species, as well as juveniles from 2 of these species. Precision is estimated; see Garcia *et al* (2007).

inter-quartile ranges from the third quartile). Next, a second value of σ is chosen, and a second population of 20 agents feed, with the maximum food gathered again recorded. This process continues for 46 values of σ ranging from 0.1 to 10 rad, constituting a single trial. The result of a trial is a curve of maximum food gathered as a function of σ . We perform 100 such trials, and then calculate the particular value of σ which results in the peak of the curve for each trial. These 100 values of σ are averaged, and the average (and standard deviation) is reported in table 1 as the optimal SR noise intensity.

For a more detailed description of the EVO and SR algorithms, see the supplementary material stacks.iop.org/PhysBio/5/044001.

Results

Figure 1(a) shows the food gathered by the most successful agent in the EVO simulation as a function of the number of generations. The food gathered plateaus after a number of generations depending on the value of inheritance parameter h , with larger values of h leading to stasis in earlier generations,

as expected. Insets show examples of the evolving TADs which begin with wide characteristic widths (large σ) and become narrower (smaller σ) in later generations. Similar plateaus arise often in both natural and artificial selection (Falconer 1981, Robertson 1980). Note that these plateaus are achieved in remarkably few generations, a testament to the power of natural selection (Endler 1986). Surprisingly rapid evolutionary processes have also been shown in other natural selection-based (albeit model-dependent) simulations, such as Nilsson and Pelger's model for the evolution of the fish eye (1994).

Asymptotically achieved TADs, together with Gaussian fits and representative trajectories, are shown in figures 1(b)–(d). The choice of normal fitting curves is the result of statistical analysis of the asymptotic distributions. The shapes of the evolving and asymptotic distributions, and consideration of the experimental data, suggest null hypotheses that correct fits would either be Laplacian (double-exponential) or normal. We calculated the Cramér–von Mises W^2 , the Watson U^2 , the Anderson–Darling A^2 and the Kolmogorov–Smirnov D statistics (D'Agostino and Stephens 1986, Efron and Tibshirani 1993, Puig and Stephens 2000) for the empirical distribution functions to help discern between the two possibilities. Although one might immediately expect normal distributions based on the central-limit-theorem, we point out that this applies only in the limit of a large number of observations, which may not apply to the foraging situation under investigation here. Our model, for instance, does not involve an infinite number of experiments with infinite sets of turning angles; nor do we model either an infinite feeding time or a food patch of infinite size.

A table detailing the results of our statistical analysis is provided in the supplementary material. Briefly, assessment of the Laplacian null hypotheses for the hop length value 1.0 mm gave $W^2 = 0.191$, $U^2 = 0.151$, $A^2 = 1.191$ and $D = 1.102$, qualifying the null hypothesis to be rejected at the 0.025, 0.01, 0.025 and 0.01 levels, respectively. However, for the normal distribution, the statistic values of $W^2 = 0.084$, $U^2 = 0.080$, $A^2 = 0.512$, and $D = 0.814$ reject the normal null hypothesis at the 0.25 level for the first three statistics, and at the 0.1 level for D . The significance levels we report show that neither distribution has been rejected outright by all tests, although there is convincingly less evidence that our resultant distribution is Laplacian.

Figure 2(a) shows σ as a function of generation for three different values of h , while (b) shows σ as a function of generation for different hop lengths. In each case, as in figure 1(a), stasis is achieved as the number of generations increases. Note that, in figure 2(b), the evolved value of σ increases as hop length increases. Stasis values of σ shown in figure 2(b) are reported in table 1. It is these final asymptotic values of σ that we consider to be evolved quantities. But the question immediately arises: are these evolved quantities optimal for foraging success? If they indeed arise from natural selection, then we expect that they might in fact be optimal as consistent with a 'strict Darwinian' interpretation of natural selection. We independently test this assertion using the stochastic resonance simulation to extract optimal values of

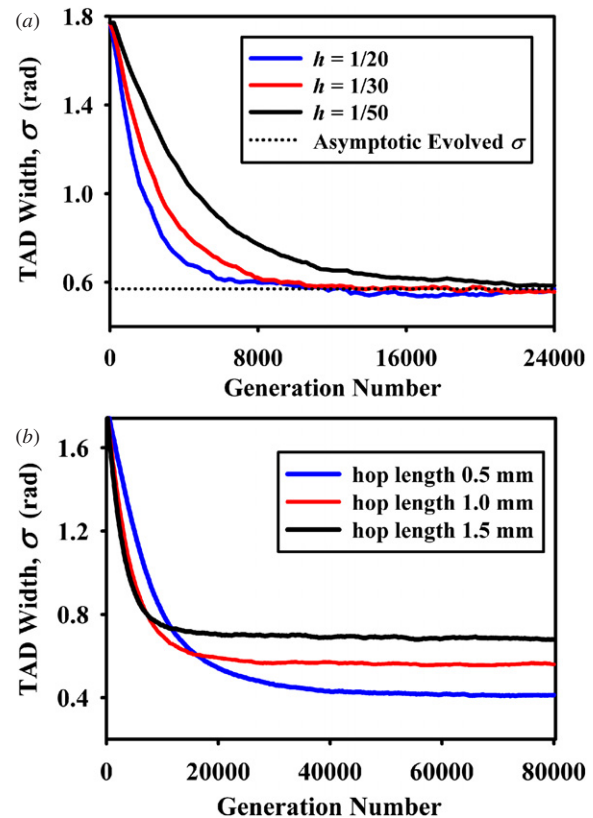


Figure 2. (a) Evolution of σ using different values of the inheritance, h , with the hop length parameter fixed at 1 mm shows an asymptotic approach to similar values of σ . Note lessening variability in curves with lesser inheritance. Curves represent averages over two trials. (b) Evolution of σ using different values of fixed hop length shows asymptotic behavior to different values of σ . Curves represent averages over ten trials.

σ , which are then compared with the experimental findings of Garcia *et al* (2007), and with the predictions of EVO, in table 1.

In the SR simulation, the maximum value of food gathered was averaged over 100 trials for each value of σ . Plotting these values for food gathered versus σ results in classic SR curves, shown in figure 3, wherein a beneficial feature (food gathered) is maximized at optimum noise intensity (σ). We find that the optimum noise intensities for SR are typically intermediate values of σ ; in other words, TADs that are either too narrow or too wide lead to less than optimal foraging efficiency. We also note that the optimum noise intensity increases as hop length increases, a result that 'tracks' similar findings from the EVO simulation (see figures 1(b)–(d), 2(b) and table 1).

Discussion

Comparison of figures 2(b) and 3 (and the first three columns in table 1) shows that our evolutionary simulation converges on a solution to the foraging problem similar to that achieved with the SR algorithm. Optimal foraging is achieved at increasing values of σ for increasing hop length. This is found both in the values of σ for which the SR algorithm achieves maximum food gathered, and in the asymptotic values of σ achieved with

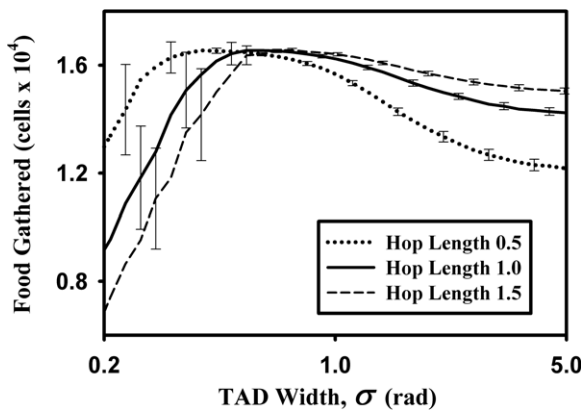


Figure 3. Food gathered versus σ for the three hop lengths indicated, calculated using the SR simulation. Curves are averaged results from 100 trials; error bars, shown every third point on each curve, represent the standard deviation. Each trial incorporates 20 independent determinations of the food gathered by an agent for each of 46 values of σ . Here, we only show values of σ from 0.2 to 5 rad on the horizontal axis.

EVO. Furthermore, the two algorithms lead to very similar optimal noise intensities. While these results do not *prove* the two hypotheses stated above, they offer substantial support in their favor.

Since both algorithms are performing optimizations independently, it is quite remarkable that they converge on similar solutions. The result that both optimal (SR) and asymptotically achieved (EVO) values of σ increase with hop length can be explained at a ‘geometrical’ level with the following argument (see also the discussion in Dees *et al* (2008)). It is clear that larger turning angles (distributions with larger σ) lead to more compact trajectories, while smaller turning angles lead to straighter trajectories. The latter case, combined with larger hop lengths, leads to the feeding agent quickly leaving the food patch, and hence to a decreased feeding efficiency. Thus, optimal feeding will be achieved at wider turning angle distributions for longer hop lengths, a result shown both in the SR and the EVO simulations.

How does one interpret the shapes of the evolved distributions? Higher animals, such as albatrosses (Viswanathan *et al* 1996), monkeys (Boyer *et al* 2006) and marine predators (Sims *et al* 2008), including humans (Bertrand *et al* 2007), searching in *non-uniform* environments can make complex cognitive decisions about where food is located (Boyer *et al* 2006). Their foraging behavior has been described using Lévy-shaped distributions, though this description has recently been revised in the cases of some animals (Edwards *et al* 2007). Trajectories of smaller animals such as *Daphnia* cannot be described using Lévy statistics since the animals move through short hops of limited distance. In contrast, experimental studies of slime mold cells (Liang *et al* 2008), and the studies of foraging *Daphnia* (Garcia *et al* 2007, Dees *et al* 2008) which motivated our present paper suggested exponential turning angle distributions. Maxima can be obtained from the SR algorithm regardless of whether it is based on exponential distributions as in Dees *et al* (2008), or based on normal distributions as in the present

study. Our model-free approach in EVO, however, seems to ‘prefer’ the Gaussian distribution.

The areas of largest disagreement between the Gaussian fits and the evolved distributions in figures 1(b)–(d) lie near the extremities of the distributions. This is even more apparent when looking at individual rather than averaged distributions (data not shown). This may be a result of the algorithm itself, which consists of repeated percentage-wise subtractions from the ‘parent’ distribution followed by the addition of the inheritance. This may lead to a gradual tapering of the evolving distribution in low-percentage areas, possibly diminishing the outer edges of the tails. Furthermore, looking at the final results, for each hop length tested, the peak noise intensities extracted by SR are slightly less than those predicted by EVO. We suggest that because foragers in SR are selecting angles from perfectly formed TADs, they have access to all angles throughout the entire distribution $[-\pi$ to $\pi]$, including the furthest reaches of the tail. If EVO does indeed systematically diminish some of the tail, the only way that foragers in EVO will have access to these angles is to foster slightly wider distributions, where the angles they need are no longer in the outer tail regions. Still, the values of table 1 show definite agreement between the two models.

Our results follow the conventional view of natural selection as an ‘optimizing’ mechanism, famously critiqued by Gould and Lewontin (1979). Ultimately, however, the problem is deeper—and evolution more subtle—than that. Natural selection is constrained by the physical limitations of animal morphologies, as well as by historical contingencies that may privilege less-than-optimal solutions. Nonetheless, traces of optimization remain, as, perhaps, in the observed turning angle distributions of real *Daphnia* and the single cells of slime molds.

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