

Neuronal Dynamics and Spatial Foraging

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Abstract

Foraging is an embodied cognitive process which balances the search constraints of exploration versus exploitation. As such, foraging strategies and mechanisms offer useful insight into abstract forms of search such as visual search, problem solving, and semantic recall. We performed a series of simulations using artificial neural networks to relate metastable neuronal dynamics to observed foraging behaviors. We show that the velocity and tortuosity of the foraging paths are influenced by metastable neuronal activity, while resource collection is unaffected. These initial results indicate that neuronal metastability may contribute to foraging behaviors but additional mechanisms are needed to optimally exploit environmental resources.

Keywords: foraging; neural networks; critical branching

Introduction

Foraging is an embodied cognitive process. Animals move continuously through physical space searching for food, mates, or other resources. Increasingly, evidence indicates that common neurophysiological mechanisms support a broad range of search behaviors. Thus, cognitive search tasks such as visual search, problem solving, and semantic recall share many of the mechanisms and constraints of foraging (Hills, Todd, Lazer, Redish, & Couzin, 2014).

Previous investigations of foraging have used probabilistic models to account for different facets of animal foraging such as group dispersal and perseveration. Many of these models can produce qualitatively similar patterns of movement to those found in animal foraging data: clustered, local movements separated by longer, straighter segments (Codling, Plank, & Benhamou, 2008). Area-restricted search (ARS) attributes this heterogeneity in movements to a division between those focused on exploiting previously discovered resources and those that explore farther away for new resources. See Figure 1 for an example of ARS in human behavioral data. ARS becomes potentially optimal if it can be related to marginal-value theorem, which holds that foraging is optimal under certain assumptions when the search agent remains in a current patch of resources until the expected rate of reward for the patch falls below the expected rate of reward for the environment as a whole (Charnov, 1976).

ARS can explain how foraging animals with minimal cognitive capabilities can approximate the marginal value theorem by modulating the rate of reorienting (Hills, 2006), but there is much debate and disagreement over which foraging data and which aspects of search agents and

environments are more or less important for theories and models (e.g. Viswanathan et al., 1996; Edwards, 2011; Planck, Auger-Méthé, & Codling, 2013). Additionally, prior models leave the cognitive and neural bases underlying the search process unspecified. These shortcomings make it currently unclear which results from the foraging literature are most relevant to cognitive search processes.

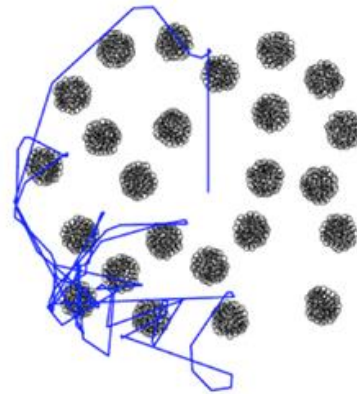


Figure 1: An example Area-Restricted Search produced by a human participant foraging (**blue**) in a virtual environment containing a patchy distribution of resources (**black**). Reproduced from Hills, Kalff, & Wiener (2013) Figure 1C.

In the current study, we focus on the balance between exploration versus exploitation as one aspect of foraging that is important and general to cognitive search processes (Hills et al., 2014). Exploration relates to the far-ranging movements of ARS, and exploitation relates to the local movements that capitalize on resources recently found. We hypothesize that the necessary balance between exploration and exploitation can be expressed in terms of *metastable dynamics*. Metastability is a property of dynamical systems which attract toward synchronous or stable states but regularly produce phase transitions between these states (Kello, Anderson, Holden, & Van Orden, 2008; Tognoli & Kelso, 2014). These dynamics facilitate propagation of information through the system and support fluctuations in activity across a wide range of scales, i.e. many small-scale fluctuations interspersed with less common but much larger-scale fluctuations (Kozma, Puljic, Balister, Bollobás, & Freeman, 2005).

Metastability can be simulated in neural networks through *critical branching* (Beggs & Plenz, 2003), which is an objective for regulating spike propagation and maximizing

information transmission through networks. Kello (2013) formulated a mechanism that is local to spiking neurons and their respective synapses, and gives rise to critical branching at the network level. The mechanism probabilistically assigns credit to individual neurons for causing action potentials. This credit is used to enable or disable synapses and achieve an average ratio of one spike propagated for each spike produced. The resulting homeostasis is metastable rather than stable, because ongoing synaptic switching drives the network from one transient state to the next (Kello, 2013).

Objective

The overarching objective of the present study was to develop a framework with which to explore neural network models of foraging. While prior work has explored various foraging models in detail, we know of no attempt to relate neuronal dynamics to observed foraging behaviors. Currently we focused on the hypothesis that metastable patterns of activity produced by critical branching networks would support movement patterns like those found in nature. More generally, we initiate work on relating neural processes to foraging behaviors, and provide the code for doing so.

Methods

We developed simulation software in which an artificial agent forages for resources. The agent is composed of an input model, a neural network, and an output model. The agent is situated in a bounded two-dimensional environment containing clusters of resources. Two groups of simulations were conducted, one in which a critical branching process actively tuned network connectivity throughout (CB) and one in which connectivity was static (NonCB) for comparison. Data on neural activity, the foraging path, and search performance were recorded and compared between CB and NonCB simulations.

The simulation software was developed using the Oracle Java SE SDK Version 8 Update 31, and the Apache Commons for statistical functions and file processing. The software and instructions for replicating our results can be accessed at cogmech.ucmerced.edu/downloads.html.

Critical Branching Neural Network

The neural network contains three layers of leaky-integrate-and-fire neurons, referred to as the source, the reservoir, and the sink (Kello, 2013). The neuron model is updated at fixed intervals (1 ms). The source layer contains 100 excitatory neurons. Each source neuron receives input directly from the input model and sends synaptic output to the reservoir. The reservoir contains 1,000 neurons (80% excitatory) which project recurrent synapses within the reservoir and feedforward synapses to the sink. The sink contains 100 excitatory neurons and its activity drives the update of the output model—sink neurons are required to absorb propagated spikes during critical branching to avoid saturation. The initial probability of a synapse between any pair of projecting and receiving neurons for all synaptic pathways is 0.1.

The critical branching mechanism described by Kello (2013) was modified for clock-based updating, but the essence of the algorithm remained unchanged. Each synapse is probabilistically ($p = 0.05$) credited for postsynaptic action potentials and uncredited for presynaptic action potentials. The mechanism results in approximately equal mean firing rates at the source and sink and the branching ratio approaching 1.0 after a period of stabilization (Kello, 2013).

Foraging Environment

The input model generates incoming stimulation for the neural network. The model evaluated here is a random spike generator which causes an action potential with a fixed probability at each source neuron for each update cycle. This

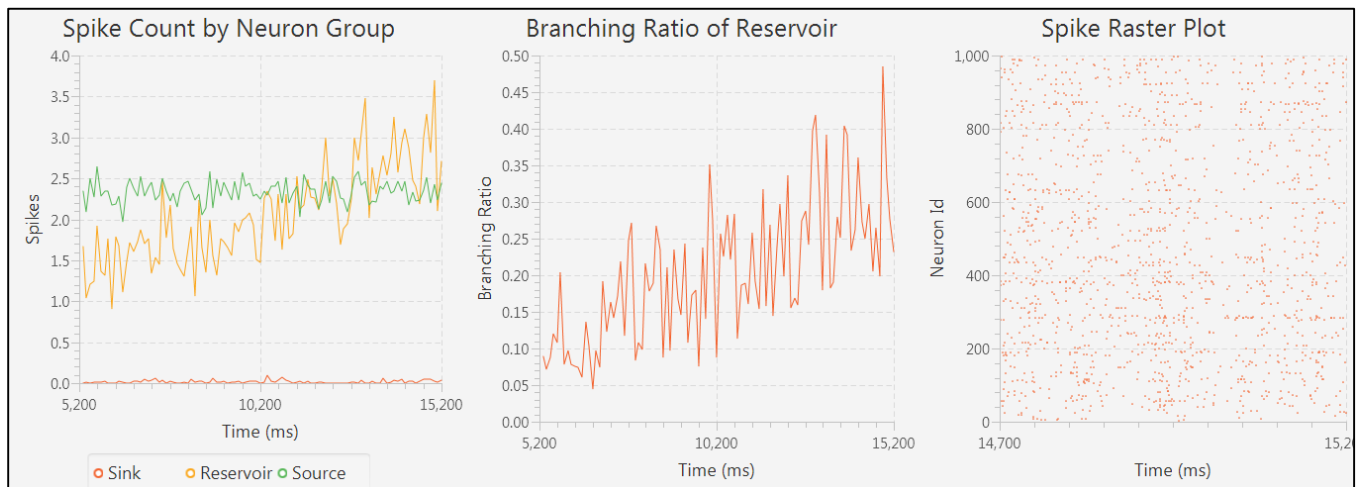


Figure 2: Continuous visualization of neural activity in the simulation software. Note that firing rates and branching ratio have not yet converged to stable values. **(Left)** Spike counts per ms are plotted for each layer of the network. **(Center)** The mean local branching ratio for the reservoir is shown. **(Right)** A spike raster plot shows spikes as they occur in the reservoir.

probability is expected to be the inverse of the mean firing rate (25 spikes/s). While the random input model is an inaccurate simulation of the sensory information available to an animal forager, it allows us to limit the uncontrolled variability in this initial work. We also tested a sequential spike train input model, which did not substantially affect network activity (not reported).

The output model transduces the spiking activity of the sink to movement of the foraging agent. We developed a simplistic output model for these simulations (see the discussion for alternatives). During each update, the model counts the number of spikes in four equally-sized subgroups of the sink. These values are then treated as the two-dimensional velocity (positive x, positive y, negative x, and negative y) of the agent in the subsequent interval. A major concern in foraging analyses of all kinds is binning and its effect on various metrics. Binning is the process of summing activity over a time window to reduce noise in the data. Unless otherwise specified, binning was performed by averaging values over 100 ms windows to preserve the time course of the data while removing excessive high-frequency noise. See Figure 3 for a sample path produced with these models.

The foraging environment was a square with sides of length 20,000 units. Movements which would end outside of these boundaries were clipped. Within the environment, 500 resource patches were uniformly distributed. The number of resources in each patch was sampled from a geometric distribution with mean 10, to yield approximately 5,000 resources total. Resource collection range was set to 10 units.

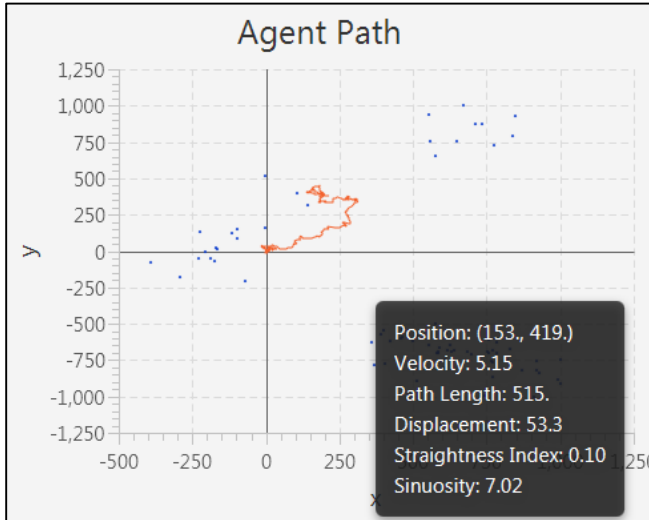


Figure 3: Continuous visualization of a foraging path with clustered resources. See Figure 6 for the full set of recorded paths.

Foraging Metrics Many models of foraging are derived from physical equations governing particle diffusion, so-called random walks. Codling, Plank, & Benhamou (2008) consolidate and extend these models, providing derivations

and a variety of useful metrics. Relevant aspects of the work are summarized below.

The probability density function for the position of a random walk is used to derive the mean displacement and mean squared displacement (MSD). MSD is particularly useful as a measure of dispersal, since it assesses the degree to which a forager has explored its environment. To calculate the MSD for an empirical distribution, we use the following:

$$(1) \quad msd(T) = \frac{\sum_{t=1}^T [x(t) - x(0)]^2}{T}$$

Where $x(t)$ is the position of the forager at time t and T is the total number of time steps observed.

Importantly, in simple random walks, steps are independent and identically distributed, such that the subsequent position of a forager depends only on the prior position, not on the path of arrival. The addition of memory to the diffusion model introduces directional correlation between subsequent steps. Thus, correlated random walks (CRW) tend to exhibit directional persistence. This extension allows CRW models to better fit movement data from animals, which generally prefer forward movement to perfectly random reorientation. The directional bias can be quantified for a foraging path consisting of a series of discrete steps using the mean sine and mean cosine of the turning angle. More valuable for the present work, metrics for the rate of turning within a given path length—the tortuosity of the path—can be derived from this series of turning angles. Straightness-Index is one measure of tortuosity, the ratio of gross displacement to path length. Another metric, sinuosity, has also been applied. The sinuosity, S , of a sequence of movements is given by:

$$(2) \quad S = 2 \left[E(L) \left(\frac{1+c}{1-c} + b^2 \right) \right]^{-1/2}$$

Where $E(L)$ is the mean step length, c is the mean cosine of the turning angle, and b is the coefficient of variation of step lengths (Codling et al., 2008). In the present study, we calculated MSD, straightness-index, and sinuosity of foraging paths.

A Lévy flight is a random walk in which step lengths exhibit power-law scaling. This kind of foraging model was first described empirically by Viswanathan et al. using data from albatrosses (1996). In practice, it has proven difficult to distinguish between power-law scaling and other distributions. Clauset, Shalizi, & Newman (2009) describe a statistical framework for estimating power-law model parameters and assessing the goodness-of-fit relative to alternative hypotheses. They apply the framework to evaluate biases in commonly used alternatives, such as simple linear regression, and demonstrate its benefits. As a preliminary investigation, we applied the graphical method for evaluating power-law scaling, in which the continuous distribution of an empirical dataset is plotted in log-log coordinates. A linear tail across at least two orders of magnitude would be considered to support power-law scaling (Newman, 2005).

Viswanathan (1999) presents a formal analysis and evidence from numerical simulations that Lévy flights are optimal foraging strategies when resources are sparse and randomly distributed. Alternatively, when resources are patchy and therefore the mean resource density within and between patches can be learned, marginal value theorem predicts transitions between behavioral regimes (Charnov, 1976). Both of these arguments rely on the intuitive rate of resource collection. We therefore record a resource collection event whenever a foraging agent approaches within a fixed collection range of a point resource and subsequently remove that resource from the environment.

Results

Network Activity

Spiking activity at the sink ($M = 1.69$, $SD = 0.78$) was 73% of the source ($M = 2.32$, $SD = 0.0048$) across all simulations ($N = 16$). The branching ratio of the reservoir, the ratio of postsynaptic to presynaptic spikes, approached 1.0 in both groups during the connectivity stabilization period. After this period, the CB mechanism was disengaged for the NonCB group ($M = 0.927$, $SD = 0.063$), which consequently exhibited greater variance than the CB group ($M = 0.946$, $SD = 0.0059$) as shown in Figure 4.

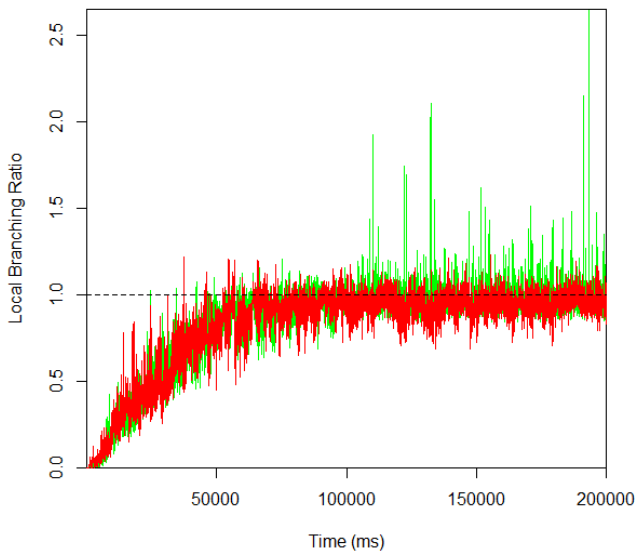


Figure 4: Local Branching Ratio for the CB group (**red**) and the NonCB group (**green**). Note the greater variability in the NonCB group after the initial stabilization period.

Interspike intervals for representative neurons in the reservoir are shown in Figure 5. Note that Kello (2013) predicts that ISIs should follow a heavy-tailed distribution. This was graphically assessed by plotting the cumulative probability distribution in log-log coordinates (Newman, 2005). The distributions in Figure 5 may exhibit power-law tails, or follow log-normal or stretched exponential distributions. Of note is the greatly increased variability in the distribution of ISIs for the NonCB group.

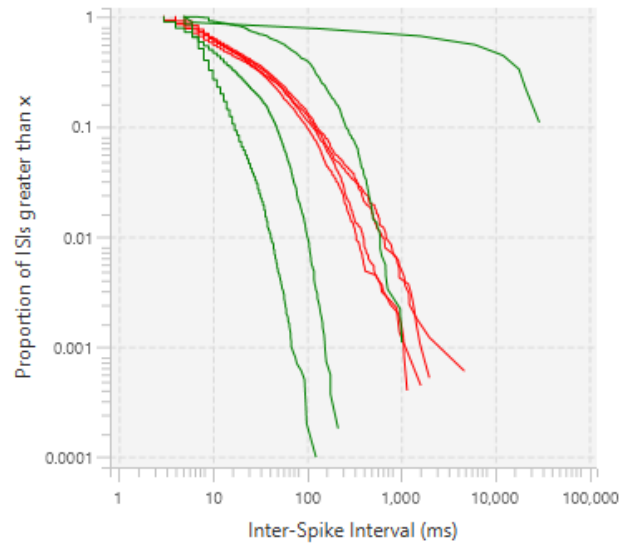


Figure 5: Interspike interval distributions of neurons (# 0, 100, 200, 300) from the NonCB (**green**) and CB (**red**) groups.

Foraging Path

Qualitatively, the critical branching foragers produced paths that were significantly more tortuous, included path crossings, and seemed to exhibit no directional bias. The non-critical branching foragers tended to perseverate along a narrow range of headings eliminating path crossings, minimizing tortuosity, and introducing an apparent directional bias.

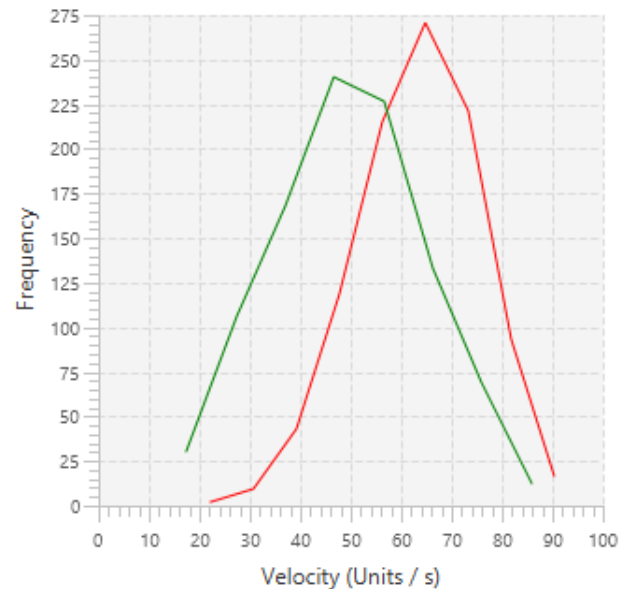


Figure 6: Velocity Histogram for CB Simulation #1 (**Green**) and Non-CB Simulation #1 (**Red**).

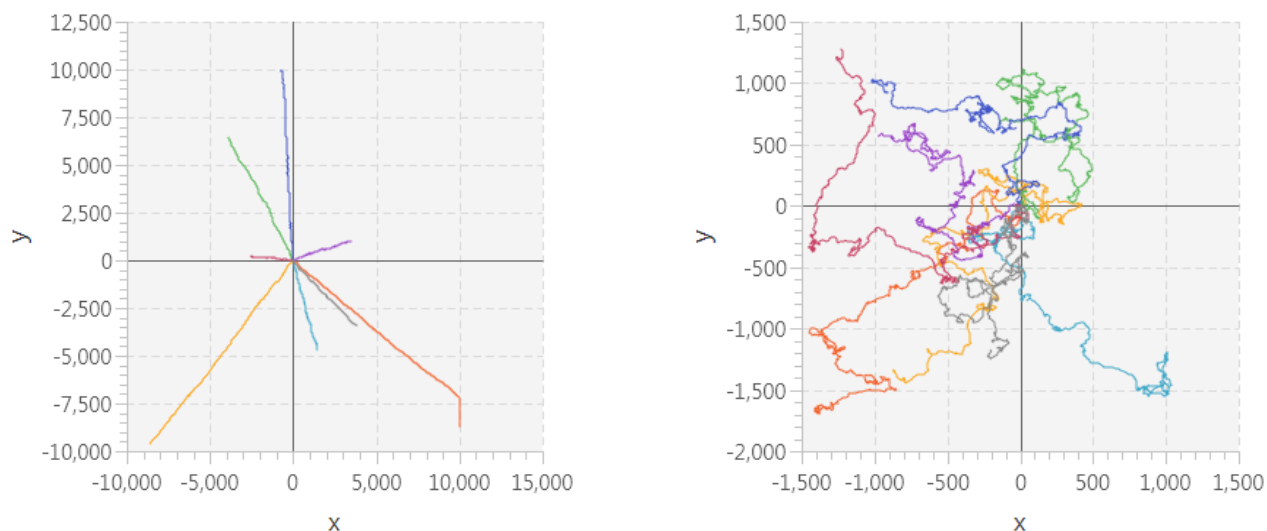


Figure 7: Group dispersal for 100 s. The non-critical branching networks exhibit little variability (**left**) resulting in much wider dispersal but little coverage. The critical branching networks (**right**) demonstrate significantly greater variability of movement. The path of each forager is translated to the origin for easier interpretation.

Velocity We did not find a significant difference in mean velocity between groups ($M_{CB} = 46.89$, $M_{NonCB} = 50.05$) but did find a strong effect on the variance of velocity ($SD_{CB} = 1.63$, $SD_{NonCB} = 20.3$, $F(7) = 0.0065$, $p < 0.001$). Velocity distributions were qualitatively similar, and we found no evidence of power law scaling in step size in either group by graphical inspection (see Figure 6).

Dispersal Group dispersal of the foraging paths are shown in Figure 7. Mean-squared displacement (MSD) was significantly greater for the NonCB group ($M = 2.54 \times 10^7$, $SD = 2.54 \times 10^7$) than for the CB group ($M = 8.32 \times 10^5$, $SD = 5.40 \times 10^5$), $t(7.0) = -2.74$, $p = 0.029$.

Tortuosity Benhamou (2004) describes three methods for estimating the tortuosity of a movement path. The non-critical branching group produced significantly straighter paths ($t(7.28) = -5.17$, $p = 0.001$) however we did not find a significant difference in sinuosity between groups ($t(7.26) = -0.093$, $p = 0.93$), which may be due to high-frequency noise in the paths despite binning.

Resource Collection We performed a paired, 2-tailed t-test on number of resources collected and did not find a significant difference between groups ($M_{CB} = 2.0$, $M_{NonCB} = 2.5$, $p = 0.66$).

Discussion

The goal of this study was to make initial progress into relating neural activity to patterns of movement observed in animal foraging. We compared two groups of spiking neural networks, one in which a homeostatic critical branching mechanism was present and a control group in which critical

branching was disabled but other aspects of the model were the same.

The recorded network activity agreed with results presented by Kello (2013), indicating that the critical branching group is exhibiting metastability at the level of neural activity. This did indeed translate to differences in foraging paths, though not in exactly the ways we hypothesized. The resulting effect on foraging paths was significantly greater variation in the direction of movement in the CB simulations. We believe the reason for the observed increase in tortuosity is that there is a constant shift in which neurons in the sink receive the greatest degree of activation from the reservoir. As synapses in the pathway from reservoir to sink are switched on or off, a new set of neurons becomes dominant, changing the foraging direction.

Interestingly, we did not identify an effect of critical branching on the distribution of step sizes. Thus our results did not support the predicted connection between power law scaling in neural activity and Lévy flights. Given that aggregated neural activity can lead to power laws (Kello, 2013), the present results indicate that not all such aggregations will do so. This suggests that consideration of other factors affecting spatial search or exploring other models of neural control will be important for understanding the relationship between neural activity and Lévy foraging.

Finally, although the foraging literature makes a variety of predictions about the relationship between tortuosity and optimality, we did not find any significant difference in resource collection rate in our simulations. We attribute this to the fact that the agents were unable to learn anything about the resource distribution in the present study.

There are several promising future directions for this research. First, qualitative pilot comparisons with several

output models demonstrated that binning the path, i.e. summing activity over an interval to produce motion on an ecologically plausible timescale, and applying physical constraints (momentum, friction) significantly alter the shape of the path.

Second, in foraging animals, tight coupling of perception and action require immediate, implicit, and continuous decision-making. The present study did not explore this coupling between perception and action, and in particular did not address how discovering a resource could be expected, through evolved mechanisms or learning, to bias subsequent movements. Making the foraging model sensitive to the history of resources collected is essential to *adaptive* foraging and may be responsible for some of the patterns that are observed in animal search paths. Encoding agent position or local environmental features as input to the neural network would be a first step to addressing this limitation and provide insight into interaction of agent and environment. Future research should also investigate the ability of critical branching foragers to optimize movement patterns by learning about the distribution of resources in the environment.

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