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).

Much of the prior work on foraging has analyzed it as a statistical process rather than the product of embedded, interactive systems. This approach has produced effective descriptive accounts of movement patterns but neglects the roles of perceptual, motor, and neural mechanisms. Statistical models have successfully characterized aspects of foraging such as population dispersal and perseveration. Some 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). In contrast, area-restricted search (ARS) describes the emergence of heterogeneity in movements as arising from direct interaction with the resources in the environment. See Figure 1 for an example of ARS in human behavioral data. ARS is adaptive in the sense offered by the marginal-value theorem, which holds that foraging is optimal when the forager transitions between resource patches as a function of the rate of success in the current patch (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).

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, 1999; 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.

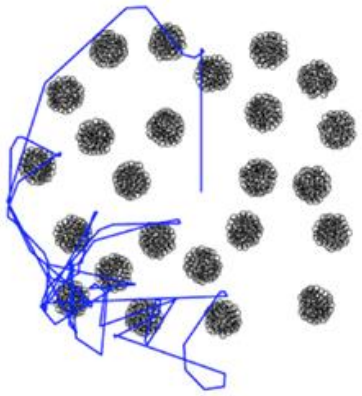

Figure 1: An example area-restricted search produced by a human participant foraging **(blue)** in a virtual environment containing a patchy distribution of resources **(black)**. Reproduced from Hills, Kalff, & Wiener (2013) Figure 1C.

In the current study, we focus on the relationship between neural dynamics and the exploratory paths agents take as they forage. Exploration refers to patterns of movement in search of patches of high resource density in the environment. We hypothesize that the exploratory paths taken will be more realistic when the neural model exhibits *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). Metastable neural activity has been proposed as a substrate around which adaptive behaviors can be organized. To successfully account for the spatial movement patterns of foragers, metastable neural activity must be capable of producing complex behavioral dynamics.

Objective

Our objective 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 metastable neural activity to observed foraging behaviors. 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 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 tuned network connectivity to produce metastable neural activity (CB) and one in which connectivity was static (NonCB) for comparison. Neural spike times and rates, movement paths, and resource collections were recorded and compared between groups.

The simulation software was developed using Java SE SDK (8u31) 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

Artificial neural networks can achieve metastability 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, local to spiking neurons and their synapses, which produces critical branching at the network level. The mechanism probabilistically assigns credit to individual neurons for causing action potentials. The 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.

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 projects synapses 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 probability of a synapse between any pair of projecting and receiving neurons for all 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. Spikes probabilistically ($\rho = 0.05$) enable axonal synapses and disable dendritic synapses causing the local branching ratio—the ratio of upstream to downstream spikes—to approach 1.0. This process self-organizes across the network to reach approximately equal mean spiking rates at the source

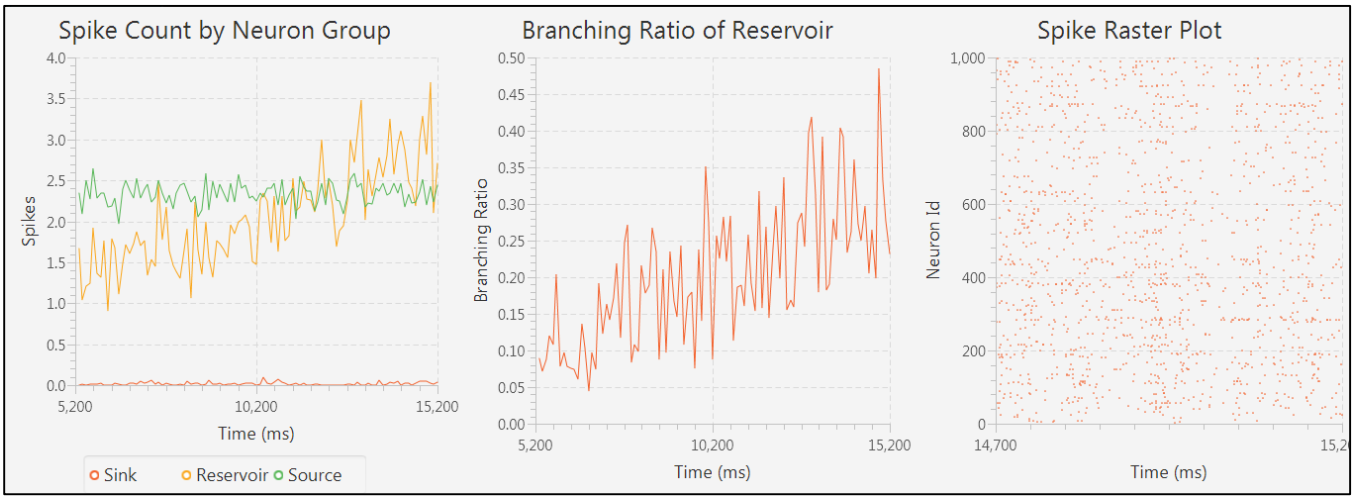

Figure 2: Continuous visualization of neural activity in the simulation software. **(Left)** Spike counts per ms for each layer of the network **(Center)** Mean local branching ratio for the reservoir **(Right)** Spike raster plot depicting spike times in the reservoir for the previous 500 ms

and sink. See Kello (2013) for a complete description of the critical branching algorithm and the resulting network dynamics.

Foraging Environment

The input model generated incoming stimulation for the neural network. The model described here was a random spike generator which caused an action potential with a fixed probability at each source neuron for each update cycle. The mean firing rate in the network was equal to the product of this probability and the number of neurons. We also tested a sequential spike train input model, which did not substantially affect network activity (not reported).

The output model transduced the spiking activity of the sink to move the foraging agent. During each update, the model counted the number of spikes in four equally-sized subgroups of the sink. These values were then treated as the two-dimensional velocity (positive x, positive y, negative x, and negative y) of the agent in the subsequent interval. A concern in many types of foraging analyses is temporal binning which in some cases can skew movement distributions to support models that would not be supported by the unbinned data (Newman, 2005). Nevertheless, movements generated on the scale of milliseconds would not be relevant to foraging behaviors. 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.

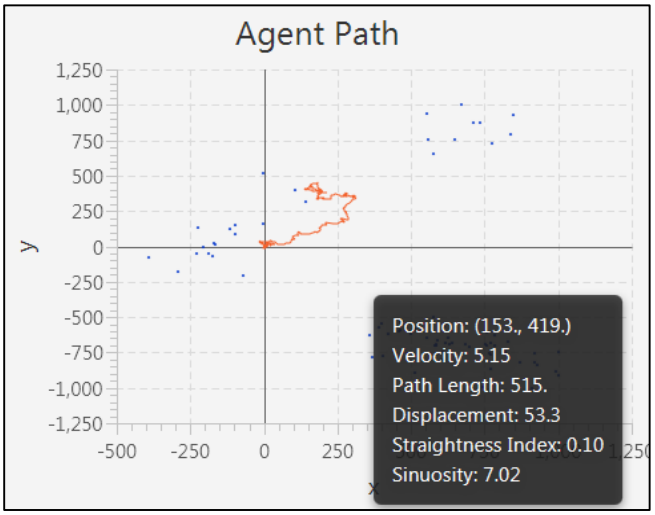

Figure 3: Continuous visualization of a foraging path with clustered resources and path statistics.

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. Resources within 10 units of the forager were automatically collected.

Thus, the forager was unidirectionally coupled with its environment. The lack of sensory information related to position or resources is a limitation, but it was necessary to directly explore the movement distributions produced by the intrinsic metastable dynamics of the network. Figure 3 depicts a sample path produced with these models.

Foraging Metrics Many models of foraging are derived from physical equations governing particle diffusion, so-called random walks. Codling, Plank, and Benhamou (2008) consolidates 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:

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

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, better fitting 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 the 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:

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

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 Lèvy flight is a random walk in which step lengths exhibit power-law scaling. This kind of foraging model was first described empirically by Viswanathan, Afanasyev, Buldyrev, Murphy, Prince, and Stanley using data from albatrosses (1996). In practice, it has proven difficult to

distinguish between power-law scaling and other distributions. Clauset, Shalizi, and Newman (2009) describes a 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 analysis, we applied the graphical method for evaluating power-law scaling, in which the cumulative probability distribution of a 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 Lèvy 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, the marginal-value theorem predicts transitions between behavioral regimes (Charnov, 1976). To test whether different neural models lead to different rates of resource collection, we record a resource collection event whenever a foraging agent gets within a fixed spatial distance from a point resource. That resource is subsequently removed 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 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 subsequently exhibited greater variance (M = 0.946, SD = 0.0059) as shown in Figure 4.

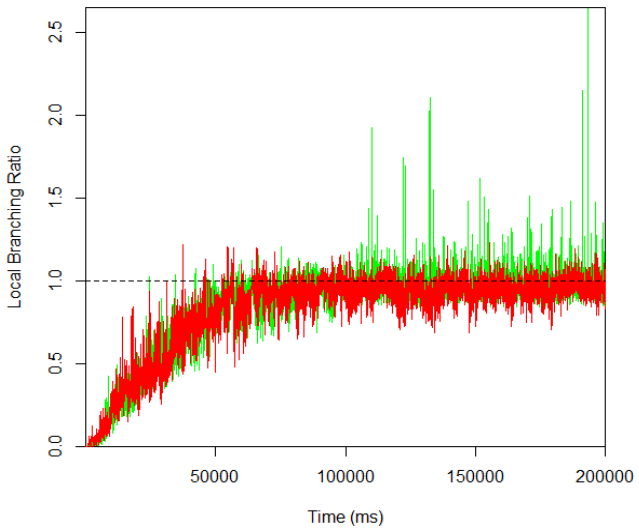

Figure 4: Local Branching Ratio for the CB group **(red)** and the NonCB group **(green)**.

Interspike intervals (ISIs) 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). Of note is the greatly increased variability in the distribution of ISIs for the NonCB group.

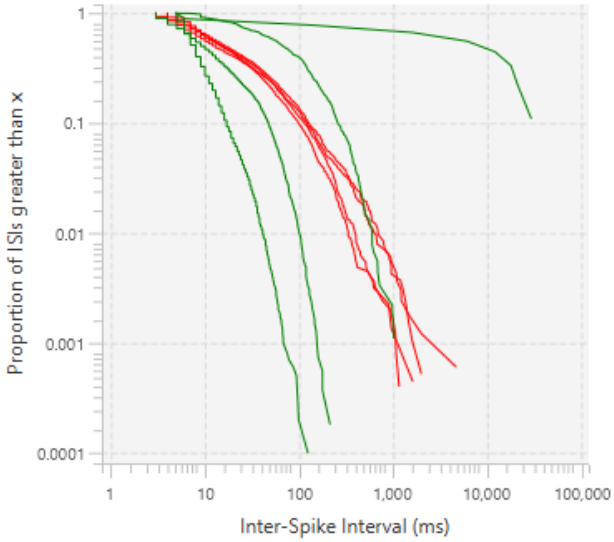

Figure 5: Interspike interval distributions of neurons (# 0, 100, 200, 300) from the CB **(red)** and NonCB **(green)** groups.

Foraging Path

Qualitatively, the critical branching foragers produced paths that were more tortuous, included path crossings, and seemed to exhibit no directional bias (Fig. 7). 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.

Velocity We did not find a significant difference in mean velocity between groups (M_{CB} = 46.89, M_{NonCB} = 50.05) but did find unequal 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 visual inspection (see Figure 6). This indicates that for our output model, metastable neural activity alone is not sufficient to produce the power law scaling of step sizes found in some empirical data.

Dispersal Group dispersal of the foraging paths are shown in Figure 7. Mean-squared displacement (MSD) was significantly greater for the NonCB group ($M = 2.54\text{x}10^7$, $SD = 2.54\text{x}10^7$) than for the CB group ($M = 8.32\text{x}10^5$, $SD = 5.40\text{x}10^5$), $t(7.0) = -2.74$, $p = 0.029$. Because the mean velocity is not significantly different between groups, this can only be caused by the increased turning rate in the critical branching group.

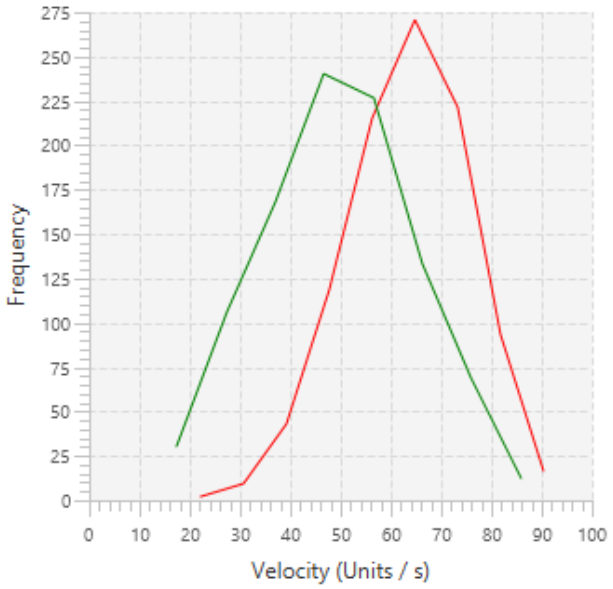

Figure 6: Velocity Histogram for CB Simulation #1 **(Green)** and Non-CB Simulation #1 **(Red)**.

Tortuosity The non-critical branching group produced significantly straighter paths ($t(7.28) = -5.17$, $p = 0.001$) as indexed by the ratio of displacement to path length (Benhamou, 2004) but we did not find a significant difference in sinuosity between groups ($t(7.26) = -0.093$, $p = 0.93$). Because this measure may be more sensitive to high frequency noise, this could be a result of insufficient 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 ($M_{CB} = 2.0$, $M_{NonCB} = 2.5$, $p = 0.66$). While our hypothesis did not specifically make a prediction regarding resource collection, prior models have found relationships between straightness of a random walk and foraging success.

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), in that the critical branching group exhibited 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.

We did not identify an effect of critical branching on the distribution of step sizes. Thus our results failed to support a

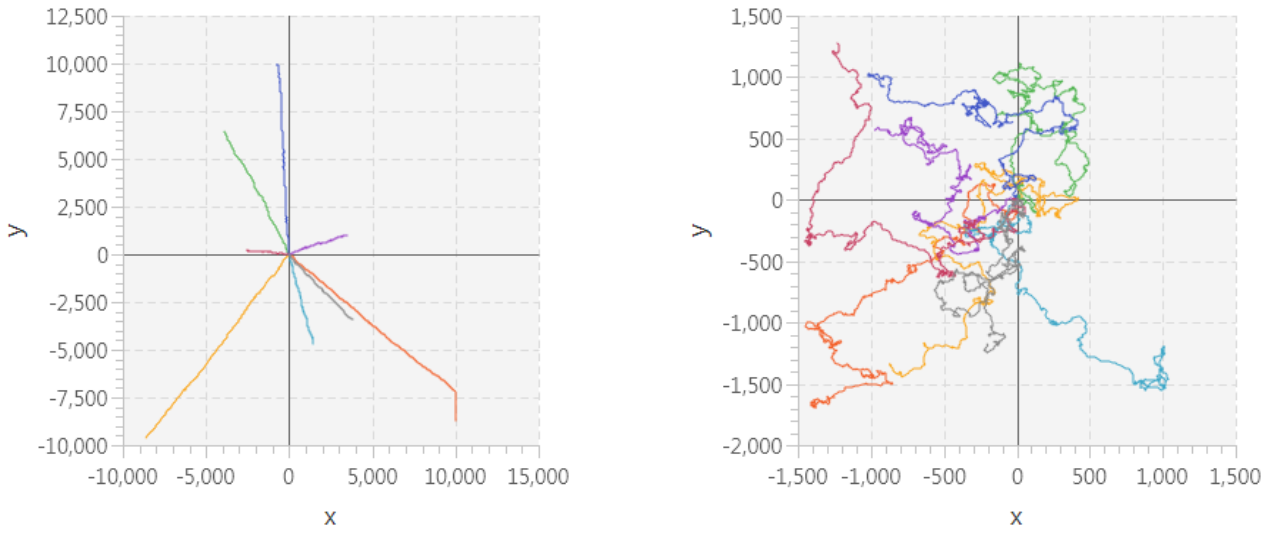

Figure 7: Group dispersal for 100 s. The non-critical branching networks exhibit little directional variability **(left)** resulting in much wider dispersal but little coverage. The critical branching networks **(right)** demonstrate more tortuous paths which include backtracking and clustered movements. The path of each forager is translated to the origin for easier interpretation.

connection between power law scaling in neural activity and Lèvy flights. Given that aggregated neural activity can lead to power laws (Kello, 2013), the present results indicate that not all aggregations will preserve this structure. This suggests that consideration of other factors affecting spatial search or other models of neural control will be important for understanding the relationship between neural activity and Lèvy foraging.

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. Despite prior literature associating random processes with optimality, we contend that optimal foraging will require adaptive mechanisms.

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. A comprehensive investigation of these factors in the computational framework we developed could provide insight into ongoing methodological debates.

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 this information as input to the neural network would be a first step to addressing this limitation.

Finally, foraging processes offer a valuable perspective with which to conceptualize diverse cognitive phenomena. For this perspective to be profitable, more work should be done on the common neural mechanisms of search-like processes and how to map these to complex neural dynamics.

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