Foraging and uncertainty

Certain food-seeking strategies, such as the Lévy-Walks, emerge product of the irreducible uncertainty the animal faces when foraging. Uncertainty then informs food-seeking behavior. However, how animals capture o process this uncertainty while searching for food has not yet been explained, such is the aim of this section.

If an animal perform any food-seeking strategy in a specific area of the environment there exists a probability of having success, which is dependent on resource density and the specific strategy. Fixing the strategy, the probability is determined by the resource density, moreover, as the resource density changes over time so does the probability of successfuly obtaining food. Moreover, in conjuntion with limited perceptual abilities (Bartumeus et al. 2016), the environment appears as being of stochastic nature (Caraco et al. 1990).

An animal which does not consider environment stochastic nature in its food-seeking behavior will act greedely upon sampled values. Acting greedely implies that the animal will always choose the option that yielded the most values in a initial random sampling. Thus, acting greedely is analogous to neglecting that the sample comes from a stochastic distributions of rewards, this is problematic as it makes food-seeking strategy insensitive to reward variation (Sutton and Barto 2018). One could relax this assumption and propose that animals will act upon the mean rewards such as the classical model by Charnov (1976), which determines the strategy based on current patch value against the global mean of the environment. Nevertheless, such rule-based models do not provide good fit to behavioral data (Nonacs 2001; Le Heron et al. 2020; Pyke 2010; Hayden, Pearson, and Platt 2011).

The competing models to rule-based ones are those which effectively consider uncertainty into its formulation. However, for this to make biological sense, animals should be able to specifically track uncertainty measures. Risk considers the spread of possible outcomes, or similarly, the standar deviation of the expected outcome (Rothwell and Stock 1988), in humans risk is readily tracked in the anterior cingulate cortex (ACC) (Christopoulos et al. 2009). Moreover, ACC tracks risk in a context-dependent fashion, that is, it considers cue-related information to determine the risk and expected value of a given option (van Holstein and Floresco 2020). While risk is the component of uncertainty that measures the spread of outcome, volatility signifies how often an environment changes its contingencies, for example, in the action and outcome probability pairing. In learning tasks ACC activity is increases when task volatility increases (Behrens et al. 2007). The main goal of tracking uncertainty is to augment the chance of success while searching for food. In that regard, being able to filter out uncertainty regarding outcomes can prove to be benefitial as the true outcome prediction does not become affected by noise. Stolyarova and Izquierdo (2017) showed that rats are able to optimally choose options with larger value (mean reward waiting time) despite large associated variability. Furthermore, lesions in

the orbito frontal cortex (OFC) showed an impaired ability to change preference when the mean rewards were up or downshifted, that is, value inference became noisy.

All previously mentioned aspects of uncertainty can be categorized within the notion of expected and unexpected uncertainty. Yu and Dayan (2005) proposed expected uncertainty as the uncertainty regarding outcomes when contingencies (outcome given a certain action) remain stable but are subject to some noise, whereas unexpected uncertainty represents a drastic change in the contigencies that likely reflects an structural change in the environment. For example, Stolyarova and Izquierdo (2017) experiment measured rat behavioral modulation with expected uncertainty, and Behrens et al. (2007) showed ACC activity increases in the case of unexpected uncertainty. Considering both kinds of uncertainties enables the animal to balance top-down and bottom-up information, if the obtained rewards present some variation is should not modify learned contigencies that maps actions with rewards in a given environment, so top-down control should have dominance over bottom-up input. On the other hand, if obtained rewards present a large amount of variation, the balance should switch in order to prioritize bottom-up input to increase learning about new contingencies (Yu and Dayan 2005; Soltani and Izquierdo 2019).

Yu and Dayan (2005) dual notion of uncertainty can be considered in terms of stationary and non-stationary environments. A non-stationary environment is one where the outcome variance remain unchanges, whereas non-stationary present a variable variance (Wu, Iyer, and Wang 2018). Thus, non-stationary environments should be the only cause of unexpected uncertainty, and stationary environments should only have expected uncertainty. However, humans while being subject only to expected uncertainty typically behave as the environment were non-stationary, and thus able to produce unexpected uncertainties (Ryali, Reddy, and Yu 2016). While the functional reasons behind this behaviors are not clear, it has been proposed that this emerge because sustatining the belief that environments are non-stationary does not prove to be problematic in stationary ones (Ryali, Reddy, and Yu 2016) or because stochasticity in decisions may provide a sufficient heuristic in many natural environments (Reverdy, Srivastava, and Leonard 2014).

Under non-stationary environments contingencies change, so animals are faced with the dilema of either exploiting or exploring (Sutton and Barto 2018). Exploiting means that behavior should be consistent with previously learned reward contingencies, on the other hand, exploring tries to re-sample the environment to improve or re-learn current contingencies. The exploitation-exploration balance has been linked to the expected and unexpected uncertainty (Cohen, McClure, and Yu 2007), as unexpected uncertainty should increase exploratory behavior to boost learning of new contingencies, whereas if only expected uncertainty is present behavior should exploit current knowledge. However, exploration could be triggered by 'boredom' when environment properties are extensible learned (Aston-Jones and Cohen 2005).

Here we briefly exposed the different environmental properties food-seeking behavior is subject to in order to generate good strategies and maximize gain. We proposed that natural environments are inherently stochastic, and animals adapted to sense various aspects of uncertainty regarding their actions within the environment. However, such a pivotal importance of uncertainty in food-seeking behavior could be contested when considering perceptual abilities as the primary means of informing foraging.

Perceptual abilities are always limited in some regard, and such limitation can be regarded as the perceptual range of a given animal (Fletcher et al. 2013). If an animal must know what is beyond such perceptual range displacement is needed. However, to inform such displacement memory, perceptual information integration, or some other strategy should come into play. In many classical models lies the assumption than animals can somehow integrate information about resource quality and distribution into a environment mean (Charnov 1976). However, perceptual omniscience is not the case, and integration of environmental information is dependent on times, so including non-local information (outside perceptual range) such as resources gradients prove useful for the foraging animal (Fagan et al. 2017).

Even when local and non-local information can improve foraging sucess, there is still an issue on how perceptual information behaves regarding movement and spatial distance. The speed-perception tradeoff describes how perceptual abilities are degraded as speed is increased (Campos, Bartumeus, and Méndez 2013), and as rapid approaching speeds are required to capture prey or obtain food-resources while relying on local perceptual inforamtion (Fagan et al. 2017) this tradeoff present an issue to food-seeking behavior. Moreover, the intensive-extensive tradeoff points how finding food-resource nearby impairs finding resources far-away (Raposo et al. 2011; Bartumeus et al. 2016). Both tradeoffs imply that in order to properly obtain knowledge about the environment, and actually achieve success in obtaining food lead to perceptual uncertainty and require a fine balance between exploration and exploitation.

In order to deal with such tradeoffs animals stablish two distinct behavioral modes: (a) local search, and (b) relocation. Local search is predominantly informed by perceptual information, while the relocation behavior show signs of a stochastic process with Lévy-like distributions (Bazazi et al. 2012). While there has been discussion of brownian-like random movements guiding local search, this is most likely a emergent property caused by frequent food encounters (de Jager et al. 2014), so this shifts from a random relocation process to a perceptually guided local search, are in part result of an increased frequency of food encounters. Thus, the overall food-seeking strategy derives from a combination of random and perceptually informed movements (Balogh et al. 2020).

Given the limitation in perceptual abilities uncertainty seems to be innescapable. Even when a experienced animal can integrate optimal foraging paths in non-stationary environments, random searched with distinct cycles of exploration/exploitation phases persist (Kembro et al. 2019). Furthermore,

introducing stochasticity in food-seeking behavior improves success as makes strategies more resilient to cognitive errors derived from perception (Campos et al. 2020). The persistance of strategies that permits the balance between exploitation, exploration and relocation (Campos, Bartumeus, and Méndez 2013), even when they are not technically needed (Ryali, Reddy, and Yu 2016) shows how relevant is uncertainty in the development of food-seeking behavior. In this section we presented how stochastic properties of the environment lead to behavioral adaptations to deal with the resultant uncertainty, by favoring strategies that favor reduction of uncertainty (Peters, McEwen, and Friston 2017). In the next section we will examine models that consider the case of foraging in uncertain environments, which inform about the underlying processes in food-seeking behavior.

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