Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Behavioral Sciences

The foraging brain

Adam J Calhoun[1] and Benjamin Y Hayden[2]

Foraging theory is a branch of behavioral ecology that deals with how animals seeking nourishment (foragers) make decisions. Neuroscientists have begun to study foraging decisions because of their ethological relevance and their unique ability to give a glimpse of decision-making as it was evolved to happen. Here we provide a brief introduction to the field, with a focus on two organisms selected to emphasize the breadth of foraging theory: nematodes and monkeys. Despite the obvious differences between these animals, it is clear that several basic principles, especially in the domain of regulation and control of sensory-motor transformations, apply to foraging decisions across taxa. These principles include the importance of the foreground/background structure in foraging decisions and the coordination of multiple input and output modalities to make beneficial long-term choices.

Addresses
[1] Princeton Neuroscience Institute, Princeton University, Princeton, NJ, United States
[2] Department of Brain and Cognitive Sciences and Center for Visual Science, University of Rochester, Rochester, NY, United States

Corresponding author: Hayden, Benjamin Y (benhayden@gmail.com)

Current Opinion in Behavioral Sciences 2015, **5**:24–31

This review comes from a themed issue on **Decision making/ neuroeconomics**

Edited by **John O'Doherty** and **Colin Camerer**

http://dx.doi.org/10.1016/j.cobeha.2015.07.003

2352-1546/Published by Elsevier Ltd.

Introduction

Foraging decisions run the gamut from simple choices like whether to bypass a reward in favor of the chance at a better one a few moments later to complex social decisions like whom to hunt with [1–3]. Laboratory studies of foraging normally rely on classic problems such as patch-leaving and diet selection, search strategies, and group foraging [4••,5•,6,7,8•]. Foraging theorists generally assume that animals are driven by evolution to seek the items (normally called prey) that yield greatest long-term benefit to themselves [1,9,10]. So basic are the principles of foraging theory that they describe behavior in creatures as diverse as insects and human hunters [11,12], and contexts as broad as plant root growth and humans searching their memories when recalling a word [13,14].

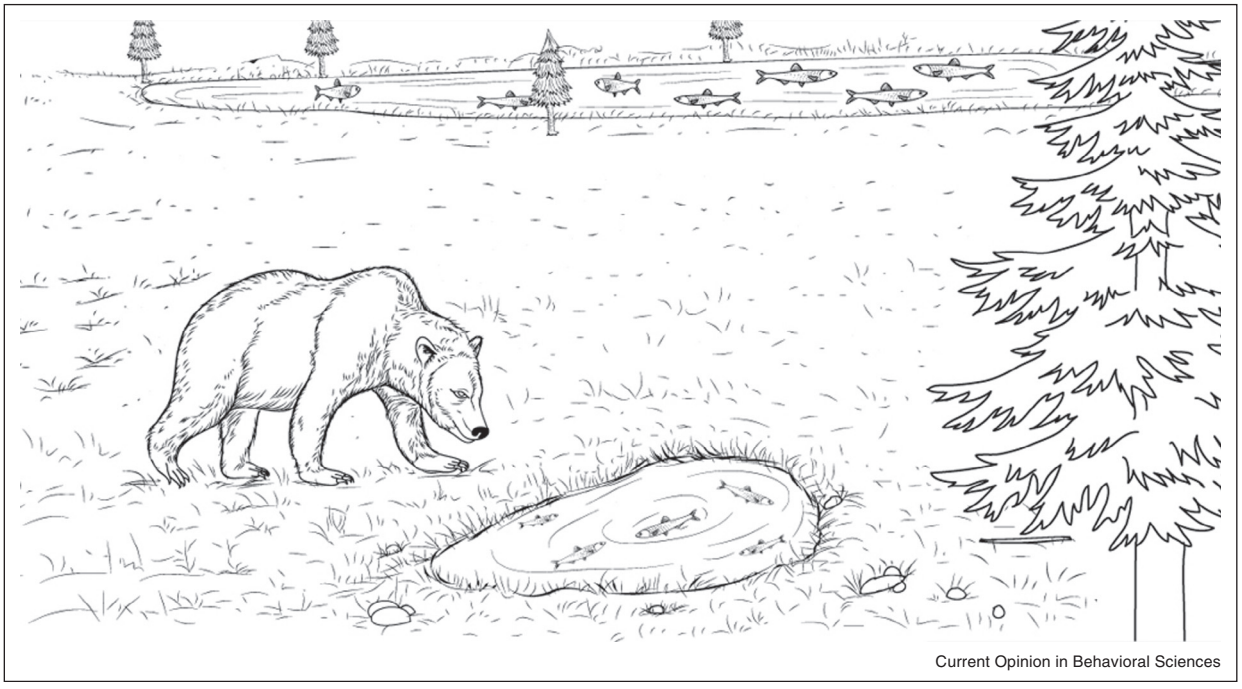
There are several reasons that foraging is important to neuroscience. First, animals have evolved to forage and thus foraging tasks and analyses reorient us toward the brain working as it is designed, by evolution, to work [15,16••,17]. Second, much of primate brain evolution is driven specifically by the cognitive demands of foraging [18]. Third, naturally evolved solutions to foraging problems may provide new and previously undiscovered techniques for understanding the processes by which good decisions are made [19]. Finally, it is often easier to train animals to perform foraging tasks than to perform other ones, presumably because they tap into natural repertoires; this in turn reduces the risk that animals use aberrant decision strategies [20,21].

Broadly, speaking foraging tasks include any task directly inspired by classic foraging problems [1]. Generally, a foraging task is one in which a decision-maker's choices on this trial affect the options available on the next one. Of course, animals may consider the effects of their choices on future options, even if that is not an intended feature of the task, so the foraging perspective may be more broadly useful [15,22••]. Another hallmark of foraging tasks is that decision-makers choose between accepting or rejecting a single option (accept and reject are often called the foreground and background options, respectively). In such contexts, decision makers generally frame the foreground option as the default and the background as the non-default option; this frame in turn determines how and where the brain represents the offers [6,23•,24]. In comparison to the standard economic frame — two equivalent options — several observers have argued that that the accept–reject type is more natural and thus methodologically preferable in animal studies [15,25•,26–28,29•]. Thus, studying the neuroscientific basis of these decisions may give more insight into naturalistic encoding schemes than other types of decisions.

Neuroscience of foraging decisions in monkeys and other mammals

In a study designed to identify the neuronal computations underlying foraging decisions, we trained monkeys to perform a computerized version of the *patch-leaving task* (Figure 1, [30]). In our implementation, the *stay* option (i.e. foreground) provided a juice reward that shrank by a small fixed amount each time it was chosen (Figure 2a). The *leave* option (i.e. background) provided no reward and imposed a long delay (called *travel time* in recognition of the ethological inspiration for the task) — but reset the stay reward to its initial high value. Thus monkeys traded off the desire for an immediate reward against the long-term benefits of leaving to replenish the reward.

Figure 1



Cartoon illustrating patch-leaving problem, a classic problem in foraging theory. In the cartoon, a bear fishes at a lake whose fish population is rapidly dwindling in quality. She spies a distant lake with richer fish population, and has to decide whether it's worth incurring the travel cost of leaving the present one, or whether to wait a bit more time.

Monkeys' patch-leaving times adjusted to changes in travel times and were nearly optimal across all conditions [22••,30]. This behavior is inconsistent with the steep discounting typically observed in intertemporal choice tasks (which are not foraging tasks), suggesting that foraging contexts can reduce biases in measures of time preferences [15,21,29•].

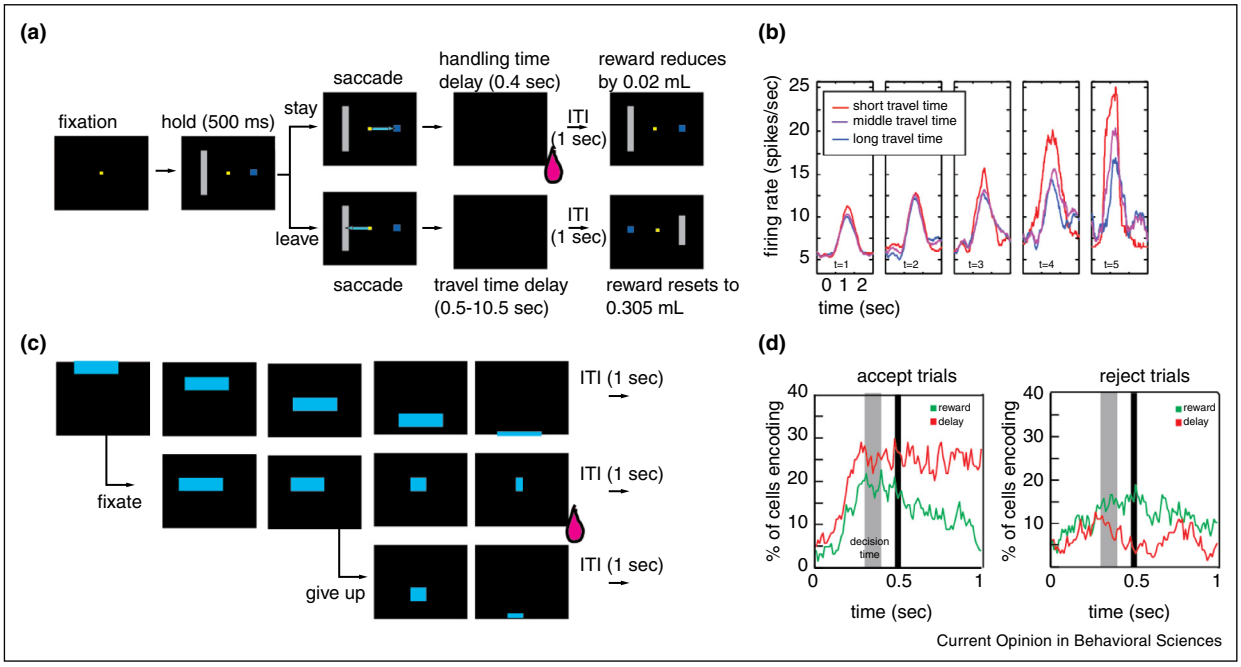
The dorsal anterior cingulate cortex (dACC) has been a focus of studies of the neural basis of foraging because it is a central node in the decision-making network — it integrates information from reward and associative regions and generates a control signal that influences selection of actions [31–34]. In the patch-leaving task, dACC firing rates rose gradually while the monkey continued to choose the depleting stay option (Figure 2b). When activity reached a threshold, the monkey left the patch. When travel time increased (and monkeys chose longer patch residence times), neural responses rose more slowly and required a higher leaving threshold. These results suggest the existence of multiple complementary control systems that operate through a single accumulation process to regulate patch-leaving. This process is consistent with an 'evidence accumulation' model of decision making in which the brain continuously gathers evidence for a single scalar variable that represents evidence in favor of a decision ([35]; cf. [36••], below). More recent work suggests a mechanism by which competitive interactions of neuronal subtypes produce this evidence variable [5•].

Just as animals must decide when to leave a patch, they must decide, when encountering a specific prey, whether to pursue it [1]. Consistent with the idea that patch-leaving and prey rejection result from common neural patterns, dACC tracks the values of rejecting or foregoing an option ([6,23•,37••]; see [38], for a different take on some of these data). The dACC also appears to regulate changes in foraging strategy in response to changing contexts [39••].

The idea that dACC tracks the value of the non-default option is confirmed by a recent study of monkeys performing a diet selection task [37••]. In the classic version of the task, birds accept or reject variously sized worms passing on a conveyor belt (itself mimicking stochastic encounters in nature [40]). In our version, monkeys accept or reject single options that appear in a continuously moving stream (Figure 2c). We found that, following choices, dACC tracked the foregone reward on reject trials and the delay (which determines opportunity cost) on accept trials (Figure 2d).

Freely moving rodents offer a look at foraging in more complex environments that require the recruitment of additional neural systems. In a maze with a series of bins

Figure 2



Neural signals in dACC associated with foraging decisions. **(a)** In computerized patch-leaving task, monkeys choose on each trial between blue and gray bars representing, respectively, staying and leaving the patch. Staying provides an immediate juice reward whose value declines on each trial; leaving provides no reward and a long delay (called travel time), but resets the value of staying to a high value. The optimal strategy, which monkeys follow, is to choose the leave option when the value of staying falls below a threshold that is determined by the travel time. **(b)** In this task, firing rates of neurons in dACC rise as the value of staying falls; when the hit a threshold the monkey leaves the patch. The rate of rise and the threshold both depend on the travel time, suggesting a control mechanism for foraging. **(c)** In a computerized diet selection task, monkeys see offers that vary in benefit (juice amount) and cost (a delay called handling time). The optimal strategy, which monkeys follow, is to accept all options with a benefit/cost ratio above a threshold determined by the average of rewards in the environment. **(d)** During the hold period, dACC neurons preferentially signal the foregone reward on reject trials and the delay — which is correlated with opportunity cost — on accept trials. Thus, neurons preferentially represent the value of the alterative to the choice made.

that offer rewards at the cost of varying time delays [4••] found that rats have a strong bias toward overstaying. They found that this behavior probably reflects a cognitive bias, in particular a 'sunk cost' fallacy of retrospection. This retrospective consideration of what might have been has a distinct neural signature and recruits spatial processing areas of the brain such as hippocampus ([41•]; see also [42,43]). This work provides a vital and as yet poorly explored link between behavioral economics and foraging theory. More generally, ongoing work using foraging paradigms in rodents has the potential to link foraging decisions with navigation, and with related processes like learning, memory and motivation. For instance, dopamine strongly influences food intake and satiety, and this is controlled via the hormone leptin [44]. This dependence of foraging on motivational aspects of behavior is an area where, in our opinion, the overlap between neuroscience and foraging theory is probably to be particularly mutually beneficial.

In dynamic foraging tasks, decision-makers must trade off the desire to exploit a known reward against the benefits of information. The k-arm bandit task has been an especially useful search task. Although the precise functional neuroanatomy, much less the neural mechanisms, of dynamic foraging remains unclear, studies have identified crucial areas, including the frontal pole, the posterior parietal cortex, and the posterior cingulate cortex [45–47]. These studies so far suggest that the tension between exploration and exploitation may be governed by competing systems specialized for particular behavioral patterns. Ultimately, we hope this line of work will be integrated into studies of the neural bases of information-seeking and curiosity — key drivers of search behavior in foraging [48,49•,50], and to search more generally [7].

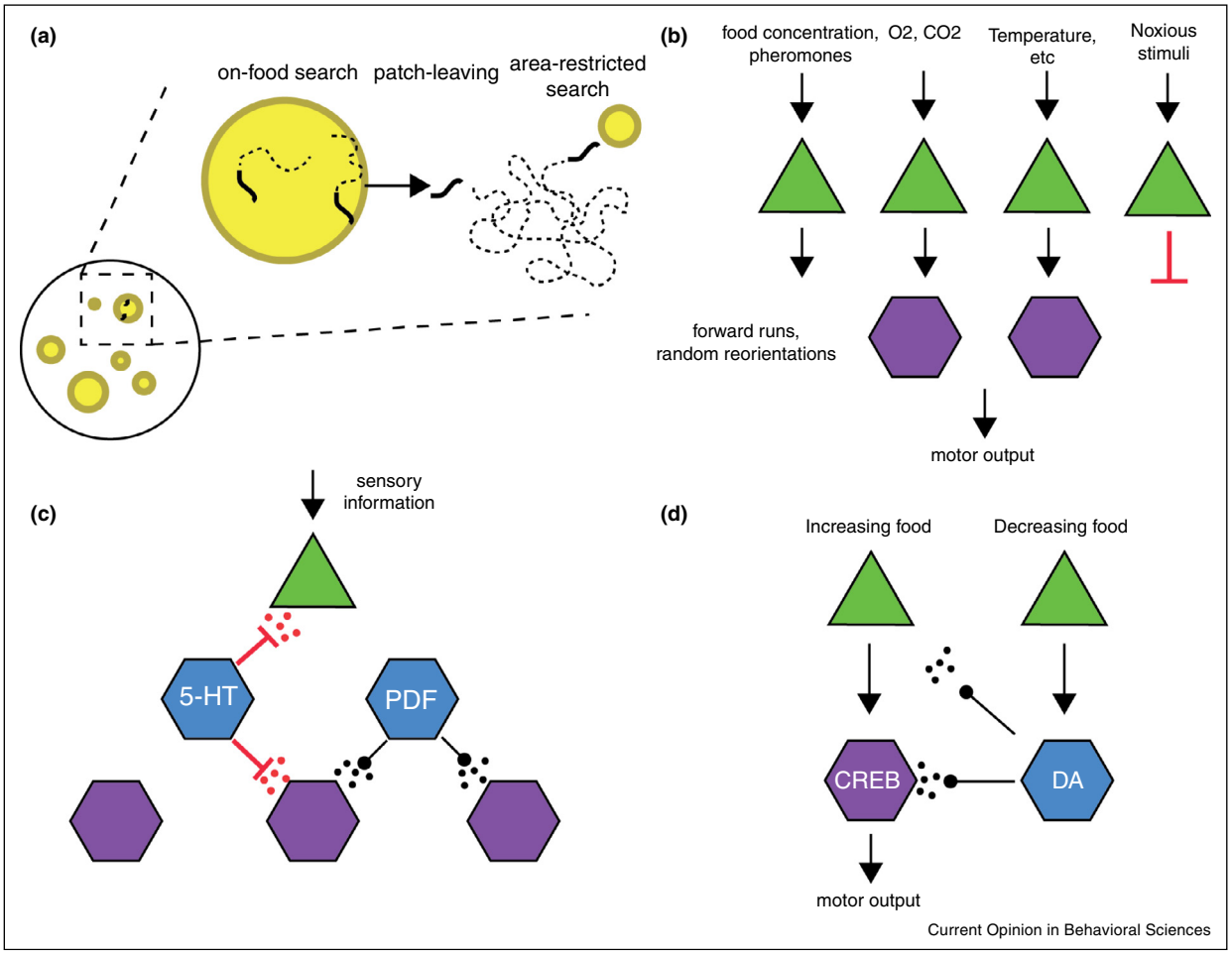
Neuroscience of foraging decisions in *Caenorhabditis elegans*

In order to understand the detailed neural circuitry underlying foraging decisions, it is useful to examine an organism with a smaller nervous system. *C. elegans* is a soil-dwelling, bacteria-eating nematode (a type of worm) with a reduced nervous system consisting of 302 neurons

whose synaptic connections are known. Its short generations and easy genetics allow rapid analysis of features of the nervous system, such as peptides, that are difficult to manipulate in larger animals. Their ease of growing also allows many different animals to be presented with the same option once, instead of one animal being presented with the same option repeatedly (in the worm equivalent of trials). *C. elegans* placed on patches of food will naturally forage for new, or better, sources of food (Figure 3a). The desirability of a given food patch is influenced by the presence of multiple resources beyond nutrition, such as temperature, oxygen and carbon dioxide levels, and light intensity. They also consider social factors such as mating opportunities and the presence of competitors (which provide information about competitive interactions) [51–54]. Thus, *C. elegans* must act as a sophisticated information gatherer and deploy its knowledge strategically to make efficient decisions.

Many neuropeptides and modulators reflect long-term signals that are probably to influence the entire nervous system [55]. Some, such as tyramine, which is released when the food environment is poor [56], act directly on sensory neurons to guide foraging decisions. Others, such

Figure 3



(a) Schematic of the foraging decisions faced by *C. elegans*. Worms must find the most nutritious portion of their current food patch (on-food search) and also decide when to leave in search of a new food source (patch-leaving). When searching for a new food source, they also must decide whether to search in the local area (area-restricted search) or to leave for the global environment. **(b)** *C. elegans* receives information about the environment through its sensory neurons. Over short time scales, these send output to neurons through classical neurotransmitter pathways such as glutamate and GABA. This causes the animal to run forward and leave the nearby rewards or halt its forward movement through random reorientation. **(c)** Long-term needs are encoded through peptides and neuromodulators. These (possibly extrasynaptic) signals modulate the nervous system in a complex fashion at both the sensory neuron and inner layers. Here, serotonin ionically inhibits several neurons in order to increase random reorientations and stay on the current food option. PDF, on the other hand, uses molecular cascades to modulate a partially overlapping set of neurons to promote forward movement to leave the current location. Lines with dots represent extrasynaptic connections. **(d)** Valuation of the environment for foraging can be learned through molecular pathways for future decisions. This circuit motif uses signals from sensory neurons that respond to large fluctuations in expected food to encode the amount of area to search (area-restricted search (a)) if the animal leaves the food patch. Lines with dots represent extrasynaptic connections.

as TGF-beta, reflect a broad 'goodness' of the environment and can be released directly from sensory neurons [57]. Peptides are also released from the sex organs: ablation of the gonad wildly increases the rate at which worms leave a food patch [51]. These different modulatory systems reveal the dynamic balancing that worms must achieve given the many competing resources they must maximize during foraging.

In order to understand how foraging circuitry [58] is dynamically regulated by the environment, we recently investigated how *C. elegans* controls its foraging decisions (Figure 3b, [36••]). We found that these animals keep track of the distribution of food (reward) that they have experienced over thirty minutes to generate their search strategy when looking for a new food source. This is guided by two pairs of sensory neurons, one of which responds to sudden large increases in food, and the other of which responds to sudden large decreases. Postsynaptic to these sensory neurons are a layer of neurons, four of which express a D1-like dopamine receptor which appears to promote exploration. Dopamine is implicated in motivated behaviors and controls both food intake satiety and allocation of rewards [44,59]. In our assay, the period over which the value is integrated is controlled by the amount of CREB protein expressed in these same neurons. These results delineate a basic circuit for foraging and its relationship to learning and memory.

These modulators also interact with each other. Consider the interaction between serotonin and pigment dispersing factor (PDF, Figure 3c, [60••]). Serotonin, which is released during different behavioral states including starvation (in practice, this is similar to hunger in other animals), increases dwelling time by activating serotonin-gated chloride channels (*mod-1*) that are expressed on a single pair of sensory neurons as well as on a series of interneurons that regulate the length of forward locomotion. Thus, serotonin is both inhibiting transmitter release from sensory neurons that can trigger leaving, as well as inhibiting downstream neurons that interpret that information. In mammals, serotonin is known to increase the amount of time that an animal is willing to wait at one foraging site in order to receive reward [61]. It is worth noting that, similar to the multidimsenional signaling of peptides in *C. elegans*, mammalian serotonin signals also display a diverse repertoire of responses to rewards [62••]. Conversely, the release of PDF reflects integration of diverse signals about the quality of the environment. Its action via Galpha-s signaling causes fast forward locomotion to promote exploration of the broader environment. Notably, PDF acts on a subset of the interneurons that are also inhibited ionically by serotonin (in addition to other neurons). Although the precise mechanism of action is unknown, artificially increasing the concentration of cyclic AMP in neurons expressing this PDF receptor replicates this behavior. Why are these opposing behaviors regulated in such different ways? Perhaps this reflects the multiple dimensions along which the stay-or-go decision is being made.

There is a strongly fixed genetic component to foraging, allowing evolution to shape foraging over timescales longer than its natural lifetime (roughly 10 days [63]). For instance, alleles in the receptor *npr-1*, homologous to the mammalian neuropeptide Y receptor, strongly influence how often an animal will leave a food patch, as well as the relative preference for quantities such as the carbon dioxide level to food level, and probably reflects an adaptation to how patchily food has been distributed in the recent environment [53]. Interestingly, worms found in the wild where food is scarce express the increased patch-leaving allele while the standard laboratory-bred animals express the alternate allele and rarely leave the abundant food patches [64]. Further, leaving rate is strongly affected by polymorphisms in the tyramine receptor gene *tyra-3* at a single sensory neuron [65].

Animals need to trade off the desire for immediate food with the need for information — which provides only indirect, though potentially rich future sources of food. There is some evidence that worms can do this [66••]. We tested the hypothesis that *C. elegans* search for information *about* food sources instead of exploiting their information for immediate reward (termed a 'greedy' strategy). This strategy balances information gained from immediate rewards (exploitation) with information gained about faraway rewards, analogous to the balance between exploitation and exploration seen in classic k-armed bandit tasks [45]. Interestingly, this strategy can result in bimodal behaviors often seen in foraging: searching a small area thoroughly followed by sudden leaving to search a globalized area (a Levy flight [67]). We found that *C. elegans* search behavior is indeed consistent with such a strategy. How might such an algorithm be implemented in a reduced nervous system? One way to approximate the information-seeking strategy is with a 1-dimensional evidence accumulator that maintains a tally of the time since food was last seen [66••]. There is direct evidence for accumulating evidence in the responses of neurons in monkey dACC before the animal leaves the local food patch [30]; it is tempting to consider that evidence accumulation may be a more general principal by which foraging decisions get made.

These data show the power of studying natural foraging behaviors in an organism with a completely mapped nervous system. It is clear that real-world foraging decisions require the animal to track a large number of internal — hunger, motivation — and external — food, competitors, mates, gas concentrations — states in order to optimize their intake. In order to make this multidimensional decision, a hidden neuromodulator network overlays a classic neural network to promote long-term

dynamics and plasticity. Given the strong preservation in neuromodulator function across taxa, we speculate that such research may provide useful insights into the role of neuromodulaton in decisions in more complex organisms. We are particularly interested in dopamine and norepinephrine (thought to be analogous to octopamine), both of which project to the ACC [68–70].

More generally, these results suggest a general layout for a control system that regulates foraging decisions: it includes both a monitor that indicates the value of the foreground option and a threshold that depends on the value of the background; it also requires a control system that governs both the monitor and the threshold. We anticipate that this basic structure may be a recurring computational motif that determines foraging decisions in diverse taxa.

Conclusion: the future of the foraging brain

The primary appeal of foraging is its potential to place animals into states that are difficult to capture in less natural laboratory tasks. Just as aspects of sensory systems have been revealed through natural stimuli (instead of white noise), natural behaviors may allow us to more efficiently explore relevant behavioral space in order to reveal naturalistic neural computations. We therefore think the primary appeal of future foraging studies will be behavior in ever more natural situations. Trivially, this means newer studies making use of the many different foraging contexts, like complex environments, social foraging, and so on [8•,39••]. Another important direction is to understand how foragers learn to forage the way they do [72•], and what aspects of decisions are so strongly hard-wired by evolution that they appear even in contexts where they are costly [71]. These tasks will naturally connect neural modules that are typically studied in isolation, such as spatial navigation and reward. Such studies will enrich our understanding of a broader array of decision contexts, and provide important generality tests for decision models.

But it also means more natural task conditions. For *C. elegans*, this means long-term single animal tracking and investigation into the many resources (e.g. oxygen) that are silently influencing their decisions. It will require disentangling the many correlated resources the worm is sensing over a very tractable (four days to maturity, 10 days to death) lifespan. For primates (including monkeys to humans), this means virtual and even real-world foraging environments. Such environments are crucial for eliciting full involvement of the brain's navigation system. They are probably to also induce more naturalistic executive control, and require more complex representations.

Conflict of interest statement

The authors declare no conflict of interest.

Acknowledgement

This research was supported by a R01 (DA038615) to BYH.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Stephens DW, Krebs JR: *Foraging Theory*. Princeton, NJ: Princeton University Press; 1986.

2. Stephens DW, Brown JS, Ydenberg RC: *Foraging: Behavior and Ecology*. Chicago, IL: University of Chicago Press; 2007.

3. Giraldeau LA, Caraco T: *Social Foraging Theory*. Princeton, NJ: Princeton University Press; 2000.

4. •• Wikenheiser AM, Stephens DW, Redish AD: **Subjective costs drive overly patient foraging strategies in rats on an intertemporal foraging task**. *Proc Natl Acad Sci U S A* 2013, **110**:8308-8313 http://dx.doi.org/10.1073/pnas.1220738110.
Rats in a naturalistic task involving sequential accept–reject decisions were overly willing to wait for food rewards. Their bias, which was akin to a sunk cost fallacy, was sensitive to environmental context, and demonstrates a novel basic bias in choice behavior.

5. • Kvitsiani D, Ranade S, Hangya B, Taniguchi H, Huang JZ, Kepecs A: **Distinct behavioural and network correlates of two interneuron types in prefrontal cortex**. *Nature* 2013, **498**:363-366 http://dx.doi.org/10.1038/nature12176.

6. Kolling N, Behrens TE, Mars RB, Rushworth MF: **Neural mechanisms of foraging**. *Science* 2012, **336**:95-98 http://dx.doi.org/10.1126/science.1216930.

7. Hills TT: **Animal foraging and the evolution of goal-directed cognition**. *Cogn Sci* 2006, **30**:3-41.

8. • Mobbs D, Hassabis D, Yu R, Chu C, Rushworth MFS, Boorman E, Dagliesh T: **Foraging under competition: the neural basis of input-matching in humans**. *J Neurosci* 2013, **33**:9866-9872.

9. McNamara JM, Houston AI: **The common currency for behavioral decisions**. *Am Nat* 1986, **127**:358-378.

10. Schoener TW: **Theory of feeding strategies**. *Annu Rev Ecol Syst* 1971, **2**:369-404.

11. Pyke GH, Pulliam HR, Charnov EL: **Optimal foraging: a selective review of theory and tests**. *Q R Biol* 1977, **52**:137-154.

12. Smith EA, Winterhalder B: *Evolutionary Ecology and Human Behabior*. New York: de Gruyer; 1992.

13. Hills TT, Jones MN, Todd PM: **Optimal foraging in semantic memory**. *Psychol Rev* 2012, **119**:431-440 http://dx.doi.org/10.1037/a0027373.

14. McNickle GG, Cahill JF Jr: **Plant root growth and the marginal value theorem**. *Proc Natl Acad Sci U S A* 2009, **106**:4747-4751 http://dx.doi.org/10.1073/pnas.0807971106.

15. Stephens DW, Anderson D: **The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences**. *Behavl Ecol* 2001, **12**:330-339.

16. •• Pearson JM, Watson KK, Platt ML: **Decision making: the neuroethological turn**. *Neuron* 2014, **82**:950-965 http://dx.doi.org/10.1016/j.neuron.2014.04.037.
In this ambitious review, the authors lay out a detailed picture of the ways in which our understanding of the brain benefits from taking the neuroethological perspective (including foraging). They argue that this perspective changes the way we look at reward processing in particular.

17. Cisek P: **Making decisions through a distributed consensus**. *Curr Opin Neurobiol* 2012, **22**:1-10.

18. Passingham RE, Wise SP: *The Neurobiology of the Prefrontal Cortex: Anatomy, Evolution, and the Origin of Insight*. Oxford, UK: Oxford University Press; 2012.

19. Passino KM: *Biomimicry for Optimization, Control, and Automation*. London: Springer; 2004.

20. Freidin E, Aw J, Kacelnik A: **Sequential and simultaneous choices: testing the diet selection and sequential choice models**. *Behav Processes* 2009, **80**:218-223 http://dx.doi.org/10.1016/j.beproc.2008.12.001.

21. Stephens DW, Kerr B, Fernández-Juricic E: **Impulsiveness without discounting: the ecological rationality hypothesis**. *Proc Biol Sci* 2004, **271**:2459-2465 http://dx.doi.org/10.1098/rspb.2004.2871.

22. •• Blanchard TC, Hayden BY: **Monkeys are more patient in a foraging task than in a standard intertemporal choice task**. *PLoS One* 2015, **10**:e0117057 http://dx.doi.org/10.1371/journal.pone.0117057.
The authors find that monkeys discount the future in the non-foraging task but not in the foraging task. These results suggest that the preferences measured in non-natural situations may not generalize well to more naturalistic (i.e. foraging) ones, and thus argue for the use of foraging tasks.

23. • Boorman ED, Rushworth MF, Behrens TE: **Ventromedial prefrontal and anterior cingulate cortex adopt choice and default reference frames during sequential multi-alternative choice**. *J Neurosci* 2013, **33**:2242-2253 http://dx.doi.org/10.1523/JNEUROSCI.3022-12.2013.

24. Boorman ED, Behrens TE, Woolrich MW, Rushworth MF: **How green is the grass on the other side? Frontopolar cortex and the evidence in favor of alternative courses of action**. *Neuron* 2009, **62**:733-743 http://dx.doi.org/10.1016/j.neuron.2009.05.014.

25. • Blanchard TC, Pearson JM, Hayden BY: **Postreward delays and systematic biases in measures of animal temporal discounting**. *Proc Natl Acad Sci U S A* 2013, **110**:15491-15496 http://dx.doi.org/10.1073/pnas.1310446110.

26. Kacelnik A, Vasconcelos M, Monteiro T, Aw J: **Darwin's ''tug-of-war'' vs. starlings' ''horse-racing'': how adaptations for sequential encounters drive simultaneous choice**. *Behav Ecol Sociobiol* 2011 http://dx.doi.org/10.1007/s00265-010-1101-2.

27. Kacelnik A: **The evolution of patience**. In *Time and Decision: Economic and Psychological Perspectives on Intertemporal Choice*. Edited by Loewenstein GF, Read D, Baumeister RF. New York: Russell Sage; 2003.

28. Pearson JM, Hayden BY, Platt ML: **Explicit information reduces discounting behavior in monkeys**. *Front Psychol* 2010, **1**:237 http://dx.doi.org/10.3389/fpsyg.2010.00237.

29. • Hayden BY: **Time discounting and time preference in animals: a critical review**. *Psychon Bull Rev* 2015 http://dx.doi.org/10.3758/s13423-015-0879-3.

30. Hayden BY, Pearson JM, Platt ML: **Neuronal basis of sequential foraging decisions in a patchy environment**. *Nat Neurosci* 2011, **14**:933-939 http://dx.doi.org/10.1038/nn.2856.

31. Shenhav A, Botvinick MM, Cohen JD: **The expected value of control: an integrative theory of anterior cingulate cortex function**. *Neuron* 2013, **79**:217-240 http://dx.doi.org/10.1016/j.neuron.2013.07.007.

32. Rushworth MF, Noonan MP, Boorman ED, Walton ME, Behrens TE: **Frontal cortex and reward-guided learning and decision-making**. *Neuron* 2011, **70**:1054-1069 http://dx.doi.org/10.1016/j.neuron.2011.05.014.

33. Hayden BY, Heilbronner SR, Pearson JM, Platt ML: **Surprise signals in anterior cingulate cortex: neuronal encoding of unsigned reward prediction errors driving adjustment in behavior**. *J Neurosci* 2011, **31**:4178-4187 http://dx.doi.org/10.1523/JNEUROSCI. 4652-10.2011.

34. Quilodran R, Rothe M, Procyk E: **Behavioral shifts and action valuation in the anterior cingulate cortex**. *Neuron* 2008, **57**:314-325.

35. Gold JI, Shadlen MN: **The neural basis of decision making**. *Annu Rev Neurosci* 2007, **30**:525-574.

36. •• Calhoun AJ, Tong A, Pokala N, Fitzpatrick AJ, Sharpee TO, Chalasani SH: **Neural mechanisms for evaluating environmental variability in *Caenorhabditis elegans***. *Neuron* 2015, **86**:1-14.
Processes such as learning and memory are important to foraging. The authors identify the minimal neural network that learns the variability in the food environment, something that *C. elegans* uses for a foraging decision, as well as its dependence on CREB and dopamine.

37. •• Blanchard TC, Hayden BY: **Neurons in dorsal anterior cingulate cortex signal postdecisional variables in a foraging task**. *J Neurosci* 2014, **34**:646-655 http://dx.doi.org/10.1523/JNEUROSCI.3151-13.2014.
In the first measure of single neuron activity in the diet selection task, the authors find preferential representation of foregone reward in dACC neurons. These findings emphasize the regulatory role of dACC in foraging decisions.

38. Shenhav A, Straccia MA, Cohen JD, Botvinick MM: **Anterior cingulate engagement in a foraging context reflects choice difficulty, not foraging value**. *Nat Neurosci* 2014, **16**:1249-1254.

39. •• Kolling N, Wittmann M, Rushworth MFS: **Multiple neural mechanisms of decision making and their competition under changing risk pressure**. *Neuron* 2014, **81**:1190-1202 http://dx.doi.org/10.1016/j.neuron.2014.01.033.
The authors take advantage of their human foraging task to see how environmental changes affect strategy. They find that subjects rapidly adjust their choice strategies to new pressures in a foraging task and explore the neural antecedents of those changes.

40. Krebs JR, Erichsen JT, Webber MI, Charnov EL: **Optimal prey selection in the great tit (*Parus major*)**. *Anim Behav* 1977 http://dx.doi.org/10.1016/0003-3472(77)90064-1.

41. • Steiner AP, Redish AD: **Behavioral and neurophysiological correlates of regret in rat decision-making on a neuroeconomic task**. *Nat Neurosci* 2014, **17**:995-1002 http://dx.doi.org/10.1038/nn.3740.Behavioral.

42. Abe H, Lee D: **Distributed coding of actual and hypothetical outcomes in the oribital and dorsolateral prefrontal cortex**. *Neuron* 2011, **70**:731-741.

43. Hayden BY, Pearson JM, Platt ML: **Fictive reward signals in the anterior cingulate cortex**. *Science* 2009, **324**:948-950.

44. DiLeone RJ: **The influence of leptin on the dopamine system and the implications for ingestive behavior**. *Int J Obes* 2009, **33**:S25-S29.

45. Daw ND, O'Doherty JP, Dayan P, Seymour B, Dolan RJ: **Cortical substrates for exploratory decisions in humans**. *Nature* 2006, **441**:876-879 http://dx.doi.org/10.1038/nature04766.

46. Pearson JM, Hayden BY, Raghavachari S, Platt ML: **Neurons in posterior cingulate cortex signal exploratory decisions in a dynamic multi-option choice task**. *Curr Biol* 2009, **19**:1-6.

47. Wittmann BC, Daw ND, Seymour B, Dolan RJ: **Striatal activity underlies novelty-based choice in humans**. *Neuron* 2008, **58**:967-973 http://dx.doi.org/10.1016/j.neuron.2008.04.027.

48. Blanchard TC, Hayden BY, Bromberg-Martin ES: **Orbitofrontal cortex uses distinct codes for different choice attributes in decisions motivated by curiosity**. *Neuron* 2015, **85**:602-614 http://dx.doi.org/10.1016/j.neuron.2014.12.050.

49. • Gruber MJ, Gelman BD, Ranganath C: **States of curiosity modulate hippocampus-dependent learning via the dopaminergic circuit**. *Neuron* 2014, **84**:486-496.

50. Kang MJ, Hsu M, Krajbich IM, Loewenstein G, McClure SM, Wang JT, Camerer CF: **The wick in the candle of learning: epistemic curiosity activates reward circuitry and enhances memory**. *Psychol Sci* 2009, **20**:963-973 http://dx.doi.org/10.1111/j.1467-9280.2009.02402.x.

51. Lipton J, Kleemann G, Ghosh R, Lints R, Emmons SW: **Mate searching in *Caenorhabditis elegans*: a genetic model for sex drive in a simple invertebrate**. *J Neurosci* 2004, **24**:7427-7434 http://dx.doi.org/10.1523/JNEUROSCI.1746-04.2004.

52. Shtonda BB, Avery L: **Dietary choice behavior in *Caenorhabditis elegans***. *J Exp Biol* 2006, **209(Pt 1)**:89-102 http://dx.doi.org/10.1242/jeb.01955.

53. Gloria-Soria A, Azevedo RBR: ***npr-1* regulates foraging and dispersal strategies in *Caenorhabditis elegans***. *Curr Biol* 2008, **18**:1694-1699 http://dx.doi.org/10.1016/j.cub.2008.09.043.

54. Milward K, Emanuel K, Joseph R, De Bono M, Olofsson B: **Neuronal and molecular substrates for optimal foraging in *Caenorhabditis elegans***. *Proc Natl Acad Sci U S A* 2011, **108**:20672-20677 http://dx.doi.org/10.1073/pnas.1106134109.

55. Li C, Kim K: **Neuropeptides**. *Wormbook* 2008, **25**:1-36.

56. Alkema MJ, Hunter-Ensor M, Ringstad N, Horvitz HR: **Tyramine functions independently of octopamine in the *Caenorhabditis elegans* nervous system**. *Neuron* 2005, **46**:247-260 http://dx.doi.org/10.1016/j.neuron.2005.02.024.

57. Gallagher T, Kim J, Oldenbroek M, Kerr R, You Y-J: **ASI regulates satiety quiescence in *C. elegans***. *J Neurosci* 2013, **33**:9716-9724 http://dx.doi.org/10.1523/JNEUROSCI.4493-12.2013.

58. Gray JM, Hill JJ, Bargmann CI: **A circuit for navigation in *Caenorhabditis elegans***. *Proc Natl Acad Sci U S A* 2005, **102**:3184-3191.

59. Cousins MS, Salamone JD: **Nucleus accumbens dopamine depletions in rats affect relative response allocation in a novel cost/benefit procedure**. *Pharmacol Biochem Behav* 1994, **49**:85-91.

60. •• Flavell SW, Pokala N, Macosko EZ, Albrecht DR, Larsch J, Bargmann CI: **Serotonin and the neuropeptide PDF initiate and extend opposing behavioral states in *C. elegans***. *Cell* 2013, **154**:1023-1035 http://dx.doi.org/10.1016/j.cell.2013.08.001.
In this elegant study, the authors identify two peptides that each independently control the exploration and exploitation phases of foraging. The action of the peptides represents long-term signals that modulate the function of the neural network to make appropriate foraging decisions.

61. Fonseca MS, Murakami M, Mainen ZF: **Activation of dorsal raphe serotonergic neurons promotes waiting but is not reinforcing**. *Curr Biol* 2015, **25**:306-315.
By photoactivating serotonin neurons in the dorsal raphe nucleus, the authors were able to increase the amount of time a mouse was willing to wait for a reward. Serotonin did not appear to be itself rewarding, or to affect reward preferences, but see Cohen *et al*. above.

62. •• Cohen JY, Amoroso MW, Uchida N: **Serotonergic neurons signal reward and punishment on multiple timescales**. *eLife* 2015, **4**:e06346.
By recording from genetically tagged serotonergic neurons in the dorsal raphe nucleus during behavior, the authors find that these neurons have diverse functions. Different serotonergic neurons will respond to reward, punishment, or both, and can respond over either short or long timescales.

63. Wolkow CA, Kimura KD, Lee M, Ruvkun G: **Regulation of *C. elegans* life-span by insulinlike signaling in the nervous system**. *Science* 2000, **290**:147-150.

64. De Bono M, Tobin DM, Davis MW, Avery L, Bargmann CI: **Social feeding in *Caenorhabditis elegans* is induced by neurons that detect aversive stimuli**. *Nature* 2002, **419**:899-903.

65. Bendesky A, Tsunozaki M, Rockman MV, Kruglyak L, Bargmann CI: **Catecholamine receptor polymorphisms affect decision-making in *C. elegans***. *Nature* 2011 http://dx.doi.org/10.1038/nature09821.

66. •• Calhoun AJ, Chalasani SH, Sharpee TO: **Maximally informative foraging by *Caenorhabditis elegans***. *eLife* 2014, **3**:1-13 http://dx.doi.org/10.7554/eLife.04220.
This study shows how an information–maximization search strategy will naturally make a foraging decision, staying in one area and eventually leaving for another. The authors provide evidence that this strategy is used in *C. elegans*, and show that it can be approximated by an evidence accumulation model.

67. Salvador LCM, Bartumeus F, Levin SA, Ryu WS, Valle C: **Mechanistic analysis of the search behaviour of *Caenorhabditis elegans***. *J R Soc Interface* 2014, **11**:20131092.

68. Aston-Jones G, Cohen JD: **An integrative theory of locus coeruleus-norepinephrine function: adaptive gain and optimal performance**. *Annu Rev Neurosci* 2005, **28**:403-450.

69. Williams SM, Goldman-Rakic PS: **Widespread origin of the primate mesofrontal dopamine system**. *Cereb Cortex* 1998, **8**:321-345.

70. Roeder T: **Octopamine in invertebrates**. *Progr Neurobiol* 1999, **59**:533-561.

71. Blanchard TC, Wilke A, Hayden BY: **Hot hand bias in rhesus monkeys**. *J Exp Psychol Anim Learn Cogn* 2014, **40**:280-286.

72. • Constantino Sara M, Daw Nathaniel D: **Learning the opportunity cost of time in a patch-foraging task**. *Cognitive, Affect & Behav Neurosci* 2015 http://dx.doi.org/10.3758/s13415-015-0350-y.