



Neuroethology of decision-making

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A neuroethological approach to decision-making considers the effect of evolutionary pressures on neural circuits mediating choice. In this view, decision systems are expected to enhance fitness with respect to the local environment, and particularly efficient solutions to specific problems should be conserved, expanded, and repurposed to solve other problems. Here, we discuss basic prerequisites for a variety of decision systems from this viewpoint. We focus on two of the best-studied and most widely represented decision problems. First, we examine patch leaving, a prototype of environmentally based switching between action patterns. Second, we consider social information seeking, a process resembling foraging with search costs. We argue that while the specific neural solutions to these problems sometimes differ across species, both the problems themselves and the algorithms instantiated by biological hardware are repeated widely throughout nature. The behavioral and mathematical study of ubiquitous decision processes like patch leaving and social information seeking thus provides a powerful new approach to uncovering the fundamental design structure of nervous systems.

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Introduction

In the natural world, animals face many difficult decision-making problems, posed by the details of their habitat and social system. Such problems can include when, where, and for what to forage; with whom to mate and where to nest; whether to flee or to ignore a potential predator; and with which conspecifics to form long-term associations. Evolutionary theory and behavioral ecology identify such decision-making problems, and the costs, benefits, and constraints associated with pursuing specific behavioral strategies for solving them.

Although the study of animal behavior has revealed a remarkable diversity of such problems and their solutions,

mathematical analysis has demonstrated that dissimilar-seeming problems can be solved with similar strategies. For example, certain foraging problems can be generalized to a broad class of resource-seeking behaviors [1]. When the fitness impact of a decision is large, strong selective pressures should produce mathematically optimal behavior. Such a constraint means that the neurobiological mechanisms mediating decisions may be highly conserved or convergent across taxa for problems with similar mathematical formulations (Figure 1).

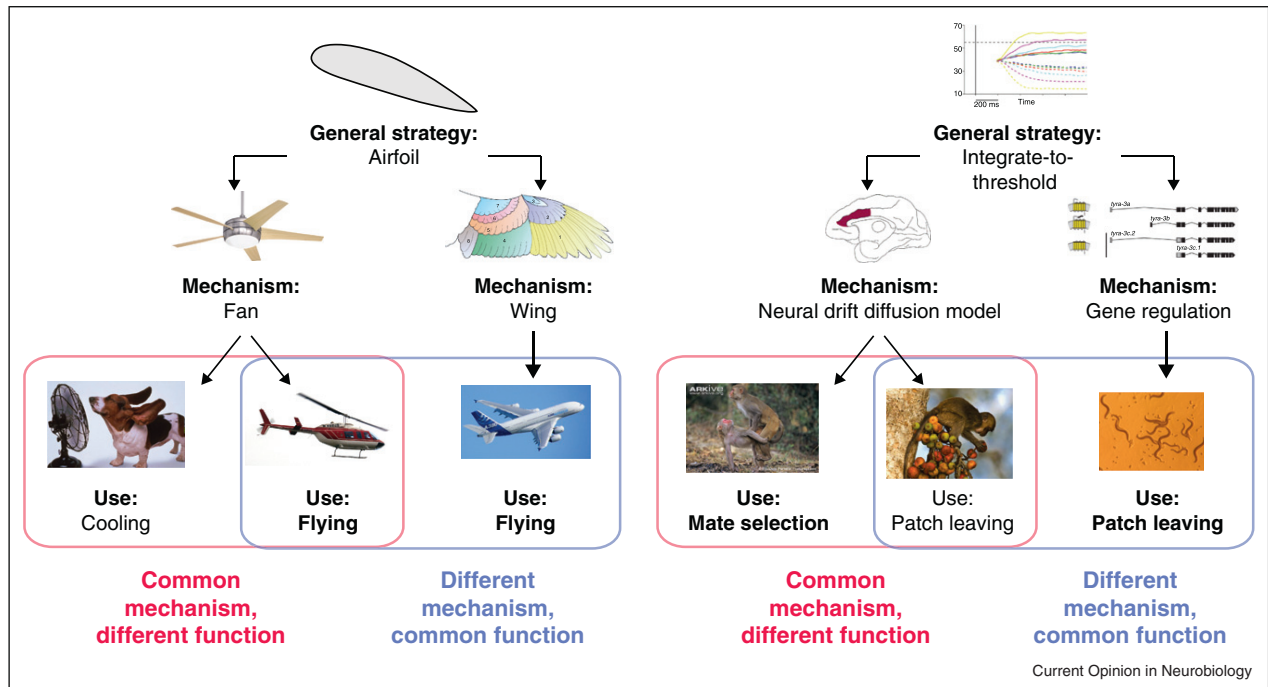
To illustrate these ideas, we will discuss two types of decision problem in behavioral ecology and their neural implementations. First, we will examine foraging, a prototype of environmentally based switching between action patterns to optimize resource gathering. Second, we will examine social information seeking behaviors in non-human primates. We conclude that this work portends a more general understanding of decision-making and, ultimately, motivates the unification of theoretical and experimental work in behavioral ecology and neuroscience.

Foraging decisions

A well-studied example of a natural foraging decision is the patch-leaving problem, mathematically analyzed by Charnov [2] and first tested in a series of experiments in birds [3]. This problem considers an animal foraging in an environment with food items distributed in sparse patches. As the animal forages in a patch, local resources are depleted, and the time required to find a new food item increases, reducing the rate of food intake. As a result, animals must balance the benefits of diminishing returns against the costs of searching for new patches. The optimal solution to this problem, the Marginal Value Theorem (MVT)—that foragers should abandon patches when the local rate of caloric return falls below the average for the environment as a whole—has been demonstrated to hold in a breathtakingly wide array of species, including worms, insects, fish, rodents, birds, nonhuman primates, and humans [1,4].

In a recent experiment investigating the neural basis of patch leaving decisions, Hayden, Pearson, and Platt [5**] designed a laboratory version of the problem in which monkeys chose between ‘stay’ and ‘leave’ options represented by visual stimuli on a computer monitor. The ‘stay’ option simulated foraging within a gradually depleting patch by initially delivering a large juice reward, followed by a decreasing payoff on each sequential selection of ‘stay.’ The ‘leave’ option simulated travelling to a new, undepleted patch by incurring a ‘travel time’ before giving a juice reward and resetting

Figure 1



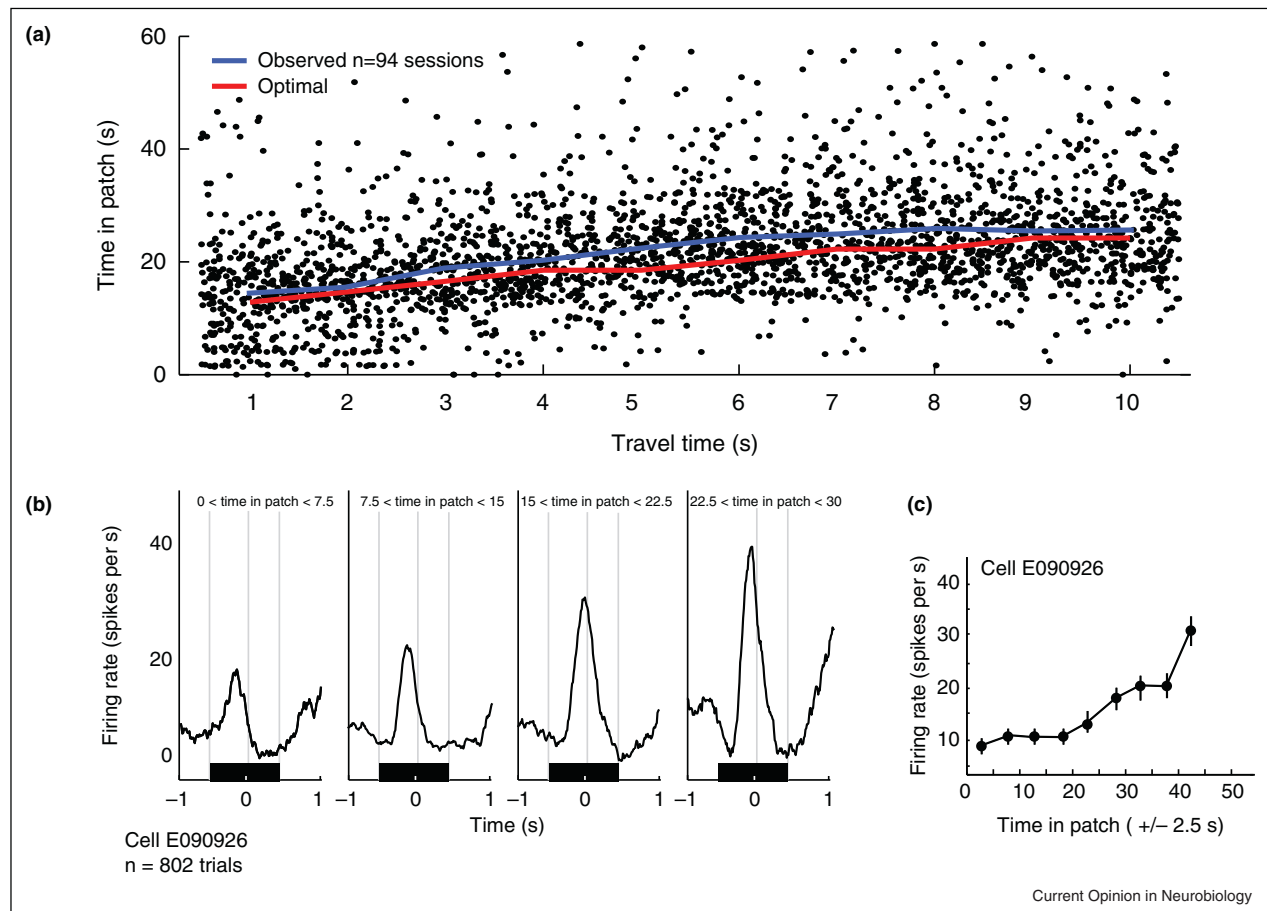
Depending on the mechanisms present in the ancestral state, dissimilar behavioral problems can be solved by common mechanisms, and similar behavioral problems can be solved by disparate mechanisms, (a) Analogy for the relationships between algorithm, mechanism, and function. A fundamental design, the airfoil, can be configured into two very different forms: the wing and the fan. These more elaborate configurations may be further modified for use in multiple, unrelated functions, as in the use of helicopter blades for flying or fan blades for cooling. (b) We posit that the integrate-to-threshold algorithm, like the airfoil, is an evolutionary ‘building block’ that will be found frequently in various species and implementations. This algorithm can be implemented by several mechanisms, such as neural computational models as well as gene-regulatory mechanisms. As in (a), these specific mechanisms are integrated into the evolutionary toolkit, and made available for modification. Duplication and subsequent refinement of a particular mechanism can then adapt it to subservise a different behavior. For example, a neural mechanism that originally evolved to guide foraging behavior needs relatively small modifications before it can be implemented to enhance mate-seeking behavior.

the payoff associated with the ‘stay’ option. The travel time was explicitly cued to the monkeys by the height of a bar presented on the computer monitor, and was selected randomly for each new ‘patch.’ Monkeys readily optimized their patch residence times (Figure 2a) and their patch-leaving decisions also depended systematically on the ‘travel time’ to the next patch, a departure from the MVT consistent with observed behaviors in other species [6]. Simultaneously, Hayden and colleagues recorded the firing patterns of single neurons in the dorsal anterior cingulate cortex (dACC), an area of the macaque and human brain linked to reward monitoring, error signaling, learning, and behavioral control. Neuronal firing rates during the peri-saccadic decision-making period rose with each successive decision to stay in a given patch, across multiple actions unfolding over tens of seconds (Figure 2b, c). An analysis of neuronal firing according to the monkeys’ patch residence times demonstrated that these responses were more closely related to the decision to leave a patch than to the monkeys’ patch residence times or reward rates [5**]. This firing pattern revealed a

strikingly simple implementation of a thresholded decision circuit. Using fMRI in humans, Kolling and colleagues [7**] investigated the function of ACC using a similar foraging task, and found that ACC tracks the value of foraging (i.e. leaving the current patch) on a scale anchored to the average value of the environment. While dACC appears to encode a signal that is compared to a threshold to determine the patch leaving decision, the mechanism by which this threshold is set remains unknown, but according to the MVT should be flexibly sensitive to environmental conditions such as average patch richness.

The rise-to-threshold process evident in the decision-related responses in ACC mirrors similar rise-to-threshold processes evident in the activity of neurons in parietal and prefrontal association cortex in monkeys rendering perceptual judgments [8]. While such perceptual judgments entail the integration of sensory evidence from a noisy environment over time until a threshold is reached, similar integration is not immediately apparent in ACC

Figure 2



Rhesus macaques forage nearly optimally in a computerized patch-leaving task, and the rising value of leaving a patch is represented by single neurons in the macaque frontal cortex. **(a)** Monkeys remain in the patch longer as travel time rises, as predicted by the marginal value theorem (MVT). Each dot indicates a single patch-leaving decision ($n = 2834$ patch-leaving events). The time at which the monkey chose to leave the patch (y axis) was defined relative to the beginning of foraging in that patch. Travel time was kept constant in a patch (x axis). Data from two monkeys are shown. Behavior (average is traced by the blue line) closely followed the rate-maximizing leaving time (red line), albeit delayed by 0–2 s. **(b)** Peri-stimulus time histograms (PSTHs) for an example cell in anterior cingulate cortex (ACC). Neurons responded phasically around the time of decision-making saccades and then fell to a baseline level between trials. Time zero indicates end of saccade, indicating choice. Black rectangle indicates the average duration of the trial. The firing rate during the peri-saccadic decision-making period rose with each successive decision to stay in a given patch, across multiple actions unfolding over tens of seconds. Each panel indicates responses selected from one range of patch residence times. **(c)** Average responses of example neuron occurring in a series of 1-s peri-saccadic epochs. Firing rates increased as time in patch increased. Error bars represent s.e.m. Firing rates peaked with the decision to abandon a patch and move on to the next. Figure after [5**], used with permission.

firing during this patch foraging task. Nevertheless, both algorithms entail threshold comparison, and variability in neural firing determines the monkeys' decisions. Further, such rise-to-threshold processes have been theorized to serve as implementations of the sequential probability ratio test (SPRT)—the optimal solution to this type of binary decision problem [9–11]. The observation that a similar process appears to govern both perceptual decisions and patch leaving decisions endorses the idea that the brain uses a small suite of similar, repeated mechanisms to solve diverse problems in multiple domains [5**].

Recent evidence also indicates that genes coding for neuromodulatory chemicals may mediate the impact of local environmental conditions on patch leaving decisions, perhaps by controlling the threshold for patch leaving. Bendesky and colleagues [12**] compared patch-leaving decisions by a nematode (*C. elegans*) strain from Hawaii with one developed in the laboratory. Hawaiian worms abandoned algae lawns at ten times the rate that the laboratory strains did. The authors found that differences in patch-leaving threshold among distinct strains resulted from polymorphisms in promoter regions of the tyramine receptor gene (*tyra 3b*), which controls the

expression of a G-protein coupled receptor analogue of vertebrate catecholamine receptors. Thus worms' patch leaving thresholds are regulated genetically, as opposed to monkeys' use of flexible thresholding, though both obey the MVT. In other words, different proximal mechanisms are capable of instantiating the same algorithm to solve a computationally equivalent biological problem.

Intriguingly, the invertebrate catecholamines tyramine and octopamine, which bind to the tyra3 receptor, are closely related structurally to the vertebrate neuromodulator norepinephrine, which has been hypothesized to regulate exploration/exploitation tradeoffs in primates and humans [13,14]. It is tempting to speculate that individual differences in exploration behavior, an innate tendency to abandon the current behavioral strategy for another potentially more profitable one, might also be mediated in humans through genetic influences on catecholaminergic neuromodulatory systems [15].

In a remarkable illustration of the idea that similar decision-making problems may be solved by widely disparate mechanisms following similar strategies, the nest site selection behavior of honeybees has been found to be governed by much the same integrate-to-threshold process as the foraging behavior of monkeys and worms [16••]. In this case, it is the individual animal that is the basic unit of information processing rather than the single neuron. Individual bees dance to accumulate evidence in favor of a nest site, while other bees that suffered predator attacks at that site 'head-butt' the dancers, a stop signal that inhibits dancing. When the evidence in favor of a nest site reaches a threshold, the entire swarm mobilizes to the selected site. Notably, this research was motivated by predictions derived from findings in macaques, demonstrating the predictive potential of the comparative neuroethological approach [17•]. Furthermore, the same dancing and head-butting mechanism is also used in the selection of foraging sites, lending support to the idea that a mechanism evolved to solve one decision-making problem may also be applied to solving a different but similar one.

Social information seeking

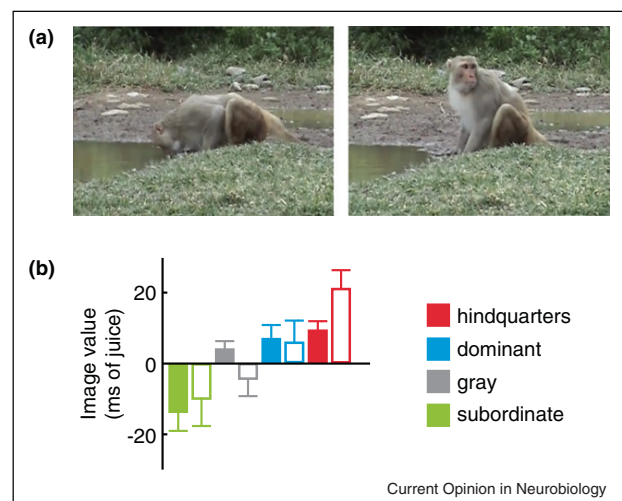
Social information seeking, like foraging, is a process of accessing a variably distributed resource, under the constraint of costs associated with the search behavior. Information about social partners can be valuable in a wide variety of contexts, such as mate choice, foraging, and nest site choice, and the strategies used to solve one class of problem, such as foraging, may also be applied to another class of problems, such as social decision-making.

Thus the primacy of information in guiding decisions is abundantly evident in the social behavior of primates. Primates have frontally oriented, mobile eyes with a central fovea composed of a high density of cone

photoreceptors, and thus are not capable of sampling all regions of the visual field simultaneously. This set of adaptations has led to the evolution of mechanisms that orient the visual system to objects with high information value via overt and covert attention [18]. In the context of foraging, information is given value as a consequence of the value of the nutriment it may yield, as when an animal evaluates a tree for the presence of ripe fruit. But animals living in complex and dynamic societies can use the same attentional strategies to gather information about others [19], including rank [20], identity [21], group membership [22], direction of gaze [23–25], and emotional state [26].

While behavioral and physiological evidence demonstrates the value of information to primates in decision-making, information seeking also has associated costs. By contrast with foraging, for which locomotion imposes high energetic costs, the metabolic costs of information seeking are quite low. However, information seeking can impose time costs, requiring animals to forego activities such as sleeping, drinking, or eating, which demand postures or behavioral states incompatible with attentive orienting (Figure 3a). Other costs are social: in the case of rhesus macaques, visual fixation on the face of another

Figure 3



Social information is a valuable resource for macaque monkeys. (a) A rhesus macaque on Cayo Santiago assumes a vulnerable posture (left) to drink from a puddle, but periodically interrupts this posture in order to visually scan the surrounding region for potential threats (right). There are no predators on the island, but aggressive social interactions are commonplace. (b) Values determined for different image classes for two male monkey subjects (open and closed bars), in ms of fluid delivery time. Positive deflections indicate the subject was willing to forgo fluid to view that image class. Negative deflections indicate the subject required fluid overpayment to choose that image class. Hindquarters refer to the perineal sexual signals of familiar females. Dominant and subordinate refer to the faces of familiar dominant and subordinate males. Gray refers to a plain gray square matched for size and luminance to the other image classes. Behavioral data depicted here correspond to neural data depicted in Figure 4, below. Photographs by K.K. Watson.

individual invites aggression [27]. Furthermore, inappropriate information seeking (e.g. directing attention to low-value information) can result in missed opportunities to gather more useful information elsewhere. These tradeoffs are part of the decision-making problem that social animals must solve in allocating their time and attention to social information seeking behaviors.

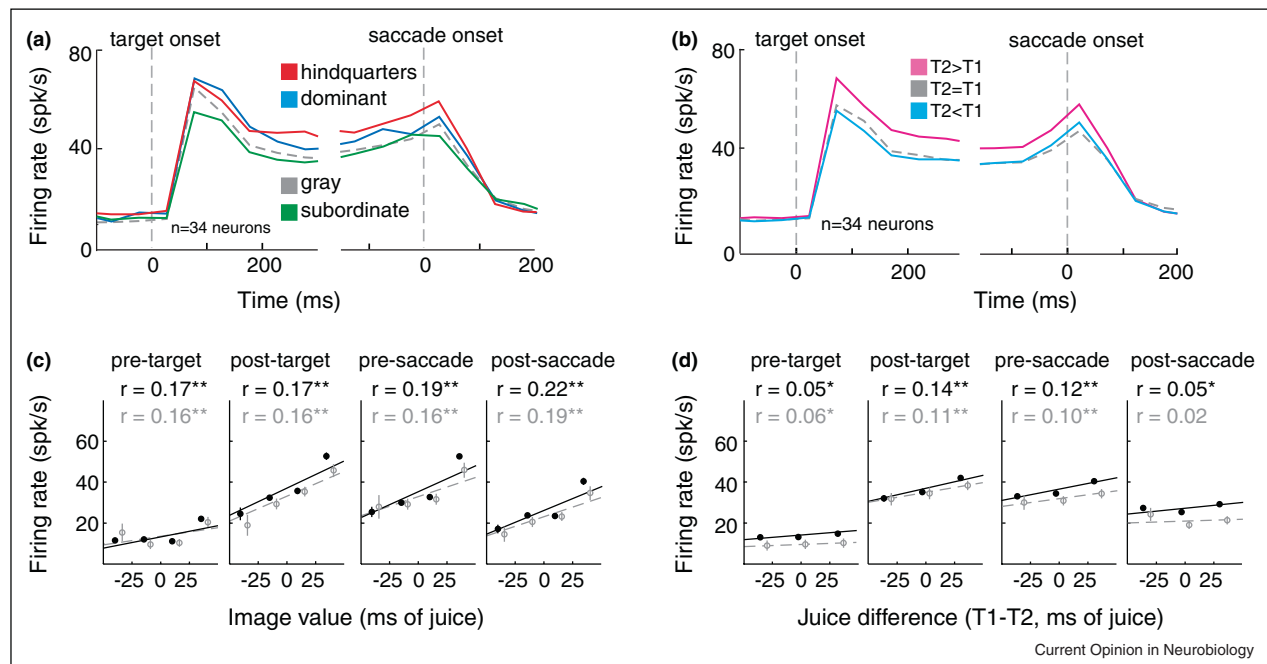
Thus, as in foraging, adaptive choices during information seeking depend on the assessment and comparison of associated costs and benefits. Deaner, Khera and Platt [28] demonstrated that thirsty male rhesus macaques will forego a small amount of juice in order to acquire specific types of social information, such as reproductive signals (i.e. female perinea) or the faces of dominant males, but will not do so for other types of social information, such as the faces of subordinates (Figure 3b). By contrast, monkeys look longest at reproductive signals but quickly avert gaze from both dominant and subordinate faces. These two observations invite the hypothesis that although both sexual signals and status-related signals contain high information value, there is a high cost associated with an extended period of direct eye contact. In support of this interpretation, a genetic polymorphism in the serotonin system associated with heightened anxiety elicits

reduced attention to the faces of other monkeys, greater pupil dilation (a somatic index of elevated autonomic arousal) in response to faces of dominant males, and reduced reward value for viewing the faces of dominant males [29**] in rhesus macaques.

Multiple cortical and subcortical brain areas are specialized for processing social information. Regions in the temporal and occipital lobes are specialized for processing social information in humans and macaques, suggesting adaptation for the rapid assessment of visual social information. Humans and macaques both possess multiple brain regions, identified by functional imaging and confirmed by recordings from single neurons, exquisitely selective for faces [30,31]. Neurons in other temporal lobe areas encode head direction [32], face identity [33], or biological motion [34]. Cortical thickness in both temporal and prefrontal areas increases with increasing social group size in macaques [35*].

Subcortical structures play a particularly critical role in encoding affective properties of social stimuli. For example, the amygdala is known to encode stimulus salience, and damage to this region disrupts face processing and produces abnormal social approach behavior

Figure 4



The value of social information is signaled by neurons in the macaque visual orienting system. **(a)** Average firing rate for 34 LIP neurons plotted against time for all trials in which the subject chose to view the image (T2) in the neuron's response field, separated by image class. **(b)** Average firing rate of the population for all trials in which the subject chose to view the image (T2) in the neuron's response field, separated by fluid value relative to the non-chosen target (T1). **(c)** Firing rates during the 200 ms after target onset, plotted as a function of image value (left) and as a function of difference in fluid payoff between T2 and T1 (right). Regressions were performed on all data in which the subject chose to view the image. The data in **(c)** were binned for display, but all regressions were performed on raw data. ** $p < 0.001$. Figure after [19], used with permission.

(reviewed in [36]). In addition, fMRI studies reveal that many parts of the canonical subcortical reward circuit, most notably the nucleus accumbens (NAcc), are activated by visual social rewards [37], social approval [38], aversion to social inequity [39], and charitable donations [40]. The special role of NAcc in social interaction is endorsed by animal research showing, for example, that D2 receptor manipulation in NAcc alters partner preference in mating voles [41], and that μ -opioid receptor manipulation in NAcc alters social play behavior in rats [42].

These populations of neurons are interconnected and feed forward from the temporal into the frontal lobe, where various features of external stimuli, including their motivational value, are integrated [43]. The architecture of this network suggests that decision-making mechanisms may have privileged access to social information in human and nonhuman primates alike. We conjecture that a common suite of algorithms, and perhaps mechanisms, subserves both 'social' and 'non-social' decision processes, with the former differentiated from the latter by the large number of specialized circuits used for detecting and processing information related to conspecifics.

Moreover, studies of neural activity in the primate brain support the notion that information itself has value for making decisions. Dopamine neurons, which respond to unpredicted primary reinforcers (such as nutritive rewards) and cues predicting reinforcers, also encode monkeys' preferences for advance information about the content of impending choices [44]. Moreover, firing of neurons in lateral intraparietal area (LIP), a region of visuomotor cortex thought to encode a salience map of the visual world [45,46], varies with the value of social images displayed in the neurons' receptive fields. Neurons in LIP not only encode the value of the juice reward monkeys will gain for orienting to a particular location [47], but also the intrinsic biological value of the social information they receive for orienting to the same location [19]. When monkeys are given the opportunity to either maximize a juice reward or display a social image, LIP neurons respond to both the amount of juice received and to the value of the social reward (Figure 4). Importantly, social and gustatory value are encoded independently along the same axis, suggesting that LIP plays a role in assigning value to a particular location in space, irrespective of the nature of the resource being sought. Thus, neurons in parietal cortex—a final common pathway for information seeking behavior—automatically integrate the intrinsic biological value of social agents into salience maps guiding orienting.

Discussion

The study of ecological decision-making suggests that natural selection has favored a set of simple, repeated design patterns: basic circuit elements capable of being implemented by many biological configurations. Instead of forming a single unified system for decisions, these

local circuits might be capable of functioning independently for specialized subclasses of action planning and selection, as well as being recruited across regions for more complicated behaviors. Just as Gigerenzer has suggested that human decision processes draw on a well-stocked 'adaptive toolbox' filled with inexpensive, approximate heuristics, so evolution appears to favor repeating algorithms, despite disparate implementations [48].

In this view, the study of a decision-making problem like patch leaving is valuable not only because it is ubiquitous, but also because the algorithm used to solve it—comparison of local returns to a fixed threshold—represents one of the simplest forms of a single-input/single-output control system, in which the controller implements a binary threshold operation [49]. Any neural system capable of implementing such a circuit is likewise applicable to an extremely wide class of problems, one that extends far beyond foraging. In fact, a more general version of such a system, the Kalman filter, is known to be an optimal solution to the problem of predicting returns under fairly general assumptions, and thus for fine-tuning behavior in response to changing environmental conditions [49,50]. That such a system is linear, that it requires only a simple architecture, and that it is robust against noise all lead us to expect that it will not only appear in a wide diversity of species, but that it may be repeated and repurposed within a single brain to solve seemingly unrelated problems. In fact, such observations motivate a neural engineering viewpoint in which the unique classes of problems faced by an organism become primary, followed by the algorithms used to solve them, and only lastly their specific neural implementations [51].

This does not mean, however, that comparative biology or neurophysiology become irrelevant for understanding decision-making. On the contrary, this evolutionary viewpoint suggests that algorithms implemented in simpler nervous systems are more generally applicable than we might have thought. Just as in vision or olfaction, the insights gained from studying flies or worms suggest possibilities at the algorithmic level in birds or primates. And though the details may differ as organisms become capable of more generalized and flexible behaviors, the same simple biological components, coupled like circuit elements, may likewise be expected to give rise to startlingly sophisticated generalizations [49].

Many models of decision-making, particularly those derived from economics, describe the decision process as a linear sequence: estimating the abstract utility of several possible outcomes or behavioral plans, directly comparing these utilities, and finally selecting the goal or behavior associated with the highest utility [52–56]. In some cases, such models leave the exact nature of the abstract utility undefined. Here, however, we have presented a 'bottom-up' as opposed to 'top-down' perspective,

in which simple, reusable decision rules are implemented repeatedly to solve various decision-making problems across a diverse range of taxa. Owing to the rules' algorithmic similarity, their output could mistakenly be attributed to a single decision-making system. We argue that these design patterns, implemented by diverse suites of neural hardware, should nonetheless prove ubiquitous on evolutionary grounds, and that their simplicity and robustness should favor them both for convergent evolution and conservation within taxa. Such ideas represent a new opportunity for both systems theory and comparative biology, since the view of decision systems as evolving primarily to solve ecological problems demands renewed interest in both engineering disciplines and animal behavior. Indeed, the search for reusable design patterns in neural systems may provide a unifying framework for biological decision making in much the same way it has for vision and motor control.

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