

Economic choice: the foraging perspective

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Foraging theory offers an alternative foundation for understanding economic choice, one that sees economic choices as the outcome of psychological processes that evolved to help our ancestors search for food. Most of the choices encountered by foragers are between pursuing an encountered prey (accept) and ignoring it in favor of continued search (reject). Binary choices, which typically occur between simultaneously presented items, are special case, and are resolved through paired alternating accept–reject decisions limited by the narrow focus of attention. The foraging approach also holds out promise for helping to understand self-control and invites a reconceptualization of the mechanisms of binary choice, the relationship between choosing and stopping, and of the meaning of reward value.

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Introduction

The need to make economic choices is often framed in bloodless terms. It is seen as the careful and dispassionate balancing of competing possibilities and the deliberate selection of a preferred one. But the brain circuitry underlying economic choice evolved to make life-or-death decisions and underwent intense selection pressure for optimization. It evolved for a specific purpose — to help us survive. The types of choice that we study in the lab have a direct analog in the natural repertoire of animals — the feeding decisions that foragers face. These decisions must be quick — otherwise we risk losing prey to flight or rivals — and they must be accurate — when survival is on the line. For these reasons we believe that a focus on evolutionary demands, rather than on economic theory, provides a firm basis for thinking about the neural basis of economic choices in humans and other animals

[1,2]. For these reasons, we believe that economic choice, and foraging choices more broadly, can be put under the rubric of survival circuits [3,4] (Figures 1 and 2).

Foraging decisions are accept–reject decisions

For most foragers, the distribution of prey in the environment is patchy in space and ephemeral in time [5]. As foragers search, prey are generally encountered one at a time and the forager's decision is whether to pursue (accept) or ignore (reject) the prey item. (Note that we use prey here in the formal sense, to refer to any pursued diet item, whether it is animal, plant, or other [5].) This principle is true for foragers searching within a patch and foragers surveying multiple patches. The elemental decision in foraging, then, is the accept–reject decision and not, as in microeconomics, a binary choice between simultaneously presented items.

Prima facie, accept–reject choices may appear to be just like other binary choices. After all, they involve selection between accepting and rejecting an option. The key difference between accept–reject decisions and other binary decisions is that the two options are asymmetric: accept and reject are different. While the psychology of accepting and rejecting has not been delineated, several hypotheses seem intuitive. Pursuing a prey item is often active. It leads to reward consumption (and has features in common with exploitative choices); in some contexts it involves a change from the current (search) state. Capture normally triggers monitoring, adjustment, and learning processes (as does failed capture following an accept decision). Rejecting a prey item is often passive, often maintains the status quo (that is, continuing to search), and, during the subsequent search, returns the decision-maker to outwardly oriented searching mode (which has features in common with exploratory choices). Note that these relationships may not hold in all contexts; determining their boundary conditions is important for future studies.

Insights into self-control from the accept/reject framework

One important example of the way the accept/reject framing matters is the performance of animal decision-makers in intertemporal choice (a.k.a. delay discounting) tasks. Such tasks, in which animals choose between delayed large rewards and immediate small rewards, are a mainstay of the psychology and neuroscience of self-control (reviewed in [6]). Animals generally appear impulsive, meaning they prefer a reward offered sooner even if it is less profitable. This observation is difficult to

Figure 1



Animals in natural environments, such as this gorilla at the Karisoke Research Center in Rwanda, generally encounter prey one at a time. Their decision-making strategies are molded by those encounters and are centered on accept–reject decisions. (Photo credit: Jessica Cantlon).

Figure 2



Animals in the laboratory, such as this baboon at the Seneca Park Zoo, are often faced with binary decisions. Some research suggests that those decisions are made as interleaved accept–reject decisions of each option. (Photo credit: Jessica Cantlon).

reconcile with evolutionary theory because it is highly maladaptive in the long run.

One possible explanation for the seeming contradiction between evolutionary pressure toward optimality and observed behavior is that animals naturally misunderstand the structure of laboratory intertemporal choice tasks and continue to do so after extensive training [6,7,8]. Specifically, the post-reward adjusting interval that is added to laboratory intertemporal choice tasks appears to present a clear learning problem for most animals; this problem is expected if animals adopt a *expectation-of-ratios* heuristic strategy, which is evolutionarily favored in most natural contexts [8]. In tasks in which post-reward delays are unambiguously cued, animals' choices are much closer to rate-maximizing, suggesting that lack of information about task structure leads to some apparent impulsivity [9,10]. Indeed, in foraging tasks with a time component, ostensibly impulsive animals are almost perfectly patient [10,11*,12,13].

Another important feature of foraging decisions absent from standard economic ones is the requirement for persistence in pursuing or handling a prey item after the decision itself is made. The neural mechanisms of persistence are just beginning to be understood [14**15**,16,17]. One key ingredient in many persistence decisions is the need to maintain an ongoing representation of the value of the prey and to update that value continuously as the receipt of the prey gets closer in time [14**,18]. Failures of this value updating process may help to explain failures of self-control, and treatments that modify this representation may help improve self-control.

How accept–reject decisions are implemented

The key decision variable in accept–reject decision is profitability: the gain weighed against the cost of the item, including opportunity costs [5]. Profitability is compared to a threshold, the average value of the environment. The most straightforward way to implement an accept–reject decision is to maintain a (dynamic) representation of the profitability of the foreground option and a (stable) representation of the profitability of the background and to compare them [15**,19,20]. Control systems in the brain then can modulate these representations regulate the threshold for accepting a presented option [20,21*,22**].

Once an item is attended, accepting the option may be a type of default action; rejecting it would then be an alternative. If so, this framing would introduce an asymmetry into binary choice. That asymmetry should be visible in the brain, and indeed it is: the two option types are associated with activation in the ventromedial prefrontal cortex (vmPFC) and dorsal anterior cingulate cortex (dACC), for default and alternative, respectively [19,23]. The relationship between coding and choice is also dependent on accept–reject status; for example,

vmPFC encodes the value of the offer if it is accepted and of the environment (negatively) if the offer is rejected [19,24]. Moreover, lesions of vmPFC in macaques disrupt the common tendency to repeat choices following large rewards — that is (to speculate a bit) these lesions disrupt regulation of the processes that determine the favored default and disfavored alternative actions, or that select them [25].

Presumably, then, choice is determined by competition between these two systems. The role of dACC in encoding the value of the alternative is also consistent with recordings of single neurons there, which show encoding of the rejected value on reject trials and of the delay — which corresponds to the opportunity cost of the accept decision — on accept trials [26]. And in a patch-leaving task, in which the decision to reject an option builds over several trials, responses of dACC neurons gradually increase as the value of rejection rises [20]. These discoveries about dACC offer a synoptic account of dACC function that was not available from standard conflict and comparator models based on conventional (non-foraging) tasks [27,28]. These regions, then, especially the dACC and the vmPFC, can be said to constitute the core of the foraging survival circuits [4,29].

Are ostensibly binary choices really paired accept–reject choices?

Binary choice is the very core of microeconomics and understanding its neural basis is a central goal of neuroeconomics. Given the importance of accept/reject decisions in foraging, however, some scholars have argued that the binary choice is at least somewhat unnatural and in some cases an artificial laboratory construct [7,30]. A forager whose brain is evolved for single encounters may treat the binary choice as two simultaneous accept/reject decisions. Key evidence for this decision mechanism comes from measures of reaction times and choice probabilities [31–34]. An implication of these results is that binary choice is better described as a paired race-to-threshold than as a single drift diffusion between two bounds.

Another psychological limitation on binary choice is the limited capacity of attention: we cannot bind abstract features (like value) to objects (offers) in the absence of attention, which is generally limited to a single spotlight [35]. In a standard visual task with two spatially separate options, the spotlight of attention likely follows the locus of gaze or, sometimes, covert attention [36]. In more abstract situations, such as when choosing between two possible options that are out of view (e.g. a monkey choosing which of two distant orchards to forage in), the locus of attention likely shifts in a more abstract manner, but still serially. Thus, it seems likely that when options are presented simultaneously, they are nonetheless evaluated and compared serially. Key evidence for this idea comes from a study that recorded ensemble

activity in orbitofrontal cortex (OFC) in a simultaneous choice task [37**]. Neuronal ensembles rapidly oscillated between two states corresponding to the two possible options, presumably tracking the focus of attention. Further evidence comes from the fact that, when attention is artificially controlled (by controlling gaze), ventromedial prefrontal cortex (vmPFC) and OFC preferentially track the values of attended offers [38,39,40*,41,42**].

How can comparison occur in serial choice models?

If attention alternates between single offers, and the brain signals the value of the attended offer only, how can a comparison occur? One possibility is that the brain computes the *relative*, not absolute, value of the attended offer (that is, the value difference or quotient). This relative value can be seen as a normalized representation of the value of the offer, but is sufficient to guide choice: if the difference is greater than zero the attended option can be selected. In other words, following appropriate normalization, no comparison other than thresholding is needed to implement the choice. There is evidence that value representation in vmPFC is relative [38,39] and may be relative in other areas as well (e.g. [43*,44–47]). To implement choice, then, such normalized value representations must be subject to some downstream (or distributed) comparison-to-threshold process.

During serial shifts of attention, what is occurring during each epoch of sustained attention on one option? One possibility is that the brain is gradually accumulating evidence in favor of or against selecting that option [36,48–50*]. That evidence is presumably stochastic, because it reflects the output of multiple noisy channels. It seems likely that at least some of that sampling corresponds to drawing recollections of stimulus and action value mappings from memory [51**]. This demand for memory is particularly likely to be required in contexts where options are defined by two dimensions [45]. These are then fed into one or more value buffers and compared to a threshold.

Foraging suggests a unification of economic and stopping decisions

An accept/reject decision is a choice between actively changing the status quo or passively maintaining it and continuing to search; accepting involves performing a planned or primed motoric response; rejection involves withholding it. In other words, an accept/reject decision has much in common with a stopping decision. And binary choice, by extension, has much in common with a pair of interacting stopping decisions. By stopping decision, I am referring to a class of decisions that is seldom conceptually linked with economic choice (except in the domain of self-control, e.g. [52]). Stopping can refer, here, to a simple inhibition of a motor plan, but can have a more abstract meaning, referring to a change in

strategy, even an abstract one, driven by observations that the payoff structure of the environment has changed.

The speculation that economic choice has stopping as its basis, if true, is important because the neural mechanisms of stopping are relatively well understood, and applying this understanding to economic decisions could rapidly advance the neuroscience of economic choice [53–55]. Indeed, if economic choice ultimately boils down to stopping, there is an opportunity for a “grand unified theory” unifying the two types of decisions.

There is some tentative evidence that the neural circuitry involved in stopping is overlapping with the circuitry involved in economic decisions. The motor and premotor cortex, for example, have clearly defined roles in stopping decisions, and also have important and complementary roles in economic choices [56,57*]. More broadly, at least some evidence supports the idea that stopping is a distributed process that reflects activity of much of the prefrontal cortex (among other regions, [55]); similar arguments have been made for economic choice [57*,58*]. In any case, future work on the relationship between stopping and choice is needed. Progress in this area promises to help shed light on important debates, such as how economic choice relates to self-control [59*,60].

Value as tentative commitment to a decision

Value is a construct that is convenient in economic models, but may not be explicitly computed; evidence that it is realized in the brain is equivocal [58*,61]. The brain has not evolved to compute value and then use that to drive choice; it has evolved to drive adaptive behavior in the natural world [1*,3,56]. Indeed, a reasonable null hypothesis would be that the brain, as an evolved system, performs a gradual rotation from an input to an output space without a special amodal value representation in a middle layer. Such a rotation would lead to sensorimotor information — that is, the details of the positions of offers and actions leading to them, in ostensibly motor areas. Recent evidence supports the idea that such signals are indeed observed throughout the reward system [40*,57*,62,63**,64]. What we call value, then, may really be a tentative commitment to accepting an offer, or, more abstractly, to a proposition (cf. [65]). In early layers, that proposition may be toward identifying the stimulus, in middle layers, it may be toward signals that can influence the action or the goal, and in later layers it may be toward the action associated with choosing it [43*,56,57*,58*]. Future studies will be necessary to test this idea; such studies are most likely to be informative if they are ethologically relevant, that is, if they embed the decision-maker in as natural an environment as possible [1*].

Conflict of interest statement

Nothing declared.

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