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Decision-making behaviors: weighing ethology, complexity, and sensorimotor compatibility[☆]

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Rodent decision-making research aims to uncover the neural circuitry underlying the ability to evaluate alternatives and select appropriate actions. Designing behavioral paradigms that provide a solid foundation to ask questions about decision-making computations and mechanisms is a difficult and often underestimated challenge. Here, we propose three dimensions on which we can consider rodent decision-making tasks: ethological validity, task complexity, and stimulus-response compatibility. We review recent research through this lens, and provide practical guidance for researchers in the decision-making field.

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“[T]here is nothing intellectually inherently good or bad about the integration of ‘field’ and ‘closet’ approaches to the study of behavior. All depends on the questions one is trying to answer.”

— Bennett Galef, Jr., 1989 [1]

In the history of behavioral research, there has often been a divide between ‘field’ and ‘closet’ biologists [2]. Modern systems neuroscience is almost exclusively in the closet — we develop controlled, albeit artificial paradigms as a means of distilling animal behavior into quantifiable variables. Yet, the full behavioral repertoire of an animal is complex and incompletely reproduced in a laboratory

setting. Recently, several groups have commented on the importance of behavior in neuroscience, arguing that reductionism and an emphasis on technology have created a significant bias in our experimental design [3,4]. They recommend that the behavior of an animal should be understood *before* engaging in studies of the neural mechanisms which implement it.

Few would disagree that it is wise to consider an animal’s ecological niche when designing a behavioral paradigm. Classic work in rodent psychology relied on natural behaviors such as navigation and foraging to establish fundamental principles of habit formation [5], cognitive maps [6], and spatial learning [7]. The challenge for more modern approaches is in figuring out exactly how to blend the natural approach with the need for experimental control. What features of the animal’s natural environment or actions can and should be recreated in the lab? What is the ideal compromise between experimental demands and naturalistic behavior? What are the risks of imperfectly recreating a natural environment? What other dimensions of behavior should be considered?

Recent technological advances in rodents have given us unprecedented access to circuits and cell types in the mammalian brain [8,9]. Mice and rats exhibit many of the same characteristics during decisions as primates — they are sensitive to risk [10], optimally accumulate perceptual evidence [11], and estimate their own confidence [12]. Indeed, advances in rodent decision-making paradigms in parallel with innovative molecular targeting and population recordings have allowed researchers to find neural mechanisms of decision-making in specific cell types within multiple brain regions [12–14,15^{*},16^{**},17].

Here, we consider the implications of the ethological approach in the field of rodent decision-making, which seeks to elucidate the neural circuits and computations that allow an animal to choose between options. As an alternative to evaluating all behaviors through the lens of ethological validity, we lay out three dimensions that capture much of the variance across rodent decision-making tasks. Then, we examine recent progress in rodent decision-making research through this framework, arguing that current behavioral tasks, taken together, strike a balance between complexity, naturalness and stimulus-response compatibility. Lastly, we offer practical insights

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to those seeking to study decision-making in quantifiable yet ethologically valid ways.

Evaluating behavioral paradigms according to multiple metrics

How should researchers adjudicate between a fully ethological approach and the realities of current neuroscience methods? Below, we argue that ethological validity alone is an insufficient metric for designing and evaluating a behavior and promote an alternative framework in its place.

Ethological validity of the stimulus and response

The simplest definition of ethologically valid behaviors is that the stimuli and/or response are within the scope of stimuli and responses that the animal would typically encounter or do (Figure 1, vertical axis). For example, mating calls would be considered ethologically valid, whilst pure tones would not. We can consider the animal's response on a similar axis: some actions are not in an animal's natural repertoire (e.g. manipulating a joystick), while others are (e.g. running).

The upside of ethological stimuli and responses is twofold. First, they may offer a fast route to understanding brain function since neural circuits are likely optimized for stimuli and responses that have been present throughout the organism's evolutionary history. For instance, auditory cortex evolved in part to process complex, time-varying vocalizations. This may explain why neural modulation tuning characteristics scale to encode natural sound statistics in cat inferior colliculus [18] and why neurons respond more reliably to real versus disorganized vocalizations in rat non-primary auditory cortex [19]. A second upside of ethological stimuli and responses is that they may be learned more rapidly. While the process of mastering a novel movement can be illuminating [20,21], the need to reduce training time is a major consideration in some studies.

Despite these advantages, the use of ethological stimuli comes at a price. Stimuli that are ethological may be difficult to parameterize and vary systematically. The opportunity to characterize and systematically manipulate the statistics of stimuli was critical in the development of the deeply influential models of visual cortex neurons [22]. Further, the use of non-natural stimuli can allow illuminating comparisons that would otherwise be impossible. For example, arbitrary electrical pulses have proven essential in comparing the timescales of activity in primary auditory, visual and somatosensory cortex [23]. Lastly, the mapping between stimuli and neural circuits is likely experience-dependent, even for innate behaviors [24] (Box 1).

Stimulus-response compatibility

The stimulus used to inform a decision and the response used to report it can either be compatible (e.g. orienting

toward a mating call) or incompatible (e.g. orienting away from a mating call; Figure 1, right axis). We can therefore place these behaviors on a scale from -1 to $+1$, where -1 indicates stimulus-response pairs that are incompatible, and $+1$ indicates pairs that are compatible. Some stimulus-response pairs may be neutral, such as licking in response to a visual grating, and can be assigned 0.

Low stimulus-response compatibility will likely increase training time. Even when an animal has mastered a stimulus contingency with low stimulus-response compatibility, a signature of the challenge of such behaviors can remain. For instance, monkeys and rodents can be trained to orient (e.g. turn head or saccade) away from a visual target; although they can achieve very reliable performance on these 'anti-orienting' tasks, their reaction times are much longer compared to the more compatible 'pro-orienting' task [14,27]. Rats trained to switch between the 'pro' and 'anti' rule also show several phenomena related to asymmetric task-switching (i.e. switching back and forth between an easy and hard task) that had previously been observed in humans [28]. This rodent model allowed for experimental perturbations that provided the first causal evidence (from any species) for the task-set inertia theory of switch cost [14,28].

In many studies, a neutral relationship between stimuli and response can be useful [29,30]. Such studies allow us to investigate learning and decision-making over time from a neutral baseline, without the biases that innate positive or negative stimuli-response relationships may introduce. However, we should be wary that two different seemingly neutral responses (e.g. a go/no-go vs two-alternative forced choice (2-AFC) odor discrimination) can produce distinct behavior strategies [31].

Task complexity

A final key consideration in choosing a behavior is how many independent variables the experimenter is modifying and how many dependent variables can be recorded (Figure 1, left axis). Here we summarize these two concepts with the term 'task complexity.' For example, no-go tasks with a single modality presented at a time (e.g. a go tone) have low complexity [32,33]. Tasks such as foraging in a virtual reality environment with multiple stimulus modalities (e.g. auditory and visual) have high complexity (sounds, sights, space, velocity).

More complex tasks take longer to learn, which is a downside. However, their use has been critical in exposing key principles of neural computation. For example, monkeys trained to judge stimuli based alternately on color or motion direction are slow to train and need constant reinforcement of the proper stimulus-response contingency [34]. However, animals who have mastered this complex task offer an unprecedented opportunity to understand how the context of a sensory stimulus

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