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Invited review

A framework for understanding and advancing intertemporal choice research using rodent models

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ABSTRACT

Intertemporal choices are common and consequential to private and public life. Thus, there is considerable interest in understanding the neural basis of intertemporal decision making. In this minireview, we briefly describe conceptual and psychological perspectives on intertemporal choice and then provide a comprehensive evaluation of the neural structures and signals that comprise the underlying cortico-limbic-striatal circuit. Even though great advances have been made, our understanding of the neurobiology of intertemporal choice is still in its infancy because of the complex and dynamic nature of this form of decision making. We close by briefly discussing recommendations for the future study of intertemporal choice research.

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1. Introduction

Among the countless behaviors studied by neuroscientists, value-based decision making engenders great fascination because of the ease with which people can think of examples from their own lives-routine decisions like selecting what/when to eat as well as more profound decisions like choosing whether to pursue an advanced degree or determining the right time to invest in a home. Such examples highlight the fact that many of the value-based decisions humans and other animals regularly face are intertemporal choices, decisions between options available at different times.

Individuals across species respond to intertemporal choices by delay discounting, a phenomenon by which their subjective valuation of reward declines with a delay (Ainslie, 1975; Mazur, 1997). Not only do individuals prefer an immediately available reward over a delayed reward when given the choice between equally-sized reward options, but their preference for an objectively larger reward is also reduced when its receipt is delayed relative to the smaller reward. Even though delay discounting is the norm, the rate at which individuals discount future reward varies greatly, with high rates of discounting correlating with a variety of psychiatric and behavioral conditions such as psychiatric diseases and behavioral disorders (Koffarnus, Jarmolowicz, Mueller, & Bickel, 2013), college GPA (Kirby, Winston, & Santiesteban, 2005), texting while driving (Hayashi, Russo, & Wirth, 2015), environmental investment (Hardisty & Weber, 2009), social policy (Weatherly, Plumm, & Derenne, 2011).

Because intertemporal choices are common and consequential to private and public life, there is great interest in enumerating the processes that underpin normal and pathological intertemporal choices. While human studies are useful for identifying neural circuits and psychological processes involved in intertemporal decisions, rodent studies are able to extend those findings by disentangling the contributions of specific brain structures and systems. Thus, the aim of this minireview is to present a framework for understanding and advancing intertemporal choice research using rodent models. We begin by briefly describing conceptual and psychological perspectives on intertemporal choice. Then, we summarize rodent studies in order to review and evaluate the neural contributions of brain structures and systems. Finally, we close by highlighting open questions and making recommendations for future study.

2. Measuring intertemporal choice

Even though it is widely recognized that the goal of value-based decision making is to maximize value, it is difficult to predict an individual's intertemporal choice because valuation is idiosyncratic and driven by delay discounting rate. Thus, to study intertemporal decision making, researchers have developed labo-

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ratory tasks to measure individual delay discounting rates. The tasks, often called delay discounting tasks, record subjects' preferences during a series of choices between small rewards available after little/no delay (usually immediately) and larger rewards preceded by a range of delays. During the course of these tasks, human subjects are asked about their preferences during novel choices between food or money rewards paired with long delays (weeks, months, or years), and rodent subjects are well-trained to learn and express preferences for choices between food rewards associated with delays on the order of seconds. [In the rodent tasks, choices are typically presented with fixed delays in a prescribed order, i.e. increasing from 0 s, but there are versions with mixed delays and versions that allow rodents' choices to determine the order.] From these tasks, subjects' choice behavior (% choice of large, delayed reward) is used to calculate delay discounting rates and identify decision making tendencies (Fig. 1A). Individuals with higher rates than the group mean are identified as 'impulsive', whereas individuals with lower rates are identified as 'patient'. Here, we use the term impulsive to refer only to impulsive choices and not impulsive actions.

Despite the differences in task structure, rodent delay discounting tasks are designed to measure the same process as human tasks. Although some have argued rodent tasks are not appropriate models for extending human research (see Hayden, 2015; Killeen, 2011 for critical analyses), the similarities in results between species has justified their continued use. Not only do measures of human and rodent delay discounting rates both remain stable over time if measured under the same circumstances (Anokhin, Golosheykin, Grant, & Heath, 2011; Kirby, 2009; McClure, Podos, & Richardson, 2014), but there is significant overlap between psychological and neural processes that have been identified using these tasks in both species (see Sections 4 and 5).

3. Conceptual basis of intertemporal choice

In light of how intertemporal decision making is measured, it is tempting to view choice as a single, standalone behavior. But, it is more accurate to view it as a complex, multistep behavioral process. The conceptual model which captures this best divides the decision making process into five subprocesses that occur every time an animal encounters an intertemporal choice: decision representation, subjective valuation, action selection, outcome evaluation, and learning/updating (Rangel, Camerer, & Montague, 2008; Fig. 1B). According to the model, animals must first represent the decision problem by determining the number and features (actions, delays, reward size) of the available options. Then, they integrate the feature information (reward and delay) to assign each option a subjective value, and next, they use that valuation to choose and perform the action(s) associated with the most valuable option. Finally, they compare the experienced value against their expected value and then update their decision representations, valuations, and choices based and what has or has not changed externally (actions, cues, delays, rewards, etc.) or internally (hunger, thirst, affect, etc.). By outlining the entire decision making process, the model expands our conception of intertemporal choice beyond just the choice itself to include an interconnected web of behavioral subprocesses.

Even though the subprocesses were initially proposed to highlight testable computational variables for neurobiological experiments, they also implicate psychological variables to be tested in behavioral experiments. Specifically, the fact that each subprocess is likely linked to numerous psychological processes (including learning, memory, perception, and motivation-related processes) raises the possibility that some or many of those processes are critical for intertemporal choice.

4. Psychological basis of intertemporal choice

To empirically determine which psychological variables support intertemporal choice, experimenters have taken two approaches. The first is to identify scenarios and manipulations that change (increase or decrease) delay discounting rates; and the second is to identify correlations between psychological measures and delay discounting rates. To date, those approaches have been little applied to rodents and very frequently applied to humans, such that many psychological variables have been identified in human subjects (for excellent reviews, see Koffarnus et al., 2013; Lempert & Phelps, 2016; Peters & Büchel, 2011) and

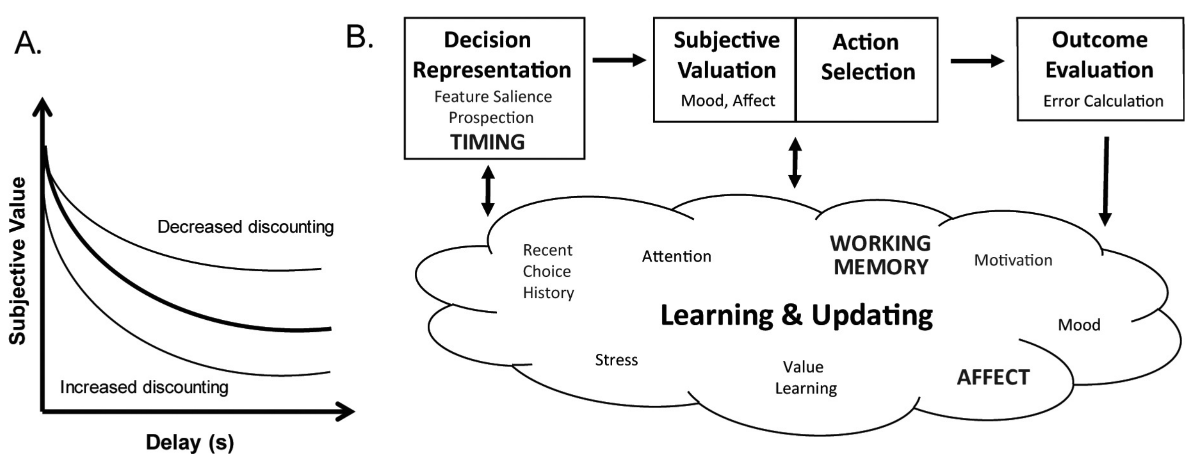

Fig. 1. (A) Example delay discounting curves. Such curves are generated using the choice behavior from delay discounting tasks, and delay discounting rates and decision tendencies are derived from them. The thick black line in the center represents a typical discounting curve, while the thin lines represent a decreased discounting/'patient' curve (top) and an increased discounting/'impulsive' curve (bottom). (B) A schematic of the five behavioral and computational subprocesses that comprise the intertemporal decision making process (adapted from Rangel et al. (2008)). First, an individual represents the decision problem. Next, they assign each option a value through a valuation process. Third, they compare the computed values and select the action associated with the greatest value (action selection). Fourth, they compare the experienced value against that which they expected (outcome evaluation); and finally, they update their decision representations, valuations, and choices through learning, memory, and motivational mechanisms. (Of note is the fact that even though it is easy to conceive of subjective valuation and action selection as distinct processes, it is difficult to disentangle the two because a basic assumption of decision theory is that the chosen option is by definition the most valuable option.) In addition to the behavioral subprocess labels, the schematic is also populated with the psychological variables that have been identified in human and rodent studies. Only those that have been identified in both species are bolded.