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Research report

Effects of striatal lesions on components of choice: Reward discrimination, preference, and relative valuation

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HIGHLIGHTS

- Lesions to dorsal and ventral striatum and free choice were examined.
- Lesion effects were observed on free choice and not serial reward responses.
- Ventral striatal lesions led to impaired optimal preference and risk aversion.
- Dorsal striatal lesions led to altered appetitive actions but minimal choice deficits.
- Striatal function is crucial to optimal free choice expression and involves diverse components of reward processing.

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ABSTRACT

The striatum is a key structure involved in reward processing and choice. Recently, we have developed a paradigm to explore how components of reward processing work together or independently during choice behavior. These components include reward discrimination, preference and relative valuation, and the goal of the present study was to determine how the striatum is involved in these dissociable components during this novel free choice paradigm. We tested choice utilizing two different outcome series with one being a more straightforward single-option discrimination anchored by a 0 reward outcome, and the other as a multi-option outcome discrimination of greater difficulty. We compared the free choice reward task to a sequential reward task and an extinction task. Striatal lesions impaired responding only in the free choice version with alterations in both appetitive and consummatory measures. Ventral striatal lesions had greater impact altering discrimination, preference and relative valuation in both the single and multi-option week studies. A major factor involved in these deficits was a significant aversion to the multi-option that contained a larger outcome option but with a longer delay to reward. Dorsal striatal lesions caused less impairment even leading to enhanced choice behavior compared to control animals during the more difficult multi-option free choice series. Overall, the results suggest that the context of action is crucial when linking striatal function to choice behavior and its diverse components. The implications include the idea that striatal involvement in decision-making is increased when responses are self-paced and diverse in a more naturalistic environment.

1. Introduction

When exploring the brain basis for choice, the basal ganglia has been one region of intense research as the labeled 'motivation-to motor interface' of the central nervous system [40,20]. These ganglia at the base of the brain house several structures all placed in a prime position to perform dense interactions with diverse inputs from all regions of the cortical mantle and many subcortical regions [2,56]. The striatum is the main input center within the basal ganglia, and striatopallidal circuits can be divided into dorsal and ventral subsections (DS & VS) which are believed to play dissociable roles in diverse functions including movement sequencing, choice and decision-making [24,23,14,55]. Recently, we have developed a new behavioral paradigm to explore the different components of choice in a relatively free 'foraging' environment [45]. The different components of choice explored included discrimination, preference and relative valuation. Each component interacts with the

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others depending upon the choice context. Most interestingly, the different components can be dissociated from one another suggesting that the neural basis for the components could vary. This strategy of parsing complex motivation processes has worked well in prior research [11,10,29] as it can lead to new ways to explore the neurobiology of motivation and novel translational approaches to mental impairment.

Previous work has linked DS and VS to distinct functional roles involved in discrimination, preference or relative valuation but no study has explored how lesions to these specific regions could impact these diverse but interactive aspects of choice during the same task. Numerous perspectives have provided insight into how the DS and VS would differentially be involved in these components of choice. In order to optimally decide between multiple options, the "critic" must be able to discriminate between the available outcomes before the "actor" is to perform the action [30]. Quantitative and qualitative discrimination, which involves the ability to distinguish between different outcomes, is a crucial task most likely dependent upon the "critic". Populations of neurons in the DS and VS may discriminate rewards through evaluation of separate criteria. When comparing firing of neurons based on encoding of temporal value versus the overall hedonic value, neurons in the DS and VS show increased activation respectively [14]. Discrimination based upon factors such as timing and magnitude of reward must be efficiently and accurately integrated for optimal decision making [53].

Once an animal develops the ability to discriminate between outcomes, it can then establish preference. Preference has historically been defined as when an "... animal consistently takes one food instead of another when equal opportunity is given to eat both." [58]; p. 309). Work in motivation has systemically examined determinants of preference using highly controlled studies focused on internal or external factors [59,41]. Recent work based on reinforcement theory, optimal foraging or behavioral economics has focused on outcome properties such as reward magnitude [52], quality [18], or timing of reward delivery [36,18]. One possible role proposed for VS function is that this brain region actively assigns value to rewards through its role of the "critic" [42], which would be the underlying factor in the preference-forming process. This framework includes the idea that once preference has been established by the VS, the DS then takes over for performance of the newly-acquired behavior of choice [44]. Dopamine manipulations of the VS lead to mixed results related to alterations in preference and choice [46,38]. For example a recent set of studies found that dopamine depletion of the nucleus accumbens spared risk-based decision-making [37,39]. This work was done using the two-lever choice task which is a valid and well-established measure of choice. Despite its usefulness, this task could be limited in how choice behavior could be expressed in a flexible way. The need for expanding our paradigms to examine choice that utilize more self-paced, open environments could reveal connections between VS, dopamine and choice masked by the use of particular behavioral choice situations.

Experiences with alternative outcomes can also influence the incentive value of an already preferred outcome [19,27,9]. Relative reward valuation occurs when the value of a reward that has already been experienced is altered based upon an interaction with a new reward. The valuation of a reward can be subjectively altered if experienced with different alternative outcomes even though its objective value remains constant [45]. Neurons in the VS will show activational patterns consistent with this behavior [21]. Balleine and Killcross [4] demonstrated that animals can maintain sensitivity to an upshift or downshift in reward value even after lesions to the nucleus accumbens (NAc), a subsection of the VS. This sensitivity remains although lesioned animals performed less lever presses than shams, possibly due to an impairment in instrumental behavior. This holds true when there is a shift in motivational state as well, as shown by effects of shifts in food deprivation level on lever pressing [4]. These findings of reduced instrumental behavior without a reduction of sensitivity to reward shift have been shown elsewhere [33]. Animals with NAc lesions will show reduced contrast effects through altered instrumental behavior when rewards are downshifted, which may indicate a role of this brain area in reward valuation as it relates to instrumental behavior [33]. The exact role of the striatum in all three aspects of choice behavior has yet to be determined.

Understanding how these three components are interwoven to influence choice can help further our understanding for neural representations of choice components in the brain. Our lab has designed a paradigm that provides us with the opportunity to fractionate the three components of choice behavior, thus providing a more definitive profile of the decision-making process. This paradigm consists of three boxes connected to each other by tunnels, creating a relatively large, free-choice environment [45]. Rats will be confronted with the option to choose between rewards of different magnitudes within a one-week session, while magnitude shifts between weeks (see Table 1). The shifting reward values in the current paradigm lead rats to make comparisons of discrimination, preference, and relative valuation. This paradigm has also been designed to permit for the recording of multiple dependent measures, also which could allow for a clearer understanding of choice behavior. Finally, it has also been designed to overcome the confound of overtraining which has been shown to lead to the formation of habits [1], thus resulting in inaccurate reflections of outcome valuation.

In the current set of experiments, we used excitotoxic lesions to investigate the roles of the VS and DS in the decision-making process. A parametric pattern of prediction (Fig. 2A) has been proposed as a guideline for optimal choice behavior. It is our hypothesis that animals without an intact VS or DS will exhibit behaviors that do not fit these predictions, thus not providing them with the capacity to maximize on the opportunity to gain optimal reward. We divided the study into two, three-week experiments. The first experiment uses a varying single options (i.e. 0 pellets in the first week, 1 in the second week) to examine discrimination. This allows us to explore free choice when the changing outcome was simpler with a clear reference to an anchor (0 pellets). A stable multi-option was used to examine relative valuation and differences between the two options in a single session reflected preference. The second experiment used a multi-option (i.e. 0 or 5 pellets in the first week, 0 or 3 in the next) variation for discrimination with the alternative being a single option outcome (1 pellet each week). Results could boost the understanding of striatal functional heterogeneity and the role of striatal functioning in diverse components of typical and abnormal choice behavior.

2. Methods

2.1. Experiment 1

2.1.1. Subjects

Thirty-two male Sprague-Dawley rats (*Rattus norvegicus*) weighing 275–415 g at the time of surgery were used for this experiment. All animals were housed in 65 × 24 × 15 cm cages with corncob bedding. They were food deprived Monday through Friday to no less than 85% of their free-feeding, baseline weight with *ad libitum* access to water in their home cages. From the end of testing Friday until approximately 24 h prior to testing on Monday, they had *ad libitum* access to food (Harlan Teklad Rat Chow #8604). The colony room was set on a 12-h reverse light/dark cycle (lights off at 8:00 a.m.) with the temperature maintained at 70 ° Fahrenheit and approximately 56% humidity. All procedures were approved by the