Behavioral investigations of the explore-exploit tradeoff in rats

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# Abstract

Humans and animals have to balance the need for exploring new options and exploiting existing options that are known to be good. This tradeoff is known as the explore-exploit dilemma. To better understand the neural mechanism underlying how humans and animals solve the explore-exploit dilemma, a good animal behavioral model is critical. Most previous explore-exploit studies in rodents used ethologically unrealistic operant boxes and reversal learning paradigms which have certain limitations. In such paradigms, the decision to abandon a currently bad option is confounded by the need for exploring a novel option for information collection, making it difficult to separate different drives and heuristics for exploration. A model-free win-stay lose-shift strategy is efficient in handling the reverse learning which discourages and doesn’t allow for observing model-based planning behavior in exploration. In this study, we investigated exploration in rats using a spatial navigation Horizon Task (Wilson et al., 2014) adapted to rats to address the above limitations. We compared the rat performance to that of humans using identical measures. Overall, we found a good correspondence between human and rats and established this task as a new rodent model for studying the explore-exploit decision making processes.

Keywords: explore-exploit dilemma, directed and random exploration, win-stay lose-shift, planning horizon

# Introduction

Humans and animals constantly face the choice between exploiting options that are known to be good and exploring unknown options in the hope of discovering better options for the future. Humans face this dilemma in scenarios from simple choices like deciding whether to explore a new restaurant for dinner, to important life decisions such as deciding whether to explore a new career, while animals face it when deciding whether to explore and forage for food, territory and mate. The cognitive ability to balance exploration and exploitation is vital to animal and human’s survival and success. In recent years, the study of explore-exploit decisions in humans and animals have become an active field (Mehlhorn et al., 2015, Wilson et al., 2020).

Although an optimal solution to explore-exploit decisions is, in general, computationally intractable (Bellman, 1954), humans and animals are thought to use approximations or heuristics in making explore-exploit decisions. Previous research revealed that subjects were likely to use one or both of two main heuristics. The first is an information-driven heuristic known as directed exploration in which action is biased towards the more uncertain option (Krebs et al., 1978, Meyer and Shi, 1995, Banks et al., 1997, Frank et al., 2009, Steyvers et al., 2009, Lee et al., 2011, Payzan-LeNestour and Bossaerts, 2012, Zhang and Yu, 2013, Wilson et al., 2014) . The second is an error-driven heuristic known as random exploration in which exploratory actions with suboptimal estimates of value are chosen by chance (Kao et al., 2005, Badre et al., 2012, Wilson et al., 2014, Gershman, 2018, 2019). In particular, recent studies showed that humans were able to adapt the extent to which they explore with the horizon context, i.e. the number of future choices remaining (Wilson et al., 2014). Horizon adaptation is thought to be a hallmark of exploration.

Relatively few studies have investigated how animals, in particular rodents, make explore-exploit decisions. To study such behavior, most existing rodent explore-exploit studies took the approach of a reversal learning paradigm. In the reversal learning design, animals choose between two options where one is better than the other. These can be options with high vs low costs (Beeler et al., 2010), options with large reward and short delay vs small reward and long delay (Laskowski et al., 2016) , or binary reward options with high vs low probabilities (Parker et al., 2016, Cinotti et al., 2019, Verharen et al., 2020). As animals explore the two options they will eventually converge to the better option and keep exploiting it, until the outcome of the two options are swapped. Deviating from the previously exploited option after reversal is considered exploration in these tasks. Rodents are reported to use a set of win-stay lose-shift strategies which are effective in solving these reversal learning problems.

However, reversal learning designs have several limitations. First, the scope of ”exploration” being examined using such designs is limited, as win-stay lose-shift is a model-free exploration strategy which works well for reversal learning. However, such design does not allow for observing planning and model-based behavior. Second, from the decision to abandon a currently bad option is confounded by the need for exploring a novel option for information collection. In such paradigms, it is impossible to dissociate directed choice from random exploration. Third, most of the tasks mentioned above are implemented in operant boxes that are not natural environments for a rat. As pointed out recently, head-fixed monkeys have the opposite risk preference compared to freely moving monkeys during the same task, suggesting that decision making may be directly influenced by the physical constraints of the experimental paradigms ([Vodicka et al., 2019](#ENREF_22)). One of the most fundamental and natural behavior of rats is to spatially navigate. It is unknown how rats would behave in a setting in which the explore-exploit dilemma taps into their spatial navigation abilities. Fourth, there is a general gap between the human and rodent literature in the context of the explore-exploit decision processes. The complexity of the tasks and their implementation are different across species, and whether similar heuristics are in play in human and rodents remain an open question. Finally, very little is known of the neural substrate of the explore-exploit decision circuits, and animal models allowing detailed investigations of the cellular and system mechanisms of this process are sorely needed.

# Methods

## Animals

4 Brown Norway rats were used in these experiments. All rats were male between 6 and 7 months of age at the start of the experiment. All rats were housed under reverse 12:12 light cycles. All animal procedures were approved by the IACUC committee at University of Arizona and followed NIH guidelines.

## Human participants

Data from forty six participants were used. All participants were from the undergraduate psychology subject pool who earn credits for participation in this study. The human experiments were approved by the University of Arizona Institutional Review Board.

## Behavioral Tasks

Rat version: The maze consisted of a circular area (1.5 m diameter) with 8 equidistant feeders at its periphery (Jones et al., 2012, Jones et al., 2015). Each feeder delivered sugar water (0.2g/L) in the form of computer controlled drops. A blinking LED was attached to each feeder and acted as a cue, when desired. The experimental sessions were divided into ‘games’. During each game, only 3 feeders were activated in an isosceles pattern. One feeder was the home base; the two others, equidistant from the home base, were the **reward areas/target feeders.** The home base was never rewarded, but animals had to reach it to trigger the 2 **rewards areas**. The home base was flanked by two Lego blocks, forcing the animal to start its navigation to the 2 **choice feeders** without bias (Fig 1A, blue rectangles). At the start of each game, depending on the conditions, the two **rewarded feeders** were associated with a fixed number of sugar water drops drawn uniformly from 0 to 5, and always gave the same number of drops during that game (‘Game1’, Fig 1A). Before making their free choices, rats were guided to one of the **target feeders** in the first N trials (only one LED was blinking, Trial1 cue, Fig 1A). Rats performed versions where N = 0, 1, or 3. (In cases of N = 0, rats were not guided to any target feeder and started with a choice between 2 **unknown feeders** instead.) Fig 1A illustrates the version with N = 1. From the N+1st trial, they were cued to make free choices (the LED of the 2 rewarded feeders blinked simultaneously, ‘Trial2 cue’ Fig 1A).

After the first game was completed, a 8s increasing sweep tone was played to indicate the start of a new game. The layout was then switched and the feeder directly opposite to the initial home base was now activated as the new home base and signaled the start of a new game (Game2, Trial1 Start, Fig 1A). The new rewarded feeders are the activated feeders opposite to the new home base (trial1 cue, Fig 1A).

Each home base was associated with a fixed horizon in each game. Horizon is defined as the number of trials after the guided trial {Wilson, 2014 #23}. In these experiments two conditions were implemented: Horizon 1: only one free choice allowed before a new game started, and Horizon 6: 6 free choices before the start of a new game. Horizon conditions were pseudo randomly chosen every day. On average, 16.1 games were ran per day.

Human version: In this task, participants were sitting in a booth, in front of a computer. They were asked to choose between two slots machines (also referred to as bandits, Fig 1B) that gave out a fixed number of reward points uniformly drawn from 1 to 5. Participants were instructed to maximize the total number of rewards. The height of the boxes indicated the number of choices allowed in the current game (i.e. the horizon condition, Horizon=2 in Figure 1 B) and each row represented a trial. Before participants made their own choices, in the very first trial, they were cued to pick one of the bandits (Trial1 cued guided, Fig 1B). The option available was cued with a green background color. Participants indicated their choices by pressing an arrow key on a keyboard. Their response was followed by an indication of how many rewards they obtained (3- XX, Fig 1B). From the 2nd trial, both bandits were available and participants were free to make their own choices. There were four horizon conditions (H=1, 2, 5, 9 free choices) and games with different horizons were pseudo-randomly interleaved. Humans ran 160 games per participant (with the exception of 4 early participants doing 80 games).

# Results

Both humans and rats were able to choose the best option (p(correct), the option with a higher magnitude between the two available sugar water locations for rats, or the slot machine with a higher payout for humans) significantly above chance for the last choice in the long horizon context. Humans could achieve an accuracy of over 90% (Fig2 right) whereas rats could achieve an average accuracy around 80% (Figure 2, left). Both improved with the number of trials given (rats: p(correct, trial 6, H6) vs p(correct, trial 1, H6), p = 5.89e-6). Interestingly, in the first free choice, both humans and rats could achieve a similar average accuracy of 70% (Figure 2, right). Because a change in home base was always accompanied by a change in horizon conditions, rats showed a difference in performance on trial 1 for H=1 and H=6 (p(correct, H = 6) vs p(correct, H = 1), p = 0.023). This result indicated that rats were less likely to choose the correct feeder if they knew their horizon was short.

The fact that the average accuracy was significantly above chance in the first non-guided trial showed that if prior information was available, humans and rats used it to guide subsequent exploration. In this particular task, with repeated games, humans and animals were able to assess the relative ‘goodness’ of the two bandits from the reward they obtained during the guided trial. For long horizons, both humans and rats performed above chance regardless of the reward size during the guided trial, but their performance was not uniform and displayed an inverted U shape (Figure 3A). When they were guided to 0 or 5 drops (or 1 and 5 points for humans), the accuracy was maximized whereas the accuracy was lower when they were guided to more ambiguous reward amounts such as 2 or 3 drops. As in Figure 2, the performance of rats for the short horizon was worse for intermediate guided rewards than for longer horizons, a phenomenon not seen in humans (Fig 3A, grey Vs blue curves). By the last game in longer horizons, the accuracy of both rats and humans also increased for positive drop sizes 1 to 5 (Figure 3B).

We computed the probability of choosing a different bandit than the one they were guided to during their first free choice (p(switch), Fig 4) as a function of the reward size during the guided trial. We found that rats were very likely to explore the other feeder if they obtained a low reward during the guided trials (e.g. 0 drops, mean = 95.4% Fig 4A), and were very unlikely to switch if they obtained a large reward (e.g. 5 drops Fig 4A). Interestingly, the long horizon conditions seemed to yield lower probability of switching than in the short horizon condition. This becomes clearer if the rat was only guided once instead of 3 times (Figure 8B). The overall shapes of the curves in Figure 4 were similar in humans with some notable differences. First, the utility of 1 to 5 drops seemed different between humans and rats in that human subjects were at ceiling for 1 and 2 points indicating that both reward sizes were equally salient (Fig 4, right). Second, increasing the horizon seems to increase the probability of switching for intermediate reward size 3 and 4 in Fig 4 right. This increase is compatible with what an optimal agent would do. Interestingly, the trend is the opposite in rats. The effect of the decrease of exploration with changes in horizon is more obvious when rats were only guided once (Fig 8B).

We also plotted the percentage of switching from the previous choice as a function of choice number within a game (Fig 5). Rats explore at a significantly higher level at trial 1 and then adopt a more constant and lower rate of exploration for later trials (20%), whereas humans explore more at trial 1 and 2, and eventually stopped switching (5%s, possibly due to boredom or motor error). For humans, the reaction time also decreased with trial number and became constant from the 3rd trial (0.1s, Figure 6B, right), indicating that the decision process was mostly settled during the first 2 trials. For rats, since travel time was included in the rats’ reaction times, this travel time may have overshadowed the decision reaction time difference proper, and we do not see any significant changes in reaction times as trial number increased (Fig 6B, left). Although, there seems to be a decrease in reaction time for the rat’s first choice after being guided to a larger reward (4,5 drops) compared to being guided to a small reward (0, 1 drops) (Fig 6A, left). This is may be due to the speed difference in travel time: with a larger reward, the rat explores less, has an overall higher motivation to run, and has a shorter reaction time.

Finally, we investigated whether self-driven exploration is any different from guided exploration during the first trial of a game. Do rats behave any differently if they are guided by sensory cues on the first trials, or if they are instead invited to choose randomly? Specifically, in two separate weeks, rats performed both a version in which they are guided to one feeder once before choosing between the 2 options (Guided), and a version in which they start off with 2 options to choose from (not Guided). In the analysis, we treated the 1st choice in the not Guided version as if it was guided (i.e. self-guided by the rat itself instead of by the blinking LED), and treated the 2nd choice as choice number 1 (Fig 7,8). We found that rats overall explored more on their first free choices if they are guided (Fig 7B, 8B) and their overall accuracy is higher if guided (Fig 7A). Regardless of whether they were guided or not, rats tended to explore more in a short horizon context than in the long horizon context, which is the opposite of what an optimal agent or a human participant would do (Fig 8B).

Discussion

In this study, we investigated the behavioral performance of rats in a new model of the Horizon task adapted to rats. We addressed the limitations of previous rodent studies by designing a novel open-field task in which rodents choose between two locations that offer different amounts of rewards. To dissociate the uncertainty in estimation of value from the ambiguity of a novel option, we manipulated the magnitudes of rewards rather than their delivery probabilities. Indeed, choosing the same option again in the probabilistic case can be, at least in part, exploratory whereas repeating the same choice is more exploitative in a purely deterministic reward setting. In our design, the rats were guided to one of the two feeder locations first, and the extent to which they explored the other unvisited feeder location in their free choices was used as a purer measure of exploration. In this way, we are also able to quantify directed exploration in a model-free manner. In addition, rats were set to perform the task in both a short and a long horizon condition to assess whether rats explored differently in different horizon contexts. Using an open field, we were able to use two sets of different locations alternatively as new games start as opposed to switching the reward conditions at the same set of locations (as in reversal learning paradigms). The two sets of feeders are associated with different horizon contexts. Moreover, we recruited human subjects to perform a version that is comparable to the rat task, and we compared the performance in exploration between humans and rats.

As with humans, we showed that rats were able to use prior information about the distribution of rewards to guide future exploration. However, rats did not alter their exploration strategies based on the horizon context to the same extent as humans.

In line with previous research using the reversal learning paradigm in an operant box setting, we showed that rats demonstrated the model-free win-stay lose-shift strategy in making explore-exploit decisions. Specifically, they chose to explore more when the exploit value was low and explored less when the exploit value was high. However, in our design, in order to assess whether the exploit value was low or high, instead of using short-term memory to recall the value at the exploit option before reversal, rats had to use their long-term memory from sessions in previous days to estimate the distribution of possible rewards. We showed that rats were indeed able to incorporate prior information in guiding exploration. In addition, in the reversal learning paradigm, the level of exploration has to be evaluated on the course of several trials (in the probabilistic case), therefore the exact timing of “exploration” decision is difficult to estimate. In our case, however, exploration can be seen in a single trial (visiting the unknown option), which is advantageous in studying the neurophysiological mechanisms underlying real-time explore-exploit decisions and its neural substrate.

Further analysis needs to be done to quantify directed vs random exploration in both the rat and the human datasets. In a model-free manner, the probability of choosing the unknown options can be viewed as a tendency for directed exploration. However, as with the reversal learning paradigm, our design cannot fully dissociate directed exploration from random exploration without model fitting. Instead, we can quantify both directed and random exploration by incorporating an “information bonus” and a “decision noise” term using the softmax action selection rule to dissociate the tendency to choose the unknown option vs. the variability in behavior.

Here is the reward subjects are guided to, is the expectation based on an estimate of the average payout using prior information, IB is the “information bonus” which is a quantification of the bias ofthe subject towards choosing the unguided option, bias is the spatial bias of choosing a particular physical side, = 1 if the guided trial is on the left, and = -1 if the guided trial is on the right), is “decision noise” which is a quantification of the level of randomness in the behavior. With this model fitting, we are able to evaluate how directed and random exploration are modulated differently by horizon context in both rats and humans.

Unlike humans, rats seemed to show an opposite adaptation of behavioral strategy to the horizon context. The use of horizon context to facilitate exploration requires planning and model-based reasoning. An optimal agent would explore more in long horizon contexts. However, rats explored more in short horizon context. This may be a combination of their tendency to use a model-free learning strategy (that shows no horizon adaptation) and low motivation in short horizon contexts as they overall gain less reward from the short horizon context (that increases randomness in rat’s behavior which would result in exploration). For humans, it takes over 40 participants to show a robust horizon effect. With only a small number of rats, statistical power with the limited sample size limits the interpretation of the horizon modulation of exploration in rats, and more work is needed.

Finally, we observed an interesting difference in the exploration strategy between when the first choice is self-driven vs guided (a condition that was not implemented in humans in this task). This suggests a different neural mechanism underlying voluntary vs guided learning. Rats explored more in the first free choice when they were guided first, but this was not observed when they were exploring by themselves. A similar phenomenon was recently reported in a human explore-exploit study (Sadeghiyeh et al., 2018). This rat model has the potential of probing the differential neural mechanism underlying active vs passive learning. Overall, our novel design provides a potentially better behavioral paradigm to investigate explore-exploit tradeoffs in future electrophysiological studies.

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