An investigation of the effects of time horizon and guided choices on explore-exploit decisions in rodents

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# Abstract

Humans and animals have to balance the need for exploring new options and exploiting known options that yield good outcomes. This tradeoff is known as the explore-exploit dilemma. and ringIn addition, these paradigms do not allow for observing model-based exploration behaviors, such as utilizing prior information and adaptation to the volatility of the environment. In this study, we investigated how rodents make explore-exploit decisions using a spatial navigation Horizon Task (Wilson, Geana, White, Ludvig, & Cohen, 2014) adapted to rats to address the above limitations. We compared the rat performance to that of humans using identical measures. We showed that rats use directed exploration as humans, but the extent to which they explore has the opposite dependence on time horizon than humans. Moreover, we found that free choices and guided choices have fundamentally different influences on exploration. Given the similarities and important disparity observed between human and rats, we revealed a more complex nature of explore-exploit behavior than previously thought.

Keywords: explore-exploit dilemma, directed and random exploration, prior information, self-guided vs free exploration

# 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 future outcomes. Humans face this dilemma in scenarios from simple choices like deciding whether to try a new restaurant for dinner, to important life decisions such as deciding whether to explore a new career. Animals face the explore-exploit dilemma when deciding whether to explore and forage for food, territory or mates. 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 of investigation (Mehlhorn et al., 2015; Wilson, Bonawitz, Costa, & Ebitz, 2021).

An optimal solution to explore-exploit decisions is, in general, computationally intractable (Bellman, 1954), leading humans and animals to use approximations or heuristics. 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 (Banks, Olson, & Porter, 1997; Frank, Doll, Oas-Terpstra, & Moreno, 2009; Krebs, Kacelnik, & Taylor, 1978; Lee, Zhang, Munro, & Steyvers, 2011; Meyer & Shi, 1995; Payzan-LeNestour & Bossaerts, 2012; Steyvers, Lee, & Wagenmakers, 2009; Wilson et al., 2014; Zhang & Yu, 2013) . The second is an error-driven heuristic known as *random exploration*, in which exploratory actions with suboptimal estimates of reward value are chosen by chance (Badre, Doll, Long, & Frank, 2012; Feng, Wang, Zarnescu, & Wilson, 2021; Gershman, 2018, 2019; Kao, Doupe, & Brainard, 2005; Wang & Wilson, 2018; Wilson et al., 2014). 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 effective exploration. Very few studies investigated how animals explore under different time horizons, the horizon adaptation has been studied in birds (Kacelnik, 1979), but it is unknown how rodents would explore differently in different time horizons.

Relatively few studies have investigated how animals, in particular rodents, make explore-exploit decisions. To study such behavior, most 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, Daw, Frazier, & Zhuang, 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 (Cinotti et al., 2019; Parker et al., 2016; Verharen, den Ouden, Adan, & Vanderschuren, 2020). As animals explore the two options, they will eventually converge to the better one and keep exploiting it, until the outcomes of the two options are swapped. Deviating from the previously exploited option after the switch of their outcome is considered exploration in these tasks. Such reversal learning paradigms have however several limitations. First, 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. In particular, it is difficult to separate directed vs random exploration in reversal paradigms. Secondly, in exploration, both good and bad outcomes should occur. However, in reversal learning after the reversal point, “exploring” the previously suboptimal option will always lead to a better outcome compared to the currently bad option. Thirdly, most of the tasks mentioned above are implemented in operant boxes that are not natural environments for a rat, and hence may not engage the decision circuitry fully. As pointed out recently, head-fixed monkeys exhibit a risk preference opposite to that of freely moving monkeys using 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 behaviors of rats is spatial navigation. 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 the rodent literature in our understanding 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 with well-defined behavioral quantifications allowing investigations of the cellular and system mechanisms of this complex process are sorely needed.

In this paper, we designed a rodent version of an exploration task that is similar to the human “Horizon Task” used in Wilson et al, 2014, which allowed us to study how rats explore under different time horizon conditions. The rat version was designed in an open maze in which rats can make explore-exploit decisions by navigating, which is more naturalistic for rats compared to using operant boxes. In addition, an equivalent version of the rodent exploration task was run in human subjects to directly compare the similarities and disparities in horizon adaptive exploration between humans and rats.

# Methods

## Animals

6 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 of the University of Arizona and followed NIH guidelines.

## Human participants

47 undergraduates from University of Arizona participated in this study. 2 were excluded for being underage, leaving 45 participants (14 males, 31 females). In addition, participates who did not perform significantly above chance were excluded. 5 were excluded for human experiment 1 (leaving 40 for analysis), and 3 were excluded for human experiment 2 (leaving 42 for analysis). All participants were from the undergraduate psychology subject pool and earned academic credits for their participation in the study. The human experiments were approved by the University of Arizona Institutional Review Board.

Experiments - rats

The rodent experiments were run in an open maze that consisted of a circular area (1.5 m diameter) with 8 equidistant feeders at its periphery (B. Jones, Bukoski, Nadel, & Fellous, 2012; B. J. Jones, Pest, Vargas, Glisky, & Fellous, 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 (Fig 1C). One feeder was the home base; the two others, equidistant from the home base, were the reward feeders**.** The home base was never rewarded, but animals had to reach it to trigger/activate the 2 reward feeders. The home base was flanked by two Lego blocks, forcing the animal to start its navigation to the 2 reward feeders without directional bias (Fig 1A, blue rectangles). At the start of each game, depending on the conditions, the two reward 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 (Fig 1A). ‘ ’ to ‘Trial 3 cue’ Critically, only one of the two reward feeders was guided to during the N guided trials, leaving the other reward feeder unknown to the rat before making free choices. . Fig 1A illustrates the version with N = 3. From the N+1st trial, they were cued to make free choices (the LED of the 2 rewarded feeders blinked simultaneously, ‘Trial 4 cue’ Fig 1A). The guided trials were followed by H free choices between the 2 reward feeders. Rats performed versions where H = 1, 6, or 15. Fig 1A illustrates the version with H = 1. startGame 2, Fig 1C, 2BThe number of free choices H is also referred to as the ‘horizon’.

## **Experiment 1: between-session version**

In this version, rats are always guided 3 times before a free choice can be made. There are 3 different horizon conditions, the short condition H = 1 in which only 1 free choice is allowed after the guided trials, the long condition H = 6 in which 6 free choices are allowed and the extra long condition H = 15 in which 15 free choices are allowed (Fig 1B). condition (Fig 1C)Rats performed games of different horizons in blocks of consecutive days before switching to the next horizon condition. H = 1 and H = 6 sessions were run in counterbalanced orders between rats, and H = 15 conditions were run after the H = 1 and H = 6 sessions were complete. Six rats participated in this experiment and completed a total of 292 sessions and 4802 games (36664 trials).

**Experiment 2: within-session version**

In this version, rats performed H = 1 and H = 6 games within the same session. A sound cue was played at each home base visit during each game indicating the corresponding horizon for that game, a low pitch sound was paired with short horizon games (H = 1) and a high pitch sound was paired with long horizon games (H = 6). For 192 out of a total of 218 sessions, one home base was always associated with the short horizon game and sound cue (H = 1), whereas the other home base was always associated with the long horizon game and sound cue (H = 6) (Fig 2B). For the other 26 sessions, long and short horizon games can occur at either home bases signaled by the sound cue. Results from these 26 sessions were analyzed separately in the supplementary figures.

In each session rats are guided nG times before a free choice can be made, nG = 0, 1 or 3 for different sessions (Fig 2A). For nG = 0, the rat will start each game by making free choices without guided trials, in order to compare nG = 0 with nG = 1 games, rats were asked to make H+1 free choices in nG = 0 games. For instance, for a long horizon game with no guided trials (nG = 0, H = 6), the rat would make 7 free choices. In the analysis, we treated the first free choice as if it’s guided in nG = 0 games (in other words, the rats guide themselves in the first trial) to contrast it with nG = 1 games in which in the first trial the rat is actually guided (by the light cue). Four rats participated in this experiment and completed a total of 218 sessions and 5587 games (28436 trials).

**Experiment 3: randomized reward**

In this experiment, we always use the long horizon condition (H = 6). However, instead of having a fixed reward for each reward feeder within a game, all reward feeders give a uniformly random number of drops between 0 to 5 through at all times. In this case, there is nothing to learn. The reward contingency is completely random. Rats are guided 3 times before a free choice can be made. 4 rats participated in this experiment and completed a total of 20 sessions and 309 games (2781 trials).

Experiments – humans

**Experiment 4 – small reward version**

experiment3Ag 3Aguided , 3A, the reward of the unchosen option will not be shown and will show up as ‘XX’Trial 1 response3AFrom10 (Fig 3B) 40 human participants completed a total of 6080 games (33440 trials).

**Experiment 5 – large reward version**

This experiment is the same as experiment 1 except that the reward points are drawn uniformly from 1 to 100. Results from this version is shown in the supplementary. 42 human participants completed a total of 6720 games (36960 trials).

Model-free analysis

We computed the following model-free measures of exploration. P(high reward) is the probability of choosing objectively the option with a higher deterministic reward, this measure gives some indication of exploitation. P(switch) is the probability of switching from the last chosen option, this gives some indication of exploration. P(explore) is the percentage of choosing the unguided option on the first free choice, i.e. P(switch) on the first free choice. P(explore) is consistent with directed exploration, akin to p(high info) in previous human studies (Wilson et al., 2014). On later free choices, p(switch) could have both a directed and random component. We computed and compared the above measures between humans and rats (Experiment 1, 4), between different horizon conditions (Experiment 2) and between guided and free choices (nGuided = 0 vs nGuided = 1 in rats, Experiment 2).

Hierarchical Bayesian analysis

We used Hierarchical Bayesian analysis to quantify directed exploration and random exploration for both humans and rats. We focus on humans’ and rats’ first free choices to be able to compare across horizon conditions.

To model choices on the first free-choice trial, we assume that subjects made decisions by computing the difference ∆Q between the reward value of the guided option, and an exploration threshold , choosing more likely to explore the unknown option when , and choosing more likely to exploit the guided option when . The level of randomness in choices are controlled by a decision noise parameter . Both a higher exploration threshold and a higher decision noise can lead to more exploration. is a model-based measure of directed exploration and is a model-based measure of random exploration. Specifically, we write

where, is the reward value of the guided option, is the exploration threshold, is the spatial bias, is 1 when the guided side is left and is -1 when the guided side is right, is the decision noise.

Each subject’s behavior in each horizon (H = 1,6 or 15 for rats and H = 1, 2, 5, 10 for humans) and in each nGuided condition (nGuided = 0, 1, or 3 for rats and nGuided = 1 for humans) is controlled by 3 free parameters, namely the exploration threshold , spatial bias and decision noise . Model fitting was done to the 3 rat experiments and 2 human experiments separately. Each of the free parameters was fit to the behavior of each subject using a hierarchical Bayesian approach (Allenby, Rossi, & McCulloch, 2005). The parameters for each subject are assumed to be sampled from group-level prior distributions whose parameters, the so-called ‘hyperparameters’ are estimated using a Markov Chain Monte Carlo sampling procedure. The hyperparameters themselves are assumed to be sampled from ‘hyperprior’ distributions whose parameters are set so that these hyperpriors are broad. The specific priors and hyperpriors for each parameter are shown in table 1. Here, the group-level mean of threshold and the group-level mean of decision noise . Posterior distributions over the exploration threshold and the decision noise are shown for each experiment (Fig 7, 8, 10, 11).

Table 1 Model parameters, priors and hyperpriors

|  |  |  |
| --- | --- | --- |
| Parameter | Prior | Hyperpriors |
| Exploration threshold |  |  |
| Decision noise |  |  |
| Spatial bias |  |  |

\* is the maximal reward in the experiment. for all experiments except for human experiment 2, in which .

\*\* = horizon, = nGuided, = subject (each rat or each human participant)

The model fitting was implemented using the JAGS package (Depaoli et al., 2016, Steyvers, 2011) via the MATJAGS interface (psiexp.ss.uci.edu/research/programs data/jags). This package approximates the posterior distribution over model parameters by generating samples from this posterior distribution given the observed behavioral data. We used 4 independent Markov chains to generate 40000 samples from the posterior distribution over parameters (10000 samples per chain). Each chain had a burn in period of 5000 samples, which were discarded to reduce the effects of initial conditions, and posterior samples were acquired at a thin rate of 1.

# Results

**As with humans, rats transition from exploration to exploitation in the course of a single game.**

Both humans (Experiment 4) and rats (Experiment 1) were able to choose the objectively best option (p(high reward), the option with a higher reward magnitude between the two available sugar water feeders for rats, or the slot machine with a higher reward point payout for humans) significantly above chance (50%) for all trials and all horizon conditions (Fig 4A, B). Both humans and rats improved their performances with the number of trials given (Fig 4A, B). Their performances are higher at the last trial of longer horizons compared to shorter horizons (Fig 6D, J). At the last trial of the longest horizon condition (H = 10), humans could achieve an accuracy of 98% (Figure 4A) whereas at the last trial of the longest horizon condition (H = 15), rats could achieve an average accuracy of 81% (Fig 4B).

Rats switched from the last chosen option at a significantly higher level at trial 1 (59.8% for H = 6 and 60.7% for H = 15) and then adopted a more constant and lower rate of switching for later trials (averaged 26.6% for H = 6 and 21.0% for H = 15, Figure 4D), whereas humans switch more at trial 1 (70.2%, 71.7% and 74.1% for H = 2, 5, 10) and trial 2 (27.9%, 33.9% and 37.4% for H = 2,5,10), and eventually stopped switching (4.8% and 4.3% at the last trial of H = 5 and H = 10), possibly due to boredom or motor error, Figure 4D). These results may be partly explained by the deterministic nature of the reward delivery in the experimental design, that in principle it only takes a single switch after the guided trials to learn the value of the unguided option. For humans, when they are guided to a good choice and switching on the 1st free choice to find out that the alternative is worse, they immediately switch back on the 2nd choice (Figure 5C). For rats, it takes them longer to switch back, the percentage of switching remains higher when guided to a good choice than to a bad choice for at least until the 4th trial (Figure 5D). Interestingly, when guided to a good option at first, both rats and humans show a better accuracy in later trials compared to when guided to a bad option (Fig 5A, B).

**As with humans, rats were able to use prior information to guide exploratory choices.**

On the first free choice of the game, participants have only sampled one of the options and thus have no information *from this game* about the payoff of the other option. Thus, if participants are to perform above chance on this first free choice, they *must* be making use of information from past trials, for example about the prior distribution of possible rewards.

Intriguingly, both humans (Experiment 4) and rats (Experiment 1) do perform above chance on the first free-choice trials with both achieving a similar average of 65-70% (Fig 6E, K). The fact that the average accuracy was significantly above chance in the first non-guided trial showed that humans and rats used prior information to guide subsequent exploration. In this particular experiment, with repeated games, humans and animals were able to assess the relative ‘goodness’ of the guided target in the current game based on the reward they obtained in previous games.

Their performances in the first free-choice trial were not uniform and displayed a U shape (Fig 6B, H). 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 (or 3 or 4 drops for humans). With prior information alone, it is theoretically difficult for humans and rats to choose correctly on the first free-choice trial when guided to intermediate rewards, but through learning in long-horizon games, their performance curves in the last trial were higher and became more uniform (Fig 6A, G).

**As with humans, rats can adapt the extent to which they explore based on the reward of the guided choice.**

We computed P(explore), the probability of choosing the option that was not selected during guided trials in the first free-choice trial (i.e. p(switch) at the first free choice) as a function of the reward size during the guided trials (Fig 6C, I). Like humans (Fig 6C), we found that rats were very likely to explore if they obtained a low reward during the guided trials (e.g. 0 drops, mean = 94.5% Fig 6I), and were very unlikely to explore if they obtained a large reward (e.g. 5 drops, mean = 29.1%, Fig 6I). Overall, when guided to the option with an objectively lower reward, rats explore the unguided feeder at around 70% on their first free choices, whereas when guided to the option with an objectively higher reward, rats only explore the unguided feeder at around 40% on their first free choices (Fig 5D, trial 1). Humans explored more than 80% on an objectively lower guided reward, and around 50% on an objectively higher guided reward (Fig 5C, trial 1). Unlike the “win-stay lose-shift” strategy in probabilistic exploration tasks, both “stay” and “shift” are outcomes of a comparison between the current reward and estimated prior distribution of rewards, and are not directly associated with a gain of reward vs an absence of reward. Unlike the reversal learning paradigms in which animals update values gradually and switch to the alternative option after experiencing a stream of bad outcomes, rats in this experiment can make exploratory decisions based on guided reward in a single trial (see Fig 8A, nGuided = 0 or 1, Experiment 2) or after a small number of guided trials (nGuided = 3, Experiment 1).

**As with humans, rats use directed exploration. However, time horizon has opposite modulation on directed exploration in rats vs humans.**

P(explore) is akin to the p(high info) measure in previous human researches as a model-free way of measuring directed exploration (Wilson et al., 2014). In line with previous research, humans explored more in long horizons than in shorter ones (Fig 6F, Experiment 4, Fig S1G, H, Experiment 5), however for rats, the long horizon condition seemed to yield slightly lower probability of exploring than the short horizon condition (Fig 6L, h=15 vs h=1, Experiment 1).

To better quantify directed vs random exploration, we turned to modeling.group-level means of exploration

While exploration threshold is theoretically tied to directed exploration, decision noise is tied to random exploration. It turns out that this task may not be suited in studying the horizon modulation of random exploration. Decision noise is consistently small in all horizon conditions for humans (Fig 7B). This may arise from the fact that reward values only take 5 different values (1 – 5) and are not deterministic, in contrast to the stochastic rewards ranging from 1-100 in the human Horizon Task (Wilson et al., 2014). In human Experiment 5, the rewards are deterministic but range from 1 to 100, decision noise in longer horizons (H = 5, 10) are higher than decision noise (H = 1, 2) in shorter horizons (Fig S1K,L), which is in line with the horizon adaptive random exploration reported in human studies (Wilson et al., 2014). In the 0-5 drops version of the task, we were not able to detect horizon differences in random exploration in either humans or rats.

One critical difference between the human Experiment 4 and the rat Experiment 1 is that human performed all horizon conditions within a single session, whereas rats had to perform the different horizon conditions in chunks of consecutive days, the amount of training a particular rat is exposed to before each condition will influence how they explore across different horizon conditions, plus the within-session version may make the difference between horizon conditions more salient to the rats. As a result, in Experiment 2, we trained rats to do two horizon conditions H = 1 and H = 6 within the same session, one home base is always associated with short-horizon games (h = 1) whereas the other home base is always associated with long-horizon games (h = 6). In this design, there is no confound of learning/training effect.

In Experiment 2, we showed that regardless of the number of guided trials, p(explore) is lower for Horizon 6 compared to Horizon 1 (Fig 8A, B). In model terms, we confirm that regardless of the number of guided trials, exploration threshold for H = 6 is lower than H = 1 (Fig 8C). By computing the posterior distribution over the differences in exploration threshold between horizons , we found that the percentage of samples that is 97.9%, 73.5% and 75.2% for nGuided = 0, 1, and 3 respectively. On the other hand, decision noise remain unchanged for H = 1 vs H = 6, regardless of the number of guided trials (Fig 8D). By computing the posterior distribution over the differences in decision noise between horizons , we found that the percentage of samples that is 50.2%, 54.0% and 56.8% for nGuided = 0, 1 and 3 respectively.

Moreover, we performed a variant of Experiment 2 in which we use low-pitch vs high-pitch sound cues to signal the horizon condition. The sound was played before the start of each game and during the guided trials to cue the rat the horizon condition of the current game. The motivation for doing this was that all horizons are interleaved in the human version whereas they are alternated in Experiment 2 when each home base is tied to a specific horizon condition. With the sound cue, we can interleave the horizon conditions pseudo-randomly in rats. Within a session, each home base can be associated with different horizon conditions. Again, we found that exploration threshold decreases as a function of horizon whereas decision noise remains unchanged (Fig S2). The fact that there is still a behavioral difference between games of different horizon conditions using only sound cues, we showed that experimentally rats can associate sounds with different time horizon conditions, which can be useful for future task development.

This opposite dependence of directed exploration on horizon in rats vs humans can arise from several factors. First, the utility of 1 to 5 drops is different for humans and rats. For humans, they get points, whereas rats are getting real sugar water proportional to the number of drops. As a result, p(explore) in human subjects were at ceiling for 1 and 2 points indicating that both reward sizes were equally salient (Fig 6C), whereas p(explore) for 4 and 5 drops are similar in rats likely due to perceptual senses (6I). Second, the efforts humans spend in making the decision is negligible, as a result,

they over-explore to find out the best possible action, whereas rats have to physically travel the maze to get sugar water, they therefore likely under-explore to secure a satisfiable amount of return for each visit. In our data, rats have lower exploration thresholds compared to humans (Fig 7A,C).

**Rats explore more in more volatile environments.**

Horizon task (Wilson et al., 2014) was originally designed in humans to assess exploratory behavior in terms of planning, that in longer time horizons, it’s more beneficial to explore as there is a longer time to benefit from the information gained from exploration. In a longer time horizon, the environment is more stable and less volatile that the rewards from the two options will remain predictable for a longer time before changes occur. As a result, rats may adapt the extent to which they explore based on the volatility of the environment, explore more when the environment is changing more frequently (shorter horizon). The may account for opposite dependence of directed exploration on horizon in rats.

In order to test this hypothesis, instead of giving deterministic rewards that’s fixed and learnable for the two reward feeders, in Experiment 3, each feeder gives an independently random reward that is sampled uniformly between 0 and 5 drops at all times. In other words, the rewards of the two feeders are not learnable and change independently from trial to trial, from game to game. The time horizon is always set to be H = 6 in Experiment 3. at 54.4% Possibly due to over training in Experiment 1 and 2, aratsin addition tomay9ACritically, the percentage of exploring the unguided feeder is higher compared to p(explore) in the constant reward scenario in Experiment 1, especially when the guided reward is high (Fig 9B).over 45% dropsconstant rewardThis could account for the horizon difference in p(explore) in Figure 6I that when guided reward is 4 and 5 drops, p(explore) is lower in H = 6 and H = 15 compared to H = 1. thatconstant case in Experiment 1 9A more volatile switch4Dswitchingless volatileThis difference in p(switch) cannot be attributed to directed exploration and can arise from random exploration. It has been proposed that relative uncertainty correlates with directed exploration whereas total uncertainty correlates with random exploration (Gershman, 2019). In a completely random environment, and uncertainty of both the guided and unguided feeder increases, and as a result, there is an increase in both relative uncertainty and total uncertainty. In line with this theory, through model fitting, we observed an increase in both exploration threshold and decision noise in the random reward condition compared to the constant reward condition (Fig 9C, D).

**Self-guided exploration is treated intrinsically differently than guided choices in rats.**

Finally, we investigated whether self-driven exploration is any different from guided exploration. Do rats behave any differently if they are guided by sensory light cues on the first trials, or if they are instead invited to choose freely? Specifically, in separate weeks and between sessions, rats performed both a version in which they were guided to one feeder once before freely choosing between the 2 options (Guided condition, nGuided = 1 in Experiment 2), and a version in which they start off with 2 options to choose from (Free choice condition, nGuided = 0 in Experiment 2). In the analysis, we treated the 1st choice in the Free choice condition 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 10).

We found that overall, rats performed better if the first trial was a free choice compared to when they were guided (Fig 10A). rats explore differently in the Free condition compared to the Guided condition. Wrats freethan in subsequent choices variants1differ from subsequent choiceskeptswitching throughout the game10B Rats switched more on the first free choice in the Guided condition compared to the Free choice condition (Fig 10D), and they explore more regardless of the guided reward and the horizon condition (Fig 10C).

We have shown earlier that the exploration threshold is lower in H = 6 compared to H = 1, regardless of whether the first trial was guided or not (Fig 8E, 10A) and decision noise remains unchanged (Fig 8F, 10C). Now we ask, whether exploration threshold and decision noise differ in the Guided vs Free choice condition. For both horizon H = 1 and H = 6, exploration threshold in Free-choice condition is lower than in Guided condition (Fig 10A). By computing the posterior distribution over the differences in exploration threshold between conditions , we found that the percentage of samples that is 99.2%, and 99.7% for H = 1 and H = 6 respectively (Fig 10B). In other words, when rats were guided, they explore more in the first free choice. Decision noise do not change much in the Guided condition vs Free choice condition (Fig 10C), by computing the posterior distribution over the differences in decision noise between conditions , we found that the percentage of samples that is 59.7%, and 63.2% for H = 1 and H = 6 respectively (Fig 10D). When self-guided in the Free choice condition, rats behave slightly more predictably in the first choice (2nd trial in Free choice condition, 1st free choice in Guided condition) by having a lower decision noise term compare to when they are guided.

Discussion

In this study, we investigated the exploratory behaviors in rats using 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 an unknown novel option, we manipulated the magnitudes of rewards rather than the probabilities of their delivery. 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 measure of exploration. This measure is an equivalent of the model-free measure of directed exploration in previous human studies (Wilson et al., 2014) . In addition, rats were set to perform the task in both a short and a long horizon condition to assess whether they explored differently in different time horizon contexts. Using an open field task, 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). Moreover, we recruited human subjects to perform a version that is comparable to the rat task, and we compared the performance between humans and rats.

Using our task design, we showed that as humans, rats were able to use prior information about the distribution of rewards to guide future exploration. Rats explored the unguided option more in their first free choice when the guided reward is low compared to when the guided reward is high. This looks very similar to the win-stay/lose-shift in reversal learning that animals choose to explore more when the exploit value is low and explore less when the exploit value is high. However, unlike in reversal learning that a “win” or a “loss” is computed by comparing the current reward with the estimated value,a “win” or a “loss” is computed by comparing the current reward(or estimated value) of the current option with the estimated distribution of rewards using prior information. Ijudgeof within the same game previous games and previous

In this study, we were able to able to separate directed exploration from random exploration. The percentage of choosing the unguided option serves as a model-free measure of directed exploration. Both rats and humans switch significantly more at the first free choice than subsequent choices. We further quantified directed and random exploration using hierarchical Bayesian model in both the rat and the human datasets. In line with previous human studies, humans have an increased exploration threshold (explore more) in longer horizons. Unlike humans, rats showed an opposite adaptation of directed exploration to the time horizon. For random exploration, with the small range of reward size (0 – 5), we didn’t observe adaptations of random exploration in either humans or rats in this specific task. However, with a larger reward range (1 – 100), in Experiment 5, we did observe a higher level of random exploration (Fig S1K, L) in longer horizons (H = 5 and 10) compared to shorter horizons (H = 1 and 2). This can be considered as a limitation of the current design, although we are able to separate directed from random exploration, with the deterministic rewards and small reward changes, it is hard to observe random exploration adaptation with horizon with the current design.

As with optimal agents, human have a higher level of directed exploration in longer time horizons since the value of the information gained through exploration is high if the remaining time horizon is long. However, our rats have instead a lower level of directed exploration. Here we speculate the possible reasons why rats explore less in longer horizons. There may be an optimize vs satisfice discrepancy in humans vs rats due to the nature of the rewards received. Humans are receiving hypothetical points with relatively effortless keypresses on a computer keyboard, whereas rats are earning their daily portion of water by running back and forth on a meter-long table. It costs little for humans to optimize by testing if the alternative reward is 5 when the guided reward is 3, however for rats, they may risk running for 0 rewards by visiting the unguided feeder when they are guaranteed to have 3 drops of water in the guided feeder. The exploration threshold in our data is overall higher in humans compared to rats (Fig 7A, C).The drive to explore is not to optimize for rats, but to satisfice. Exploring more in longer horizon may be an optimal way of exploration, but may not be an economic one. Rats may be less motivated in short horizon condition because they overall gain less reward from the short horizon context (at least in Experiment 2 when both horizons are alternated or interleaved within the same session) that increase novelty seeking and randomness in rat’s behavior which would result in exploration. Also, in short horizon, without fully understanding the structure of the task, the rat may perceive the time horizon in terms of the volatility of the environment, and thus explore more in a more volatile condition (the short horizon condition). Experiment 5 supported this view, that by having random rewards, rats still use directed exploration (only significantly higher on the first free choice compared to subsequent choices, Fig 9A) and explore more compared to the deterministic reward case in Experiment 1 (Fig 9B). Lastly, a longer horizon means that there are plenty of opportunities to explore the unguided option later on, making it less urgent to explore on the first trial compared to a shorter horizon.

Nevertheless, we note the significance of the fact that rats can modulate the level of directed exploration to time horizon. The use of horizon context to explore requires (possibly irrational) planning and model-based reasoning (a mental model of the environment that reflects the time horizon). Win-stay/lose-shift strategies which are effective in solving reversal learning problems are not working in dealing with horizon changes. Win-stay/lose-shift strategy is solely dependent on experienced and estimated rewards and does not by itself adapt to time horizon changes. To the authors’ knowledge, horizon adaption of exploration has only been examined in very limited species (humans, Wilson et al, 2014; great tits, Kacelnik, 1979), it remains an open question how other species can adapt exploration to time horizons.

we think our design has advantages in serving as a potential behavioral model in studying the neurophysiological mechanisms underlying real-time explore-exploit decisions and its neural substrate. Idesign.

Finally, we observed an interesting difference in the exploration strategy between when the first choice was self-driven vs guided (a condition that was not studied in humans in this task). This suggests a different neural mechanism underlying voluntary vs guided learning. Rats explored the alternative feeder more when they were guided first, but this was not observed when the first choice was made freely by themselves. A similar phenomenon was recently reported in a human explore-exploit study (Sadeghiyeh, Wang, & Wilson, 2018). More generally, learning differences in active and passive version of the same tasks have been shown in a number of tasks (Gureckis & Markant, 2012; Markant & Gureckis, 2014; Markant, Settles, & Gureckis, 2016).This rat model has the potential of probing the differential neural mechanism underlying active vs passive learning. Overall, our novel design provides a fruitful behavioral paradigm to investigate explore-exploit tradeoffs in future electrophysiological studies and suggest new avenues for further comparisons between rats and humans.

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