Predictive Maps in Rats and Humans for Spatial Navigation: The Successor Representation Explains Flexible Behaviour

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Abstract

Much of our understanding of navigation comes from the study of individual species, often with specific tasks tailored to those species. Here, we provide a novel experimental and analytic framework, integrating across humans, rats and simulated reinforcement learning (RL) agents to interrogate the dynamics of behaviour during spatial navigation. We developed a novel open-field navigation task ('Tartarus Maze') requiring dynamic adaptation (shortcuts and detours) to frequently changing obstructions in the path to a hidden goal. Humans and rats were remarkably similar in their trajectories. Both species showed the greatest similarity to RL agents utilising a 'successor representation', which creates a predictive map. Humans also displayed trajectory features similar to model-based RL agents, which implemented a tree-search planning procedure. Our results help refine models seeking to explain mammalian navigation in dynamic environments, and highlight the utility of modelling the behaviour of different species to uncover the shared mechanisms that support behaviour.

Key words: Artificial Intelligence, Reinforcement Learning, Spatial Memory, Decision-making, Planning, Hippocampus, Cognitive Map, Successor Representation, Detour, Shortcut

Introduction

Adapting to change is fundamental for survival. Adapting to changes in the structure of the environment has been studied in a huge diversity of psychological experiments in humans (Ekstrom et al., 2018), but also more ethologically in a remarkable range of different species (Gallistel, 1990). One challenge that unites all motile animals on our planet is spatial navigation. In particular, prime examples are finding a new path when a familiar route is blocked and exploiting a novel shortcut. Efficient detours and shortcuts are considered the hallmarks of a cognitive map - an internal representation of the environment that enables novel inferences to guide behaviour (Behrens et al., 2018; Epstein et al., 2017; Tolman, 1948; Tolman & Honzik, 1930).

Both rodents and humans can show an impressive capacity to identify shortcuts and take optimal detours (Alvernhe et al., 2008; Brown et al., 2020; Grieves & Dudchenko, 2013; Howard et al., 2014; Javadi et al., 2017; Javadi, Patai, Marin-Garcia, Margois, et al., 2019; Patai et al., 2019; Shamash et al., 2021; Tolman et al., 1946; Tolman, 1948; Xu et al., 2010). However, not all studies report successful adaptive behaviour (Spiers & Gilbert, 2015). Rats often require multiple exposures to a set of paths before they are able to shift towards an optimal detour (Grieves & Dudchenko, 2013), and may fail to select an optimal shortcut from a set of novel paths (Gentry et al., 1947). Humans too can be poor at judging the directions between locations in walled mazes, hindering the capacity to identify shortcuts (Foo et al., 2005; Marchette et al., 2011).

Much of the research into navigation implicitly assumes that rodents and humans navigate in a fundamentally similar way (Ekstrom & Ranganath, 2018; Epstein et al., 2017) and this has been used to support the integration of insights across both species (Ekstrom et al., 2018; Gahnstrom & Spiers, 2020; O'Keefe & Nadel, 1978; Spiers & Barry, 2015; Tolman, 1948). In mammals, the hippocampus is thought to form a cognitive map (O'Keefe & Nadel, 1978), evidenced by spatial-tuned cells (such as 'place cells') in the hippocampal formation of rodents and humans (Ekstrom et al., 2003; Grieves & Jeffery, 2017; Poulter et al., 2018). However, despite the wide array of human and rodent research, few experiments have sought to compare rodents and humans on a directly homologous task. Understanding the similarities and differences of these two species on the same task would be useful for allowing the better integration of findings from different methods, such as combining data from neuroimaging in humans with neural recordings and disruption methods in rodents (Barron et al., 2020, 2021; Samanta et al., 2021). Moreover, such integration could potentially benefit the translation of assessments in rodents to assessments for clinical trials in humans, for example where tests of spatial navigation may be important for the early detection of Alzheimer's disease (Coughlan et al., 2018, 2019; Laczó et al., 2012).

When considering how humans and rodents might differ during navigation, differences in sensory perception are important. Whilst humans have binocular vision, they may differ in olfaction (McGann, 2017) and lack the tactility of whiskers. Meanwhile, rodents have a larger visual field of view, lower visual acuity and can move their eyes independently

(Wallace et al., 2013). In terms of neuroanatomy, the prefrontal cortical regions associated with spatial planning differ greatly between rodents and primates (Patai & Spiers, 2021; Uylings et al., 2003); while the hippocampus and surrounding structures associated with spatial representations are relatively similar (Andersen et al., 2006). Given these similarities and differences, it is possible that rodents and humans navigate in a similar fashion or show pronounced differences in certain situations. Understanding such patterns in behavior is important not only for understanding navigation, but how the behaviour of different species is inter-related and may have emerged through evolutionary pressure.

One approach for identifying potential cross-species mechanisms underlying goal-directed behaviour is through comparison with reinforcement learning models (Banino et al., 2018; Bermudez-Contreras et al., 2020; Botvinick et al., 2020; Dayan & Daw, 2008; Momennejad, 2020; Simon & Daw, 2011). Such models can be used to examine how rapid learning and control can be developed in artificial systems, outcompeting human performance (Banino et al., 2018; Mnih et al., 2015; Silver et al., 2016, 2017) or used for comparison to patterns seen in animals or human behavior (Anggraini et al., 2018; Geerts et al., 2020; Simon & Daw, 2011; Voudouris et al., 2021; Zhu et al., 2021). Reinforcement learning (RL) is an area of machine learning that addresses the theoretical problem of how an artificial agent should act in an environment in order to maximise rewards. Specifically, it seeks to maximise the expected accumulated reward R yielded from its future states s_t, which is known as the value function V:

$$V(s) \;=\; \mathbb{E}\left[\sum_{t=0}^{\infty} \gamma^t R(s_t) \,\middle|\, s_0 = s\right] \tag{1}$$

The parameter γ is a discount factor that determines the timescale of how motivating future rewards are, such that for $\gamma < 1$ the agent exponentially discounts future rewards (Sutton & Barto, 2018).

Solutions to reinforcement learning problems have traditionally been divided into two categories: model-based methods that afford the agent a model of the environment, used to decide actions via a planning procedure (Sutton & Barto, 2018), and model-free methods that learn from experience which actions lead to the most rewarding future (Sutton, 1988; Watkins & Dayan, 1992). Provided that the model implemented in a model-based algorithm contains an accurate depiction of the environment, model-based methods are typically able to respond quickly and optimally to environmental perturbations. However, the planning procedure - for example a tree search (Silver et al., 2016) - required to successfully exploit the model brings with it computational complexity and overhead, particularly in large state spaces with deep transition structures such as navigating a city.

In contrast to model-based methods, model-free methods are generally more simple and computationally inexpensive through a reliance on temporal-difference (TD) learning rules (Sutton, 1988), however, this comes with a reduced flexibility to environmental changes. As such, model-free mechanisms are often associated with the formation of habits (Dolan

& Dayan, 2013; Lee & Keramati, 2017). To achieve this simplicity, model-free methods usually operate using the state-action value function Q instead of the state value function V. This makes it possible to disassociate the value of different actions a in a particular state s, without the need to know how the states are interconnected.

$$Q(s,a) \;=\; \mathbb{E}\left[\sum_{t=0}^{\infty} \gamma^t R(s_t) \,\middle|\, s_0 = s,\; a_0 = a\right] \tag{2}$$

Whilst model-free and model-based methods appear to function at opposite ends of an algorithmic spectrum, intermediary methods do exist. One such algorithm that has increased in application recently is the successor representation (SR) (Dayan, 1993). The SR somewhat combines parts of model-free and model-based learning (Gershman, 2018; Russek et al., 2017) by using experience to learn a predictive map M between the states in an environment. For a one-step state transition matrix T, the predictive map can be learned via TD learning and is equivalent to the discounted sum of future state transitions:

$$M \;=\; I \;+\; \gamma T \;+\; \gamma^2 T^2 \;+\; \ldots \;=\; \sum_{t=0}^{\infty} \gamma^t T^t \tag{3}$$

This discounting of transitions means M can be readily combined with a separately learned reward R associated with each state s in order to explicitly compute value (equation 1), thus negating the need for a complicated planning procedure in order to use the predictive map to guide action selection.

$$V(s) = \sum_{s'} M\big(s, s'\big) R\big(s'\big) \tag{4}$$

The SR has been able to provide a good account of behaviour and hippocampal representations in humans (Bellmund et al., 2019; Brunec & Momennejad, 2019; Garvert et al., 2017; Momennejad et al., 2017; Russek et al., 2021) and rodents (de Cothi & Barry, 2020; Geerts et al., 2020; Stachenfeld et al., 2017). The tasks often used to draw these comparisons with RL agents typically focus on small state-spaces, with 2-step transition structures – as such the extent of planning often requires one or two actions. Furthermore, due to the conceptual nature of the underlying task space, translational research usually requires differing sensory implementations for humans (Daw et al., 2011) and rodents (Miller et al., 2017).

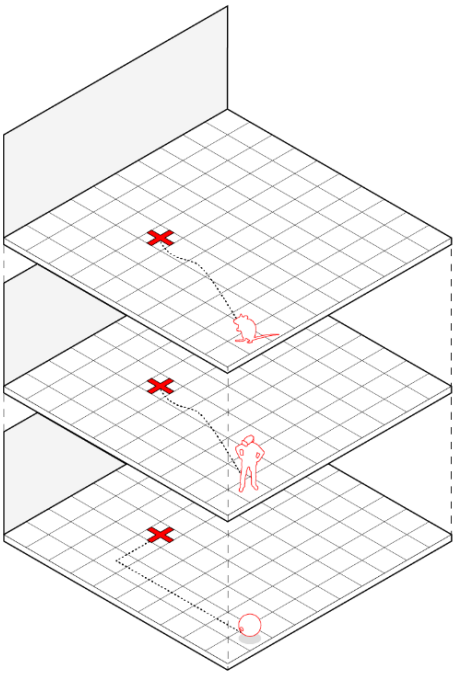
Here, we created a configurable open-field maze with a layout of barriers that reconfigured after a set of trials (Tartarus Maze). We tested the navigation of rats in a physical instantiation of the maze, humans via an immersive head-mounted display virtual environment and RL agents in a simulation. Using a range of analytic methods we probed how rat and human spatial behaviours compare to each other and to model-free, model-based and SR reinforcement learners. We found a strong similarity in the trajectories of rats and humans. Both rats and humans showed the greatest likelihood

similarity to SR based RL agents, with humans also displaying trajectory features similar to model-based RL agents implementing a tree-search planning procedure.

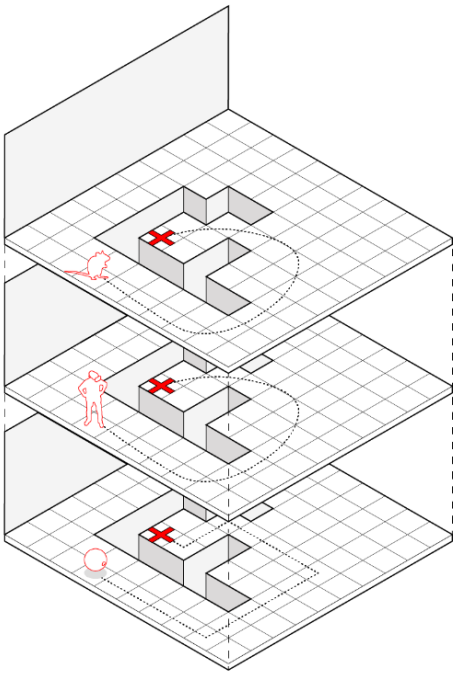
Results

Navigation was tested in a large square environment with a fixed hidden goal location and a prominent directional black wall cue in one direction (Fig. 1, Video S1 - rats, and Video S2 - humans). The maze was divided in a 10x10 grid of moveable sections that could either be removed, leaving impassable gaps to force detour taking, or added, creating shortcuts. During training, all 10x10 maze modules were present and the rats and humans were trained to reach the goal within a 45s time limit, (Fig 1A), while RL agents were initialised with the optimal value function. During the testing phase of the experiment, maze modules were removed to block the direct route to the goal (Fig 1B). Humans (n=18), rats (n=9) and agents were tested on the same sequence of 25 maze configurations each with 10 trials in which a set of defined starting locations were selected to optimally probe navigation (Fig 1C). See Methods for details.

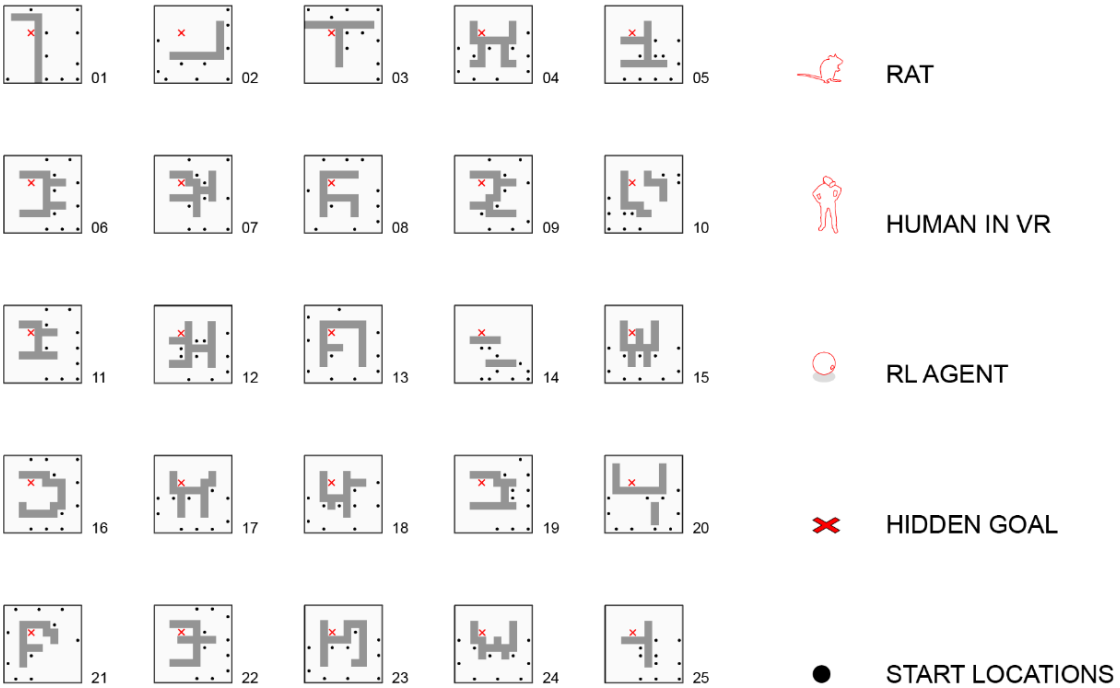
A Training (example trial)



B Testing (example trial, maze 21)



C Maze Configurations



D Sequence of Trials

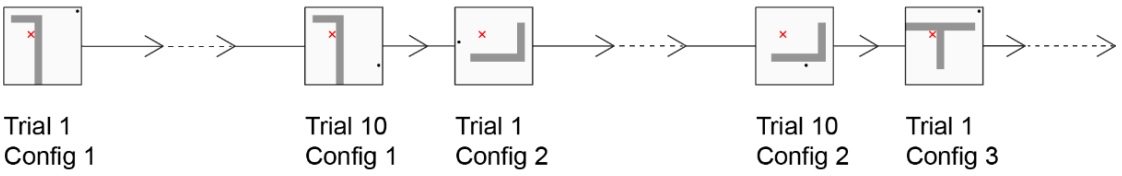


Figure 1: The Tartarus Maze. A) Schematic of the maze composed of 10x10 units for humans, rats and RL agents. For rats each unit (20x20cm) had a port to potentially deliver chocolate milk reward after the rat waited 5 sec at the goal (See Video S1). For humans each unit could be associated with a hidden gold star linked to financial reward, which appeared after waiting 5 sec at the goal location. Gaps between units were not visible to humans to avoid counting distance to the hidden goal (see Video S2). Example trial shows one of the possible pseudo-random starting locations on the edge of the maze. **B)** After training, flexible navigation was tested by removing units from the maze to create gaps between traversable surfaces. Example configuration for trial 21 is shown with one of the 10 starting locations tested shown. Each configuration was tested for 10 trials each with a different starting location. **C**) Sequence of 25 maze configurations used. **D)** Illustration of the trial sequence, highlighting the transition in layout every 10 trials across the 250 trials tested in the 25 maze configurations.

Behavioural performance is relatively similar between rats and humans

We first asked how well humans and rodents were able to complete the task during the test sessions. As expected, repeated exposure over trials to a new maze configuration corresponded to a general increase in the ability of both the humans and rats to navigate to the goal within the 45s time limit (Fig 2C; first 5 trials vs last 5 trials: humans $t(17)=6.3$, $p<.001$; rats $t(8)=4.0$, $p= .004$). Humans were also generally better than the rats at finding the goal across the 25 maze configurations (Fig 2D; humans vs rats: $t(25)=3.0$, $p=.006$). There were 3 mazes in which rats outperformed humans (mazes 2, 10 and 19). We saw a strong correlation between the places visited by the rats and human participants (occupancy correlation, humans vs rats: $\rho=.67$), in particular towards the later trials when both were better at navigating to the goal (Fig 2E; occupancy correlations for first 5 trials vs last 5 trials: $t(8)=3.2$, $p=.013$). The routes used were also more efficient (Fig 2E; deviation from optimal path, first 5 trials vs last 5 trials: human $t(17)=-5.0$, $p<.001$; rats $t(8)=-4.0$, $p=.004$) with humans generally choosing more optimal routes than the rats (deviation from optimal path humans vs rats: $t(25)=-8.2$, $p<.001$). Inspection of trajectories showed that in some cases near optimal paths could be observed in both species even on the first trial of a maze (see Video S1&2).

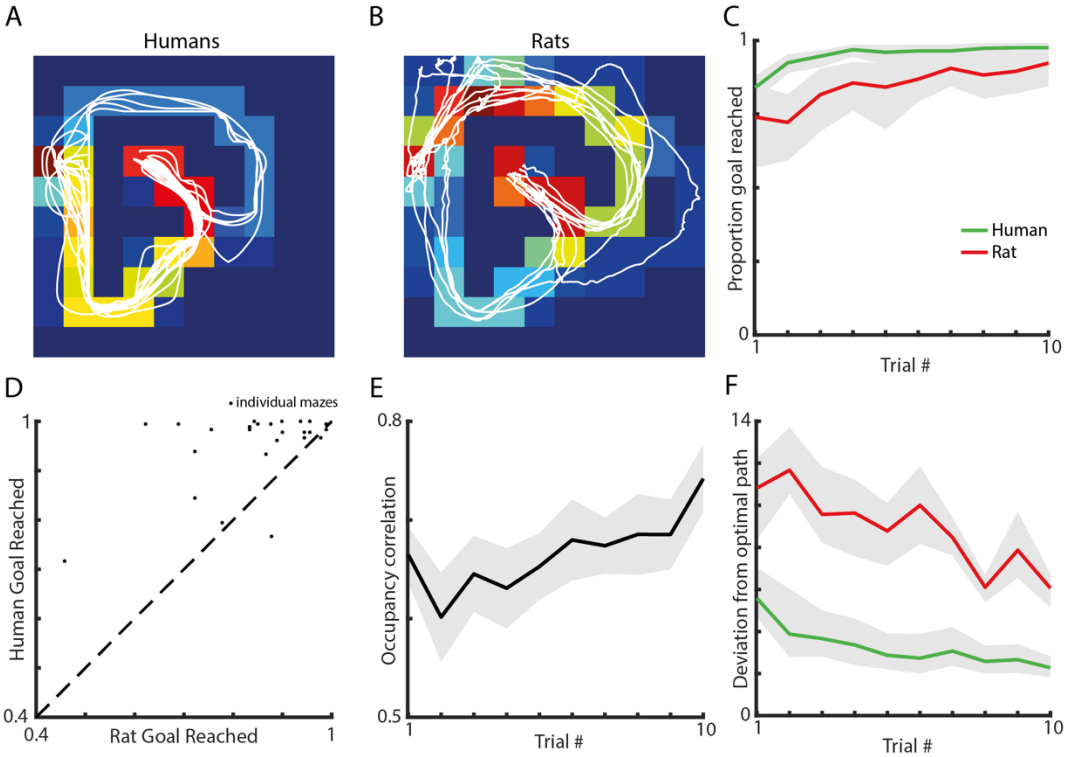


Figure 2: Humans and rats were able to successfully navigate to the hidden goal and generally did so using similar routes. Examples of the human (A) and rat (B) trajectories overlaying occupancy maps for a given trial. (C) Proportion of trials where the goal was reached averaged over all configurations as a function of trial number, for rats (red) or humans (green). Grey areas indicate 95% confidence intervals. D) Proportion of goals reached by humans and rats during the time limit. Configuration 2 is the only configuration where rats out performed humans. Configuration 1 was the configuration both species performed most inaccurately on. (E) Correlation between the human and rat occupancy maps. Note the increase across exposure to a maze configuration implying they take increasingly similar routes. (F) Average deviation from optimal path (measured in extra maze module visitations) for rats and humans as a function of trial number; humans navigate to the goal with more efficient routes.

Observations of the behaviour of the RL agents

Examining the trajectories of the RL agents we observed a number of consistent patterns. As expected, model-free agents were relatively unable to adapt to changes in the maze layout; whenever there was a barrier obstructing the learnt route to the goal the model-free agent would remain in a similar region of space and often fail when the new path required travelling away from the goal or around obstacles (Video S3). This behaviour logically follows from the fact that it has no representation of the transition structure and relies on previously cached optimal actions to select which transitions to make. The model-based RL agents chose more optimal routes as the trials progressed, but initially made poor choices in paths (Video S4). This is consistent with them requiring an accurate model of the environment in order to conduct a useful tree-search over routes to the goal. However when a change in the transition structure occurred and that model was no longer accurate, they do not have cached values to rely upon and must extensively explore to acquire a model of the new environment they can exploit. SR RL agents appear to make errors like model-free agents, but adapt more efficiently to the change in the transition

structure, for example avoiding deadends after a few trials (Video S5). This is consistent with them updating a stored transition structure using past experience. Thus, unlike the model-based agents, SR agents have a learned set of biases they will fallback to which can aid choice-making after changes in the environment.

Likelihood analysis of actions reveals rats and humans are both most similar to an SR agent

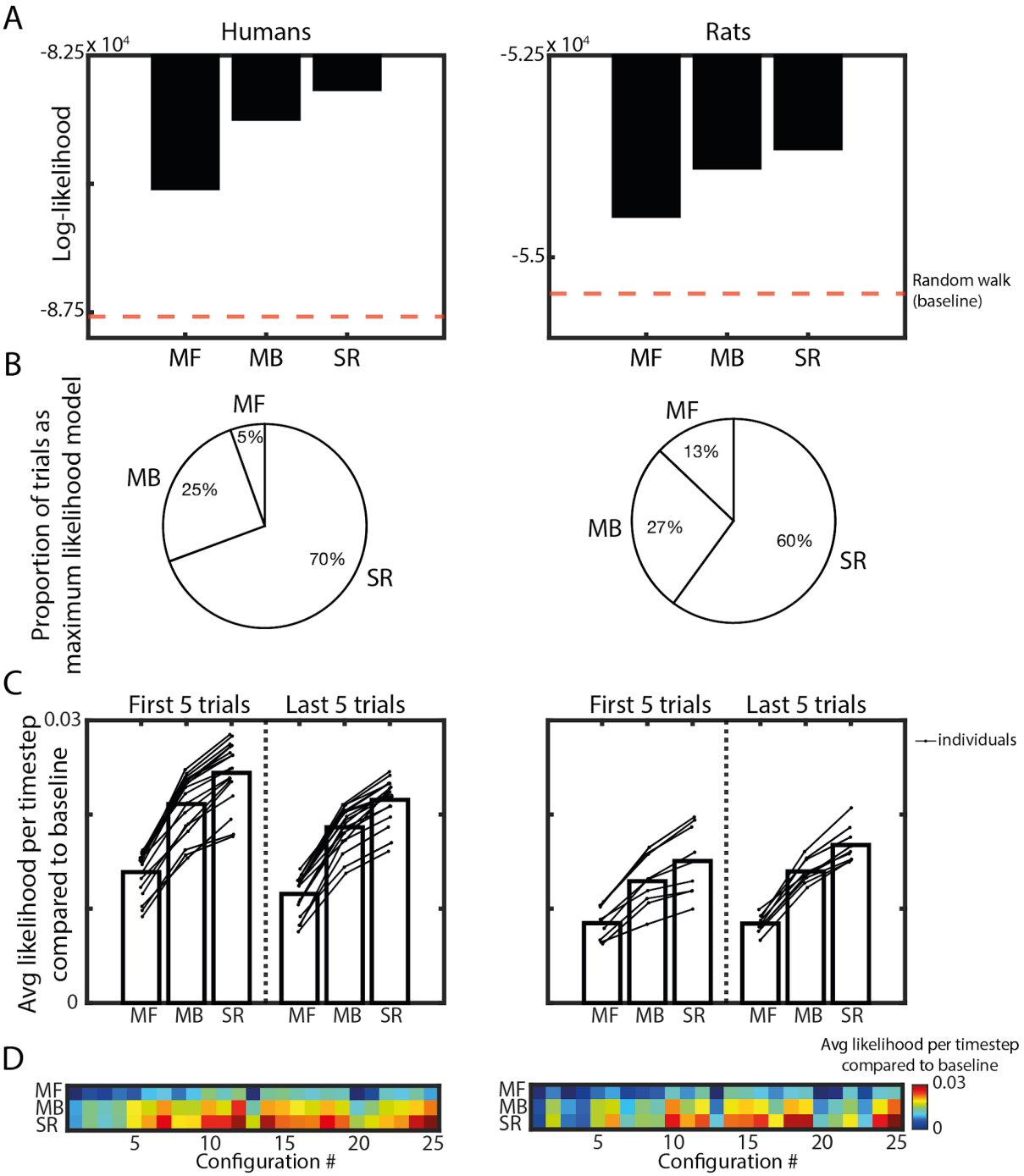
We next investigated how the human and rat trajectories compared to the RL agents' representation of optimal actions. To do this, we computed the likelihood of the human and rat behaviour matching each model by using their trajectories as input to the RL agents. We then used the agents' internal value estimates to compute a softmax probability distribution over the available actions at each timestep. Using these probabilities to compute the likelihood of the biological data for each agent, we calculated the maximum likelihood parameter estimates for each model's learning rate and discount factor across individuals, as well as pooled across the subject sample (Table 1).

	α		γ	
Model	Human	Rat	Human	Rat
MF	0.45	0.22	0.75	0.65
MB	1	1	0.81	0.79
SR	0.93	0.81	0.79	0.79

Table 1: Maximum likelihood parameters for learning rates α and discount factors γ for the model-free (MF), model-based (MB) and successor representation (SR) agents, pooled across individuals.

Comparing the model-free, model-based and SR algorithms, the value representation of the SR agent consistently provided the most likely fit to the biological behaviour (Fig 3A; Likelihood-Ratio (LR) test: SR vs MF for human data ln(LR) = 1911.1; SR vs MB for human data ln(LR) = 538.2; SR vs MF for rat data ln(LR) = 842.0; SR vs MB for rat data ln(LR) = 225.2), with the model-free agent consistently providing the worst fit (MF vs MB for human data ln(LR) = -1372.9; MF vs MB for rat data ln(LR) = -616.9). Consequently, the SR agent was the maximum likelihood model for 70% of the human trials and 60% of the rat trials (Fig 3B). Normalising these likelihoods by trial length and using a uniform random walk as a baseline, we observed this trend was robust throughout the time spent on a maze configuration (Fig 3C) and across individuals (SR vs MF for human data: $t(17) = 29.2$ $p<.001$; SR vs MB for human data: $t(17) = 11.9$, $p<.001$; SR vs MF for rat data: $t(8) = 13.0$, $p<.001$; SR

vs MB for rat data: t(8) = 9.6, *p*<.001). We also observed that the agent likelihoods for humans and rats varied from maze-to-maze (Fig 3D), with a strong correlation between the fits to the biological data (r=.57, *p*<.001).



<u>Figure 3</u>: Maximum likelihood analyses of the human and rat trajectories. Likelihood analysis reveals that humans (left) and rats (right) are more similar to a successor representation agent (SR) than model-based (MB) or model-free (MF). (A) The value estimates generated by the SR agent provide a more likely explanation of the biological behaviour than either the MF or MB agents. (B) The SR agent was the maximum likelihood model to explain the biological behaviour for the majority of trials. (C) This trend is true across all individuals in both species (humans n=18; rats n=9) and robust throughout exposure to a maze. (D) Likelihood estimates vary from maze-to-maze, with a strong

correlation between the model likelihoods for the human and rat behaviour across mazes ($r = .57$, $p<.001$).

Simulating agents using parameters derived from the human and rat data reveals closest match to SR agent

To investigate whether these differences in agent likelihoods transfer into differences in the resulting behavioural performance, we simulated the agent's trajectories using the pooled maximum likelihood parameters (Table 1) and an epsilon-greedy policy with epsilon=0.1. This policy makes the agents exploit (i.e. choose the action with maximum expected value) 90% of the time and explore (i.e. choose a random action) on the remaining 10%. To accurately depict the distribution of trajectories generated by an agent under such a policy, we simulated each RL algorithm 1000 times, with the maximum number of state transitions set to the mean from the humans and rats on unsuccessful trials (humans: T = 42, rats: T = 29).

The biological behaviour consistently outperformed all RL agents. Beyond that, the model-based algorithm was the most successful agent (Fig 4A-B; Mann-Whitney test, human parameters: MB vs SR, $z=29.6$, $p<.001$; MB vs MF, $z=38.7$, $p<.001$; rat parameters: MB vs SR $z=14.5$ $p<.001$, MB vs MF $z=38.7$ $p<.001$), with the model-free agent consistently the worst (human parameters: MF vs SR, $z=-38.7$, $p<.001$; rat parameters: MF vs SR, $z=-38.7$ $p<.001$). As with the humans and rats, the model-based and SR agents progressively improved throughout the trials on a given maze configuration (Fig 4A-B; first 5 vs last 5 trials, human parameters: MB, $z=-18.1$, $p<.001$; SR, $z=-30.1$, $p<.001$; rat parameters: MB $z=-14.2$, $p<.001$; SR: $z=-11.0$, $p<.001$). Meanwhile, the model-free agents became progressively worse at reaching the goal (first 5 vs last 5 trials: human parameters, $z=38.6$, $p<0.001$; rat parameters, $z=38.8$, $p<.001$) – indicative of the increasingly complex trajectories required from successive starting positions on a maze. Goal-reaching performance for the RL algorithms varied maze-to-maze (Fig C-D), with mazes that had a contradictory optimal policy to the preceding maze seeming particularly difficult (i.e. mazes 4, 8, 13, 21 – see Fig 1C for mazes). Conversely, mazes that possess a high degree of overlap in optimal policy with the previous maze (i.e. mazes 2, 7, 25) were consistent with higher levels of agent goal-reaching - due to the improved accuracy of the initial value representations. Ranking maze difficulty by order of goal-reaching performance revealed a significant positive correlation between the human and rat difficulty rankings with the SR agent (Fig 4E-F; human-SR rank correlation: $\rho=.52$, $p<.001$; rat-SR rank correlation: $\rho=.40$, $p=.049$). No significant correlations were detected between the human and rat difficulty rankings with either of the other agents (human-MF rank correlation: $\rho=.15$, $p=.48$; human-MB rank correlation: $\rho=-0.18$, $p=.39$, rat-MF rank correlation: $\rho=.37$, $p=.066$; rat-MB rank correlation: $\rho=.085$, $p=.69$).

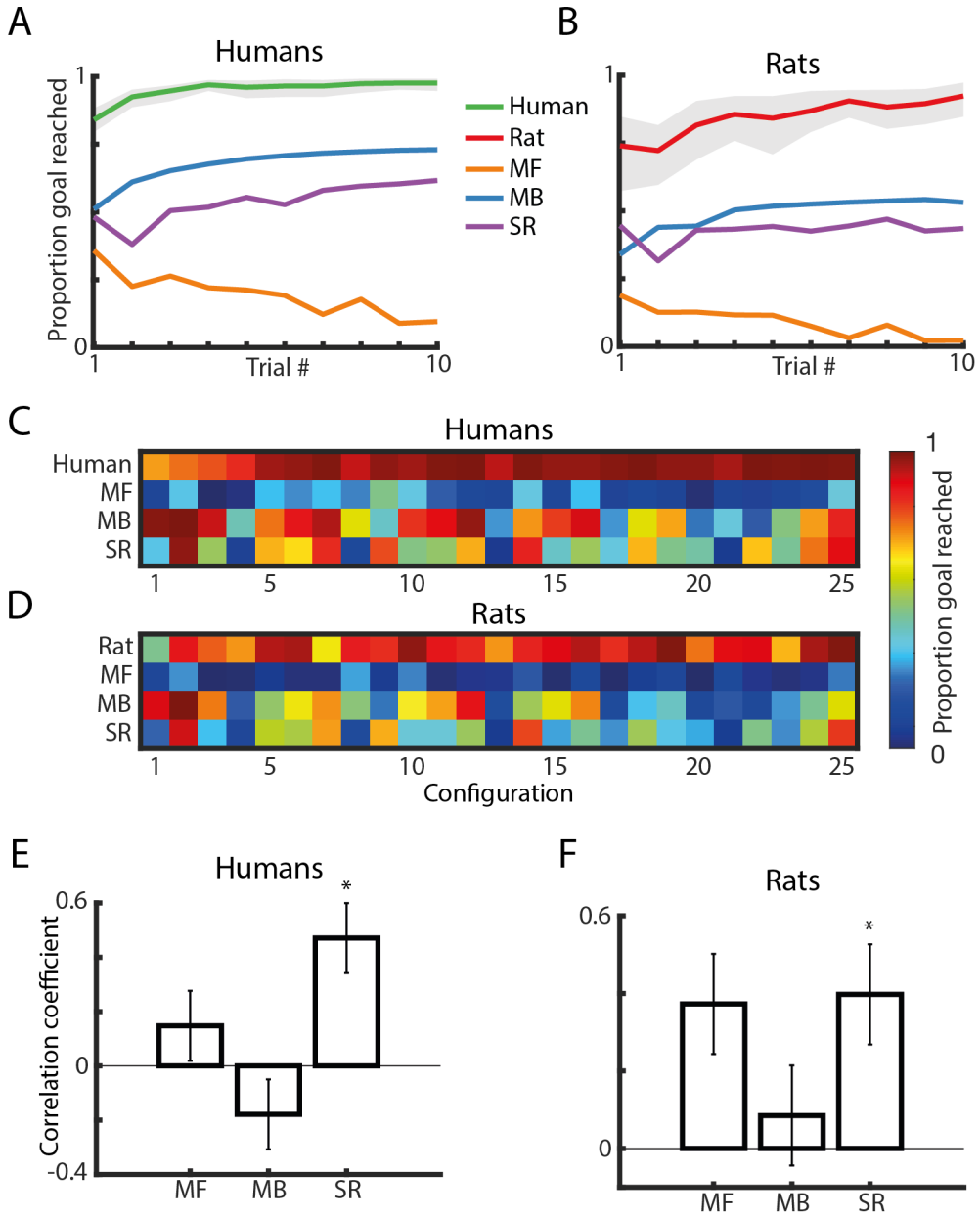
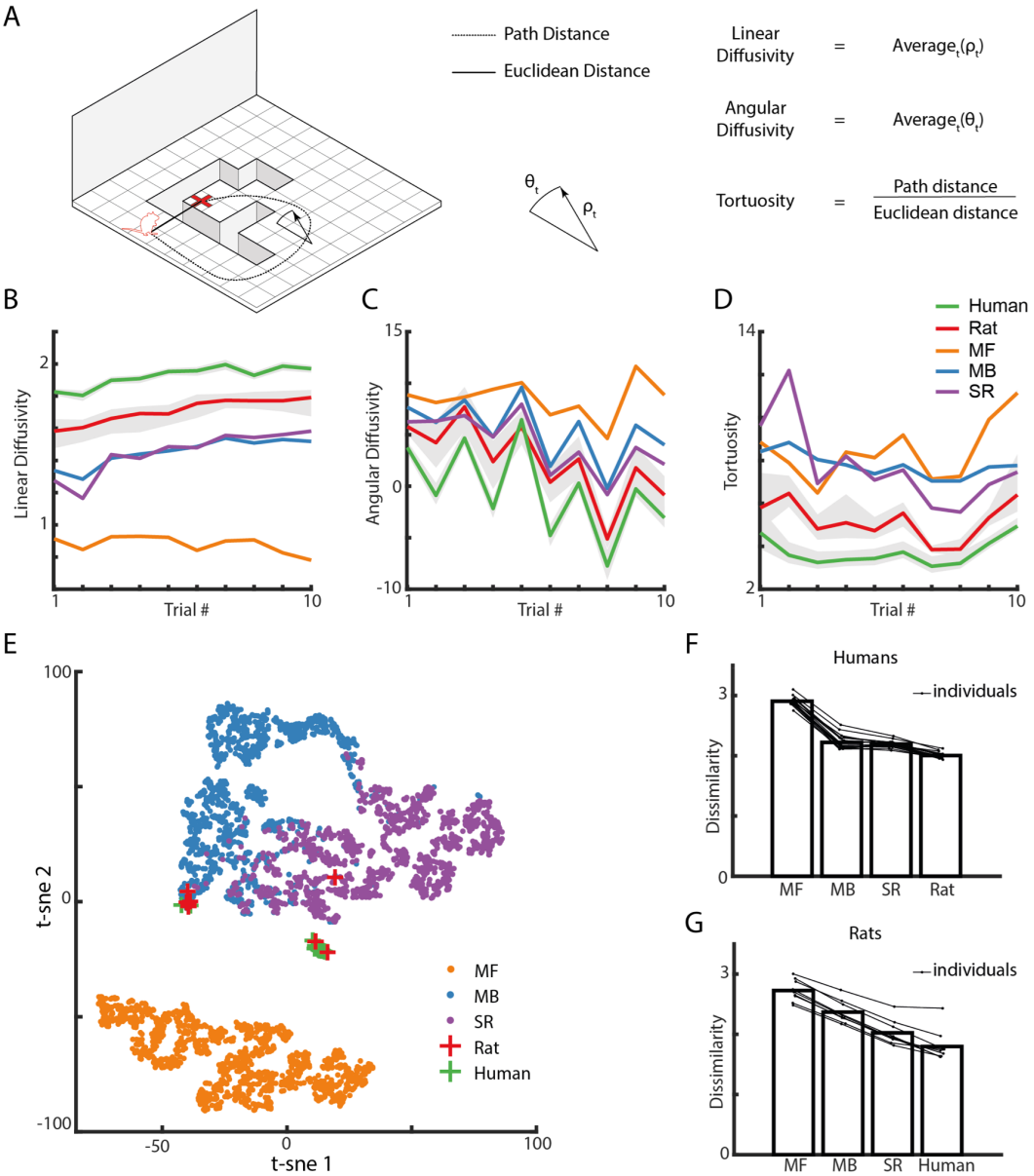


Figure 4: Human and rat performance compared with maximum likelihood reinforcement learning agents. Goal reaching for agents (n=1000) using the maximum likelihood parameters fit to the human (A) and rat (B) trajectories. Grey areas indicate 95% confidence intervals. (C-D) Goal reaching varied across maze configurations. Using this to rank maze configurations difficulty reveals a significant positive correlation between the human (E) and rat (F) difficulty rankings and the successor representation agent's (humans, ρ=.52, *p*<.001; rats, ρ=0.40, *p*=.049), but not with the model-free (humans, ρ=.15, *p*=.48; rats, ρ=.37, *p*=.066) or model-based (humans, ρ=-0.18, *p*=.39; rats, ρ=0.085, *p*=0.69) agent. This is in spite of the model-based agent generally being better at navigating to the goal than the other agents. Error bars indicate standard error from the mean.

In order to compare the similarity of the routes taken by the rats, humans and RL agents, we next quantified each trajectory using three measures: the linear diffusivity, the angular

diffusivity and the tortuosity (Fig 5A). Linear and angular diffusivities describe the overall directness and direction of the route, whilst tortuosity describes general trajectory complexity. In all measures, rats and humans values are closer to each other than to any of the reinforcement learners (Fig 5B-D).

Visualising the quantified trajectories across all trials revealed distinct clustering of behaviour (Fig 5E). We then used the Mahalanobis distance to calculate the dissimilarity between the biological and agent trajectories per trial. The Mahalanobis distance was used as it accounts for the covariance between the trajectory measures when calculating dissimilarity. We found that human and rat trajectories were significantly more similar to each other than to any of the reinforcement learners (Fig 5FG; humans to rat cluster vs SR cluster: $t(17)=-26.3$, $p<.001$; rats to human cluster vs SR cluster: $t(8)=-6.0$, $p<.001$). Of the RL agents, the SR was the most similar to the rat (SR vs MF: $t(8)=-27.5$, $p<.001$; SR vs MB: $t(8)=-34.6$, $p<.001$) and human trajectories (SR vs MF: $t(17)=-97.7$, $p<.001$; SR vs MB: $t(17)=-2.4$, $p=.03$), with the model-free agent consistently being least similar (humans to MF cluster vs MB cluster: $t(17)=37.6$, $p<.001$; rats to MF cluster vs MB cluster: $t(8)=20.7$, $p<.001$).

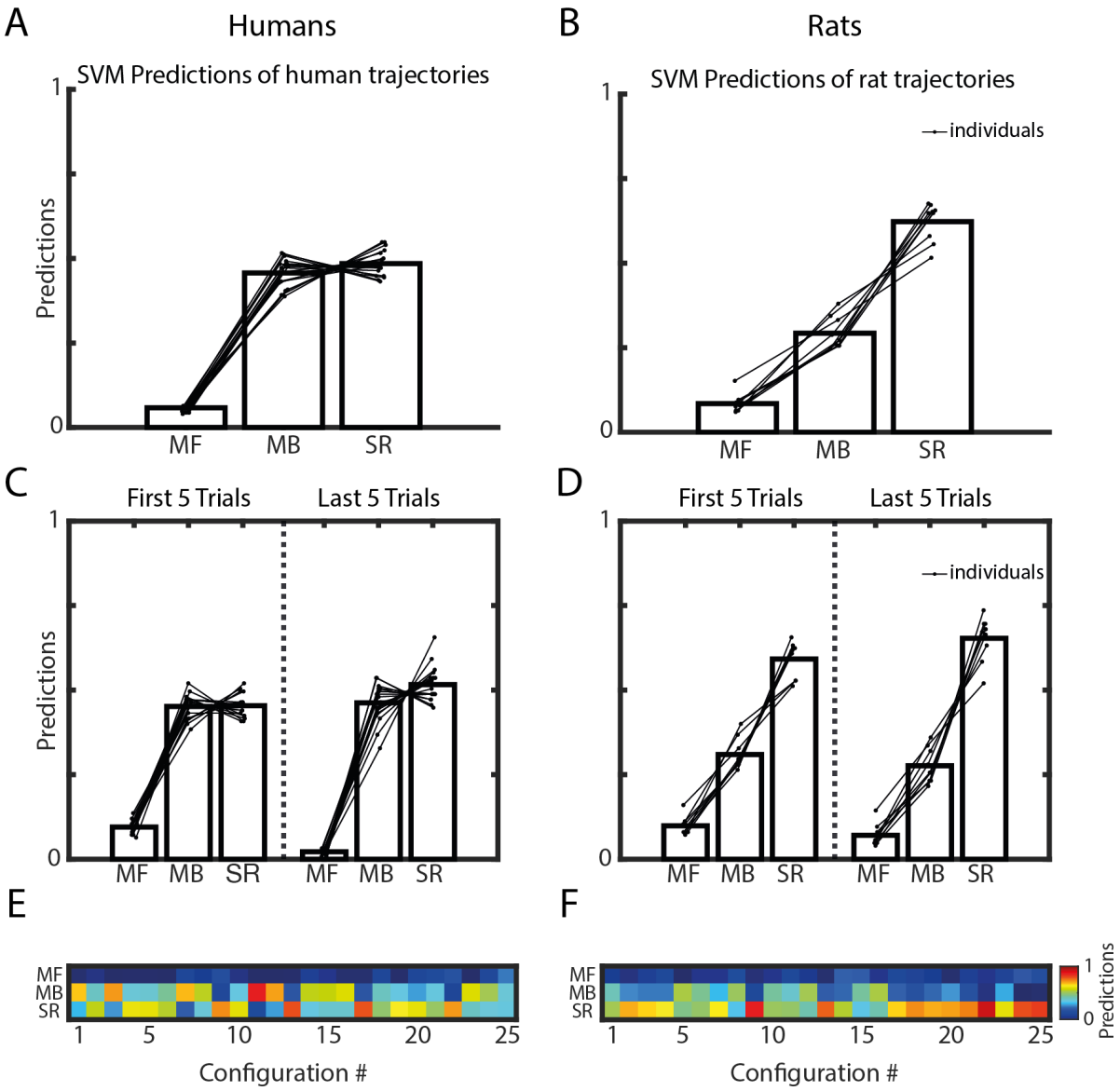


<u>Figure 5</u>: Trajectory similarity analysis. Analysis reveals that rat trajectories are most similar to a successor representation agent, whilst human trajectories are similar to both successor representation and model-based agents. (A) The shape of each trajectory was quantified using three metrics: the average diffusivity (B) and average angular diffusivity (C) provide a measure of the general dispersion and direction of a trajectory, whilst the tortuosity (D) gives a description of larger scale complexity. (E) Using these metrics to quantify trajectories across all trials, agent behaviour can be seen to form clusters (shown here via t-sne), where each point represents an individual human, rat or agent. Note, that for different embeddings a similar pattern emerges with MF agents forming a highly distinct cluster. Calculating the Mahalanobis distance between clusters reveals the human (F) and rat (G) behaviour is most similar to a successor representation agent.

Support-vector machine classification identifies agent patterns in human and rat data

Finally, to test if the differences in these measures of the trajectory are sufficiently robust to allow categorisation, we trained a support-vector machine (SVM) classifier to accurately predict trajectories as either model-free, model-based or SR agents (SFig3). When the decoder was given data from the biological behaviour, the SVM classifier most frequently predicted those trajectories to be an SR agent for rats (Fig. 6AB; SR vs MB: $t(8)=9.8$, $p<.001$ SR vs MF: $t(8)=11.8$, $p<.001$). Interestingly, there was no discernible difference in SR and model-based agent predictions in humans until the latter half of trials - when the routes to the goal were longer and more complex (Fig6CD; first 5 trials $t(17)=0.14$, $p=.89$; last 5 trials $t(17)=2.1$, $p=.048$). Viewing how SVM predictions change from maze to maze again reveals noticeable variation (Fig 6EF), with configurations that have little overlap in optimal policy with the preceding maze often leading to increased SVM predictions of the SR agent.

In summary, we used three approaches to compare RL agents to rats and humans: a likelihood analysis of rats and humans actions under different agents, the similarity of RL agents performance and trajectories to rats and humans ones, and an unsupervised categorisation of rat and human trajectories by a support-vector machine (SVM) classifier. Our results show that both species match more closely the SR RL agents' performance patterns than MF or MB agents, and that there are features of rodent and human navigation that remain more similar than the simulated agents.



<u>Figure 6</u>: Support-vector machine (SVM) classifies rat trajectories as SR agents and humans as SR or MB agents. A SVM classifier trained to decode model-free (MF), model-based (MB) and successor representation (SR) agents most often classified human trajectories (left column) as MB and SR agents (**A**; SR vs MB: t(17)=1.51, p=0.15), and rat trajectories (right column) as an SR agent (**B**; SR vs MB: t(8)=9.8, *p*<.001). Later trials on a configuration are more likely to be classified as an SR agent for both the human (**C**; SR vs MB prediction on last 5 trials of maze, t(17)=2.1, *p*=.048) and rat data (**D**; SR vs MB prediction on last 5 trials of maze, t(8)=11.1, *p*<.001). The level of these predictions varied from maze-to-maze (**E-F**) with a strong correlation between the humans and rats (rank correlation: ρ = .71, *p*<.001).

Discussion

To understand the underlying processes that support flexible navigation in rats and humans we compared their navigation performance with three classic instantiations of RL agents in a maze environment using a dynamic layout of barriers. Using a combination of likelihood, trajectory similarity and support-vector machine classifier analyses, we find that both rats and humans rapidly adapted to the dynamic environments, producing similar navigation choices and trajectory patterns that most resembled successor representation RL agents. This was most evident for rats, while humans were also found to show some trajectory pattern similarity to model-based RL agents. Our findings provide novel convergent cross-species insights into spatial navigation behaviour and mechanistic understanding of the different choices made when adapting to a changing environment. In doing so we identified a set of metrics that would allow the prediction of future behavioural and neural dynamics across a wide range of methods in humans and animals. We discuss: i) how these results inform our understanding of mammalian navigation, ii) insights into RL models, iii) similarities and differences between rodent and human behaviour, and iv) directions for future research.

A predictive map for navigation?

Stereotypically, one might view rats as 'creatures of habit', while humans could be considered deep thinkers, mulling over future possibilities. These two stereotypes map, to some degree, onto model-free RL (habit-like) agents and model-based RL (flexible planning) agents. Rather than finding such a dichotomy between rats and humans, we found the behaviour of both species is best captured by an RL agent that creates a predictive map of the environment to guide navigation: the successor representation. SR has been proposed as an efficient alternative to the relatively inflexible model-free RL and the computationally expensive model-based RL. SR stores a matrix of the possible transitions within the environment and integrates this with information about reward (Dayan, 1993). Recently, it has been proposed that the hippocampus may implement a system similar to a successor representation to create a predictive map to guide navigation (Stachenfeld et al 2017; de Cothi and Barry, 2020; Sosa and Giacomo 2021). Here we find behavioural evidence to support the proposal that both rats and humans use such a predictive map to guide flexible navigation behaviour.

A range of previous experiments comparing human behaviour to RL agents have generally focused on a competition of model-free vs model-based agents to capture behaviours in small conceptual state spaces with 2-step transitions. These have found evidence for model-based planning in humans (Daw et al., 2011; Vikbladh et al., 2019; Wunderlich et al., 2012). Using a much larger state space with potential for recursive transitions (i.e. loops leading back to the same state), we extend this approach into a more complex and naturalistic framework. Our findings add to recent evidence that the choices of humans are best explained by a combination of SR and model-based behaviours (Garvert et al., 2017; Momennejad et al., 2017; Russek et al., 2021). Since the SR encodes the environment's transition structure, it is itself a model that can be leveraged for intuitive planning (Baram et al., 2018) or more explicit planning procedures such as a tree search -

which may partially explain the trajectories observed during hippocampal replay (Mattar & Daw, 2018; Momennejad, 2020; Momennejad et al., 2018; Pfeiffer & Foster, 2013).

A few studies have explored human navigation in VR environments and compared navigational choices with RL agents, reporting that behaviour matches a mix of model-based and model-free choices (Anggraini et al., 2018; Simon & Daw, 2011). For example, when paths are short but decision times are longer, model-based RL agents were found to better match human behaviour (Anggraini et al., 2018). However, these past studies did not compare performance with a successor representation, nor were the trajectories examined in relation metrics such as the diffusivity and tortuosity to understand the match to the different RL agents. Here we show that navigation in humans is most similar to SR and that using trajectory information is useful in providing convergent evidence to understand this.

In our experiment the model-free RL agents showed poor adaptation to the changes in maze layout. Rather than improving over trials, performance declined. This could be accounted for by our task structure; the minimum trajectory length increased as trials progressed, requiring longer and more complex routes to the goal. Our mazes were designed to be simple but to include dead-end zones and/ or regions where the barriers extended around the goal zone requiring extended trajectories away from the goal to then reach it. It is possible with different layouts model-free learners would succeed more efficiently. While overall in our analyses the SR model provided the best fit, the SVM classifier interpreted rat behaviour as a model-free agent to some degree. This suggests that on some mazes or trials rodent choices matched those of model-free agents, which were predominantly characterised by slower updating to an optimal policy, leading to dwell at deadends and on the wrong side of barriers near the goal. Examining trajectory patterns, and in particular the likelihood analysis, revealed that while there was some fit, the general pattern of routes taken by the rats were a poor match to the model-free agents. Such results highlight the value of using different analytical approaches to examine behaviour when fitting models. Understanding how the structure of the task and state space leads to the emergence of different policies is an important question for future research.

An important observation in our data is that it is not sufficient to conclude on the basis of overall performance which simulated agents will best fit the biological agent's data. While the model-based RL agent was the closest overall to rat and human performance, the SR RL model produced the greatest match in terms of the proportion of trials as the maximum likelihood model. This is because the patterns of choices made by the model-based RL fail to capture aspects of choice and trajectory patterns in the rats and humans to the same degree as the successor representation agents. This highlights the utility of an environment in which a wide diversity of trajectories can be achieved by the rats and humans to allow models to be discriminated.

Similarities and differences in the flexible behaviour of rats and humans
Past research has suggested that rats do not always optimally adapt to selecting appropriate alternative routes when navigating (Grieves & Dudchenko, 2013) and can take time to adjust to such changes to select the optimal route (Alvernhe et al., 2011; Shamash et al., 2021). Similarly, humans can struggle to take optimal shortcuts when presented with options (Brown et al., 2020; Foo et al., 2005; Marchette et al., 2011). Here rats and humans had to reach the correct goal from a set of 100 possible locations within a 45 second time limit. Since the maze transition structure was re-configured every 10 trials, achieving this was non-trivial. Despite this, both species were able to reach the goal on the first trial of a new layout on many trials. This parallels recent evidence from mice learning new paths remarkably fast in a large labyrinth (Rosenberg et al., 2021). In several cases we saw examples of routes near the optimal path on the first attempt for both species (e.g. see Videos S1&2). Moreover, the occupancy correlation between rats and humans was relatively high even from the first trial, and improved as performance increased across trials in a configuration. These results show that our Tartarus maze, with its visual access to landmarks, boundary geometry and canyon-styled barriers, provides a useful assay for goal-directed navigation across two species, revealing a remarkable similarity in the patterns of navigation across species.

Despite similarities in behaviour, there were noticeable differences between species. Humans were more successful adapting to the changes in maze layout and learning. Rats spent more time on the perimeter of the maze's edge. The overall difference in learning likely relates to the physical differences in our maze used between rats and humans (real vs VR) and the biological differences between species (e.g. differences in vision, movement, whisking, olfaction, grooming). Further research would be needed to disentangle the various contributions that give rise to the differences we observed. One particularly salient feature of the human mazes to explore further would be the amount of fog obscuring the maze floor. This was designed to recapitulate the reduced visual capacity of the rat to observe the layout at a distance. It would be useful to understand how human behaviour changes as more fog is added. As the overall performance of the humans approaches that of the rats do the trajectory patterns match? It seems likely important differences will be evident. Humans do not need to groom fur periodically in the way rats do.

In most maze configurations humans outperformed the rats. The one configuration where rats outperformed humans (configuration 2) had a much larger open space around the goal, which required more search across the space to find the goal if uncertain about its exact position. Rats may have encoded the movement in the open space more efficiently. While the olfactory cue of extra chocolate milk at the goal may have aided guidance for the rats, we suspect that it alone is insufficient to explain this performance due to the ballistic trajectories observed in many of the rats. Rats were much more likely to explore the edges of the environment, consistent with prior studies examining exploration (Kubie & Fenton, 2009). In future research it will be useful to explore interventions that increase the similarity of performance between rats and humans, such as the use of a comparable seized walking space in humans and wireless VR.

Benefits of a dynamic open field environment with barriers

Prior studies examining navigation in mazes have generally either used track-based or open field environments (Poulter et al., 2018; Small, 1901; Wiener et al., 2009). While open field environments place more demands on self-localisation and vector-based navigation (Morris, 1984; Pfeiffer & Foster, 2013; Tessereau et al., 2021), mazes with tracks enable to testing of blocked paths and shortcuts on behaviour (Alvernhe et al., 2011; Grieves & Dudchenko, 2013; Small, 1901; Tolman & Honzik, 1930). By contrast the Tartarus maze places demands on both vector based navigation and the capacity to take detours and shortcuts, as occurs with much of the terrain in the real world. The recent development of the honeycomb maze for rats (Wood et al., 2018) provides a parallel approach to self-localisation and obstructed paths to goals, where rats sequentially navigate to a goal over a number of hexagonal platforms that are made available in pairs sequentially until the goal platform is reached. Such an approach allows for a precise assessment of choice options at different time points, whilst placing demands on self-localisation in relation to distal cues. While the tartarus maze also demands choices and navigation to distal cues it allows continual, often ballistic trajectories to be taken to the goal, mimicking naturalistic behaviours that enable integration with more ethological approaches to navigation (Mobbs et al., 2021).

A number of rodent studies have examined how maze layout and changes in layout relates to exploration behaviour (Alonso et al., 2020; Alvernhe et al., 2012; Poucet & Herrmann, 2001; Rosenberg et al., 2021; Uster et al., 1976; Vallianatou et al., 2021) or escape behaviour (Ellard & Eller, 2009; Shamash et al., 2021). Here we found rats and humans rapidly adapted to changes in the maze structure, by exploring the new layout. By matching to RL models it is possible to provide a more mechanistic account of how goal-directed behaviour is organised during the navigation of a dynamic environment. In the case of Rosenberg et al. (2021) mice had to learn the paths in a maze with a large number of options. Akin to our task, learning was rapid. This differs from many non-spatial learning tasks where learning is typically slow (see Rosenberg et al., 2021). Other recent rodent studies exploring navigation behaviour have shown the capacity to model behaviour in goal learning and homing vectors for safety (Dollé et al., 2018; Shamash et al., 2021; Tessereau et al., 2021; Vallianatou et al., 2021). Such studies highlight the value in careful modelling of behaviour to understand the mechanisms guidening that behaviour. Here, we demonstrate the added benefit of modelling behaviour with simulated agents, examining the trajectory properties (e.g. diffusivity) and comparing across two different species.

Prior human virtual navigation studies exploring flexible navigation behaviour have tended to involve complicated VR environments that would likely be too demanding for rodents to learn (Howard et al., 2014; Javadi, Patai, Marin-Garcia, Margois, et al., 2019; Javadi, Patai, Marin-Garcia, Margolis, et al., 2019; Marchette et al., 2011; Patai et al., 2019; Simon & Daw, 2011; Spiers & Maguire, 2006; Zhu et al., 2021). Here, we sought to recreate an environment that would challenge human participants generating sufficient variation in performance and to allow comparison to rodents within the same maze structure. Being able to integrate behavioural data from humans, rodents and RL agents, opens the possibilities for incorporating data from a wide array of neuroscience methods in humans

and rodents. Recent students have shown the utility of this approach (Barron et al., 2020, 2021; Samanta et al., 2021). A recent study by Zhu et al. (2021) highlights the benefit of examining eye-movement dynamics during the navigation virtual environments presented using a similar head-mounted display VR set up to our human VR, but where the whole transition structure was visible to look at. Their results show patterns of eye-movements that sweep across key points in mazes, maximally important for planning, showing forward sweeps to the goal, as well as backward sweeps from the goal. Furthermore, they show evidence that patterns in eye-movements that scan relevant available transitions relate to SR agent performance. Future work with eye-tracking integrated into our task for humans would be useful to study the selection of sub-goals and eye-movements during updating the mazes; could eye-movement predict future choices of routes and the match to different RL agents in subsequent behaviour? Eye-tracking in rodents is a bigger challenge but may also hold some promise (Meyer et al., 2020). Finally, it may also be useful to explore the search behaviour of RL agents, humans and rats in relation to models of utility and biased search (Kryven et al., 2021).

How might the RL agents be improved?

The learning efficiency of RL agents could be improved using offline replay of randomly sampled past experiences (Momennejad, 2020; Momennejad et al., 2017; Russek et al., 2017; Sutton, 1990). These replays are typically implemented between agent timesteps, and the manner in which they are sampled can further accelerate learning by prioritising the most useful learning experiences to replay (Mattar & Daw, 2018). Prioritised replay also has strong parallels to the phenomenon of hippocampal replay of place cell activity during sleep or quiescence (Liu et al., 2019, 2021; Pfeiffer & Foster, 2013). However, we did not implement agent replay in this study in order to keep the value representations and consequently the likelihoods of agents deterministic enabling fair model comparison. An alternative way to improve the goal-reaching of agents could be through improving their exploration policy. The agents simulated here relied on an epsilon-greedy policy through which exploration is purely driven by chance. However, methods that include curiosity (Still & Precup, 2012) or uncertainty in the value function (J. Geerts et al., 2019; Gershman, 2015) could be used to guide more efficient exploration of a new maze and consequently lead to faster learning. Finally, navigation using an options-framework might allow for more efficient navigation (Stolle & Precup, 2002). Rather than planning step by step, efficient navigation in our mazes can be achieved by selecting a clockwise vs a counter-clockwise path to the goal. Being able to exploit a hierarchical segmentation of the environment might allow RL agents to better approximate human and rat behaviour (see e.g. Balaguer et al., 2016). More broadly, new approaches to RL (Piray & Daw, 2021) and deep learning methods may provide new ways to examine navigation (Banino et al., 2018; Frey et al., 2021), as well as integrating our approach with biologically-inspired network models that seek to explain neural dynamics during navigation (Erdem & Hasselmo, 2012; Kubie & Fenton, 2009).

Exploring the neural substrates of a predictive map

Recent neuroimaging in humans has shown that activity in hippocampal and connected regions tracks the modelled parameters from a successor representation (Brunec &

Momennejad, 2019; Garvert et al., 2017; Russek et al., 2021; Stachenfeld et al., 2017) (Brunec & Momennejad, 2019; Garvert et al., 2017; Momennejad et al., 2018; Russek et al., 2021; Stachenfeld et al., 2017). Convergent evidence in rodents suggests that the place cell activity in the dorsal CA1 of rodents may operate as a successor representation (de Cothi & Barry, 2020; Sosa & Giocomo, 2021; Stachenfeld et al., 2017). Our protocol would allow for evidence from both rodent and human data to be integrated within a single framework to consider how patterns in the data may interrelate across species and in relation the parameters from RL modelled agents. Evidence from other recent approaches shows the utility of such an approach (Barron et al., 2020, 2021; Samanta et al., 2021). Our recent analysis of CA1 place cell activity found little evidence for changes in the place field maps when the state space changed due to blocked doorways in a 4-room maze (Duvelle et al., 2021), showing that it is not a given that hippocampal activity conforms to SR model predictions (Stachenfeld et al., 2017). It would be useful to determine how the activity of spatial cells in the hippocampus and connected regions is modulated in our task. Recent work modelling multi-scale SR agents (Momennejad & Howard, 2018) has shown patterns similar to the goal distance tuned activity of CA1 cells in navigating bats (Sarel et al., 2017). Might such patterns emerge in our task? An important step in better understanding the neural systems for navigation would be to examine the impact of temporally targeted inactivation of the hippocampal regions, as well as the prefrontal cortex which is thought to support route planning (Patai & Spiers, 2021). Such an approach would provide more causal evidence for the role of brain structures for supporting our task. More broadly, the task we have developed could be adapted for study with a range of other species which have been examined in isolation: ants, bees, drosophila, bats, birds and other primates. Integrating across invertebrates and vertebrate species may further our understanding of the common mechanisms for goal-directed behaviour and adaptations that occurred through evolution.

Conclusion

In summary, we found that rats and humans both display behaviour most similar to a successor representation RL agent, with humans also showing some behaviour matching model-based planning. Future work exploring single-unit recording or disruption to neural activity may be useful in revealing how distance to the goal may be coded, as past studies have failed to dissociate path and Euclidean distance. Moreover it will be useful to examine how neural activity in humans and rodents relates to the parameters from RL agents with behaviour adjusted to match the humans and rats. More broadly, the approach provided here could be adapted to allow comparison of behaviour across a wide range of species and iterations of RL models to help understand the broad spectrum of navigation behaviours shown by the diverse species on our planet.

Materials and Methods

General methods

Navigation was tested in a large square environment with a fixed hidden goal location and a prominent directional black wall cue in one direction (Fig. 1, Video S1 and S2). The maze was divided in a 10x10 grid of moveable sections that could either be removed, leaving

impassable gaps to force detour taking, or added, creating shortcuts. During training, all maze modules were present. Rats, humans and RL agents were trained to reach the goal within a 45s time limit, (Fig 1A). During the testing phase of the experiment, maze modules were removed to block the direct route to the goal (Fig 1B). Humans (n=18), rats (n=9) and agents were tested on the same sequence of 25 maze configurations each with 10 trials in which a set of defined starting locations were selected to optimally probe navigation (Fig 1C). These maze configurations were generated from a pilot testing with 9 rats and the maze sequence chosen maximized the differences in the layouts between trials. The starting positions on each maze gradually increased in the required tortuosity (path distance / Euclidean distance) of the shortest path to the goal to test complex trajectories whilst keeping the rodents motivated.

Upon reaching the goal module, rats and humans had to wait 5s to receive their reward. Human participants were rewarded with a financial bonus and rats received chocolate milk delivered in a well (supp. fig 1). In order to better match the visual acuity and depth perception between rodents and humans (Heffner & Heffner, 1992), a thick virtual fog lined the floor of the maze enabling them to only see adjacent maze modules and the distal black wall cue (supp. fig 2; Video S2). Modules were made visually indistinct to avoid humans counting them when traversing the space. Human participants were informed that reward was hidden in the environment and that their task was to maximise their financial return as quickly and efficiently as possible. The human and rat trajectories were discretised into the underlying 10x10 modular grid (Fig 2A-B) in order to facilitate comparison between each other and the RL agents.

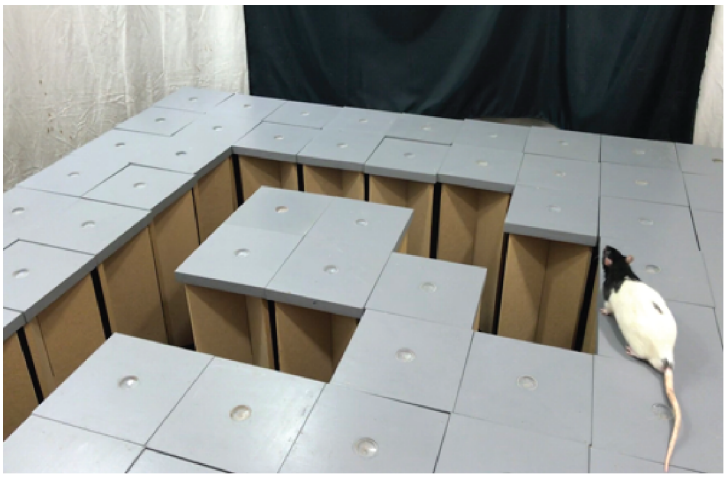
In all versions of the experiment, the environment (raised off the floor) consisted of a 10x10 grid of maze modules. These modules could be removed from the grid in order to form impassable barriers in the environment. One of the modules was rewarded and thus was the location of the goal in the maze. Navigation was facilitated by a single distal cue consisting of a black curtain that spanned the majority of one side of the maze. The goal was kept in the same position with respect to this distal cue throughout all versions of the task. All participants, rats and learning agents were initially trained to navigate to the goal module on the open maze, without any maze modules removed. Once trained, they were all put through the same sequence of 25 mazes, with the same sequence of starting locations on each maze

Rodent methods

Nine adult male Lister Hooded rats were handled daily (at start of training: 10-20 weeks old, 350-400 g) and housed communally in groups of three. All rats were subjected to a reverse light-dark cycle (11:11 light:dark, with 1 hour x2 simulated dawn/dusk) and were on food-restriction sufficient to maintain 90% of free-feeding weight, with ad libitum access to water. The free-feeding weight was continuously adjusted according to a calculated growth curve for Lister Hooded Rats (Clemens et al., 2014). Six rats were naive, while three rats had previously been trained for 2-3 weeks in a shortcut navigation task for a different maze setup. The procedures were conducted according to UCL ethical

guidelines and licensed by the UK Home Office subject to the restrictions and provisions contained in the Animals Scientific Procedures Act of 1986.

All procedures were conducted during the animals' dark period. The experiment was carried out in a custom-made modular 2x2m square maze composed of 100 identical square platform tiles elevated 50cm above the ground (supp. fig 1). The maze was constructed from Medium Density Fibrewood, with the platforms painted in grey. Each platform contained a plastic well (32mm diameter) at its centre, which could be attached to a polymeric tubing system installed beneath the maze. This tubing allowed the experimenter to reward the rat at the goal module filling the well with chocolate milk (0.1 ml). Importantly, all modules in the rodent maze were identical in appearance and construction with chocolate milk rubbed into the well of non-goal modules to lower reliance on olfactory navigational cues. The maze was surrounded on all sides by a white curtain, with a black sheet overlaid on one side to provide a single extra-maze cue. To ensure that no other cue could be used by the animal (uncontrolled room cues, olfactory traces on the maze) the black sheet was rotated 90° clockwise between sessions. The goal module was always in the same position with respect to this cue. Moreover, the experimenter stayed next to the maze inside the curtained area throughout all sessions, his positions relative to the goal were randomised.



Supplementary Figure 1: The maze environment used for the rat experiment. The environment consists of 100 removable mazes modules with a black curtain over one of the surrounding edges to provide a single extra-maze cue. Reward can be dispensed at the goal module by filling the well with chocolate milk via polymeric tubing beneath the maze.

Familiarisation: During the first day, the rats received a small amount (0.1ml per rat) of chocolate milk in the home cage to decrease neophobia in the maze. For the subsequent two days, each rat underwent two 15 minute maze familiarisation sessions, in which the rat was placed at the centre of the maze and would forage for pieces of chocolate cereal (Weetos) scattered throughout the maze. More cereal was concentrated in the centre to encourage the animal to be comfortable in the middle of the maze.
Training: Training consisted of two stages, rats were given 2 training sessions per day. In each training trial the rat had 45s to find the goal module.

For stage 1 of training the goal well was filled with 0.1ml of chocolate milk and the rats were initially placed on the modules adjacent to the goal, facing the goal. If the rat made two consecutive direct runs to the goal (without exploration of other parts of the maze), the next trial began one module further away from the goal. Conversely, if the rat failed two consecutive training trials, the next trial began one module closer to the goal until the rat was back at the goal-adjacent modules. On day 1, this procedure was continued until 15 min had elapsed.On the following days, the number of trials was fixed to 16. This procedure was followed every day until the rat was able to make direct runs from the far edges of the maze.

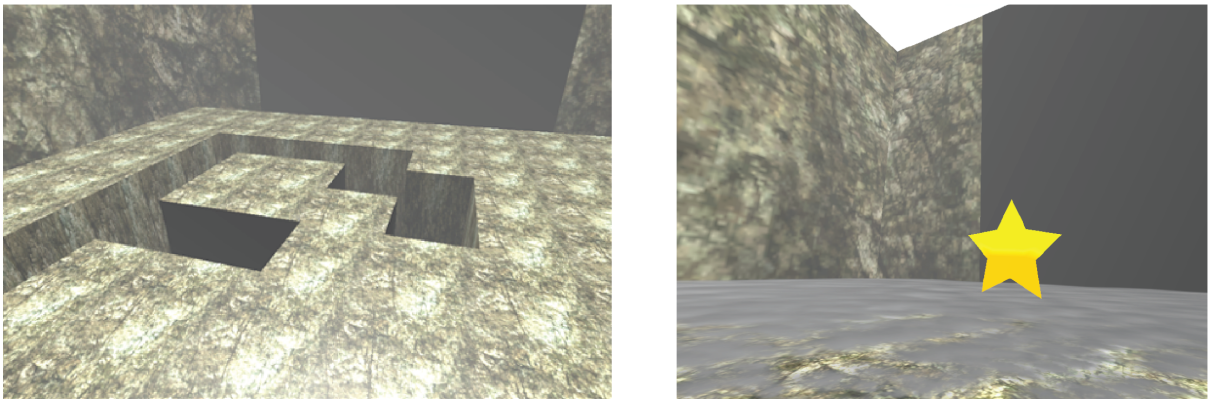
Stage 2 was similar to stage1 but a delay in the release of chocolate milk was introduced. This delay started at 1s and was gradually increased until the rat could wait at the goal location for 5s before the chocolate milk was released. Furthermore, the rat's starting position and orientation were randomised. The number of daily trials could be increased up to 25. This procedure was followed until the rats were able to successfully navigate directly to the goal and on at least 90% of trials. The training phase took on average 24 sessions.

Tartarus Maze testing: Rats were run on the 25 maze configurations. For each maze configuration, rats were given 10 trials, starting from with the starting positions indicated in figure 1. Trials were 45s long and rats were required to navigate to the goal within this time and wait for 5s in order to receive the reward (0.1ml of chocolate milk). If the rat failed to reach the goal, it moved onto the next trial. The rats would usually complete 3 configurations per day. At the beginning of each day, rats were given a brief reminder session that consisted of 5 trials from phase 2 of the training phase.

Human methods

For the human version of the task, 18 healthy participants (9 female; aged = 24.6 ± 5.9, mean ± sd) were recruited from the UCL Psychology Subject Pool and trained to navigate to an unmarked goal in a virtual arena of approximately the same relative proportion as for the rats. All participants gave written consent to participate in the study in accordance with the UCL Research Ethics Committee. Participants were reimbursed for their time as well as a bonus of up to £25 for good performance in the testing phase. Participants experienced the virtual environment via a HTC Vive virtual reality headset whilst sat on a swivel chair. They were able to adjust movement speed using the HTC Vive controller and movement direction was controlled by the participant's orientation on the chair. Upon successful navigation to the goal module, participants were informed of their financial reward along with the presence of a revolving gold star (supp. fig 2) at the goal location. In accordance with the rodent experiment, navigation was aided by the presence of a black distal cue that took up the majority of one of the walls. Goal location, maze configurations and starting positions were all defined with respect to this distal cue and were identical to the rodent experiment. Importantly, a fog lined the floor (supp. fig 2, Video S2) of the maze

to prevent the participants from understanding what maze modules were missing until they were at adjacent locations. This also provided a better match to visual information available to the rats - which are known to have less visual acuity and binocular depth perception (Heffner & Heffner, 1992). Seamless textures were applied to the floor and walls of the virtual environment, and these were rotated every 10 trials to prevent them from being used as extraneous cues for navigation.



Supplementary Figure 2: The virtual environment used for the human experiment. The environment had the same proportions as the rat environment and consisted of 100 removable mazes modules with a black curtain over one of the surrounding edges to provide a single extra-maze cue. A seamless texture was applied to the maze modules and walls and a fog lined the floor of the maze (see right image) to ensure humans had to rely on spatial memory to understand the maze structure. Reward was indicated by a gold star that would appear at the goal module when the participant successfully navigated to it.

The experiment took place over four sessions on four consecutive days. The majority of the first session was usually spent training the participants to navigate to the goal module. To accelerate this learning process, the participants were initially able to see a revolving gold star in the goal location. As they progressed through the training session the star became increasingly transparent until invisible, with the star only appearing again upon successful navigation to the goal module. Along with the decreasing visibility of the goal, the participants' starting positions were moved progressively further from the goal in a similar manner to the rat training phase. All training and testing trials were 45s in length. Training was terminated when the participants were able to navigate to the hidden goal on at least 80% of trials after being randomly placed at the far edges of the environment. Mean time to complete this training was 41 ± 21 minutes. In order to make the participants' experience similar to that of the rodents, they were not given any explicit information about the nature of the task - only that financial reward was hidden in the environment in the form of a gold star and their task was to maximise their financial return as quickly and efficiently as possible.

The testing took place over the remaining sessions and on average lasted 125 ± 25 minutes, with participants encouraged to take short breaks every 10-20 trials to reduce virtual reality sickness. At the beginning of each testing session, participants completed a short reminder task, which consisted of 5 trials from the end of the training phase.

Reinforcement learner simulations

The reinforcement learning agents were implemented in a 10x10 grid world. At the beginning of the experiment, all agents were endowed with the optimal policy on the open maze to simulate the training phase undertaken by rats and humans. They were then run consecutively on the 25 maze configuration, carrying over all value and model representations between trials. All agent behaviour was simulated using the maximum likelihood parameters fit to the rat or human data, along with an ε-greedy policy where ε = 0.1. This means the agents choose the greedy action 90% of the time and a random action 10% of the time (in order to manage the exploration-exploitation tradeoff). Due to the behavioural variance introduced by this policy, each algorithm was implemented 1000 times to produce the distribution of behaviour used for comparison with the rats and humans.

The model-free agents were simulated by implementing equation 5 at every time step to update the action-value function. The SR agents were simulated by implementing equations 7 and 8 at every time step to update the SR.
The model-based agent updated its model at every time step by observing the states adjacent to its current state and implementing the update in equation 6.
It would then sample a map from the model and use it to plan the shortest route to the goal from its current position (shortest routes were calculated using the A-star search algorithm (Hart et al., 1968). In the event of multiple equally short routes to the goal, their respective actions were sampled with equal probability.

Model-free agent

The model-free agent uses a Q-learning algorithm (Watkins & Dayan, 1992) to experientially update the state-value function Q (equation 2). Specifically, after taking action a_t in state s_t and transitioning to state s_{t+1} where it receives reward r_t, the agent will update the state-action value according to:

$$Q(s_t, a_t) \leftarrow Q(s_t, a_t) + \alpha\Big[r_t + \gamma \max_a Q(s_{t+1}, a) - Q(s_t, a_t)\Big] \tag{5}$$

where α is the learning rate and γ is the discount factor of the value function. Under a greedy policy, the model-free agent at decision time will choose an action a in state s with the highest state-action value $Q(s, a)$.

Model-based agent

The model-based agent is provided with an internal 10x10 binary grid representation of which maze modules are present or not in the environment. Every state s in the agent's model χ corresponds a module in the maze (see Fig 1A-B); as it transitions through the environment, it updates the internal model at every timestep according to the adjacent states s'.

$$\chi(s') \leftarrow \begin{cases} 1 & \text{if module } s' \text{ is present} \\ 0 & \text{if module } s' \text{ is missing} \end{cases} \tag{6}$$

At decision time, the model-based agent uses its model χ and to plan the shortest route to the goal from each possible next state. Shortest routes were calculated using an A* tree search algorithm (Hart et al., 1968), and that the value of each prospective future state was computed via equation 1.

Successor representation agent

The SR agent uses temporal-difference learning to update the successor matrix M

$$M(s,:) \leftarrow M(s,:) + \alpha[\mathbb{1}_s + M(s',:) - M(s,:)] \tag{7}$$

which can be combined with the state-rewards R at decision time to compute the value of prospective future states via equation 4.

$$R(s) = \begin{cases} 1 & \text{if } s \text{ is the goal} \\ 0 & \text{otherwise} \end{cases} \tag{8}$$

All agents implement an ε-greedy policy with $\varepsilon = 0.1$, meaning at each timestep they will choose the highest value next state with probability 0.9, or a random next state with probability 0.1. All internal representations used by the SR agent and both other RL agents were carried over onto the first trial of the subsequent maze.

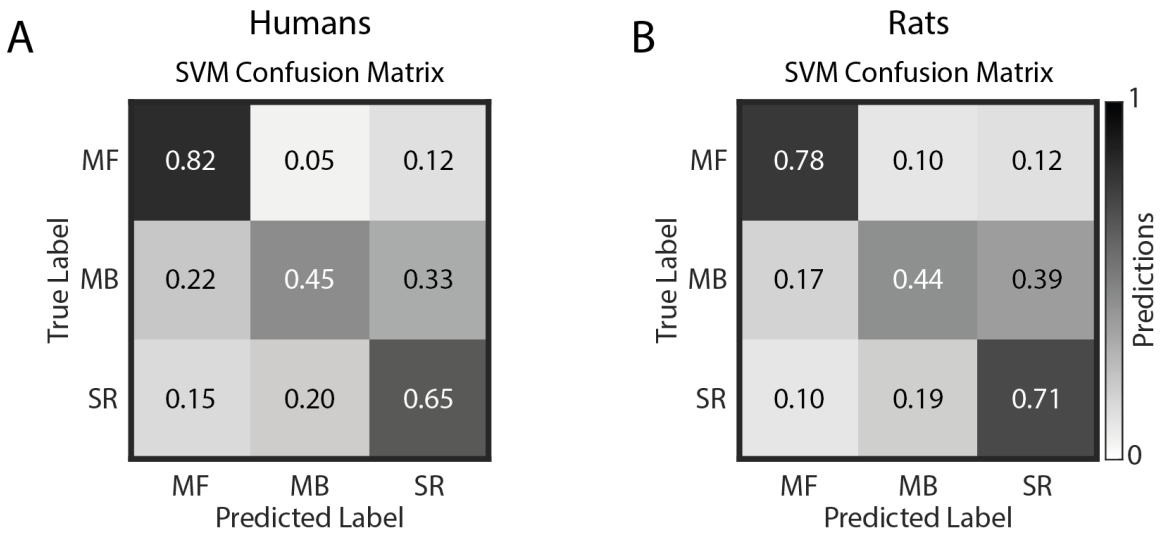
Quantification and Statistical Analysis

Optimal paths were calculated using the A* tree search algorithm (Hart et al., 1968)in the 10x10 grid state space, with path length measured in terms of state visitations. Occupancy correlations were calculated using the Pearson correlation between the proportion of time spent in each state of the 10x10 grid state space.

Likelihoods were calculated by inputting individual human/rat state trajectories to a given RL agent and calculating the internal value estimates of the available state transitions conditional on the human/rat's past trajectories. Finally, these value estimates were used in a softmax function to calculate at each time point, the probability that the agent would take each of the available actions conditioned on the human/rat's past. Maximum likelihood parameters were estimated using MATLAB's fmincon function to minimise the negative log-likelihood.

Mahalanobis distances were calculated per trial using MATLAB's pdist2 function on the trajectory metrics for the humans, rats, model-free, model-based and successor representation agents.

Support-vector machine (SVM) classifiers were trained and assessed using 5-fold cross validation to decode RL agent identities simulated with the human (SFig3a) and rat (SFig3b) maximum likelihood parameters. Individual SVM's were fit per trial using MATLAB's fitcecoc function and a one vs one coding scheme.



Supplementary Figure 3: Confusion matrices for the support-vector machine (SVM) classifier. The SVM classifier was able to accurately decode model-free (MF), model-based (MB) and successor representation (SR) agent identity based on a 5-fold cross-validation and the maximum likelihood parameters estimated from the human (A) and rat (B) behaviour.

Supplementary Videos

Video S1: An example of 10 trials (configuration 11) from the rat version of the task. Video is sped up x2 after the first trial.

Video S2: An example of 10 trials (configuration 11) from the human version of the task. Video is sped up x2 after the first trial.

Video S3: An example of 10 trials (configuration 11) of a model-free agent from the reinforcement learning simulation of the task.

Video S4: An example of 10 trials (configuration 11) of a model-based agent from the reinforcement learning simulation of the task.

Video S5: An example of 10 trials (configuration 11) of a successor representation agent from the reinforcement learning simulation of the task.

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