# Introduction

"Should I take the familiar route to work or try a new path today? Should I choose for a new dish in the menu or go for my usual one?" Everyday dilemmas like this are an example of decision-making under uncertainty. In such scenarios, individuals must constantly weigh the known against the unknown, making choices that can range from trivial to life-altering. This process becomes more important when the environment is dynamic where one’s adaptability and decision-making flexibility become key survival tools. One classic illustration of this is the exploration-exploitation dilemma, which poses a fundamental question: in an uncertain environment, how does one balance the choice between exploiting a known resource and exploring potential new ones? Exploration is a risk-taking behaviour that may come with a cost. However, without exploration, we will perseverate with same strategies and miss the opportunity to find a better option. This classical dilemma questions the current understanding of the neural underpinnings of such complex behaviours, inviting us to venture deeper into the cognitive processes involved in the same.

## Exploratory Behaviour and Attentional Resource Allocation in the Brain

Foraging is a fundamental behavior seen in many species, where individuals search for food in their environment. It inherently involves a critical decision-making process where an individual must choose between staying with a known resource (exploitation) and venturing out in search of potentially better options (exploration). This choice, fundamental in foraging behavior, becomes a complex problem of resource allocation within the brain. Decisions about leaving a current resource ("patch") rely on probabilistic and often dynamic environmental information. This decision-making process, guided by principles like the Marginal Value Theorem (Charnov et al 1996), is observed universally, from insects to humans, suggesting an underlying commonality in behavioral and neural strategies (Constantino and Daw, 2015). Exploration is influenced by various factors, including travel costs and food predictability (Lottem et al., 2018). In humans, studies on gambling (Daw et al., 2006; Raja Beharelle et al., 2015), attentional shifts to environmental changes (Müller, et al., 1995; Chetverikov et al., 2017), and visual search patterns (Kristjansson et al., 2014, Wolfe et al., 2019) reveal the brain's efficiency in adapting to subtle reward changes and environmental shifts, paralleling animal foraging behaviors.

## Prefrontal Cortex and Exploratory Decision-Making: Insights from Human and Primate Studies

Numerous studies have established the crucial role of the prefrontal cortex in decision making across species ([Bechara et al., 2003](https://www.frontiersin.org/articles/10.3389/fnbeh.2015.00007/full#B3); [Bechara, 2005](https://www.frontiersin.org/articles/10.3389/fnbeh.2015.00007/full#B2)). In humans, the anterior prefrontal cortex (aPFC), particularly the frontopolar cortex (FPC), plays a decisive role in decision-making, significantly influencing exploratory resource allocation. Notably, the FPC activates during exploratory decisions in contexts such as gambling, indicating its significant role in choosing to switch to alternative actions (Daw et al., 2006; Boorman et al., 2009). Additionally, anodal and cathodal transcranial direct current stimulation experiments involving the FPC have demonstrated a direct and polarizing impact on exploratory behavior, highlighting a causative relationship (Raja Beharelle et al., 2015).

In non-human primate studies, disruptions such as lesions in the aPFC have been linked to increased persistence in following task rules, suggesting its crucial role in shifting focus from current tasks to exploring alternative reward sources (Mansouri et al., 2015). This distinct causative role of the aPFC sets it apart from more posterior regions of the lateral prefrontal cortex, such as the inferior frontal junction area (IFJ), which primarily activates only when a task switch occurs. Furthermore, the coactivation of the frontopolar area (FP1) and IFJ observed during exploratory behaviour from functional imaging studies suggests a modulatory role of aPFC on IFJ to achieve exploratory attention shifts (Bludau et al., 2015). These functional evidences backed by the FP1’s complex dendritic spine system (high spine density but low cell body density) that offers an excellent architecture for integrating different inputs (Jacobs et al., 200, Ramnani & Owen, 2004) suggests an underlying neurocognitive circuit suitable for the comparison of current task aspects with novel information required for exploratory decisions.

In rodents, although exploratory behaviors are observed, the specific role of their frontal cortex in such behaviours remains less clear. This project aims to bridge this gap and explore the neural underpinnings of attentional resource allocation in rodents.

## Role of prefrontal cortex in exploratory behaviour in rodents?

The role of the prefrontal cortex (PFC) in rodents, particularly in terms of exploratory behavior and attentional resource allocation, represents a multifaceted and dynamic area of research. Studies have shown the medial prefrontal cortex (mPFC) to be central to decision-making processes, particularly in scenarios involving risk assessment and environmental adaptation (Orsini et al., 2018). For instance, sudden increase in mPFC neural activity was correlated to environmental changes during a tone-cued behavioural task in rats (Karlsson et al., 2012). Moreover, enhanced neuronal activity in the mPFC has been observed in mice during social approach behaviors, suggesting its active role in processing social cues, an essential requirement for exploratory behaviour (Lee et al., 2016). Additionally, accumulating evidences demonstrated that the mPFC plays an instrumental role in encoding various forms of decision-making including exploratory behaviour mainly due its strong projections from CA1, thalamus and amygdala that helps to integrate inputs from different regions and update its information about the surroundings ([Herry et al., 1999](https://www.frontiersin.org/articles/10.3389/fnbeh.2015.00007/full" \l "B23); [Thierry et al., 2000](https://www.frontiersin.org/articles/10.3389/fnbeh.2015.00007/full#B41); [Bechara et al., 2003](https://www.frontiersin.org/articles/10.3389/fnbeh.2015.00007/full#B3); [St. Onge et al., 2012](https://www.frontiersin.org/articles/10.3389/fnbeh.2015.00007/full#B38), Tang et al., 2021).

Although, mPFC was the focus point in exploring the role prefrontal cortex in decision-making research in rodents, the precise role of the rodent frontal cortex in decision-making, particularly in the context of exploratory behavior, has been a subject of considerable discussion and controversy. This debate arises primarily from the inconsistencies in nomenclature and the anatomical definition of the prefrontal cortex (PFC) in rodent models. Laubach et al. (2018) emphasize that the varied use of terms, often borrowed or adapted from primate research, has led to a fragmented understanding of the PFC’s role in rodents. Unlike in primates where the PFC is well-defined and its functions extensively studied, in rodents, the boundaries of this region are less clear, and its functions less distinct. The lack of a standardized approach in defining and researching the rodent PFC makes it challenging to draw direct comparisons with primate studies, thereby complicating the integration of rodent research into a broader neuroscientific context. This ambiguity in defining the boundaries of rodent PFC, encompassing areas like the medial prefrontal cortex (mPFC), orbitofrontal cortex (OFC), and anterior cingulate cortex (ACC), poses significant challenges in understanding its full functional spectrum, particularly in higher cognitive processes such as decision-making and attentional resource allocation.

## Mongolian Gerbils as a rodent model for exploratory behaviour

The Mongolian gerbil is a popular animal model with a long history in multiple research topics such as animals’ social cognition (Tchabovsky et al., 2019), neurological diseases – epilepsy (Cutler andMackintosh, 1989), auditory processing (cite max and Frank) and hearing loss (Scheich, 1991; Otto and Jürgen, 2011). Previous research has proved that gerbils are able to quickly learn experimental rules, adapt to environmental changes and learn complex auditory behavioural tasks such as reversal learning showcasing higher cognitive functions such as adaptive decision-making (Cite Frank and Max). Moreover, in the wild, the gerbils live in deserts making them natural foragers in one of the most dynamic environments in the world. Considering these adaptive behaviours of the gerbils, in this study, we decided to use them as a rodent model to investigate the neural underpinnings of decision making during an exploration-exploitation dilemma.

Furthermore, the gerbil atlas created by () extensively maps their cortical boundaries and connections enabling researchers to develop techniques for chronic recordings and optogenetic manipulation on these animals (Brunk et al., 2019; Zempeltzi et al., 2020). In regards to prefrontal cortex, the atlas avoids the usage of common nomenclature such as mPFC or dlPFC. Instead, just maps the anterior region of frontal cortex as frontal region A (FrA) that lies between the olfactory bulb and the secondary motor cortex. This clear anatomical distinction unlike in mice and rats forms a better analogue of human and monkey aPFC, whose role we are interested to study.

## Probabilistic Foraging as a tool to induce the exploration-exploitation dilemma

To investigate decision-making under uncertainty in Mongolian gerbils, we adapted the probabilistic foraging task from a study by Lottem et al., 2018, originally conducted with mice. This study presents a sophisticated setup to simulate an exploration-exploitation dilemma by incorporating probabilistic rules that govern the availability of rewards In this task, mice were trained in a controlled environment featuring an elongated chamber with two water-reward ports at each end. In each trial, the mice performed a sequence of nose-pokes at one of the reward ports, with each nose-poke having a decreasing probability of yielding a water reward. Such an arrangement forces the animal to constantly reassess whether to continue exploiting the current, but increasingly less rewarding resource or to explore other, potentially more rewarding options. The task was structured into three trial types, each defined by different starting reward probabilities. The introduction of varying initial reward probabilities further adds layers of uncertainty, compelling the animals to make decisions in an environment where the chances of reward are dynamic and unpredictable.

This paradigm effectively models real-life foraging scenarios and offers an excellent experimental framework to explore how rodents navigate the balance between exploitation and exploration under uncertainty. By adapting this task for Mongolian gerbils and introducing simultaneous chronic recordings, we can closely investigate the neural mechanisms of attentional resource allocation in the frontal cortex during an exploration-exploitation dilemma.

## Chronic Laminar Recordings as a tool to study frontal activity

Chronic electrophysiology recordings, used extensively in conjunction with behavioral paradigms, offer profound insights into the neural mechanisms underlying various cognitive functions. This methodology involves long-term recordings of neural activity, allowing researchers to study brain function in awake, behaving animals over extended periods. In our study, we will employ chronic laminar recordings to explore the mesoscale population activity (Local Field Potential (LFP)) across the cortical layers of the frontal region A (FrA) in Mongolian gerbils. This approach has been successfully implemented in previous studies (Happel et al., 2015; Deane et al., 2019, Zempeltzi et al., 2019), demonstrating its efficacy in capturing the dynamic neural processes in awake, behaving gerbils.

### Current source density as an analytical tool to investigate local neuronal population activity

Current Source Density (CSD) profiles, derived from laminar LFP recordings, is a critical tool in our research. CSD profiles offers a reference-free insight into the spatiotemporal sequence of neural activations across cortical layers, representing ensembles of synaptic population activity with high spatial and temporal precision (Happel et al., 2010). Unlike single-unit and calcium-imaging, CSD provides a functional readout of cortical micro-circuitry, encompassing a wider, mesoscopic view of brain function (Buzsáki et al., 2012). This methodology is particularly effective in revealing task-dependent differences in cortical activation patterns across layers from laminar recordings. Therefore, laminar CSD recordings will allow us to investigate the underlying local layer-specific FrA micro-circuit activity during the foraging behaviour, making it an ideal tool for investigating the local circuit physiology in the context of decision-making.

### Layer specific analysis and importance of it in decision making

Layer-specific analysis in the cortex is pivotal to get a nuanced understanding of different cognitive processes as studies have revealed how different layers of the cortex integrate various inputs to facilitate cognitive processes such as decision making. For instance, in mice primary auditory cortex (A1), layer 2/3 neurons exhibit task-related modulation of activity, reflecting the sum of sensory input, attentional gain, and behavioral choice (Francis et al., 2018). Furthermore, research in the gerbil auditory cortex (A1) indicates that various layers of the cortex differentially encode task- and choice-related information. Infragranular layers dominated the cortical processing modes during action selection within a detection context, while supragranular layers gained relevance when stimulus features needed to be integrated during discrimination (Zempeltzi et al., 2019). These findings expand our understanding of how individual layers contribute to the integrative circuit in the sensory cortex in order to code task-relevant information and guide sensory-based decision-making.

Accumulating evidences show that cortical layers encode relative value representations of stimulus, mirroring the principles observed in reinforcement learning models. Dopamine, a key neurotransmitter in reinforcement learning, modulates neural activity across cortical layers, influencing how information is integrated and processed for decision-making. For instance, optogenetic manipulation of VTA dopamine neurons showed reward-related modulation of auditory signal processing in the auditory cortex via a gain modulation of thalamic inputs in infragranular layers Vb/VIa (Brunk et al., 2019). Similarly, dopaminergic modulation of frontal layer-specific processing modes may set ground for the neural resource to code the salient representation of behaviourally-relevant stimuli (Homma et al., 2017; Brunk et al., 2019). Translaminar processing principles in the frontal cortex share certain common principles with the canonical cortical activation patterns (Douglas and Martin, 2007; Godlove et al., 2014). Hence, it is important to understand how the layer-specific micro-circuit activity in FrA integrates and updates the reward-related information in our probabilistic foraging task and helps the animal to adopt adequate search strategies.

# Objective

This study delves into the complexities of decision-making under uncertainty in Mongolian gerbils. Particularly, it aims to uncover the neural mechanisms and underpinnings of attentional resource allocation during the exploration-exploitation dilemma. To this end, the research will utilize a probabilistic foraging task in conjunction with chronic laminar recordings from the frontal region A (FrA), an analogue of frontopolar cortex, recognized for its significance in human decision-making. This approach allows for an in-depth analysis of the gerbil’s decision-making processes in an environment that simulates real-world uncertainties. The primary objectives of this study are:

1. To analyze the exploratory behavior of gerbils during the foraging task, particularly focusing on their decision-making strategies in response to uncertain and changing reward probabilities.
2. To investigate the role of the FrA, examining how it influences the dynamics of decision boundaries in response to varying reward probabilities.
3. To examine the layer-dependent processing within the FrA, exploring how different cortical layers adaptively contribute to the selecting adequate search strategies under varying conditions of resource availability.