

EXPLORATORY ATTENTIONAL RESOURCE ALLOCATION IN A PROBABILISTIC FORAGING PARADIGM IN THE MONGOLIAN GERBIL

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ABSTRACT

Neuronal resource allocation is essential for any cognitive function of the brain. Human and monkey studies have revealed that the anterior prefrontal cortex plays a crucial role in exploratory resource allocation processes. In rodents also, the prefrontal cortex region has been studied to assess exploration/exploitation trade-offs using various behavioral paradigms. However, in the context of such variable switches of exploratory resource allocation, the role of the frontal cortex is still under discussion. In the current study, a probabilistic foraging paradigm was developed using the Mongolian gerbil (*Meriones unguiculatus*) as the animal model abetted by food restriction. A critical parameter for the investigation of exploration/exploitation trade-offs is the so-called economic switching costs. In order to manipulate these, three different foraging setups were used with a difference in their travel distance between two foraging spouts where the animal was able to approach consecutively. With each new approach, the reward probability was reduced exponentially in order to force a trade-off to explore another food source. Firstly, a food restriction paradigm was developed that evoked sufficient motivational search behavior while the animals still exhibited stable physical conditions measured by dense body weight monitoring. A quantitative analysis of different foraging parameters was used to characterize the

foraging behavior in early and established (performing) phases. By applying various statistical analyses (Wilcoxon rank-sum test, two-way ANOVA), it was found that the change in travel distance between the foraging spouts has a less influence on the behavior of the animals. The findings of this study pave the way for investigating the neuronal resources in the frontal cortex during exploratory resource allocation in the food-searching gerbil.

Keywords: aPFC, Mongolian gerbils, food restrictions, foraging task, travel distance, Wilcoxon rank-sum test, two-way ANOVA

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INDEX OF NOTATION

ANOVA	Analysis of Variance
aPFC	anterior Prefrontal Cortex
BA	Brodmann Area
BBW	Baseline Bodyweight
CSD	Current Source Density
fMRI	Functional Magnetic Resonance Imaging
FPC	Frontopolar Cortex
IPI	Inter Poke Interval
lFP	left Frontopolar Cortex
LFP	Local Field Potentials
mPFC	medial Prefrontal Cortex
MVT	Marginal Value Theorem
rFP	right Frontopolar Cortex
ST	Setups
TT	Trial Types
WCST	Wisconsin Card Sorting Test

1. INTRODUCTION

1.1. RESOURCE ALLOCATION

Performing a deterministic task relies on the coordination of different brain mechanisms involving various brain regions. The decisions made during the task require the allocation of scarce processing resources to the brain systems that involve task understanding, response planning, and action implementations. In the course of a task, a population of neurons was recruited in the brain system relevant to the task which fires in response to certain inputs. The metabolic resource-dependent (oxygen and glucose) neuron firing transmits the information to another neuron population via electrical impulses and chemical signals so that the choices were made during the task and signals sent to the motor system for executing the action (Alonso et al., 2013). The metabolic resources lineate with the neuronal resources, as only limited amounts of neuronal activity can be used at a time. In certain tasks, this metabolic resource limitation also means cognitive limitation. This study focuses on the cognitive resource of attention which can be distributed to focal or global aspects of the sensation and henceforth the exploration and exploitation concepts were examined.

1.2. EXPLORATION/EXPLOITATION

The choice of deciding between exploration and exploitation in search of a reward is hard for any species in this world. At times, humans tend to shift away from actions with known outcomes (exploitation) and experiment with untried options (exploration) which could possibly increase their long-term success (Beharelle et al., 2015). The exploration/exploitation dilemma can be resolved by adopting different exploratory strategies, and different theoretical frameworks that deliver

exploration driving factors. The explorations could be random processes in accordance with reinforcement learning theory while they were regarded as directed or intentional processes in optimal decision-making theories (Dezza et al., 2017).

1.3. ROLE OF ANTERIOR PREFRONTAL CORTEX IN EXPLORATION-EXPLOITATION TRADE-OFF

In humans, the Brodmann area (BA) 10 is mostly related to the anterior region of the prefrontal cortex covering a remarkably larger proportion of the cortex. The anterior prefrontal cortex (aPFC) could be involved in problem-solving, which implies more than one discrete cognitive process. This leads to speculation that the aPFC may play an important role in the coordination of processing and transfer of information between numerous cognitive operations (Ramnani & Owen, 2004).

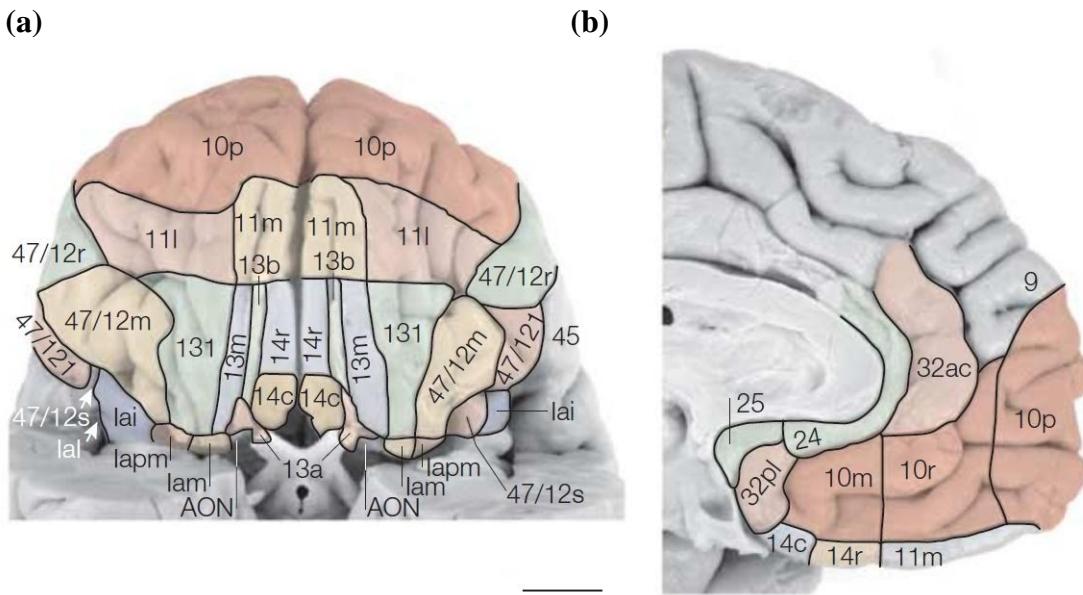
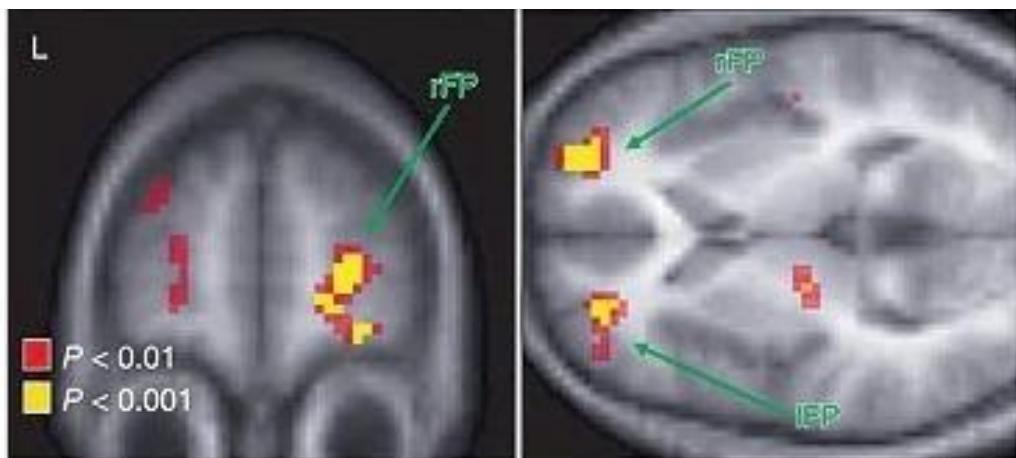


Fig. 1.1. Location of cytoarchitectonic BA 10 (shaded in red) surface rendered onto the (a) orbital and (b) medial surface of the human brain (From Ramnani & Owen, 2004)

An fMRI study in human participants performing the four-armed bandit task that demands a choice among the four slot machines alongside the classification of trials as the dominant slot machine with the highest expected value (exploitative) or lowest expected value (exploratory), revealed that the anterior frontopolar cortex could be considered as the driving mechanism that facilitates the switching between the behavioral strategies of exploratory and exploitative approaches (Daw et al., 2006). A similar kind of bandit task in humans along with transcranial stimulation over the frontopolar cortex (FPC) showed that exploratory behavior was intensified by excitatory neuronal stimulation of the FPC but the reduction of such excitatory stimulation resulted in more exploitative choices (Beharelle et al., 2015).



**Fig. 1.2. Significantly increased activation in the regions of left (lFP) and right (rFP) frontopolar cortex on comparison of exploratory with exploitative trials
(From Daw et al., 2006)**

The FPC-lesioned macaque monkeys displayed enhanced performance by exploiting the current task in Wisconsin Card Sorting Test (WCST) by possessing a strong working memory for maintaining the information of the appropriate rule of the current task while facing many interruptions (other irrelevant samples and

alternative rules). The FPC has a unique role in redistributing the executive control resources among potential goals existing in complex, changing situations (Mansouri et al., 2015).

1.4. EXPLORATORY RESOURCE ALLOCATION IN RODENTS

Examination of the neural dynamics of the medial prefrontal cortex (mPFC) of a rat performing the tone-cued behavioral task of making choices between two reward probabilities (high or low), exhibited a sudden, coordinated, and extensive shift in neural population activity in the mPFC when the animal recognizes a change in their environment (Karlsson et al., 2012).

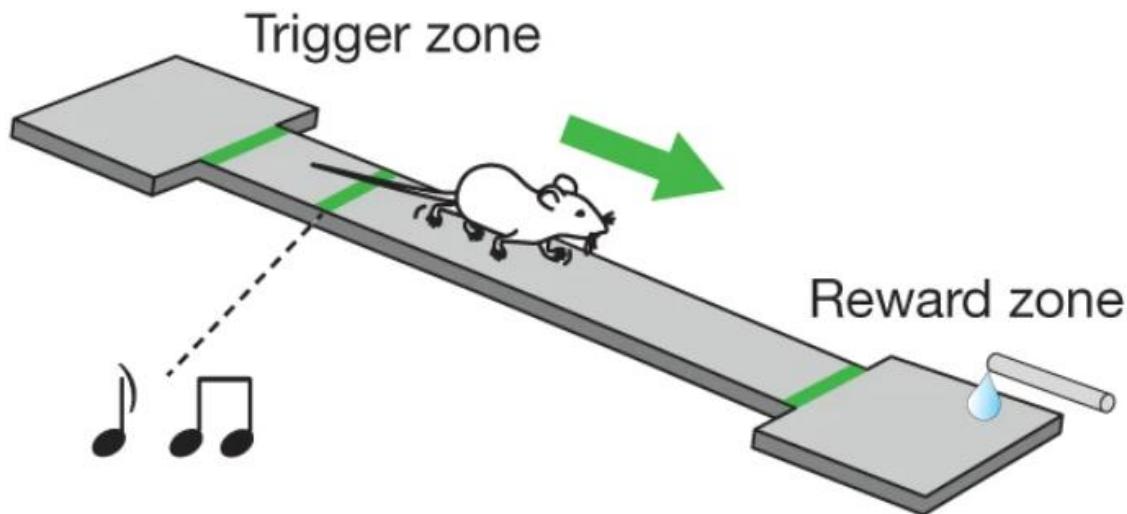


Fig. 1.3. Caricature of a mouse performing the water-rewarded foraging task in the foraging platform with trigger and reward zone of at the ends
(From Kvitsiani et al., 2013)

Electrophysiological recordings from two classes of inhibitory interneurons (parvalbumin and somatostatin) in the mouse prefrontal cortex while executing the foraging task between the trigger and water-reward zones show that the responses of these interneurons are accountable for the animal's foraging decisions i.e.

approach for staying and leaving the reward zone (Kvitsiani et al., 2013). Specifically, the somatostatin neurons had a selective response for the exploratory behavior, i.e. when the animal approached the reward zone, and the parvalbumin neurons responded at the reward leaving approach.

1.5. APPROACH FOR INVESTIGATING THE EXPLORATION/ EXPLOITATION TRADE-OFF

Animals have the ability to show flexible behavior based on their previous experiences in that environment but the mechanism of the information encoded in animal's brains pertaining to their behavior remains unclear. Different behavioral tasks have been given to the animals for studying their frontal cortex activity during active exploration of the environment. Nevertheless, the role of the frontal cortex in exploration behavior is still debatable (Karlsson et al., 2012). This raises the need for a well-designed behavioral paradigm to study the exploration/exploitation trade-off in animals.

1.5.1. PROBABILISTIC FORAGING TASK

In the present study, the well-known animal model, Mongolian gerbil (*Meriones unguiculatus*), was used as their cortex is well described in systems neuroscience. Also, studies have been performed with them to show the role of the frontal cortex during decision making (Stark et al., 2004) which requires considerable space for building the behavioral setup. Furthermore, techniques for chronic recordings and optogenetic manipulation were also developed on these animals (Brunk et al., 2019; Zempeltzi et al., 2020). Here, the animals were food-restricted for carrying out the probabilistic foraging task but the water was supplied ad libitum.

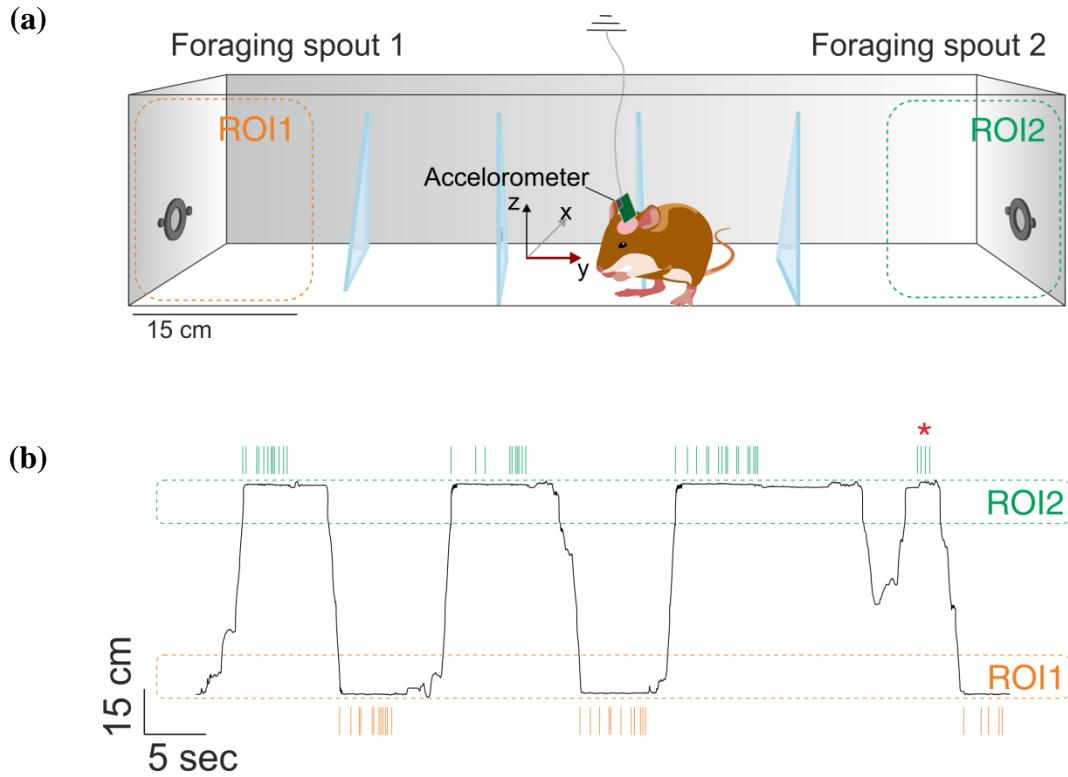


Fig. 1.4. The probabilistic foraging task. (a) Schematic representation of the foraging setup with foraging spouts at the ends of the setup; (b) One-dimensional location of an example animal along the axis of the box plotted as a function of time (green & orange ticks: nose-pokes, red asterisk: error trial) (From Lottem et al., 2018)

For studying the exploration/exploitation trade-off in Mongolian gerbils, the probabilistic foraging setup adapted from Lottem et al., 2018 was built. The random probability schedule for the rewards in this foraging task allows the animals to forage between the foraging spouts, yielding many trials that account for both exploration and exploitation strategies.

As the advent of rewards was not cued to the animals during the task, the foraging approach was based on the actual rewards received in the trial so that a fixed, reward-independent behavioral strategy would be avoided. Moreover, by adopting the probabilistic foraging paradigm, many foraging parameters (Fantino & Abarca, 1985) can be studied easily.

In the current study, the probabilistic foraging task was also helpful in investigating the impact of the travel distance between the foraging spouts with the support of three different foraging arenas with various travel distances (short box and long box foraging setups).

1.6. AIM AND OBJECTIVES OF THE STUDY

The aim of this study was to establish a probabilistic foraging paradigm in food-restricted Mongolian gerbils for investigating the exploration/exploitation trade-offs. This Master's Thesis mainly focuses on developing a probabilistic foraging paradigm (Lottem et al., 2018) in food-restricted Mongolian gerbils which is a new development of a procedure in this animal model that has never been tested before.

The discrete objectives of the current study were:

1. Establishing a suitable food restriction regime in the Mongolian gerbil to allow the titration of sufficient motivational drive and keep the animals in a healthy physical state. Hence, the daily food intake and bodyweight of the animals was closely monitored with respect to the behavioral performances of the animals.
2. Constructing the foraging setup in which probabilistic foraging paradigm would be used to examine the exploration and exploitation approaches of the animals. Then, distinct behavioral parameters of the probabilistic foraging task were analyzed to assess the performance of the animals in the foraging task. In the end, the best foraging parameter for identifying the performing phase of the animals would be enumerated.
3. Replication of the foraging setup with various travel distances between the foraging spouts and using a statistical tool (Wilcoxon rank-sum test) to

- inspect the impact of different travel distances in between the spouts of the foraging setup on animals' behavior in the probabilistic foraging task.
4. Comparing the performances of the animals in different trial types across different forms of the foraging setups by applying various statistical analyses (Wilcoxon rank-sum test, 2-way ANOVA) to check whether the trial types influenced any change in the foraging behavior of the animals in the probabilistic foraging task.

2. MATERIALS AND METHODS

In this study, a probabilistic foraging task was performed with food-restricted Mongolian gerbils (*Meriones unguiculatus*). The main purpose of this study was to develop a probabilistic foraging paradigm based on food restrictions for the animals which was adapted from the water restricted probabilistic foraging task (cf. Lottem et al., 2018).

2.1. ANIMAL SUBJECTS

Experiments were carried out with adult male Mongolian gerbils (n=8, in-house breeding). The age of the animals was 3 to 4 months while performing foraging tasks in the short box. When the same eight animals were used in the foraging task with the long box, their age was 4 to 7 months. All animals were housed at a temperature of 25°C and humidity 30 - 50% under a 12-hr dark/light non-inverted cycle. The conventional cages (Type IV) with raised wire lids were used, which allows nesting. Their cages were filled with hay, woodchips, and paper-based bedding. For the enrichment of their environment, tunnels were placed inside the cage.

2.2. FOOD RESTRICTION

The animals had free access to water but were food restricted from three days before the start of the foraging task. The bodyweight of the animals was monitored daily from the day of food restriction. The average of bodyweights measured during the three days of food restriction before the start of the foraging task was called baseline bodyweight (BBW). The BBW of the animals was 70 - 80g before starting the foraging task in the short box, while the BBW was 80 - 95g in the case of the long box. To keep the animals' bodyweights above the critical level (85% of

BBW) during the foraging task period, food was supplemented inside the cage at least 2 hours after the end of the foraging task. The daily food intake of animals was maintained between 3 - 7g based on the performance of the animals in the foraging task.

2.3. FORAGING SETUP

The foraging setup consisted of an arena/foraging box where the animal performed the task. There were two foraging spouts present on opposite sides of the box where the food was dispensed. Food dispensers were controlled by custom-built Arduino hardware, which was operated by an experimenter using a custom-written Application program in MatLab.

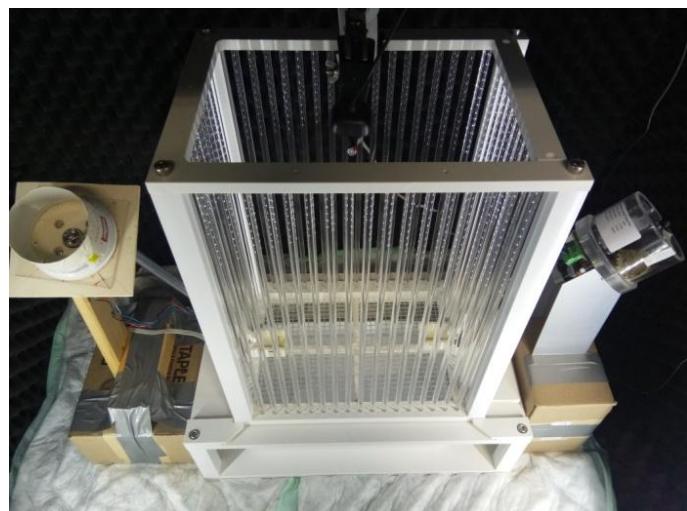
2.3.1. FORAGING BOX

The foraging box was placed in an electrically shielded and sound-proof chamber. The framework of the box was made with wood while the walls of the foraging box were made up of cylindrical plastic bars placed 1cm apart from each other. The floor of the box was made up of plastic mesh; therefore underneath the floor, a large tray was placed to collect animals' excrement. The two spouts were placed on the ends of the box. Each spout was attached to a food dispenser (Campden Instruments Ltd., USA) placed outside the foraging box. On the sides of the spouts, an infrared emitter/sensor pair was located to measure the nose-pokes of the animals.

The dimensions of the foraging box were 37cm x 26cm x 48cm (short box, **fig 2.1 (a)**) and 70cm x 31cm x 45cm (long box, **fig 2.1 (b)**). The distance between the spouts was 36cm (short box) and 67cm (long box). In the long foraging box, there were provisions for placing walls in between the spouts. Three walls were placed

in which two were kept at a distance of 17.5cm from the ends of the box and one was kept at the middle of the box.

(a)



(b)



Fig. 2.1. Foraging setup (without walls) with spouts at the ends attached to food dispensers with a camera at the top. (a) Short box; (b) Long box

2.3.2. OTHER DEVICES AND SOFTWARE

The whole experimental session was recorded with a camera (Microsoft LifeCam HD-3000) placed above the foraging box. The camera was positioned in such a way that the field of view included the whole floor of the foraging box, spouts, and lower parts of the walls to properly monitor animal behavior during the experiment (**fig 2.3**).

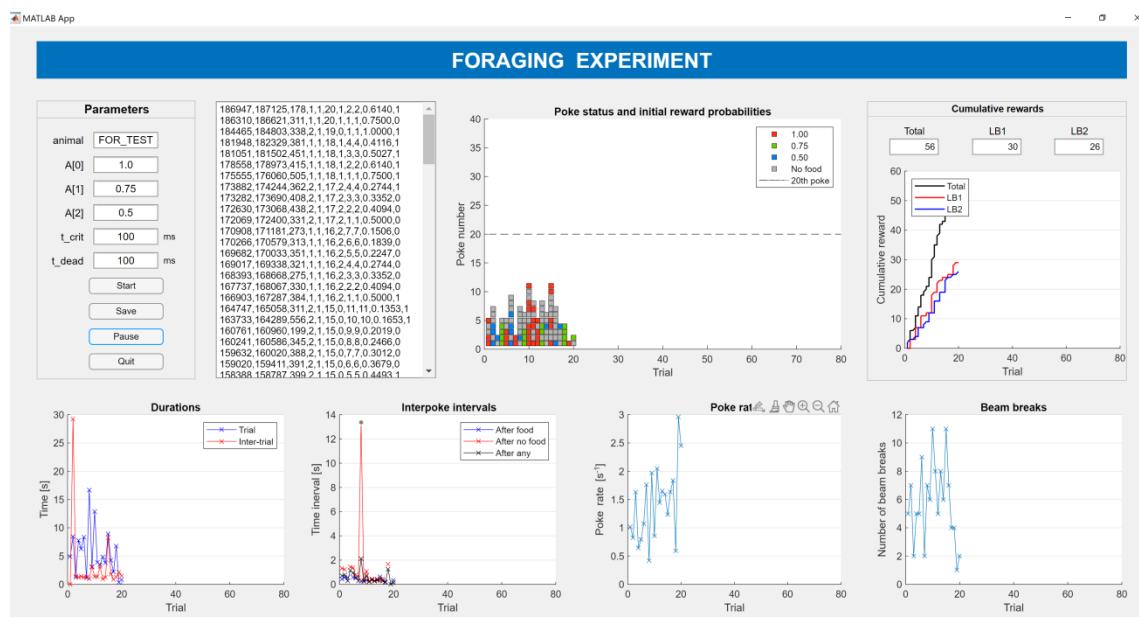


Fig. 2.2. MatLab application showing an animal's performance during foraging task

A red LED light positioned below the camera for detecting hit pokes (see section **2.4**) was also covered during the video recordings. The light source was provided in the form of two vertical light panels attached on both sides of the chamber door to aid the recordings.

The food dispensers were controlled by a custom-made microcontroller device which was commanded by a custom-written Arduino codenamed “Foraging_02”. The whole foraging setup was governed by a MatLab code “Foraging_05_App”. This MatLab code receives the input from the user and the Arduino commands

were passed through to obtain the information regarding each animal's behavior in foraging task (**fig 2.2**). For video recording the whole foraging task, OBS 25.0.8 software was used.

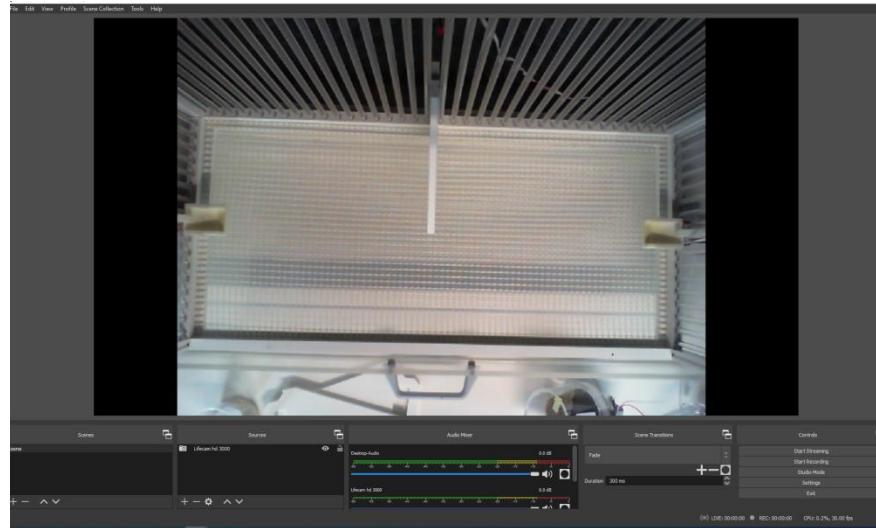


Fig. 2.3. Video recording during foraging task using OBS software

2.4. PROBABILISTIC FORAGING PARADIGM

The probabilistic foraging task (cf. Lottem et al., 2018) was carried out without any prior trainings or habituation in the foraging setup. Each animal was trained for one session per day. In each session, the animal could perform the foraging behavior for a maximum of 30 minutes.

Each foraging session consisted of an 'N' number of trials in accordance with the animal's behavior. Every trial contained a sequence of nose-pokes in one of the two foraging spouts. Error pokes were the ones that lasted for less than 100ms while the pokes that lasted for at least 100ms were called hit pokes. The error pokes were unrewarded and the hit pokes were either rewarded with 20mg of commercially available food pellet or unrewarded based on the reward probability

and reward outcome of that poke (for details see below). The reward probabilities decreased after each hit poke, forcing the animal to alternate between the spouts during the foraging session.

Three different reward probabilities were used, which decreases exponentially with each increasing hit poke number according to the equation,

$$P(o_n = 1|t_i) = A_i e^{-(n-1)/5}$$

where t_i is the i^{th} trial type ($i = 1, 2, 3$) corresponding to different exponential scaling factors of $A_1 = 1.0$, $A_2 = 0.75$, $A_3 = 0.75$ (fig 2.4). ‘ n ’ marks the hit poke number within a trial, and o_n is the outcome of the n^{th} poke (1 for reward and 0 for no reward). Trial types (exponential scaling factors) were randomly interleaved and trial type identity was not cued to the gerbils. Reward probability was set to zero during error pokes. To obtain more trials from the animals and to maintain the motivation of the animals for a longer period, the reward probability was set to zero after the 20th nose-poke of a trial. A dead time of 100ms was set to pause the session whenever the rewarding hit poke had occurred.

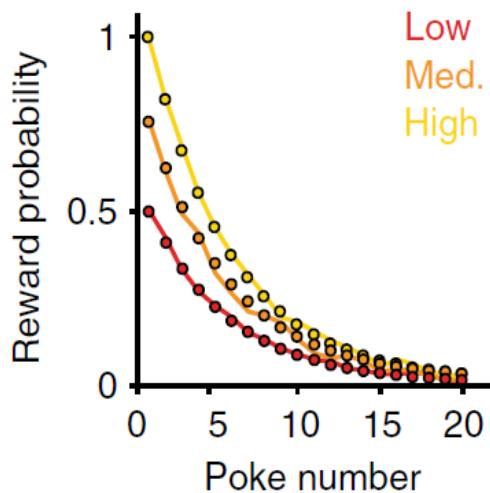


Fig. 2.4. Exponential decay of reward probabilities for three different starting reward probabilities (From Lottem et al., 2018)

Once the animal had learned the foraging task well, they might have done other activities like biting the bars on the walls of the foraging box and jumping along the sides of the foraging box. In such a case, the foraging task was suspended and the animal was taken out of the foraging box.

The foraging paradigm was accomplished in three different foraging setups such as,

- without any walls in between the spouts - short box
- without any walls in between the spouts - long box
- with three walls in between the spouts - long box

2.5. DATA ANALYSIS

All data analysis was executed using custom-written codes in MatLab Software.

2.5.1. ANIMALS' WEIGHT AND FOOD INTAKE

The baseline bodyweight measurement of each animal (n=8) was used to calculate the respective animal's weight in percentage for each foraging session. Then, the average percentage of animals' weights was calculated for each session. Likewise, the averages of the amount of food pellets eaten in the foraging task, quantity of food ingested inside the cage, and total food consumed for each foraging session were calculated.

2.5.2. SESSION-WISE ANALYSIS

In session-wise analysis, five foraging parameters were analyzed as follows:

2.5.2.1. TIME SPENT FOR NOSE POKING IN THE FORAGING SPOUT

In each trial, the food-restricted animals will stay near one of the foraging spouts and nose-poke to obtain the food pellet as their reward. The time taken by the animals for the nose poking in the spouts was calculated as:

$$\text{Duration of nose-pokes (in s)} = \text{Time of last nose-poke} - \text{Time of first nose-poke} \\ (\text{within the same trial})$$

2.5.2.2. TOTAL NUMBER OF NOSE-POKES

Within a trial, the animals can nose-poke to their maximum extent but no reward will be given after its 20th hit poke. Therefore, the animals exploit the current foraging spout by nose-poking a few times and move to the opposite spout. The nose-pokes consist of both the hit pokes and the error pokes.

2.5.2.3. RATE OF NOSE POKING

The nose-pokes by the animals in the foraging spout were done at a particular rate which was evaluated as:

$$\text{Rate of nose poking (pokes/s)} = \frac{\text{Number of nose-pokes}}{\text{Duration of nose-pokes (s)}} \quad (\text{within the same trial})$$

2.5.2.4. INTER POKE INTERVALS BETWEEN TWO SUCCESSIVE NOSE-POKES

Inter poke intervals (IPI) were the duration between two successive nose-pokes in which the preceding nose-poke was a rewarded or unrewarded hit poke.

$$\text{Inter poke interval (in s)} = \text{Time of } n^{\text{th}} \text{ nose-poke} - \text{Time of } (n-1)^{\text{th}} \text{ hit poke}$$

where, n^{th} nose-poke could be a hit or error poke

$(n-1)^{\text{th}}$ nose-poke would have been rewarded or unrewarded

2.5.2.5. TIME TAKEN TO TRAVEL FROM ONE SPOUT TO ANOTHER SPOUT

Travel time was the time taken by the animals for making the movement between the foraging spouts. It was calculated as,

$$\text{Travel time (in s)} = \frac{\text{Time of the first poke in the current trial}}{\text{Time of the last poke in the preceding trial}}$$

2.5.2.6. STATISTICAL METHODS

As the data inside each session were not normally distributed, the median was taken as the best measure of each foraging parameter. For each parameter, the median was evaluated for each session of each animal. Then, the median of medians of all animals across each foraging session was visualized using conventional box plots.

A decision criterion (see Results section 3.2) was assigned in the foraging parameter of travel time to distinguish between animals' non-performing phases and performing phases. The sessions that fulfill the decision criterion were called performing phase sessions of the animals. Likewise, the performing phase sessions were noted down for each foraging setup. The median of medians of each of five parameters in the performing phase sessions was compared across the setups and their significance levels were enumerated using Wilcoxon rank-sum test.

2.5.3. TRIAL-WISE ANALYSIS

In this part of the analysis, five different trial-based parameters were analyzed as given below:

2.5.3.1. TOTAL NUMBER OF NOSE-POKES

The animals were trained to nose-poke in the foraging spout to obtain their rewards. Depending upon the duration of the nose-pokes, they were split into two types as hit pokes and error pokes.

2.5.3.2. TOTAL NUMBER OF UNREWARDED NOSE-POKES

In every trial, the error pokes in the foraging spout which lasts for less than 100ms was unrewarded while the hit pokes lasting for at least 100ms were either unrewarded or rewarded with a food pellet based on the reward probability and reward outcome of that particular hit poke. Therefore, there could be more unrewarded nose-pokes than rewarded nose-pokes in each foraging trial.

2.5.3.3. NUMBER OF CONSECUTIVE UNREWARDED NOSE-POKES BEFORE SPOUT LEAVING

The animals exploited the foraging spout by nose poking and consumed the food pellets obtained as rewards. When the animals sensed that the rewards had depleted in the current foraging spout, they traveled to another foraging spout located on the opposite side of the setup. Hence, before leaving the current spout, the animals tended to do a few unrewarded nose-pokes consecutively.

2.5.3.4. TOTAL NUMBER OF REWARDS

The hit pokes in the foraging spout with the reward outcome of 1 were always rewarded with a 20mg food pellet. This could be measured as the number of rewards or rewarded hit pokes in each trial.

2.5.3.5. POKE NUMBER OF THE FIRST REWARD

In all of the foraging setups, the trial type with the starting probability of A=1 was always rewarded for its first hit poke. But for the other two trial types, the first reward was obtained based on the reward outcome of that particular nose-poke.

2.5.3.6. STATISTICAL METHODS

At first, the individual trials done by the animals in the performing phase sessions were listed down for each foraging setup. The medians of each parameter were compared across different setups for each starting reward probability and also compared across different starting reward probabilities for each setup. Wilcoxon rank-sum test was carried out to inspect the level of significance difference between the medians for each parameter. As the number of hypotheses tested here was large ($m=18$), the statistical test was conducted for Bonferroni corrected significance values (α/m). For the trial-wise parameters, two-way ANOVA (analysis of variance) was also carried out to assess the main effects of each independent variable (setups (ST) and trial types (TT)) and the interaction between them.

3. RESULTS

The number of sessions varied between the short box and the long box for few animals. Hence, for our analysis, the first 15 sessions in the short box and the 15 sessions of the long box of all the animals ($n=8$) were taken. Concurrently, the 5 sessions performed by all the animals in the long box by placing the walls in between the spouts were also considered for our analysis.

3.1. EFFECT OF FOOD INTAKE ON ANIMALS' BODYWEIGHT IN FORAGING SESSIONS WITH DIFFERENT FORAGING SETUPS

3.1.1. SHORT BOX

In foraging sessions with the short box, the daily food intake was altered between 3-7g during the initial phases. It is evident from **fig. 3.1(a)** that the total food consumption was between 5-7g at the ending phases. The amount of food eaten via food pellets received during the foraging session was also increasing for succeeding sessions. At the same time, the animals' bodyweights were also above the critical level (85% of BBW).

3.1.2. LONG BOX

For the foraging task in the long box, the sessions without any walls in between the spouts and sessions with walls were executed one after the other without any pause in between. Unlike the sessions in the short box, the daily food intake was altered between 4-7g throughout the sessions in the long box. Here also, the food consumed in the foraging task increased for the later sessions, and the animals' bodyweights were also kept above the minimum level.

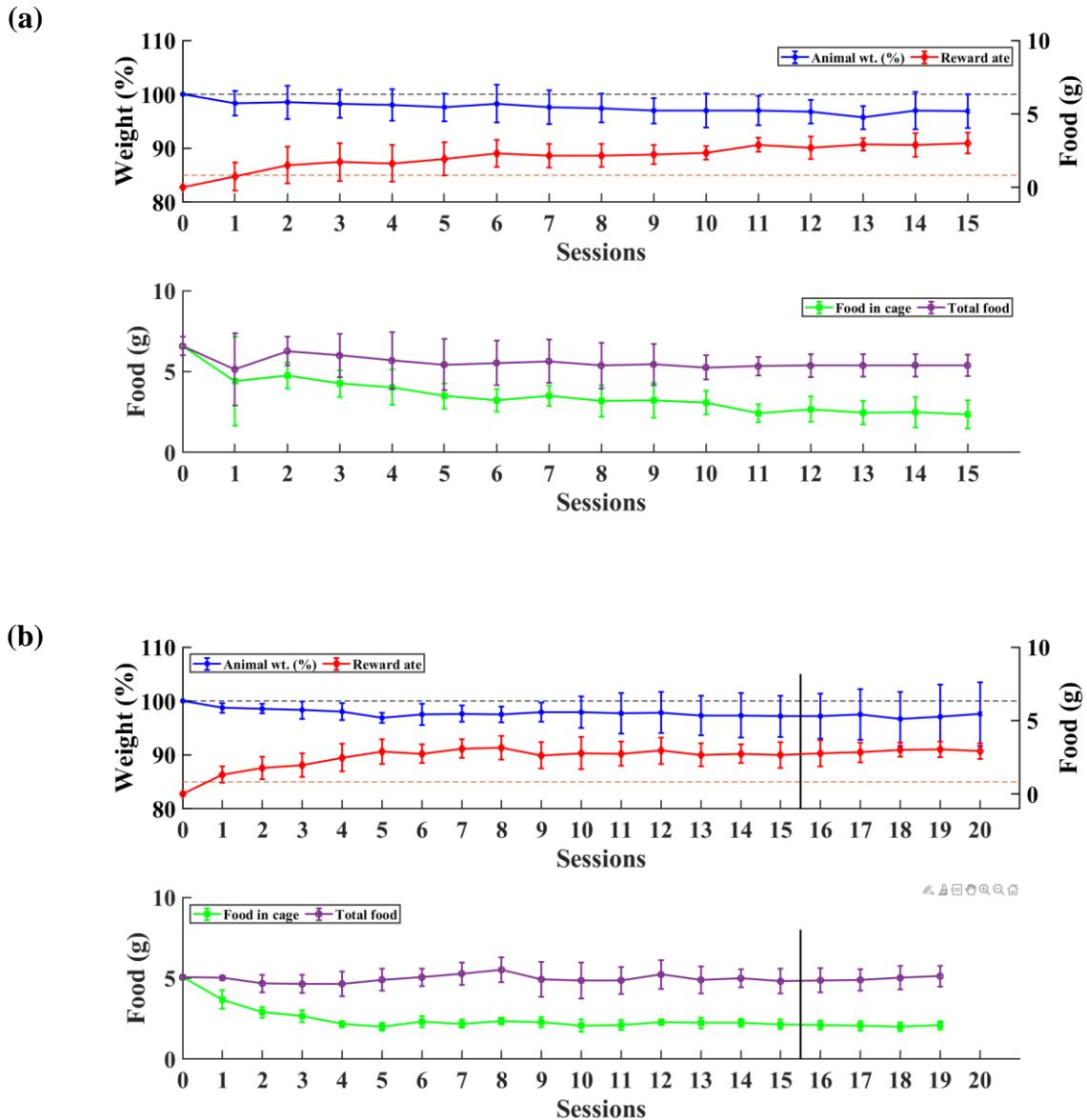


Fig. 3.1. Bodyweight of the animals and daily food intake during foraging sessions in different foraging setups. Average of animals' bodyweights in percentage (blue line) represented with the average consumption of rewards (red line); Average consumption of food kept in the cage after foraging session (green line) with average total food consumed (purple line) by the animals. All the four lines represent mean \pm std. ($n = 8$). (a) Short box; (b) Long box, the line before 16th session marks the start of foraging sessions with walls in between the foraging spouts.

3.2. SESSION-WISE ANALYSIS

Altogether, five different foraging parameters (see Methods section **2.5.2** for definitions) were analyzed for overall sessions of all the animals in each setup (see supplementary figures **S1-S10** in Appendix).

Prior to the start of the foraging sessions in the long box setup with walls, all the animals were already well trained for the foraging task in other two forms of the foraging setup. Therefore, all the sessions in this foraging setup were considered as the performing phase sessions and it is evident from the supplementary **fig. S10(C)** that the median of the travel time is always less than 5s for each session. Hence, the travel time of lesser than or equal to **5s** was considered as the criterion to separate the performing phase sessions from the non-performing phase sessions for all the animals in each foraging setup.

Primarily, when the foraging tasks were performed in the short box without any walls in between the spouts, the foraging sessions **7-15** met the criterion for performing phase. Similarly, the foraging sessions **3-15** and **1-5** were the performing phase sessions for the long box experiments without and with the walls respectively.

For all the parameters analyzed here, Wilcoxon rank-sum test was conducted to check for the level of significant difference between the median of medians of the performing phase sessions of different foraging setups.

3.2.1. TIME SPENT BY THE ANIMALS FOR NOSE POKING IN THE FORAGING SPOUT

In every trial, the animals spent some time at one of the foraging spouts for nose poking which was calculated as the difference between the times of the last poke and the first poke in that trial.

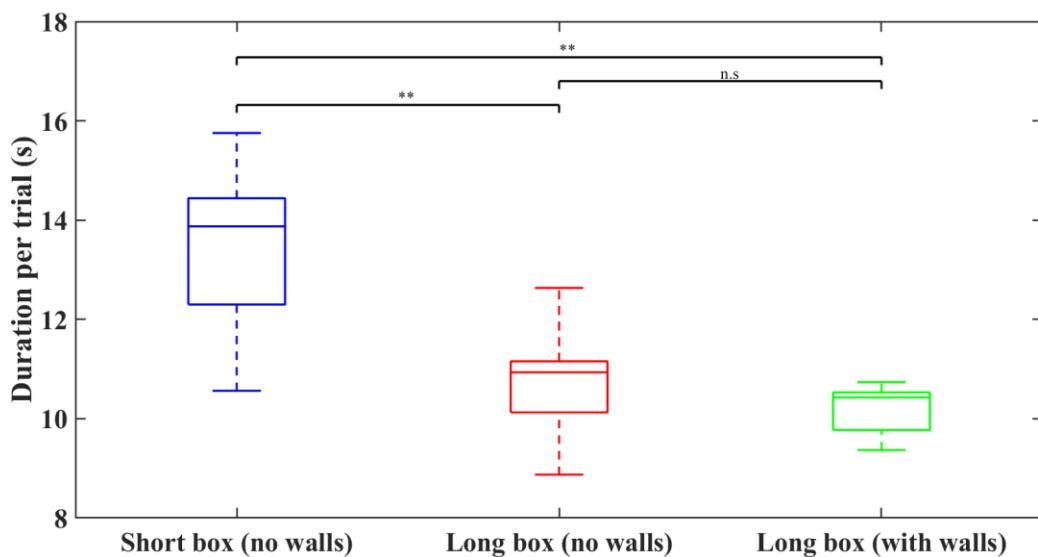


Fig. 3.2. Duration of nose-poking at the foraging spout in performing phase sessions of different foraging setups. Box plots represent the median and inter-quartile range and the significance bars indicate the differences given by Wilcoxon rank-sum test ($p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

For nose poking, the animals spent a significantly longer time at the foraging spouts in the short box compared to both of the long box foraging setups (fig. 3.2). But, there was no significant difference between the two conditions in the long box setup (with vs. without walls).

3.2.2. NUMBER OF NOSE-POKES MADE BY THE ANIMALS IN THE FORAGING SPOUT

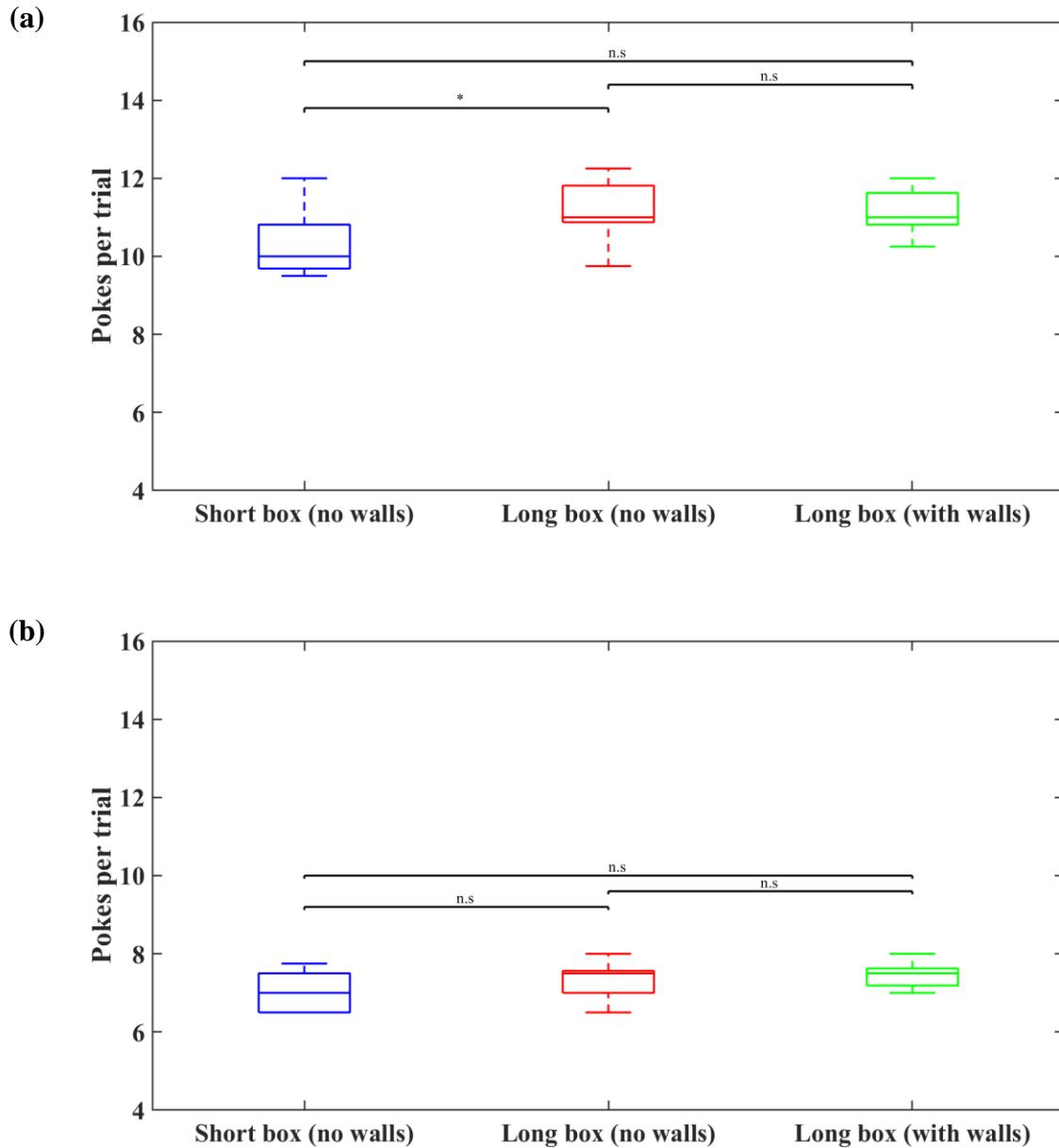


Fig. 3.3. Number of nose-pokes in the foraging spout in performing phase sessions of different foraging setups. (a) Total number of nose-pokes (both hit and error pokes) made by the animals; (b) Total number of hit pokes made by the animals. Box plots represent the median and inter-quartile range and the significance bars indicate the differences given by Wilcoxon rank-sum test ($p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

In search of a reward, the animals make numerous hit pokes and error pokes in each trial. The total number of nose-pokes (both hit and error pokes) made by the animals was significantly higher in the long box than the short box (**fig. 3.3 (a)**) when no walls were placed in between the foraging spouts. No significant difference was found between the long box setup with and without walls.

In the case of considering only the number of hit pokes (**fig. 3.3 (b)**) made by the animals, the median of all the foraging setups was highly similar — showing no significant effects in Wilcoxon rank-sum test.

3.2.3. RATE OF NOSE POKING IN THE FORAGING SPOUT BY THE ANIMALS

The total number of nose-pokes and the time spent by the animals for nose poking in the foraging spouts determines the rate of nose poking which denotes the quickness of the animals in exploiting the foraging spouts. In both the instances of the total number of nose-pokes (both hit and error pokes) and the total number of hit pokes, the medians of the rate of nose poking were lower in the short box than both the long box foraging setups.

It is also noticeable that the level of significant difference between the medians for all the three comparisons was the same ($p < 0.01$) for the poking rates in both the cases of the total number of nose-pokes (**fig. 3.4 (a)**) and the total number of hit pokes (**fig. 3.4 (b)**).

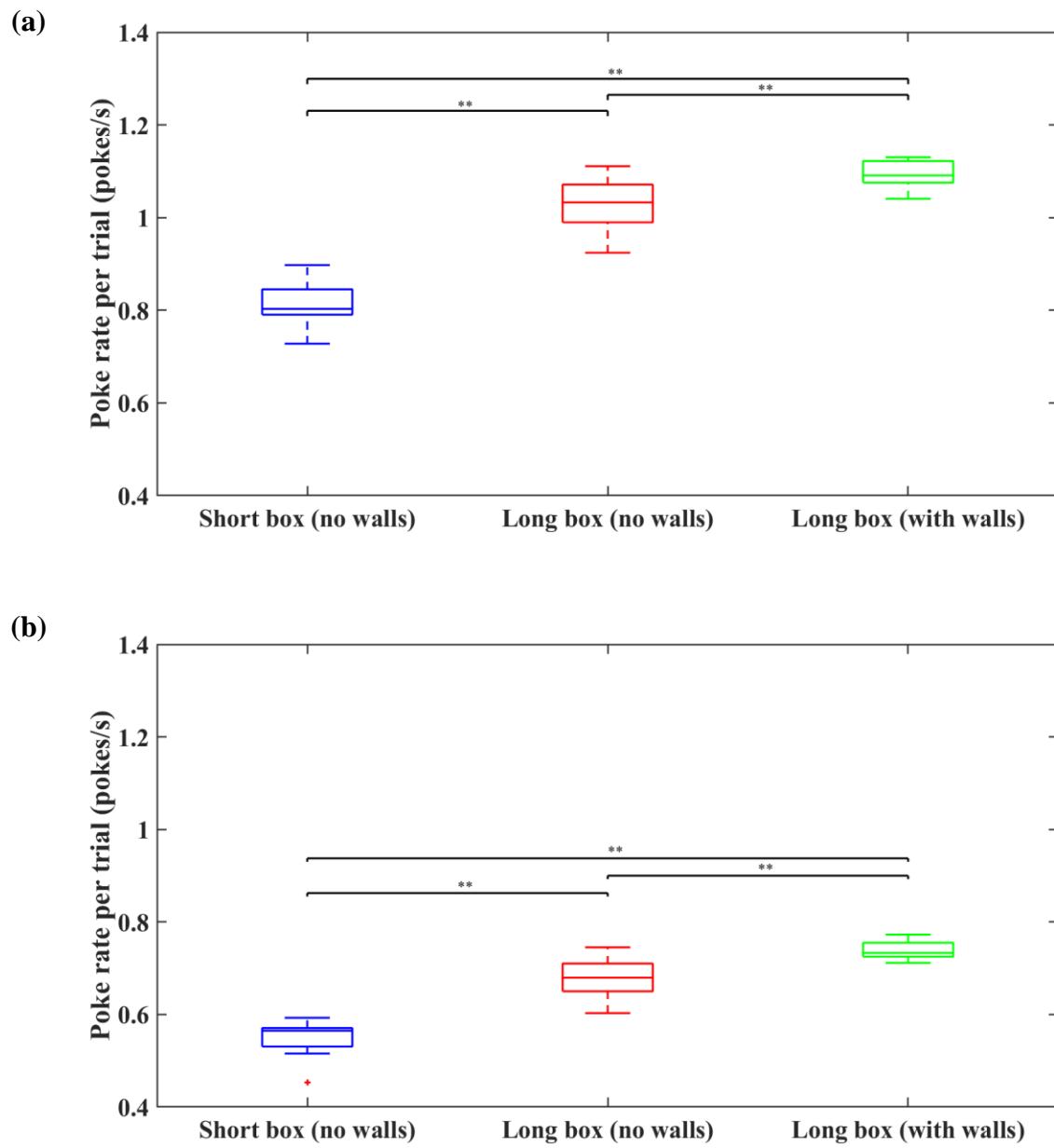


Fig. 3.4. Rate of nose poking in the foraging spout in performing phase sessions of different foraging setups. (a) Rate of nose poking for the total number of nose-pokes (both hit and error pokes) made by the animals; (b) Rate of nose poking for the total number of hit pokes made by the animals. Box plots represent the median and inter-quartile range and the significance bars indicate the differences given by Wilcoxon rank-sum test ($p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

3.2.4. INTER POKE INTERVALS BETWEEN THE SUCCESSIVE NOSE-POKES IN THE FORAGING SPOUT

During the course of a trial, the animals were rewarded with a food pellet or unrewarded for hit pokes based on the reward probability and reward outcome at that moment. Therefore, the animals tended to nose-poke the foraging spout after a rewarded hit poke in search of another reward or else seeking for a reward after an unrewarded hit poke. The time differences between the preceding hit poke and the latter nose-poke were called as inter poke intervals.

When the preceding hit poke was rewarding (**fig. 3.5 (a)**), the inter poke intervals were higher in the long box foraging setup with walls compared to the setups without the walls. Also, the inter poke intervals in the short box were lesser than both of the long box foraging setups. The level of significant difference between the medians for all the three comparisons was also the same ($p < 0.01$). But in the event of unrewarded preceding hit pokes (**fig. 3.5 (b)**), no significant differences were seen between the three foraging setups.

On enumerating the difference between the inter poke intervals of the two outcomes for the preceding hit poke (**fig. 3.6**), the median of the short box was significantly lesser than both the long box foraging setups as the medians of both the long box foraging setups were almost equal.

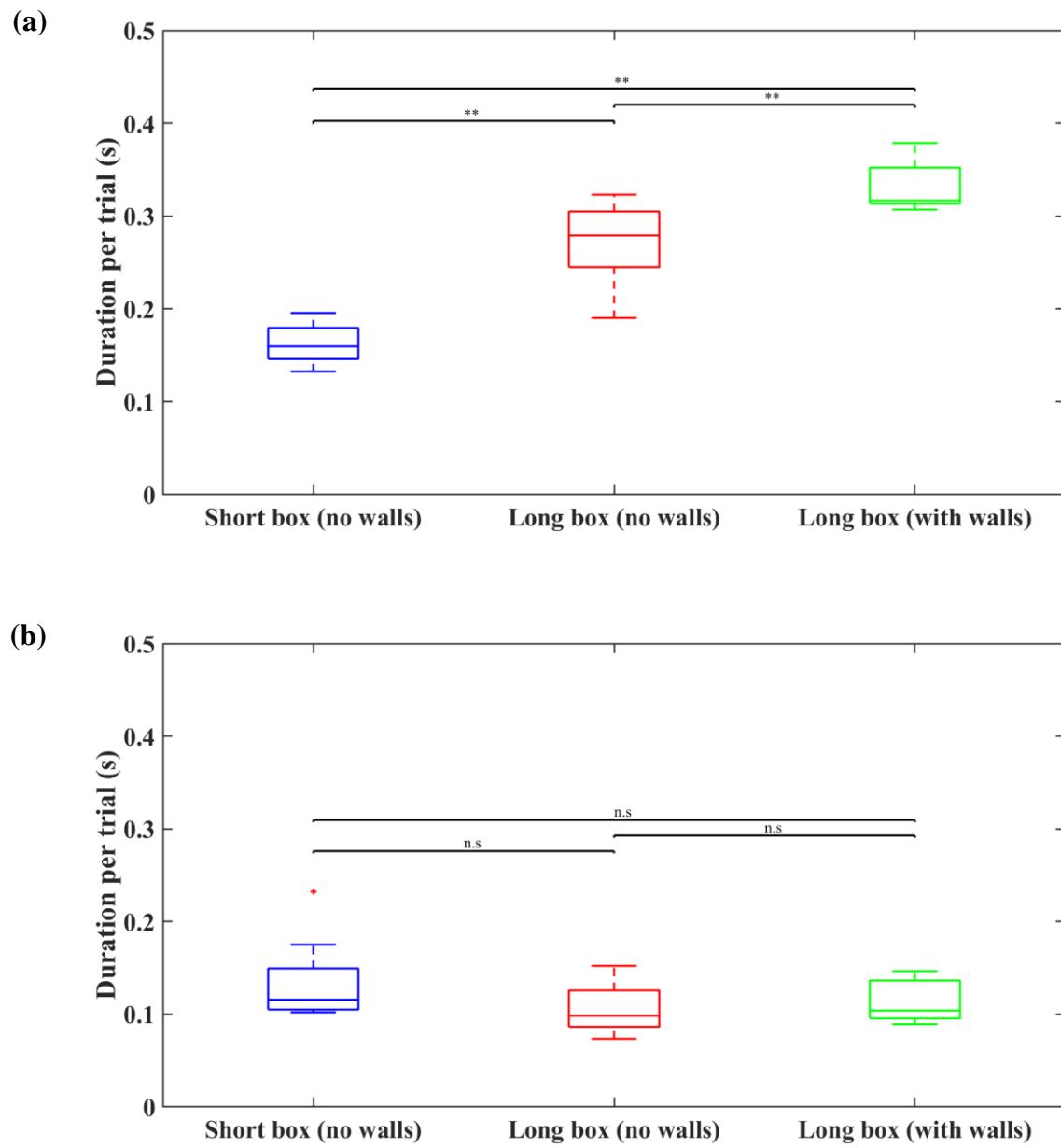


Fig. 3.5. Inter poke interval between the successive nose-pokes in the foraging spout in performing phase sessions of different foraging setups. (a) Inter poke interval in which the preceding hit poke was rewarded with a food pellet; (b) Inter poke interval in which the preceding hit poke was unrewarded. Box plots represent the median and inter-quartile range and the significance bars indicate the differences given by Wilcoxon rank-sum test ($p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

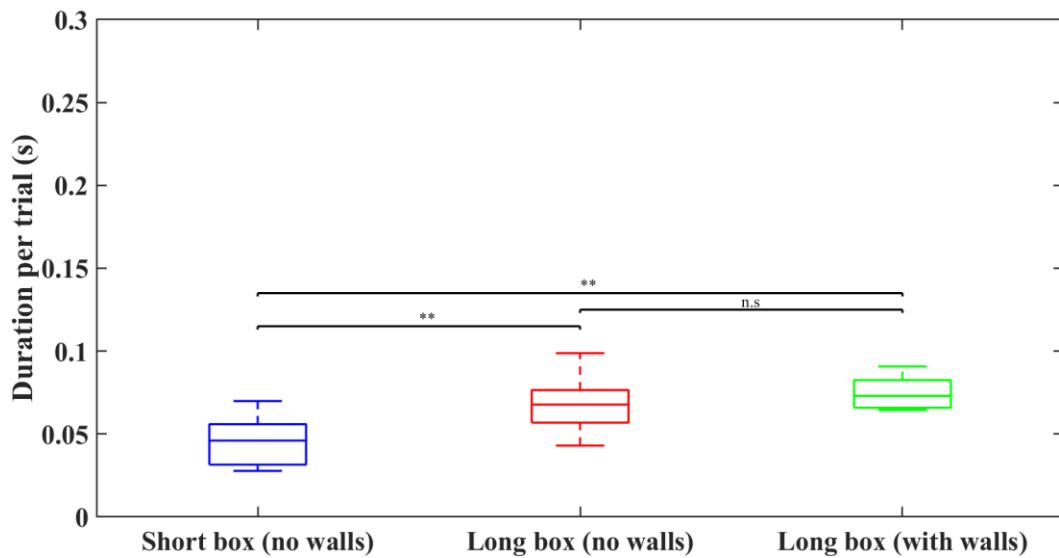


Fig. 3.6. Difference between the inter poke intervals of rewarded and unrewarded preceding hit poke in performing phase sessions of different foraging setups. Box plots represent the median and inter-quartile range and the significance bars indicate the differences given by Wilcoxon rank-sum test ($p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

3.2.5. TIME TAKEN BY THE ANIMALS TO TRAVEL FROM ONE SPOUT TO ANOTHER SPOUT

At the moment at which the animals want to stop exploiting the current foraging spout, they move towards another foraging spout placed at the opposite side of the foraging setup. The time taken by the animals to travel between the foraging spouts was termed as travel time.

As we took the same decision criterion of travel time for all the foraging setups, we could not witness any significance difference between the medians of travel time across different foraging setups (**fig 3.7**).

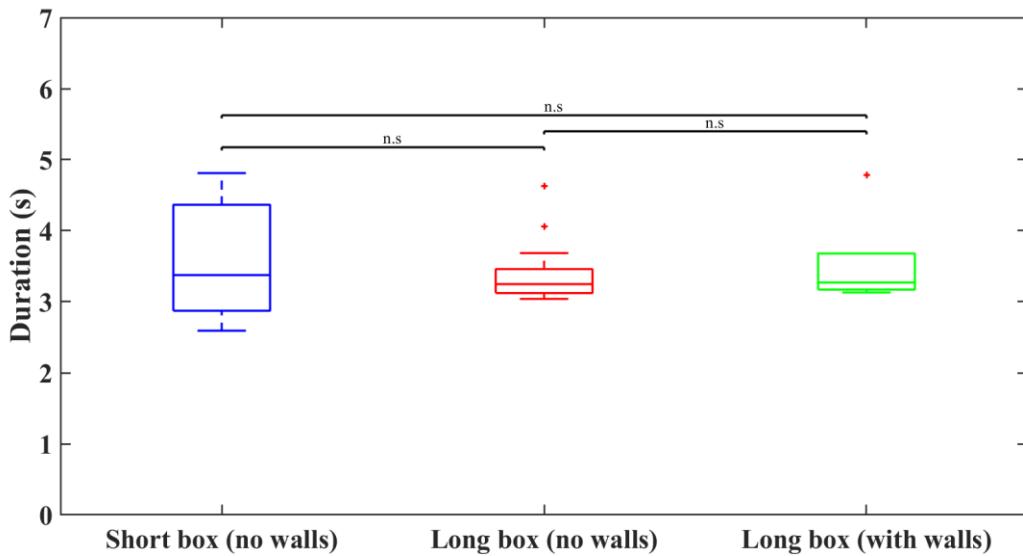


Fig. 3.7. Time taken to travel between the foraging spouts in performing phase sessions of different foraging setups. Box plots represent the median and inter-quartile range and the significance bars indicate the differences given by Wilcoxon rank-sum test ($p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)

3.3. TRIAL-WISE ANALYSIS

The individual trials in the performing phase sessions of each setup were enumerated, and five separate parameters (see Methods section 2.5.3 for definitions) were analyzed in each trial. For the foraging setups without any walls in between the spouts, 3100 trials and 4432 trials were observed for the short box and the long box respectively. In the case of the long box setup with walls, the trial count was 1760 (see supplementary table S16).

The significance levels of difference were estimated using Wilcoxon rank-sum test for Bonferroni corrected significance values. The comparison was done across different setups for each trial type (starting reward probability) and also across different trial types for each setup. Simultaneously, a two-way ANOVA test was conducted for each trial-based parameter.

3.3.1. NUMBER OF NOSE-POKES MADE BY THE ANIMALS IN THE FORAGING SPOUT

To obtain a reward, the animals explored the foraging arena and exploited one of the foraging spouts by nose poking it. For comparison of the total number of nose-pokes between different foraging setups for the same trial type, a significant difference was seen only for the trial type with the starting probability A=0.5 (**fig. 3.8 (a)**) where the long box foraging setup with walls was seen significantly higher than the rest of the two foraging setups.

Nevertheless, seven out of nine comparisons between different trial types for each foraging setup showed higher significant differences. In the two-way ANOVA for the main factors (setup type (ST) & trial type (TT)), the significant effects were found for ST: $F_{2,9283} = 7.73$; **p=0.0004** and TT: $F_{2,9283} = 114.42$; **p<0.0001**, but no significant interaction was found; ST x TT: $F_{4,9283} = 0.91$; **p=0.4543**.

On considering the number of hit pokes made by the animals (**fig. 3.8 (b)**), the long box foraging setup with walls significantly differed from both the setups without walls for the trial types with the starting probabilities of A=1 and A=0.5.

Here also, the higher significance level of differences was seen for all of the comparisons between different trial types of the same foraging setup. In the two-way ANOVA for the main factors (ST & TT), the significant effects were found for ST: $F_{2,9283} = 10.55$; **p<0.0001** and TT: $F_{2,9283} = 190.67$; **p<0.0001**, but no significant interaction was seen; ST x TT: $F_{4,9283} = 0.97$; **p=0.4209**.

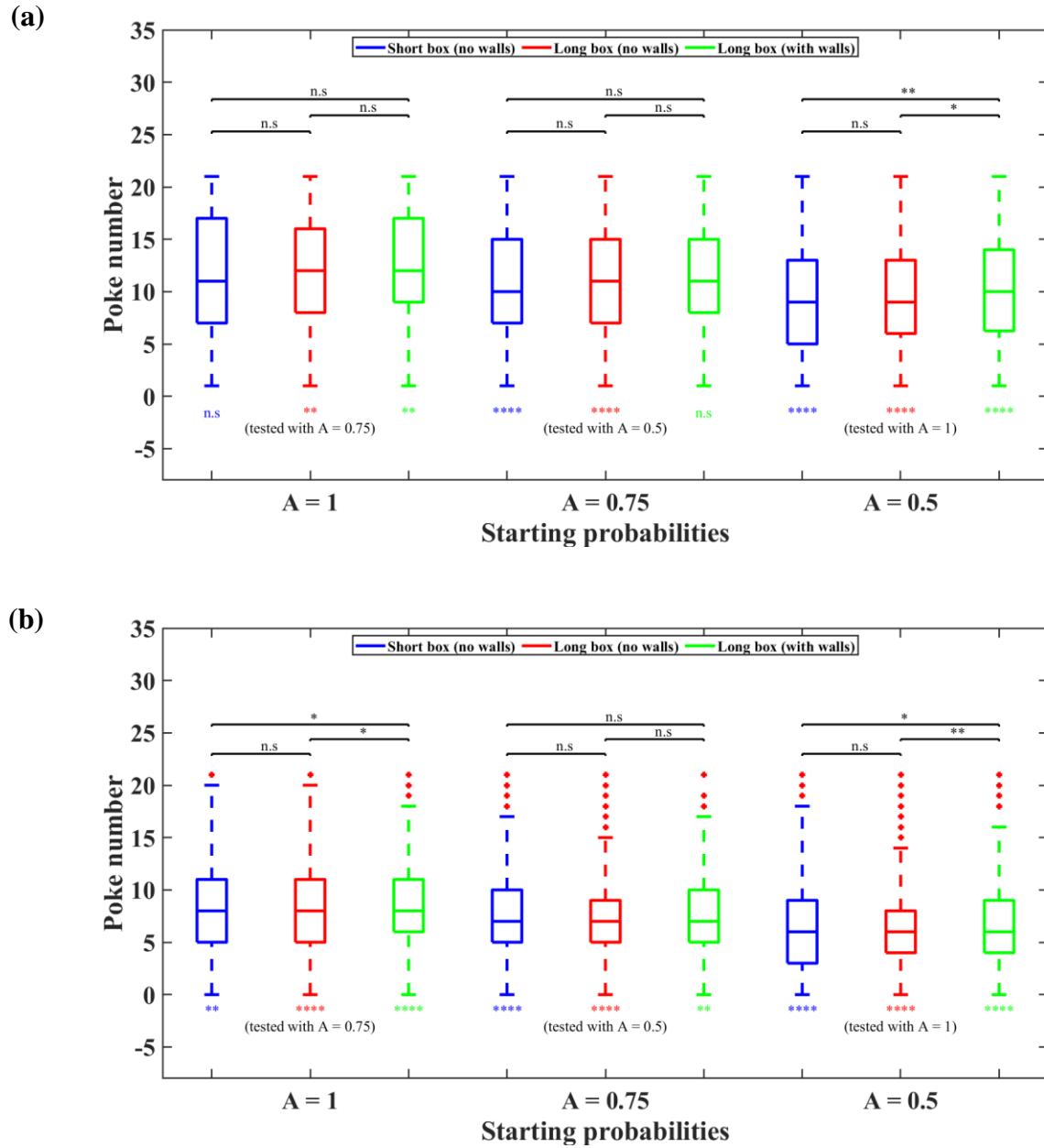


Fig. 3.8. Number of nose-pokes in the foraging spout indifferent to trial types of performing phase sessions of different foraging setups. (a) Total number of nose-pokes (both hit and error pokes) made by the animals; (b) Total number of hit pokes made by the animals. Box plots represent the median and inter-quartile range; the significance bars indicate the differences between different foraging setups for each trial type; the significance stars below each box plot represent the differences between different trial types (given in braces) for each setup given by Wilcoxon rank-sum test for Bonferroni corrected p-values ($p < 0.05/18(*)$, $p < 0.01/18 (**)$, $p < 0.001/18 (***)$, $p < 0.0001/18 (****)$)

3.3.2. NUMBER OF UNREWARDED NOSE-POKES MADE BY THE ANIMALS AT THE FORAGING SPOUT

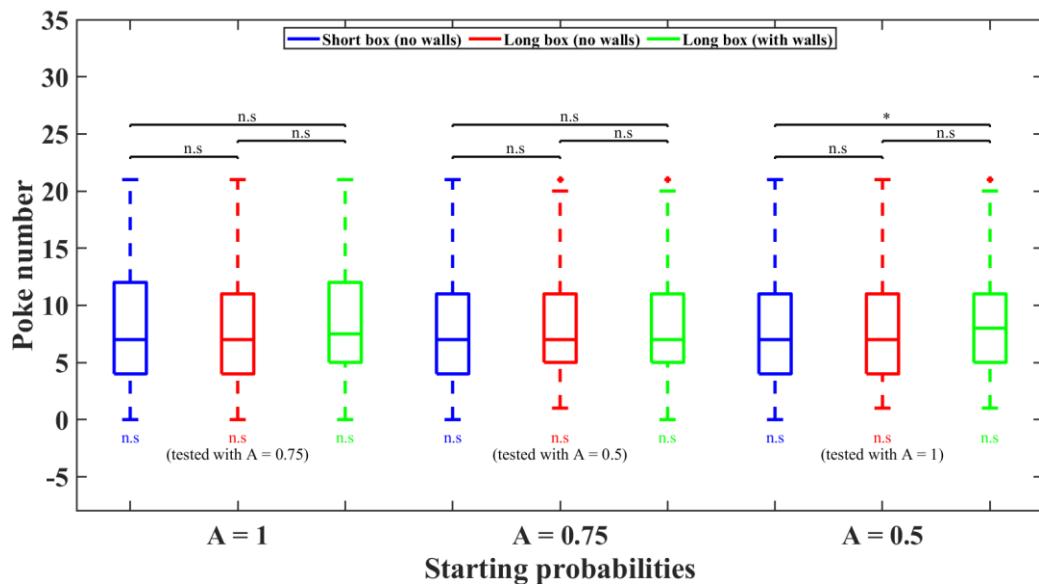
Most of the nose-pokes at the foraging spout will be unrewarded as the probability of getting a reward decayed exponentially after each hit poke. On analyzing the number of unrewarded nose-pokes, the trial type with the starting probability of A=0.5 only showed a significant difference between the short box without walls and the long box with walls when all the types of unrewarded nose-pokes were examined.

The other comparisons did not have any significant effect in Wilcoxon rank-sum test for Bonferroni corrected p-values. In the two-way ANOVA for the main factors (ST & TT), the significant effect was found only for ST: $F_{2,9283} = 3.39$; **p=0.0337** but not for TT: $F_{2,9283} = 2.62$; **p=0.0732**, also no significant interaction was found; ST x TT: $F_{4,9283} = 0.91$; **p=0.4556** (**fig. 3.9 (a)**).

When the unrewarded hit pokes were taken alone, the two long box foraging setups differed significantly for the trial types with the starting probabilities of A=1 and A=0.5. In conjunction, the one significant difference seen for the unrewarded total number of nose-pokes was also observed for the unrewarded hit pokes. For the comparisons across different trial types in the matching foraging setup, the long box setup without walls exhibited a lower significant difference between the trial types with starting probabilities of A=1 and A=0.75.

In the two-way ANOVA for the main factors (ST & TT), the significant effect was found only for ST: $F_{2,9283} = 11.11$; **p<0.0001** but not for TT: $F_{2,9283} = 2.96$; **p=0.0519**, also no significant interaction was found; ST x TT: $F_{4,9283} = 0.89$; **p=0.4718** (**fig. 3.9 (b)**).

(a)



(b)

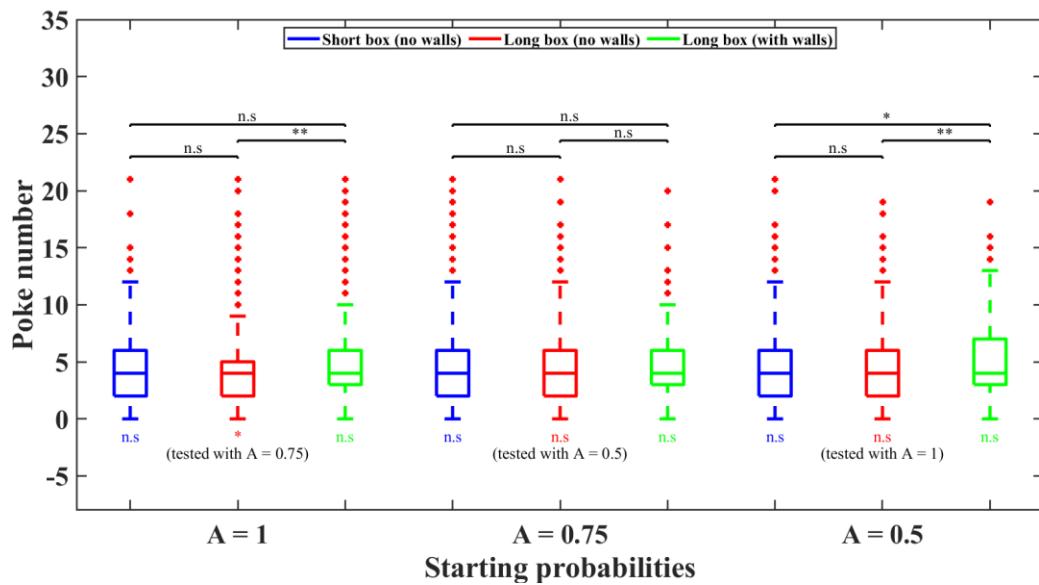


Fig. 3.9. Number of unrewarded nose-pokes at the foraging spout in different trial types of performing phase sessions of different foraging setups. (a) Total number of unrewarded nose-pokes (both hit and error pokes) made by the animals; (b) Total number of unrewarded hit pokes made by the animals. Box plots represent the median and inter-quartile range; the significance bars indicate the differences between different foraging setups for each trial type; the significance stars below each box plot represent the differences between different trial types (given in braces) for each setup given by Wilcoxon rank-sum test for Bonferroni corrected p-values ($p < 0.05/18$ (*), $p < 0.01/18$ (**), $p < 0.001/18$ (***), $p < 0.0001/18$ (****))

3.3.3. NUMBER OF CONSECUTIVE UNREWARDED NOSE-POKES MADE BY THE ANIMALS BEFORE LEAVING THE SPOUT

In most of the trials, a consecutive number of unrewarded nose-pokes were observed when the animals stopped exploiting the current foraging spout. On noticing both unrewarded hit and error pokes done consecutively before leaving the current foraging spout (**fig. 3.10 (a)**), no significant differences were seen across the foraging setups for each trial type.

But for both the foraging setups without walls, significant differences were seen between the trial types with starting probabilities of A=0.5 and A=1. In the two-way ANOVA for the main factors (ST & TT), the significant effects were found for ST: $F_{2,9283} = 4.56$; **p=0.0105** and TT: $F_{2,9283} = 8.78$; **p=0.0002**, but no significant interaction was seen; ST x TT: $F_{4,9283} = 0.78$; **p=0.5394**.

When consecutive unrewarded hit pokes were only considered, significant differences were seen between the long box setups for the trial types with the starting probabilities of A=1 and A=0.5 (**fig. 3.10 (b)**). For all the foraging setups, significant differences were observed between the trial types with starting probabilities of A=0.5 and A=1. In the short box setup alone, a difference was seen also between A=1 and A=0.75.

In the two-way ANOVA for the main factors (ST & TT), the significant effects were found for ST: $F_{2,9283} = 9.67$; **p=0.0001** and TT: $F_{2,9283} = 10.28$; **p<0.0001**, but no significant interaction was seen; ST x TT: $F_{4,9283} = 1.68$; **p=0.1508**.

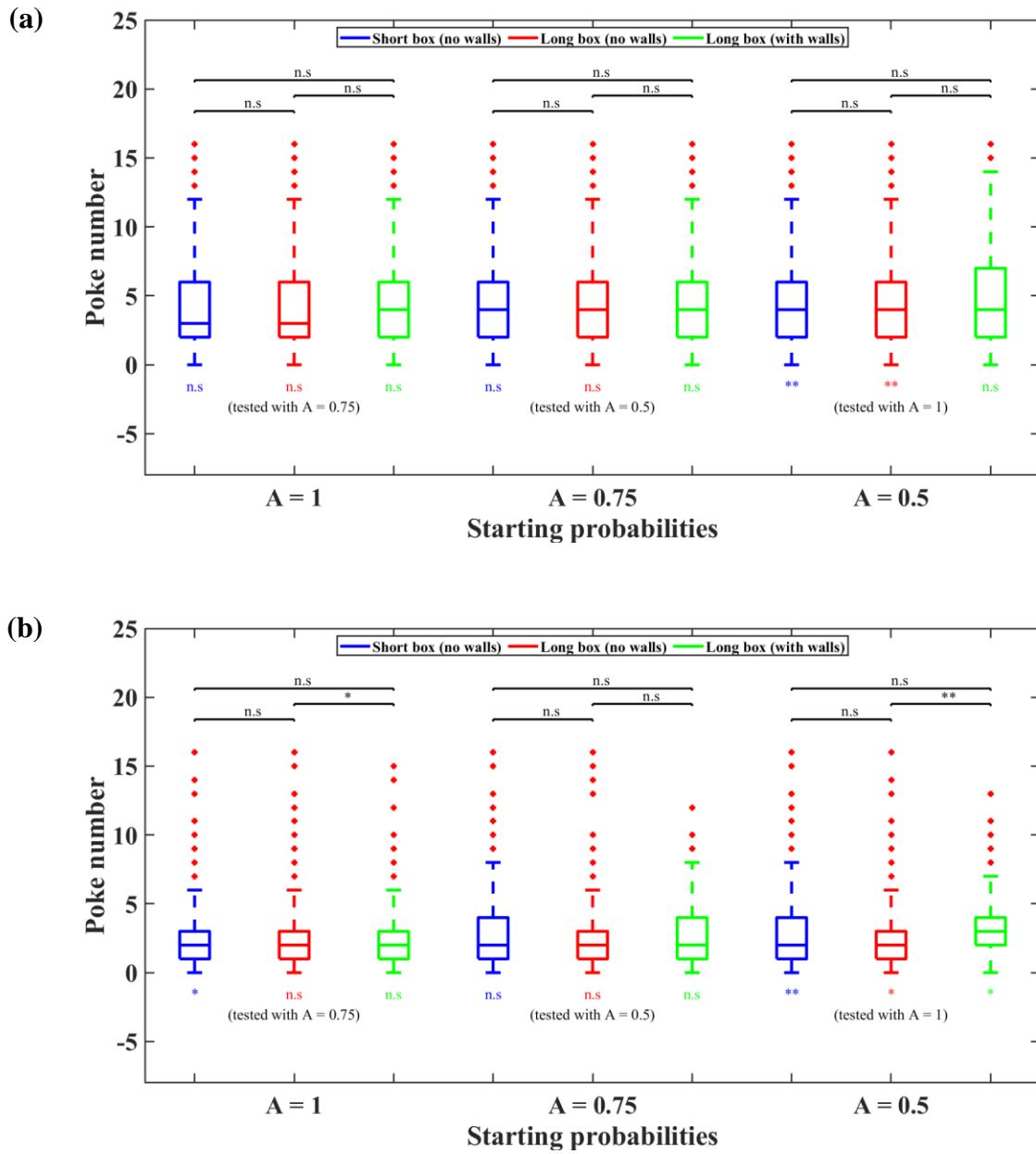


Fig. 3.10. Number of consecutive unrewarded nose-pokes before leaving the foraging spout in different trial types of performing phase sessions of different foraging setups. (a) Total number of consecutive unrewarded nose-pokes (both hit and error pokes) made by the animals; (b) Total number of unrewarded consecutive hit pokes made by the animals. Box plots represent the median and inter-quartile range; the significance bars indicate the differences between different foraging setups for each trial type; the significance stars below each box plot represent the differences between different trial types (given in braces) for each setup given by Wilcoxon rank-sum test for Bonferroni corrected p-values ($p < 0.05/18$ (*), $p < 0.01/18$ (**), $p < 0.001/18$ (***) $p < 0.0001/18$ (****))

3.3.4. NUMBER OF REWARDS OBTAINED BY THE ANIMALS

Based on the reward probability and reward outcome, hit pokes were rewarded with a food pellet. On comparing the number of rewards obtained in each trial across different foraging setups in the same trial types, only one comparison in the trial type with the starting probability of $A=1$ showed a lower significant effect. On the other hand, all the comparisons across different trial types in the same foraging setup showed higher significance differences. In the two-way ANOVA for the main factors (ST & TT), the significant effects were found for ST: $F_{2,9283} = 7.43$; **p=0.0006** and TT: $F_{2,9283} = 1347.91$; **p<0.0001**, but no significant interaction was seen; ST x TT: $F_{4,9283} = 0.87$; **p=0.4832**.

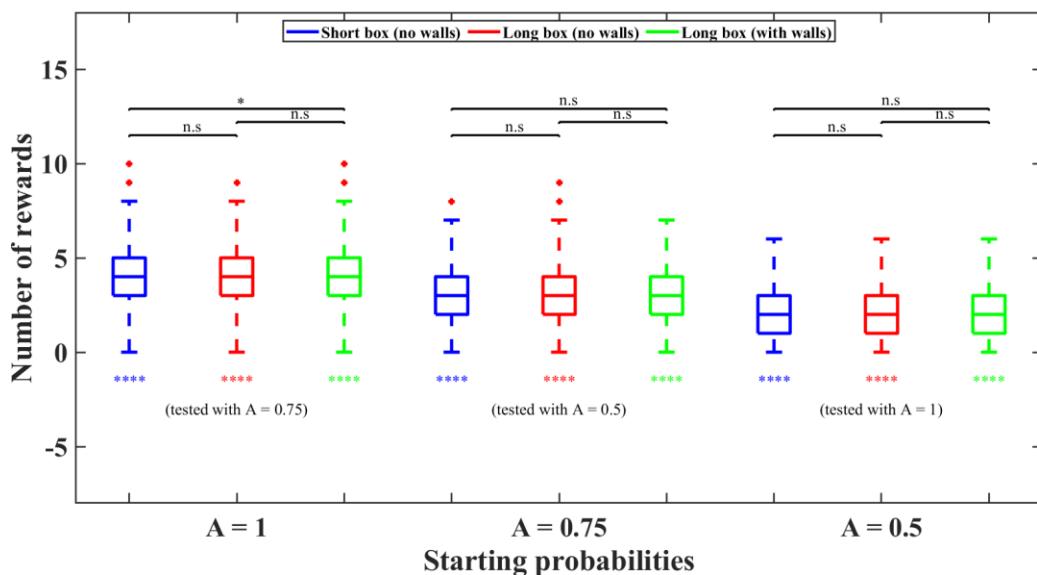


Fig. 3.11. Number of rewards obtained in different trial types of performing phase sessions of different foraging setups. Box plots represent the median and inter-quartile range; the significance bars indicate the differences between different foraging setups for each trial type; the significance stars below each box plot represent the differences between different trial types (given in braces) for each setup given by Wilcoxon rank-sum test for Bonferroni corrected p-values ($p < 0.05/18$ (*), $p < 0.01/18$ (**), $p < 0.001/18$ (***) $p < 0.0001/18$ (****))

3.3.5. POKE NUMBER OF THE FIRST REWARD OBTAINED BY THE ANIMALS

When the first reward was observed by considering both the hit and error pokes (**fig. 3.12 (a)**), a significant difference was seen between the short box and both the long box foraging setups in the trial type with the starting probability of A=1. Similarly, a high level of significant difference was observed in each setup between the trial types with starting probabilities of A=1 and A=0.75 & A=0.5 and A=1. In the two-way ANOVA for the main factors (ST & TT), the significant effects were found for ST: $F_{2,9283} = 5.31$; **p=0.005** and TT: $F_{2,9283} = 173.88$; **p<0.0001**, but no significant interaction was seen; ST x TT: $F_{4,9283} = 1.25$; **p=0.2862**.

On noticing the first rewarded hit poke (**fig. 3.12 (b)**), the comparison between different setups in the same trial type showed a similar kind of difference. For the other set of comparisons between the trial types of the same foraging setup, most of them had a high level of significant differences.

In the two-way ANOVA for the main factors (ST & TT), the significant effects were found for ST: $F_{2,9283} = 4.26$; **p=0.0141** and TT: $F_{2,9283} = 304.23$; **p<0.0001**, but no significant interaction was seen; ST x TT: $F_{4,9283} = 0.81$; **p=0.5204**.

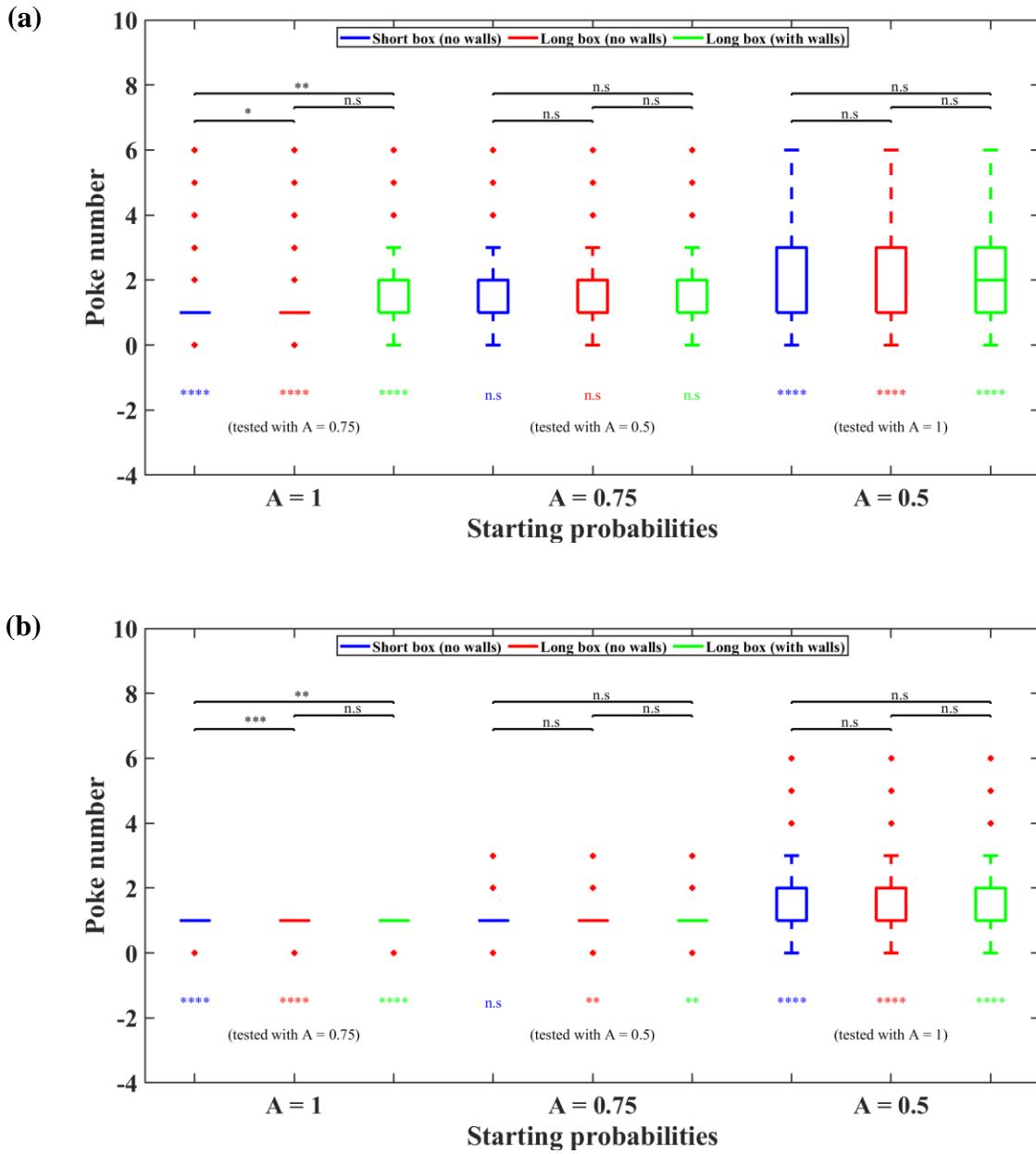


Fig. 3.12. Poke number of the first reward in different trial types of performing phase sessions of different foraging setups. (a) Total (both hit and error pokes) poke number of the first reward obtained by the animals; (b) Hit poke number of the first reward obtained by the animals. Box plots represent the median and inter-quartile range; the significance bars indicate the differences between different foraging setups for each trial type; the significance stars below each box plot represent the differences between different trial types (given in braces) for each setup given by Wilcoxon rank-sum test for Bonferroni corrected p-values ($p < 0.05/18$ (*), $p < 0.01/18$ (**), $p < 0.001/18$ (***) $, p < 0.0001/18$ (****))

4. DISCUSSION

All organisms must make decisions for their survival while facing uncertainty in their environment. Animals and humans tend to perform actions that are likely to lead to desirable outcomes. But they must also consider the possibility that environmental conditions may change and outcomes of their actions may vary over time. Such behavioral flexibility requires a delicate balance between harnessing (exploiting) known resources and exploring alternative options that may become beneficial. The trade-off between exploration and exploitation can be seen as a challenge for the allocation of attentional resources.

Foraging behavior in Mongolian gerbils is a suitable model to study such flexible behavioral strategies. When a foraging site is depleted, the gerbil is in an exploitation/exploration dilemma. Should current attentional resources be used to continue foraging at the current site, or should the environment be explored for alternative options, i.e., moving on to the next foraging area, at a time cost to the gerbil but enjoying potentially higher foraging density (cf. Shuai & Song, 2011)? This decision must be made based on probabilistic information (how much reward is typically available in the alternative area?). The trade-offs between exploration and exploitation has been studied in many animal species, in different domains, and with numerous paradigms (marginal value theorem, MVT; Charnov, 1976; Constantino & Daw, 2015). The behavior of all species, from insects to birds to mammals and humans, obeys the MVT, indicating basic behavioral patterns and possible conserved neural mechanisms.

In this study, a probabilistic foraging paradigm was established in Mongolian gerbils along with developing a food restriction regime convenient for the animals

that helped in enhancing the motivation of the animals to perform well in the probabilistic foraging task. In total, three different foraging setups were constructed and food-restricted Mongolian gerbils ($n=8$) were put in the probabilistic foraging paradigm to receive food pellets as the rewards based on their decisions to exploit and explore the foraging spouts in the setup. At first, the animals were trained in the short box foraging setup in which no walls were kept in between the foraging spouts, followed by a resting period for few weeks. Then the animals were placed in the long box foraging setup and foraging sessions were accomplished without and with walls consecutively.

The quantitative analysis of different foraging parameters was done using various statistical methods (Wilcoxon rank-sum test, two-way ANOVA) to enumerate the optimal food quantity needed for the gerbils during the foraging task, and animals' behavior in various trial types in different forms of the foraging setup which will be discussed in this section to evaluate the probabilistic foraging paradigm in Mongolian gerbils aided by the food restriction practices on them.

4.1. FEEDING OF THE ANIMALS

The animals received their food as rewards (20mg food pellets) during the foraging task and normal food pellets that were kept inside their cages to maintain the bodyweights above the critical level of 85% (Kvitsiani et al., 2013). In all forms of the foraging setup, the average reward intake increased in successive sessions and the average total daily food consumption was about 4-7g depending upon the animals' performances in the foraging task. Except for few sessions, the bodyweights of all the animals were seen above 90% of BBW (**fig. 3.1 (a),(b)**). On average, all the animals performed more than 40 trials (supplementary **fig. S1**) after they had learnt the foraging task well — which was sufficient (60 trials were

taken for analysis in Lottem et al., 2018) for analyzing the performance of the animals in the probabilistic foraging task. Therefore, the implementation of a food restriction regime on Mongolian gerbils (Tolnai et al., 2017) had worked properly in encouraging the animals to do more trials in the foraging task and also in keeping the bodyweight of the animals in check.

4.2. PERFORMANCE OF THE ANIMALS IN DIFFERENT FORAGING SETUPS

Five foremost foraging parameters were taken for analyzing the behavioral performances of the animals in the probabilistic foraging task. As the short box foraging setup (without walls) was novel for the animals, the duration of foraging spout exploitation was higher in this setup comparing to the other two foraging setups (supplementary **fig. S2**). Although the total number of nose-pokes and the total number of hit pokes were highly similar in all three foraging setups (supplementary **fig. S3 & S4**), the animals have nose poked much faster in both of the long box foraging setups (supplementary **fig. S5& S6**). Similar to the time taken for exploitation, the inter poke intervals (both rewarded and unrewarded preceding hit poke) and the travel time parameters also appeared to be high in the short box foraging setup (supplementary **fig. S7 - S10**). The medians of all the foraging parameters observed in the latter part of the foraging task in the short box setup were quite similar to the medians seen in the long box setup which shows that the animals had adapted some learning strategies during the latter part of foraging sessions in the short box setup which they implemented throughout the foraging sessions of the long box setup.

Among all the analyzed foraging parameters, the travel time seemed to be a good estimate for identifying the performing phase sessions of the animals in each

foraging setup (see Results section **3.2**). Similar to the trend of overall sessions, the exploitation time duration in performing phase sessions was significantly higher in the short box (**fig 3.2**) which could be due to the learning effect on animals. It is evident from these results that the exploitation time reduced as the animals learned the foraging task well.

The poking rate (**fig 3.4**) of the animals signifies that when the travel distance was increased, the animals poked quickly in search of a reward. The inter poke interval after a rewarded preceding hit poke (**fig 3.5 (a)**) had the same outcome of the exploitation period. This leads to the speculation that animals briskly search for their rewards and also take more time to consume the food pellets received as the rewards in long box foraging setups. As expected there was not that much difference between the travel times among different setups in performing phase sessions since we considered the travel time (5s) as the decision criterion for recognizing the performing phase sessions of the animals in each foraging setup.

4.3. PERFORMANCE OF THE ANIMALS IN DIFFERENT TRIAL TYPES OF THE PROBABILISTIC FORAGING TASK

For a comprehensive understanding of the behavior of the animals, the individual trials in the performing phase sessions of each setup were examined. Especially the trials of the three different trial types were taken into consideration. In each setup, the amount of poking (**fig 3.8**) done by the animals significantly differed highly between the trial types as the animals poked in fewer numbers in trial types with lower starting probabilities. This could be due to the availability of more rewards in trial type with higher starting probabilities (**fig 3.11**).

As most of the nose-pokes in the foraging spouts were unrewarded (**fig 3.9**) due to the exponentially decaying nature of reward probabilities, more trials were

observed in the performing phase sessions in each foraging setup (supplementary **fig. S1**) indicating the tendency of the animals to explore the foraging spouts alternatively. Interestingly, the animals made a similar amount of unrewarded nose-pokes consecutively before leaving the foraging spouts in all of the trial types of different foraging setups. Therefore, the probability of the animals' eagerness to leave the foraging spout after a sequence of unrewarded nose-pokes can be predicted from the supplementary **fig. S14**.

According to the design of the trial types in the probabilistic foraging paradigm, the trial type with the starting probability of $A=1$ was rewarded in the first hit poke which was almost the same in the case of the trial type with the starting probability of $A=0.75$ since most of the trials in this trial type were also rewarded for its first hit poke (fig. **3.12 (b)**). The first reward in the first hit poke itself could have also influenced the food-restricted animals to poke more times in the foraging spout in the trial type with higher starting probabilities.

In the analysis of the individual trial types, highly significant differences were mostly seen between the trial types of the same kind of foraging setup for all of the trial-wise parameters. In contrast, the comparison between different foraging setups for the same trial type did not show many significant differences. On putting together the results obtained from both the analysis of session-wise and trial-wise parameters, few differences were seen between the foraging setups in the performing phase sessions. Overall, the result of the study could reveal that the change in travel distance between the foraging spouts by using different foraging arena architectures had only a minor impact on the foraging behavior of the food-restricted Mongolian gerbils.

4.4. EVALUATION OF THE PROBABILISTIC FORAGING PARADIGM IN FOOD-RESTRICTED MONGOLIAN GERBILS

In this study, the animal received the food both inside the foraging setup and also in the home cage. This linedated with the open economy policy of feeding the animals — where food was provided in limited amounts at least 2 hours after the foraging session and this does not affect the animals' performances in the probabilistic foraging task (Fantino & Abarca, 1985).

Animals forage in their habitat for survival and the Marginal value theorem (MVT) describes the optimal strategy which decides the point of leaving when the instantaneous rate of rewards drops below its average value (Charnov, 1976). As the MVT assumptions were not realistic in the actual environment, another optimal solution remains relevant (Lottem et al., 2018). In accordance with this, the switching decisions between the foraging spouts were made in this probabilistic foraging task by the Mongolian gerbils. To be precise, the foraging behavior exhibited by the animals in the foraging setups could be explained by the diffusion decision models (Drugowitsch et al., 2019) in which decisions were made based on the trial-by-trial feedback during foraging sessions as each foraging approach (trial) was uncertain for the animals in the probabilistic foraging task. In this experiment, the rewards (food pellets) hold the key (for uncertainty) to such decision making (Vertechi et al., 2020).

The switching between the foraging spouts, as observed in the presented study, could be seen as flexible allocation of attentional resources in which the anterior prefrontal cortex is considered as a crucial brain structure for the neural realization of exploratory resource allocation in humans (Daw et al., 2006), non-human primates (Mansouri et al., 2015), and rodents (Kvitsiani et al., 2013).

Whenever the travel distance was increased, the time spent by the animals at the foraging spouts should have increased (Fantino & Abarca, 1985), and facing various travel distances, animals could adopt various strategies for maximizing their rewards (Shuai & Song, 2011). But, in the present foraging experiments, the time spent at the foraging spouts (**fig. 3.2 & S2**) decreased in the long box foraging setups which takes more time for the animals to alternate between the foraging spouts. This complies with the learning behavior of the Mongolian gerbils (Cheal, 1986) as we used the same animals in all the foraging setups consecutively. Nevertheless, this could be rectified by using novel animals in various foraging setups.

5. CONCLUSION

The food restriction regime had been successful in the Mongolian gerbils and that helped the animals to perform well in the probabilistic foraging paradigm (cf. Lottem et al., 2018) in all of the three types of foraging setups. In the travel-time-dependent, performing phase sessions, the post-hoc Wilcoxon rank-sum test, assisted by the two-way ANOVA test, revealed that the variation in travel distance between the foraging spouts affects the animals' behavior in the foraging task very minimally.

5.1. PERSPECTIVES

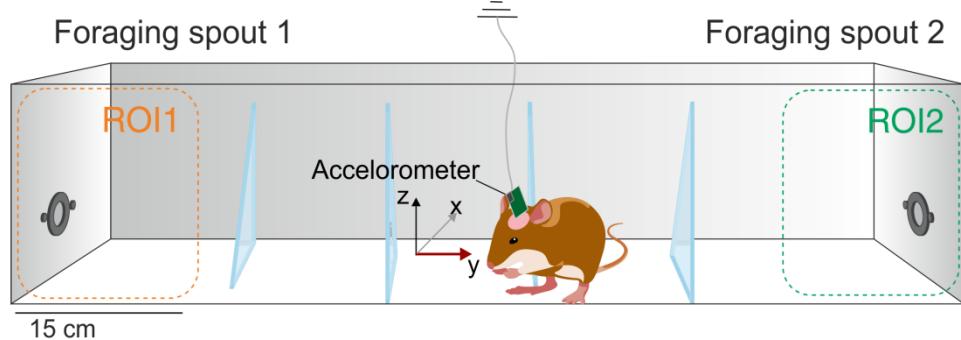
This thesis was a pilot study in developing the probabilistic foraging paradigm for the food-restricted Mongolian gerbils. The ultimate goal of the present experimental project is to pave the way for investigating the basic brain processing principles of attentional resource allocation through a novel approach of combining a foraging behavioral experiment (Lottem et al., 2018) with *in vivo* physiology (Zempeltzi et al., 2020) in a laboratory rodent model (Mongolian gerbil).

In order to achieve this, chronic electrodes will be implanted in the anterior prefrontal cortex (aPFC) of the Mongolian gerbils and an electrophysiological recording unit will be incorporated with the foraging setup to record local field potentials (LFPs). From the aPFC, LFPs will be analyzed to visualize the current source density (CSD) profiles of the Mongolian gerbils performing the probabilistic foraging task.

One other important prospect is finding out a criterion based on the foraging behavioral parameters to distinguish exploration and exploitation in the probabilistic foraging task. With this criterion, we will be able to create a better

model for understanding the exploration and exploitation behavior that enables us to study the attentional resource allocation processes occurring in the anterior prefrontal cortex.

(a)



(b)

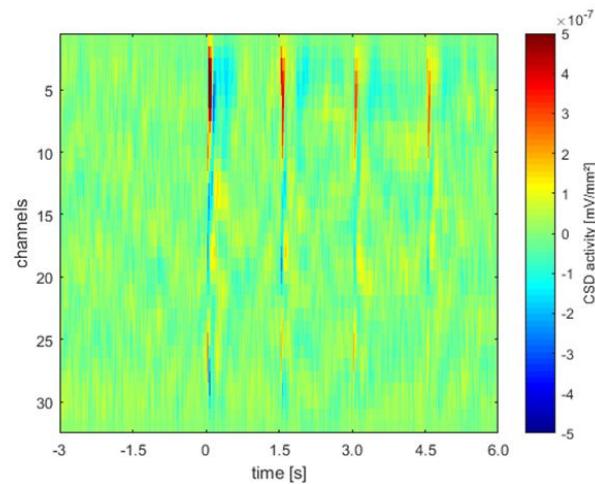


Fig. 5.1. Perspectives. (a) Multichannel recordings from aPFC of the Mongolian gerbil performing the probabilistic foraging task; (b) An example of a CSD profile relating to synaptic subpopulation activity in aPFC

6. APPENDIX

A. SUPPLEMENTARY FIGURES

A.1. SESSION-WISE ANALYSIS

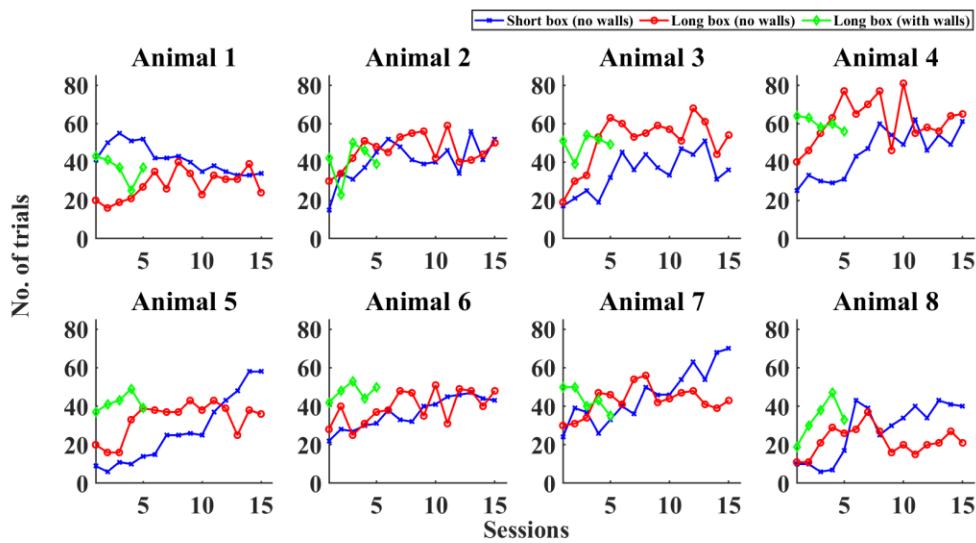


Fig. S1. Number of trials done by the animals in each session in three different foraging setups. 15 sessions were taken for both short box (Blue) and long box (Red) foraging tasks done without any walls in between the spouts; 5 sessions for long box (Green) setup with walls in between the spouts.

The following figures represent the results of session-wise analysis done for the nine parameters for each foraging setup. Every box plot constitutes for the median (middle line), 25th percentile (lower line), 75th percentile (upper line), lowest data point (lower whisker), largest data point (upper whisker), and outliers (red-colored + symbols) of each parameter in each session for all animals (n=8). The dots depict the median of each animal for that particular session. In every figure, A (Blue) denotes the short box without any walls in between the spouts; B (Red) stands for the long box without any walls in between the spouts, and C (Green) marks the long box with walls in between the spouts.

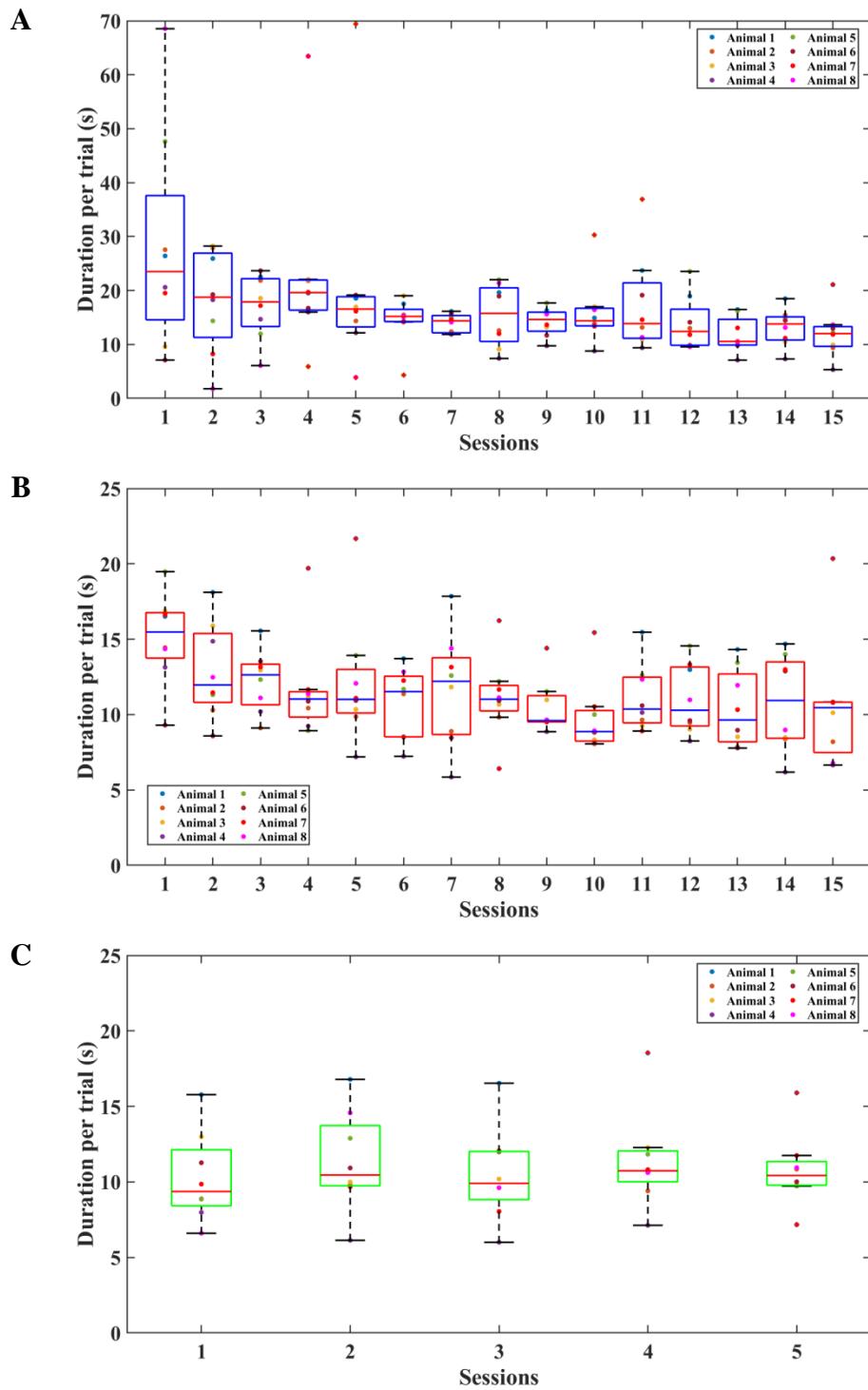


Fig. S2. Time (in s) spent by the animals for nose poking in the foraging spout

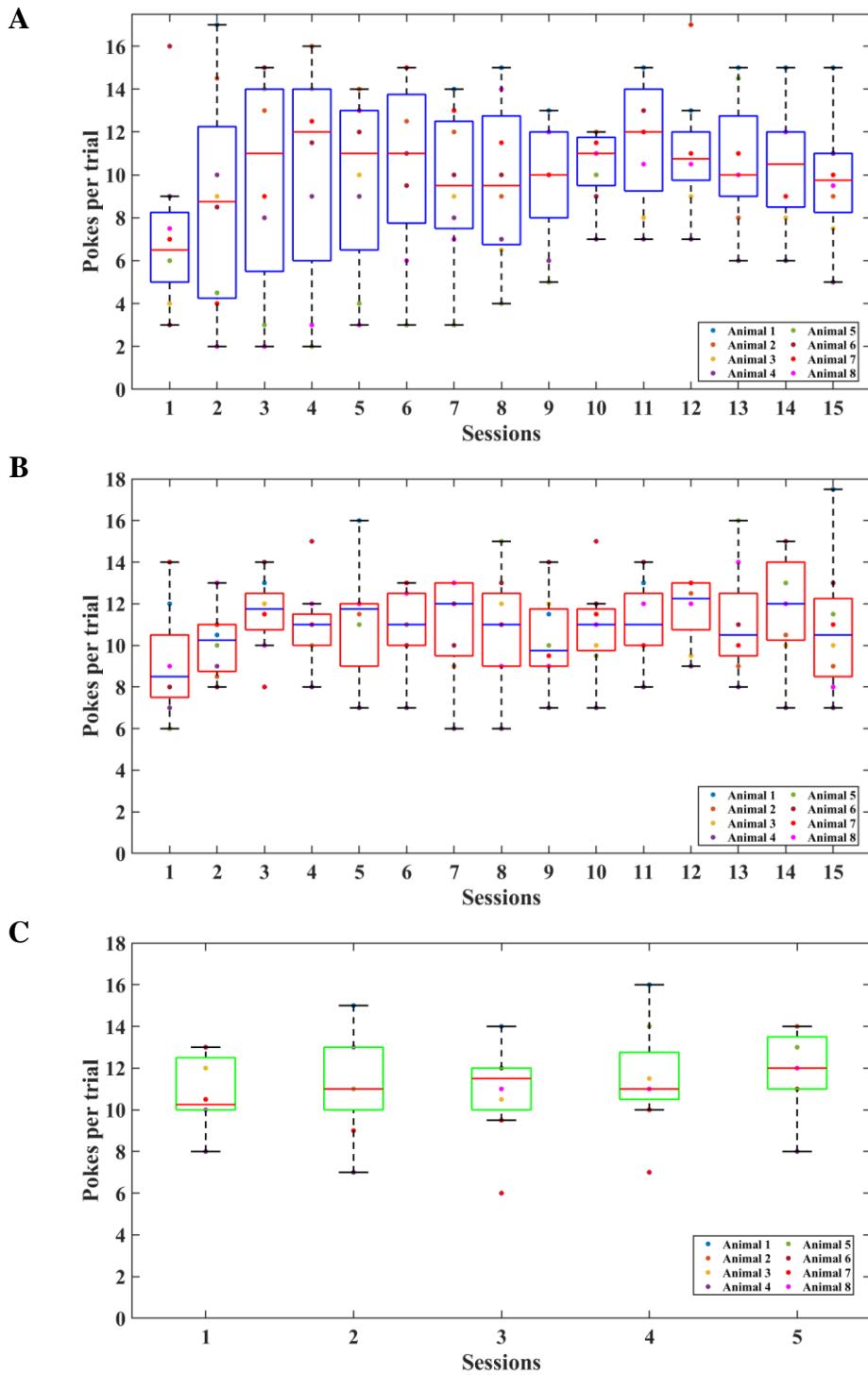


Fig. S3. Total number of nose-pokes (both hit and error pokes) done by the animals

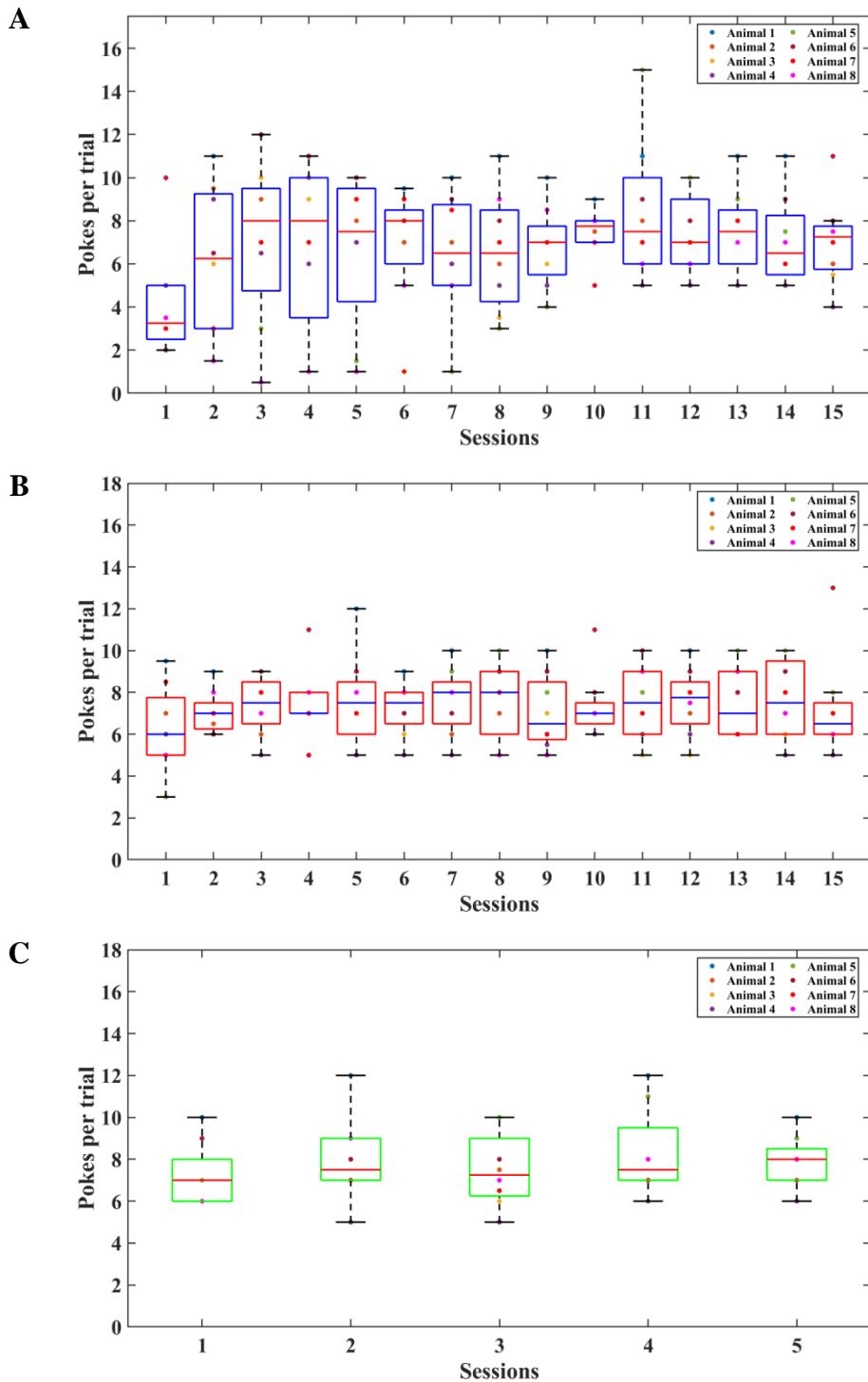


Fig. S4. Total number of hit pokes done by the animals

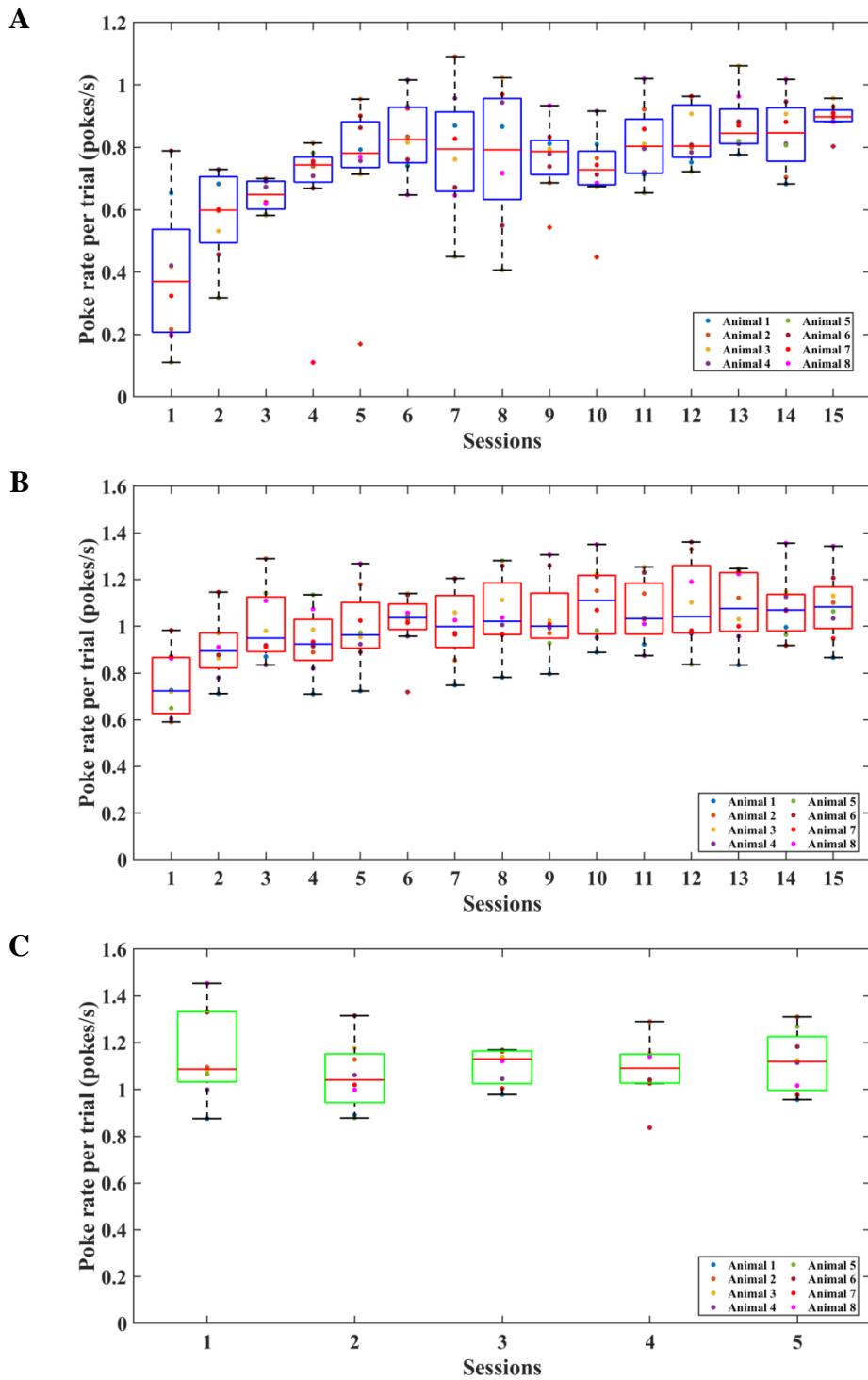


Fig. S5. Poke rate (pokes/s) of the total number of nose-pokes (both hit and error pokes) done by the animals

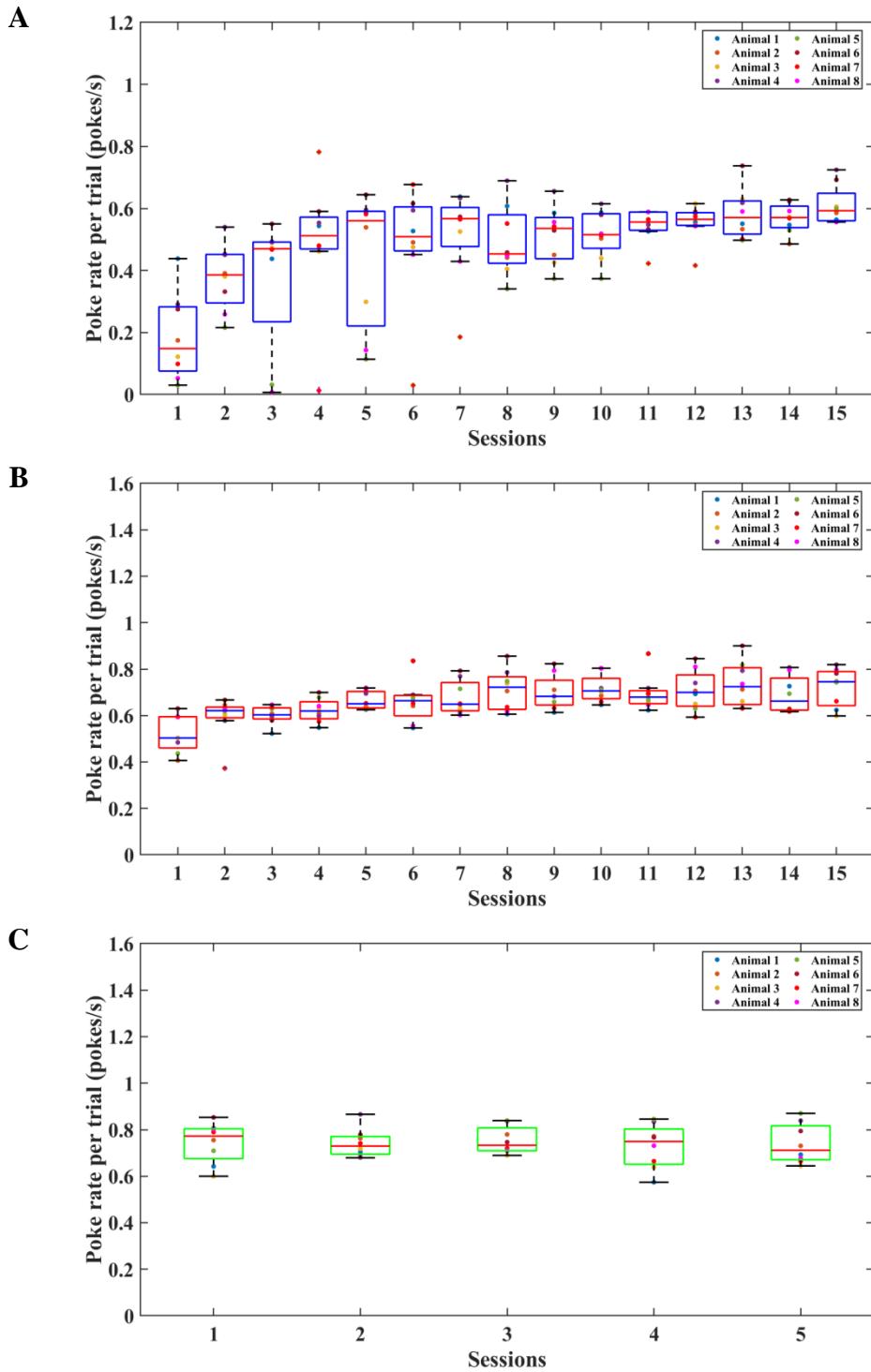


Fig. S6. Poke rate (pokes/s) of hit pokes done by the animals

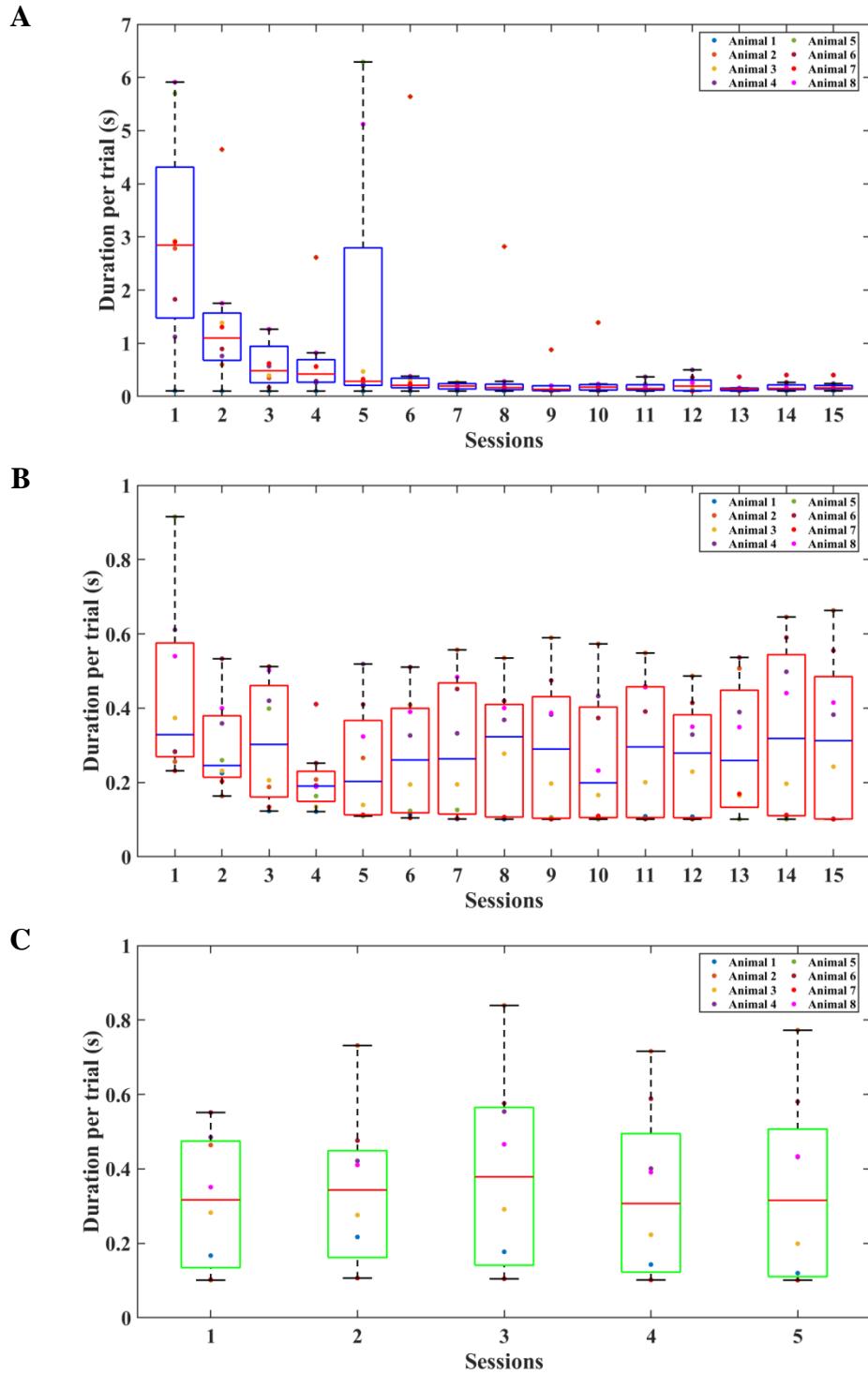


Fig. S7. Inter poke interval (in s) in which preceding hit poke was rewarded

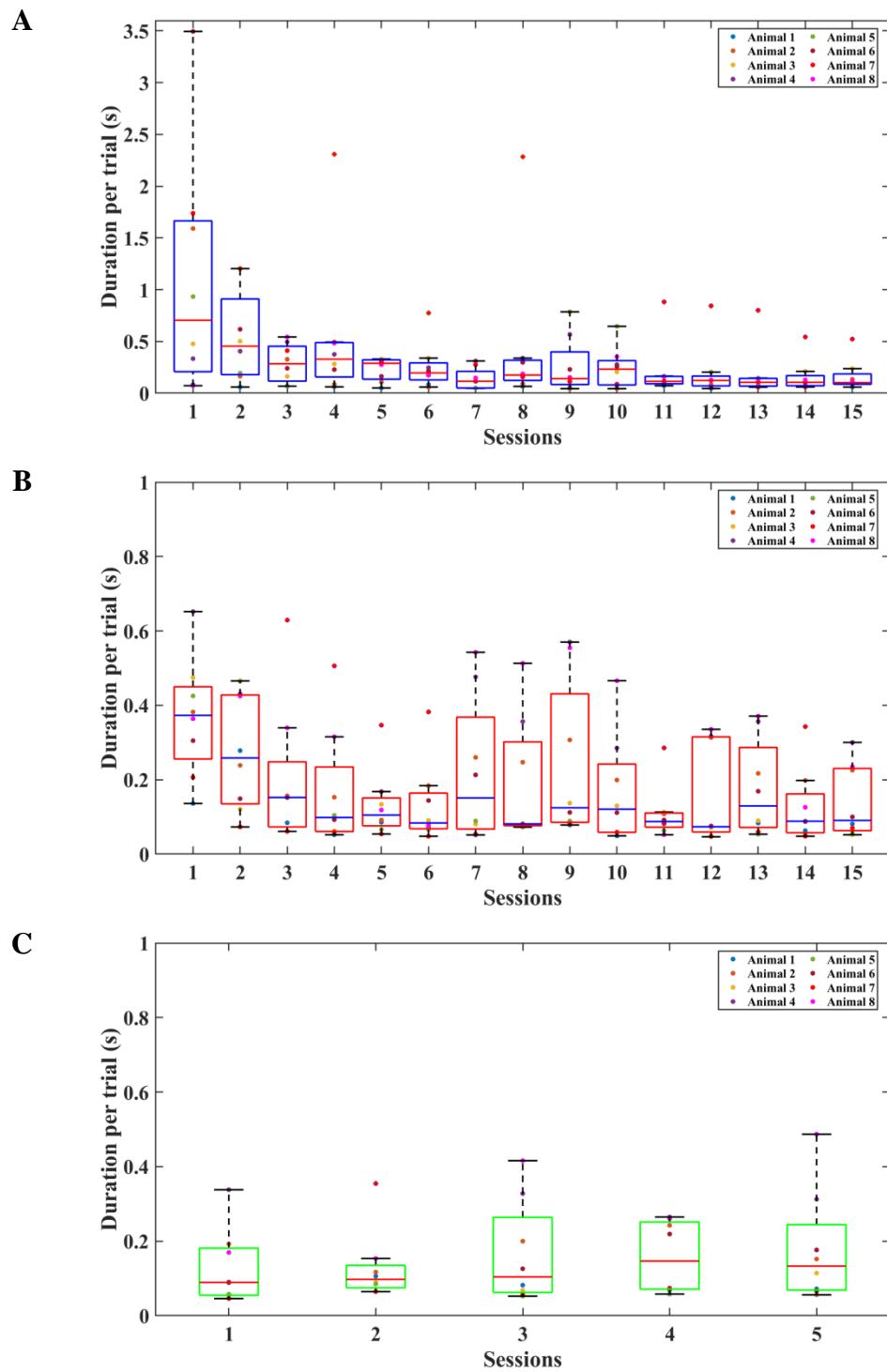


Fig. S8. Inter poke interval (in s) in which preceding hit poke was unrewarded

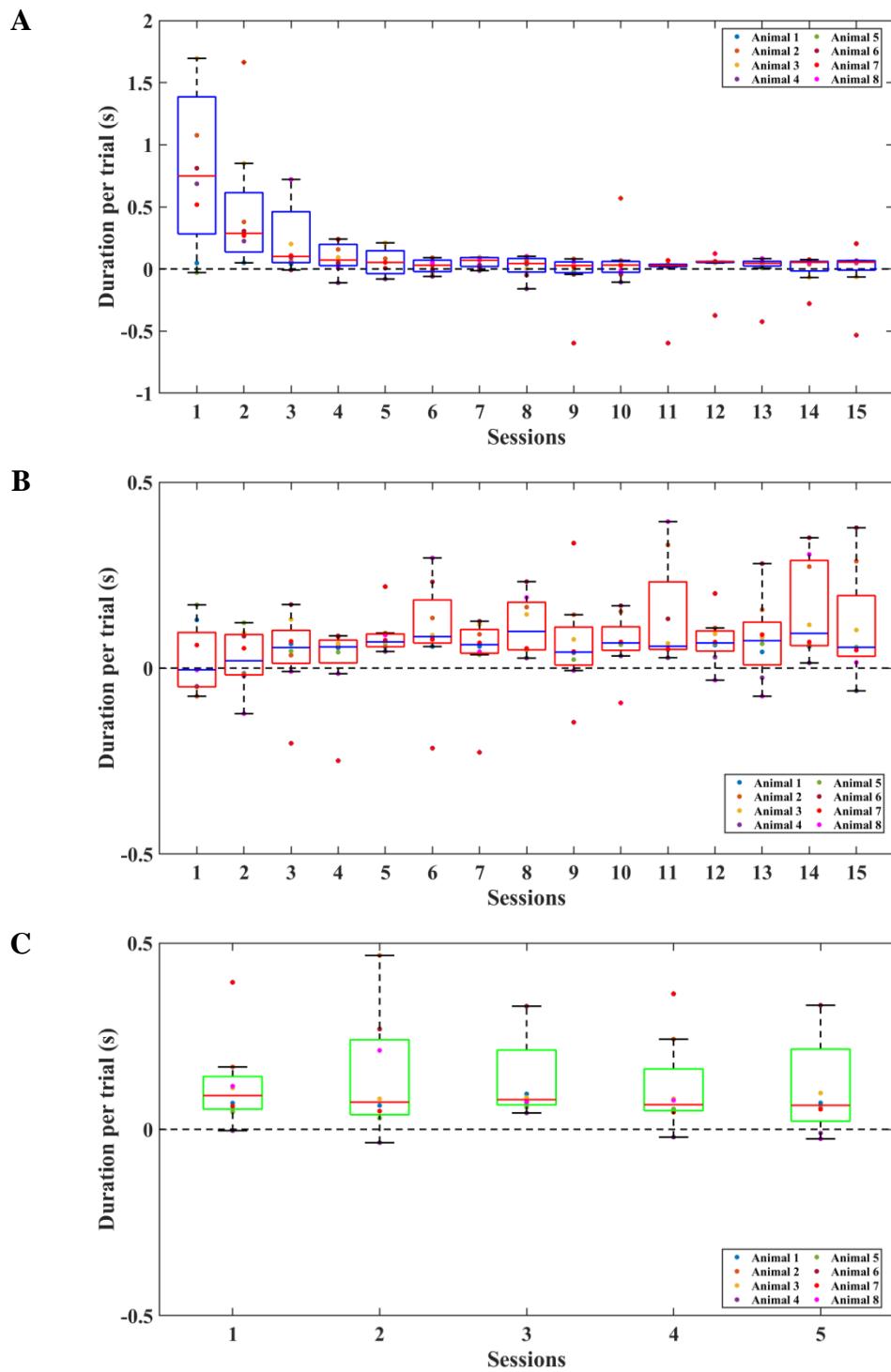


Fig. S9. Difference between inter poke intervals (in s) of rewarded and unrewarded preceding hit poke

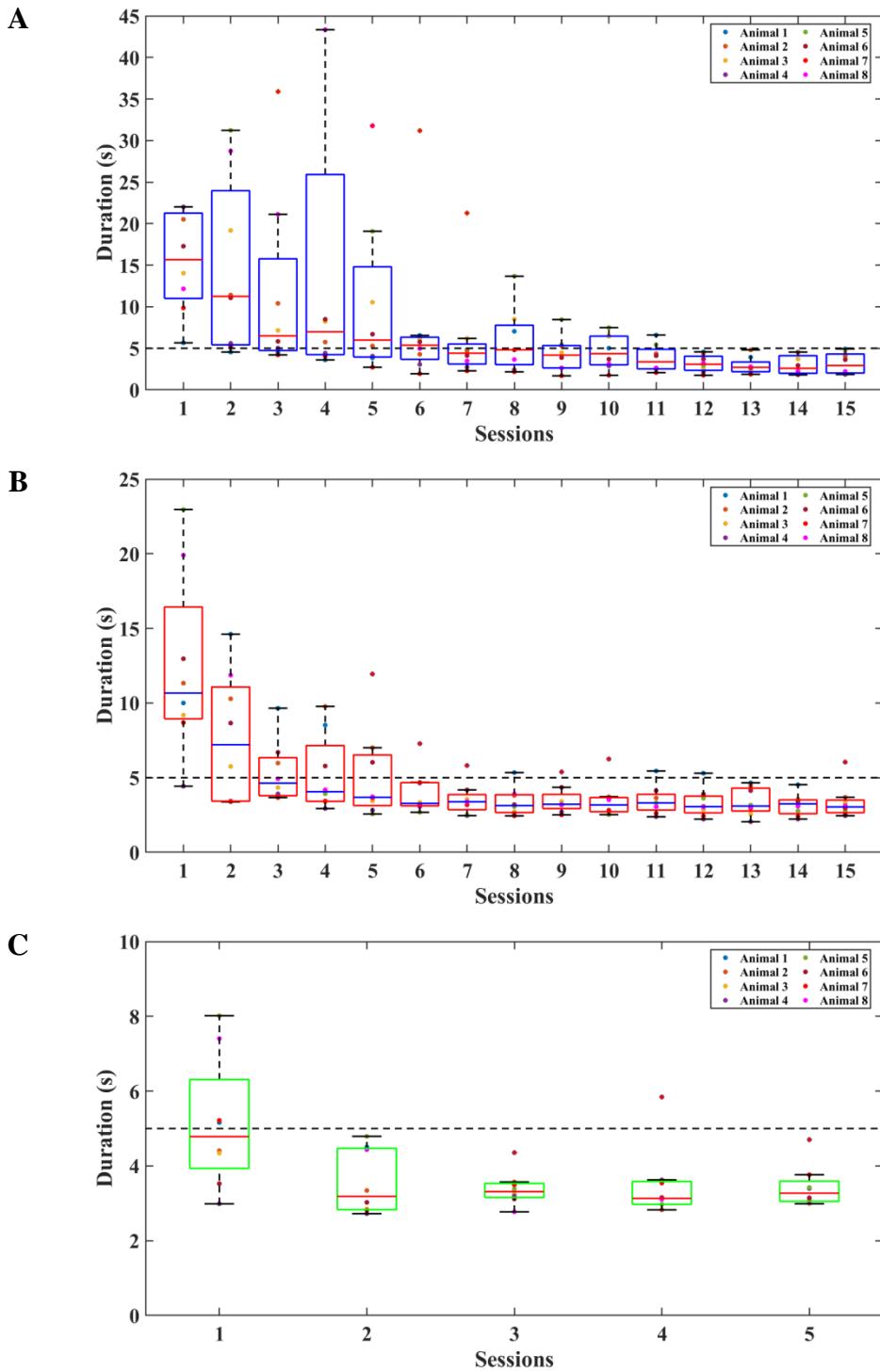


Fig. S10. Time (in s) taken by the animals to travel from one spout to another spout in the foraging setup

A.2. TRIAL-WISE ANALYSIS

The figures of the parameters analyzed in a trial-wise manner represent the proportion or fraction of trials of the performing state sessions constituting a particular value for that parameter. In each figure, the top plot represents the overall fraction of trials for each foraging setup (see the legends for the color codes of each setup). Similarly, the below three plots are representing three different starting reward probabilities of $A = 1.0$, $A = 0.75$, and $A = 0.5$ respectively.

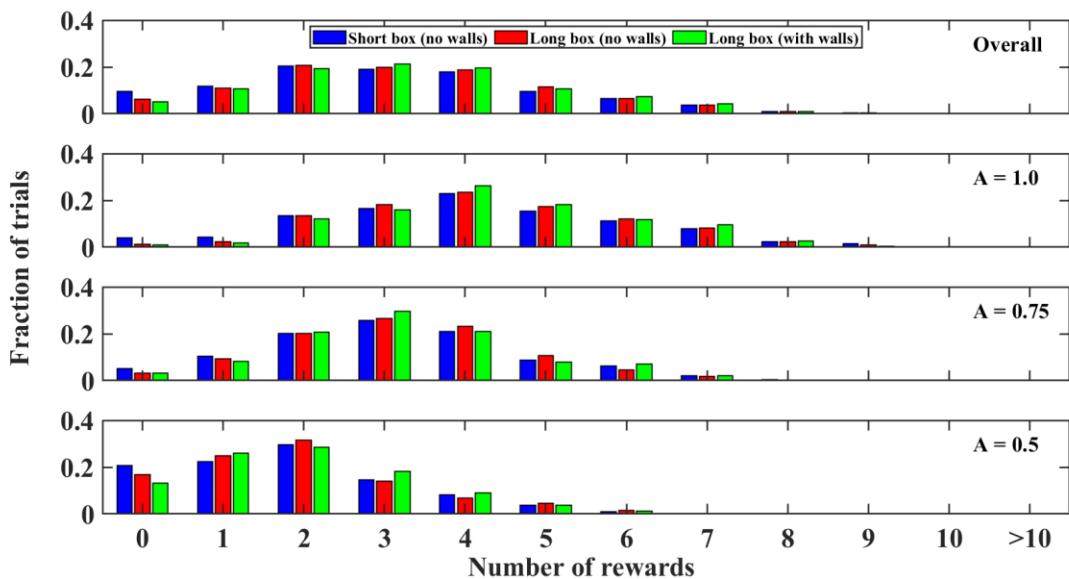


Fig. S11. Total number of rewards (food pellets) obtained by the animals in each trial. The value of zero in the x-axis of this plot represents the trials that were not rewarded during the foraging sessions.

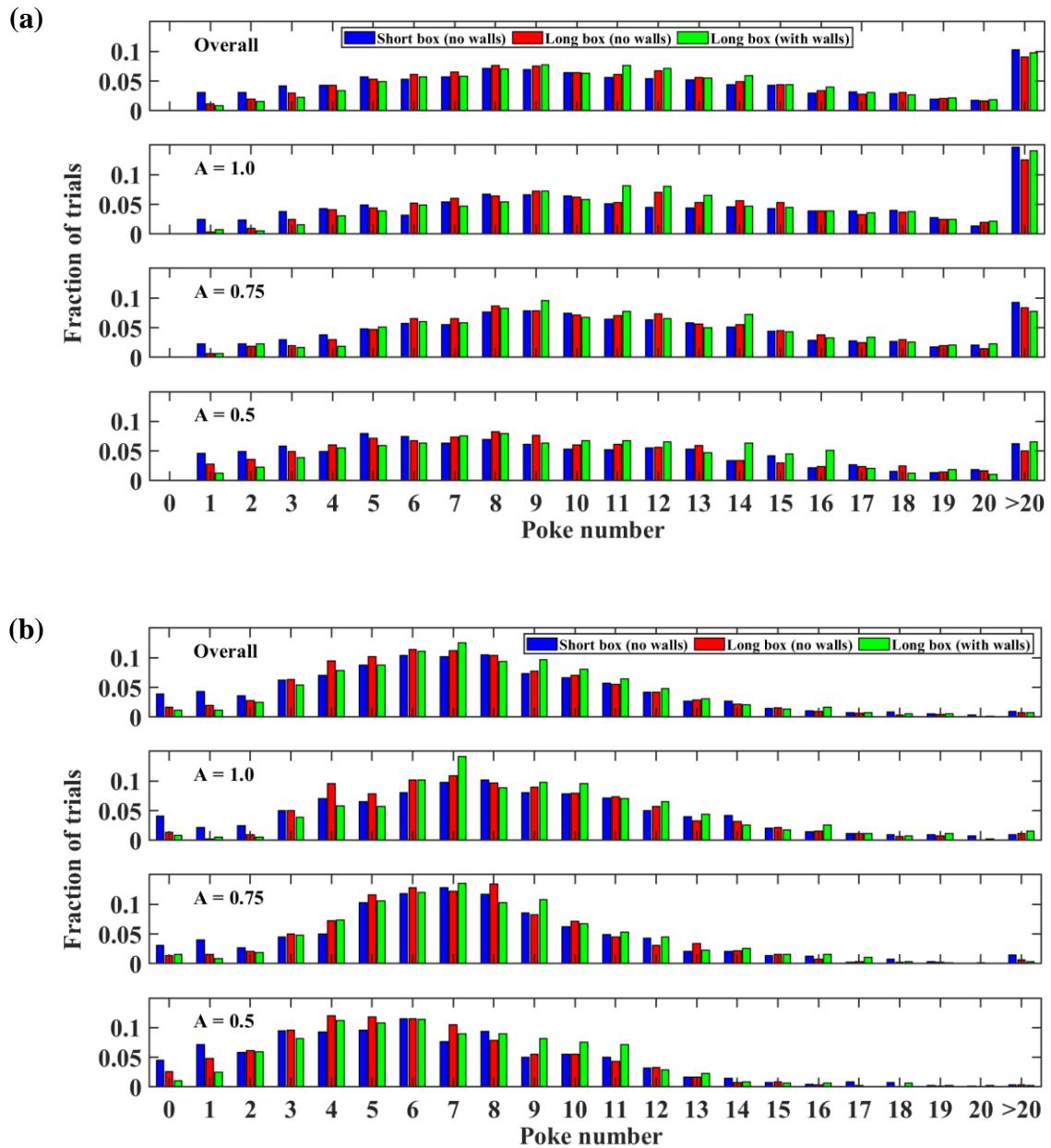
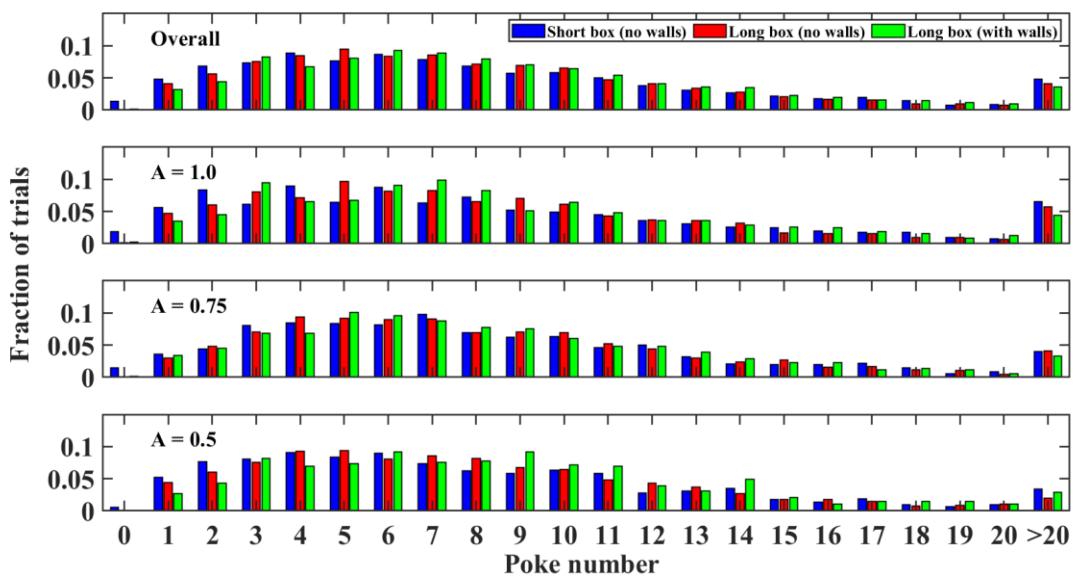


Fig. S12. Number of nose-pokes done by the animals in each trial. (a) Total number of nose-pokes consisting of both hit and error pokes; (b) Hit pokes

(a)



(b)

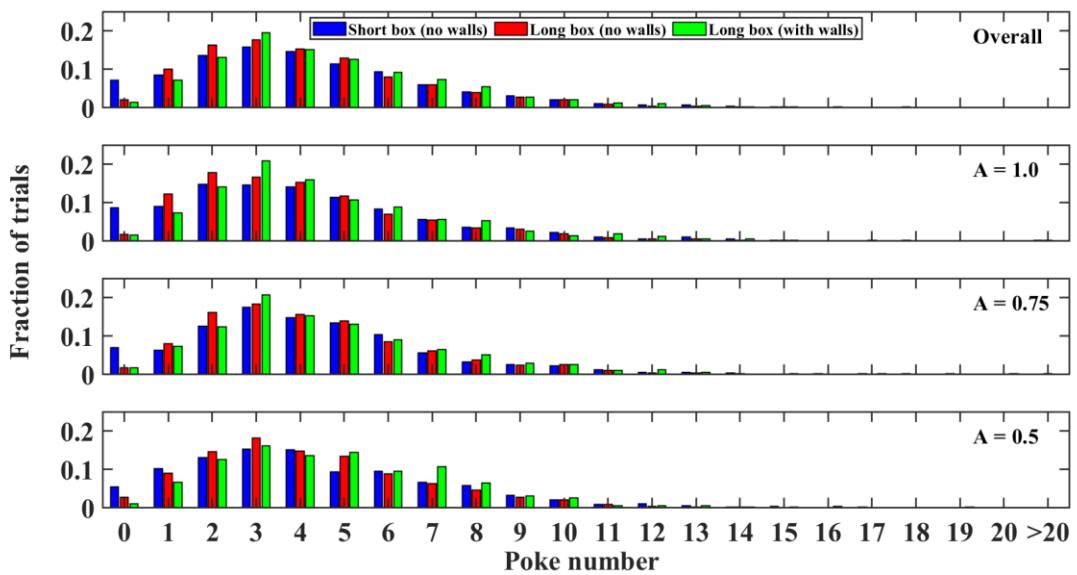


Fig. S13. Number of unrewarded nose-pokes done by the animals in each trial. (a) Total number of unrewarded nose-pokes consisting of both hit and error pokes; (b) Unrewarded hit pokes

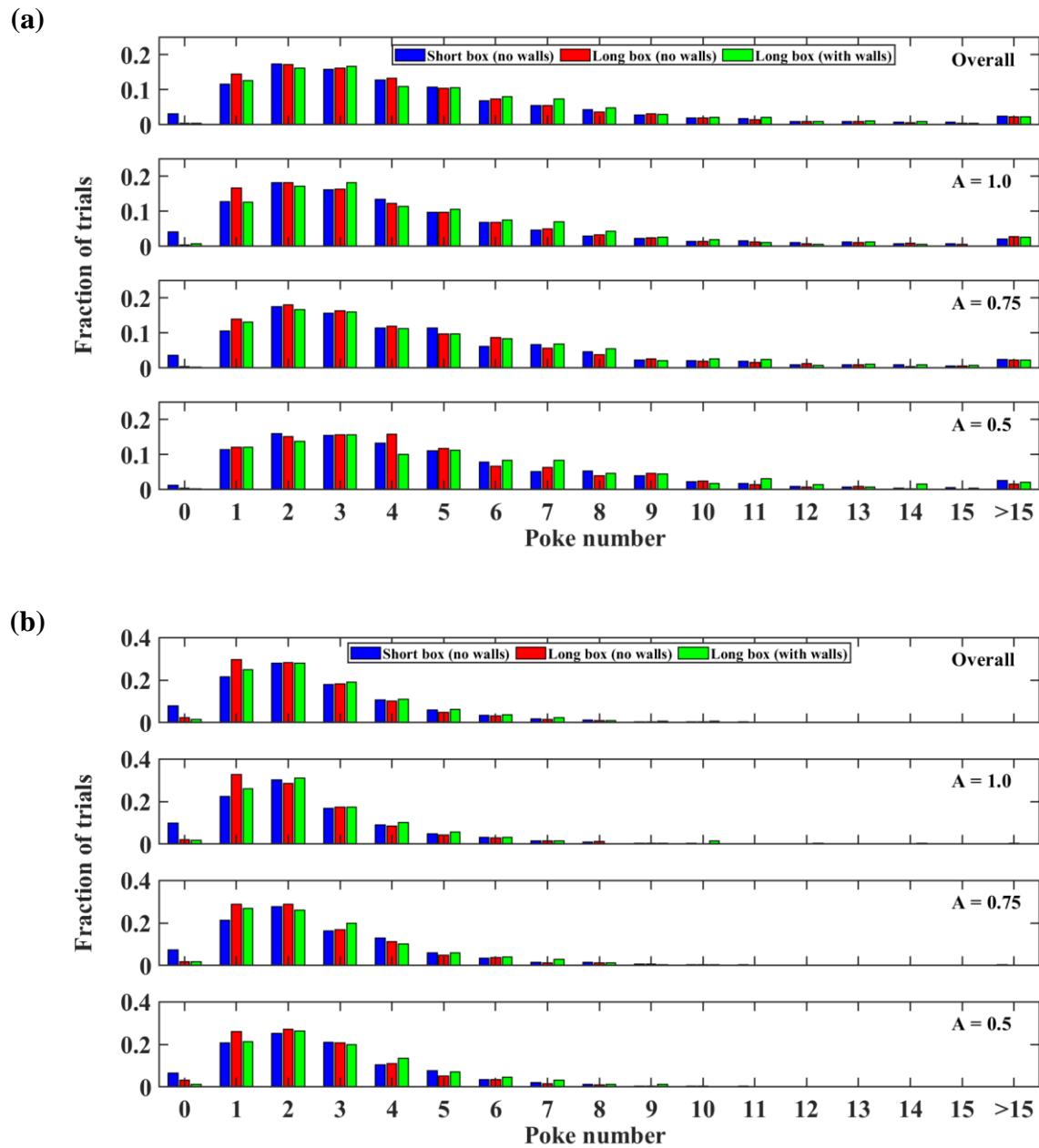


Fig. S14. Number of consecutive unrewarded nose-pokes done by the animals before leaving the spout in each trial. (a) Consecutive unrewarded nose-pokes consisting of both hit and error pokes; (b) Consecutive unrewarded hit pokes

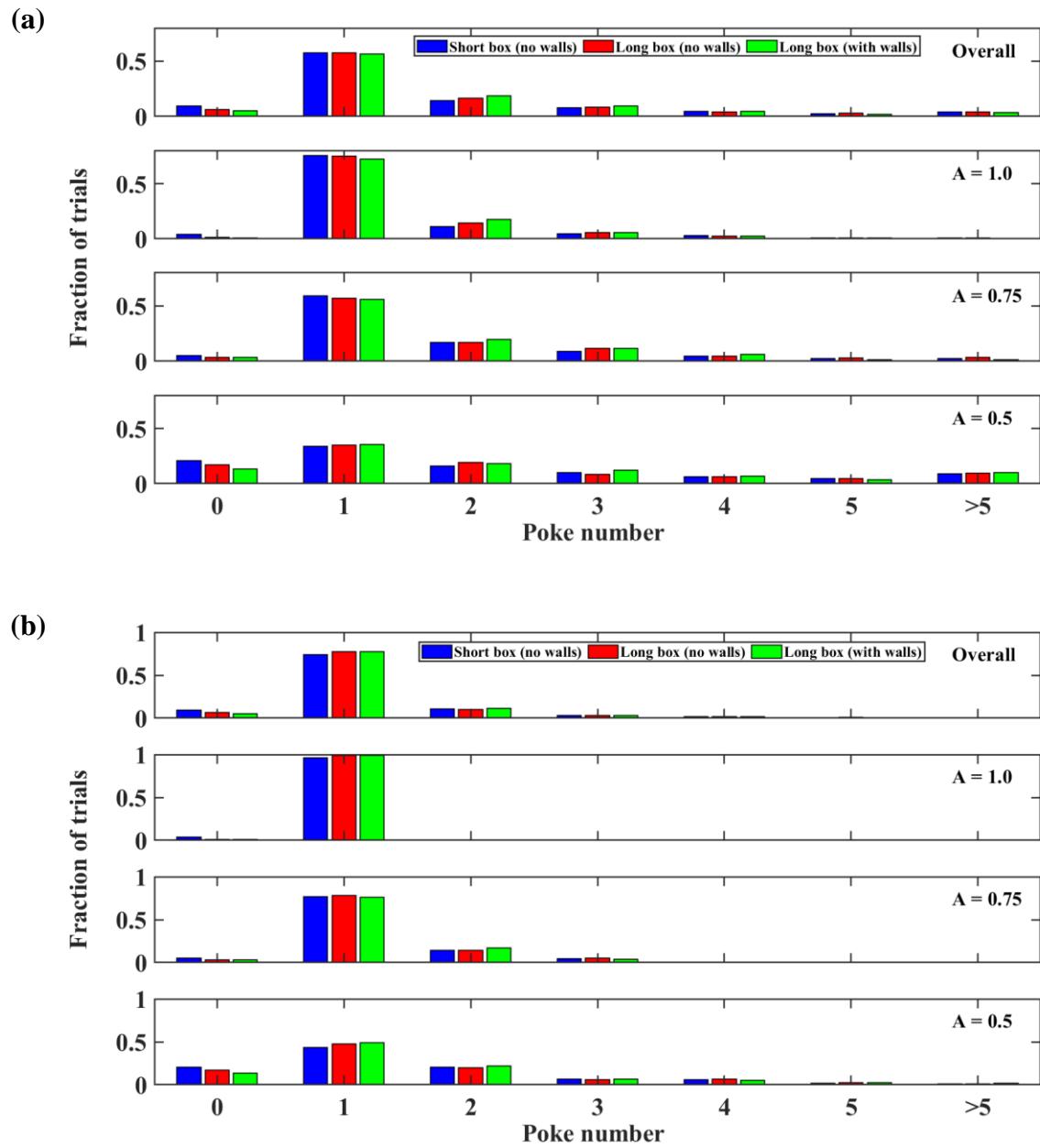


Fig. S15. Poke number of first reward in each trial. (a) Poke number consisting of both hit and error pokes; (b) Hit poke number

B. SUPPLEMENTARY TABLE

Setup/Trial type	Overall	A = 1.0	A = 0.75	A = 0.5
Short box without walls	3100	1126	1038	936
Long box without walls	4432	1737	1427	1268
Long box with walls	1760	686	583	491

Table S16. Total number of trials in different trial types (starting probabilities) in performing phase sessions of different foraging setups

C. VIDEO RECORDINGS OF FORAGING EXPERIMENTS

Scan the following QR code to view the video recordings of the foraging experiments in different setups.



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DECLARATION

I hereby declare that this thesis entitled "**Exploratory attentional resource allocation in a probabilistic foraging paradigm in the Mongolian gerbil**" is my original work, and has not been submitted for an award of a degree in any other university.

Signature

Date