

**Cognitive Science Honors Thesis: Translation from Top-Down View to First-Person View
for Spatial Navigation in Rats**

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Abstract

The ability to relate spatial perspectives is vital for navigational tasks. The holistic perspective, which often manifests in the top-down view, can reveal information that is not readily available in the first-person view. Our experiment uses high-resolution electrophysiology to study how one relates the two viewpoints on the level of single neurons. We recorded 15 subiculum neurons as the rat performed a navigational task that required the animal to use information gained from the top-down perspective in a first-person context. While the rats quickly learned the schema of the task, they have yet to consistently demonstrate the ability to relate the top-down and first-person perspectives. However, we have observed three broad categories of subiculum neurons that exhibit interesting firing patterns. The first category almost includes all recorded subiculum neurons. These cells have distinct firing fields on different levels. This ubiquitous global remapping might be evidence that subiculum neurons are sensitive to elevation. The second category of cells consistently fires at specific task phases. The third category of cells shows a directional preference and their firing fields center around reward locations.

Introduction

Imagine stepping into a descending elevator. You first notice the interior: the buttons, the marble floor, and the glass panel that allows you to look down at the busy street. Your sensory organs gather distance information and a representation of the elevator interior is quickly drawn in your brain. The objects in the elevator's interior now have spatial coordinates relative to each other, and your position in this space is apparent. You look down at the people and cars. From where you are standing, people are as small as ants and cars matchboxes, but they are getting bigger as the elevator descends. Visual flow data and your vestibular system confirm the schema of going down in an elevator. You scan the surroundings and find familiar places: the bus station a block away, the Greek restaurant just around the corner, and your favorite bakery across the street. With the aid of these landmarks, you form the representation of a much bigger space. You also see the destination and the reason for all the hassle. Your silly partner forgot their wallet and is now apologetically waving up at you from the lobby door. The elevator dings and the doors open. You already have plotted the path to your better half.

We unknowingly execute complex transformations of spatial perspectives in daily life. Information and knowledge gained from the holistic perspective can be insightfully applied in the first-person perspective. But how are we achieving this? Our project uses high-resolution electrophysiology to record activities in the CA1 region and the subiculum of a trained animal performing a novel task to investigate how the animal relates the two perspectives on the level of single neurons.

The hippocampus is a critical area for spatial navigation and episodic memory. It receives inputs from the entorhinal cortex and outputs to the subiculum. We are interested in recording from the CA1 region, which is part of the trisynaptic circuit and is where a lot of place cells

reside. The hippocampus is also vital for the formation of cognitive maps, map-like mental representations of the environment. The CA1 place cells only fire at specific spatial locations, and these neurons, along with grid cells, border cells, head direction cells, and other spatially receptive cells for the egocentric representation of allocentric space (O'Keefe & Dostrovsky 1971; Epstein et al. 2017).

The subiculum is one of the major output areas of the hippocampus and is the most responsible for delivering spatial information to the rest of the brain. It has been shown that when multiple CA1 cells carry different task-related information output to the same subiculum neuron, it can store visual scenes and choice information in subfields (Lee et al. 2022). Additionally, subiculum neurons have demonstrated encoding of spatial geometry or the features of places. A small subset of the subiculum neurons, or “corner cells” have demonstrated sensitivity to the geometric properties of corners (Sun et al. 2024).

Methods

Subjects

Four adult male Sprague-Dawley rats were used as subjects. The rats were housed individually in plastic cages and kept on a 12-hour light-dark cycle. All animals were maintained on a food restriction (80-90% of free-feeding weight) to motivate them to perform the task.

Water was available *ad libitum*.

Arena

The layout and structure of the arena alter according to the obstacles encountered in behavioral training and recording. The base arena consists of two levels made from black gloss plexiglass (33" × 33"). The two levels are separated by 35.8 inches of vertical distance. The second level has sets of guiding walls centered around an observational hole. The first level has

three landmarks with isomorphic markings so the rats see the same patterns no matter the perspectives (Fig. 1). A plastic cage lid is modified into an elevator to transport animals between two arena levels.

A long track leads to a decision point on the first level. Two target areas are on the left and right of the decision point. There are four reward locations, two in each target area. An observational hole is located 11.4 inches from the edge on the second level.

Short walls were added to the first level to better distinguish spatial locations and quantify successful trials. This makes the first level resemble a simple multiple T-maze. A blinking landmark was added to more saliently signal to the rats the desired location. Cameras are mounted on the second level and suspended overhead to detect LED mounted to the recording headstage. Unique colorful wall paintings are displayed in all training and recording rooms to provide distal visual cues.

While four reward locations exist, the current task is designed to discriminate the left and right target areas. In the spirit of progressively increasing the task difficulty, until a consistent 80% correct rate is obtained with two target areas, there is no need to teach the animals to discriminate the four locations.

Behavioral Training

Animals were first introduced to a long track to develop running behavior. Rewards are given at the two ends of the track, encouraging the rats to run back and forth. After showing stable behavior for a period of time, the rats are moved onto a circular arena with one start location and two reward locations. They are trained to alternate going to the two reward locations and returning to the start location. After again showing stable behavior for some time, the rats are moved to the final arena to learn the task.

A list of randomized trials of left and right-turning types is generated before each training session. The elevator operator would clearly state the type of the next trial when the animal is at one of the reward locations (which indicates the completion of the current trial). The target controller chooses either the lower or higher reward location in the corresponding target area and moves the blinking landmark near that reward location when the animal is fully back on the elevator. Sequentially, the animal would start the trial on the second level, run to the observational hole, look down to check the location of the blinking landmark, run back to the elevator to be lowered, run to the highlighted location on the first level to be rewarded (for the successful trial), and run back to the elevator for the next trial. The rat is expected to use the information from the top-down view in the first-person navigational task (Fig. 2).

At the beginning of the behavioral training with the final arena, more reward locations are added to the task to encourage the habituation of schematic behavior. All reward locations are as follows: observational hole, elevator, reward locations at the target areas, and the elevator again. When animals display stable behavior without rewards for some time, these additional reward locations are removed. The reward locations at the target areas should always dispense the most rewards, so a weighted significance of accomplishing correct trials is impressed upon the animals.

Surgery and Recording

Recordings were obtained from one adult Sprague-Dawley rat. After demonstrating a good understanding of the task schema, the rat was surgically implanted with tetrodes—twisted sets of four 12-micrometer polyimide-insulated tungsten wire arrays integrated into a custom microdrive. Each microdrive held 16 tetrodes. Under isoflurane anesthesia, animals were positioned in a stereotaxic device (Kopf Instruments). Following craniotomy and resection of the

dura mater, microdrives were implanted bilaterally. Microdrives were implanted relative to bregma with targeting coordinates consistent across animals. CA1: A/P -3.24 mm, M/L +/- 1.8 mm.

After a week of recovery from surgery, the animal was retrained for at least two weeks before starting the recording, ensuring adequate behavior and running ability with the new weight of the implant (~20 grams). Electrodes were moved in 50-80 micrometer increments between recordings to maximize the number of distinct units collected for each animal. Each microdrive had 2 electrical interface boards (Neuralynx) connected to a single amplifying headstage. These signals were input in the acquisition computer running Plexon SortClient software. Waveforms from single units were isolated in Plexon OfflineSorter software. Waveform parameters used were peak height, peak valley, energy, average voltage, full width at half maximum, and principal components. Recordings typically lasted 30-60 minutes.

Animals' positions were tracked during neural recordings using a camera located 2.6m above the recording room floor. The recording room was dimly lit during recording. Plexon CinePlex Studio software detected two LED lights on the animal's surgical implant separated by approximately 5cm. Location tracking was captured at 60 Hz. At any given moment, position and orientation were determined using the average location of the two lights and the orientation of the vector between the lights. All animal movement data such as location, head direction, and derivatives are calculated from these values.

This manuscript represents putative recording data of 15 principal neurons in the subiculum from the animal. Brainwave oscillations - theta rhythms - characteristic of subicular and CA1 region neurons as well as anatomical boundaries of the regions of interest (Paxinos & Watson, 2006) guided an estimation of the source of each microdrive for each set of recordings.

Results

Behavior

Animals had a major left-turning bias at the start of the recorded behavioral training sessions. They would fixate on the left reward locations and always turn left even after trials without rewards. Remedial trials were administered to correct the behavior and weaken fixation (Fig. 3). These randomized trials would include runs that encourage the animals to run in the opposite of the fixated direction to get rewards. All remedial trials ended on March 26th.

In order to prevent the development of directional fixation after remedial trials, we have adopted a training scheme that utilizes a semi-randomized list of trials that have two maximum repetitions in one direction. This means that the total number of left and right-turning trials are always roughly the same, and no three consecutive trials would be turning in the same direction.

More than 20 days of behavioral training data is collected for DN 38, 39, and 42. DN 43 was moved off the maze due to its behavior of climbing down from the second to the first level being deemed unsafe. The compiled percentage correct statistics and dates show unpromising results. Rats quickly learned the schema of the task and can routinely perform single trials in under 20 seconds. However, their percentage correct statistics fluctuate drastically and are not significantly better than chance (Fig. 3). We believe that the animals were not consistently relating top-down and first-person views. This is because animals use other strategies or hybrid strategies to get rewards.

Initially, running an unsuccessful trial by going to the target area without the blinking landmark is not punished by denying the reward. Animals exhibit checking behavior, entering and scanning one target area first, and in the absence of a reward, going to the other target area to look for a reward. This exploitation is later fixed by denying the reward if the animal performs

an unsuccessful trial. This means that only successful trials are rewarded. Animals also tend to repeat successful trials in the hope of being rewarded again. This helps explain why just a few trials of repeating the same direction invite fixation on that direction's reward locations. To combat this, we selectively lowered the body weights of rats that frequently use this strategy to between 80 and 85%, incentivizing them to perform more successful trials and be rewarded.

Ultimately, it is unknown if rats can perform this novel task with the current arena setup. It is advised for future studies to decrease the vertical distance between levels and use more salient signals. Animals should also be introduced to the arena at a much younger age.

Electrophysiology

We observed multiple categories of subiculum neurons that exhibit interesting activity patterns that warrant further investigation. We have not yet observed notable activities by CA1 neurons during the task, indicated by theta rhythmic activities.

The first and most numerous category consists of neurons that exhibit different firing patterns on the two levels (Fig. 4A). Our arena has analogous parts at the entrance of the tracks on both levels. One would expect the same neuron to show similar activities across levels, but it is difficult to find any analogous activity. Most subiculum neurons we have recorded show vastly dissimilar firing patterns on different levels (Fig. 4). The only notable exception is cell 3 (Fig. 4B). This neuron fires at the entrance of tracks on both levels. These positions are only separated by 35.8 inches of vertical distance and are thus analogous. However, the shapes of the firing fields are still dissimilar: the firing field on the first level is elongated while there are two smaller firing fields at the entrance of the track and near the observational hole on the second level.

The second category is task-phase-specific neurons (Fig. 4B). These neurons fire during a specific task phase, such as running on a segment of the arena, staying relatively still to retrieve

the reward, or performing non-locomotor tasks. As mentioned, cell 3 (Fig. 4B) shows prominent firing at the track entrances on both levels and near the observational hole, but it also fires at the decision point. The size of this latter firing field is massive, but the neuron is relatively quiet when the animal is in the target areas.

The third category includes neurons that have a directional preference. They might exhibit more activities in either the left or right target area (Fig. 4C). This category of neurons is the most similar to traditional place cells, as they usually have one prominent firing field on the first level. Curiously, these cells show little activity on the second level. The firing fields of these neurons center around reward locations at target areas. Rate maps show that they can even finely distinguish between two reward locations within the same target area, as these firing fields are seldom at the centroid of the target areas.

This was stated by implication, but these categories are in no way mutually exclusive. Cells can match the descriptions of two, or even three categories. Cell 4 (Fig. 4B) has different firing patterns on the two levels. It shows the most prominent firing when the animal is moving along the track on the first level to the decision point, a vital navigational phase. Additionally, it shows more firing at the lower reward location of the left target area. The firing field of this cell is elongated, like that of a subiculum boundary vector cell (Bicanski & Burgess 2020). While the animal is in proximity to the short walls on the first level when the cell fires, it doesn't exhibit firing at other locations with similar distance and direction. For example, why doesn't it fire near the decision point where conditions are similar? Does the animal's straight-running behavior modulate the firing rate of this cell?

Discussion

Our task is similar to the visual scene memory task (VSM). Animals have to choose a direction associated with the reward for both tasks. The difference is that for our task, the hint of where the reward is can be glimpsed in the top-down view. Subiculum neurons can undergo rate remapping in response to the visual scenes and choice responses in a VSM task (Lee et al. 2018). But what we have observed is more akin to global remapping.

It is still unclear if elevation triggers global remapping for analogous locations in subiculum neurons. Two other factors might also contribute to their field remapping: differences in accessibility and level layouts. The rat ran two vastly different routes on the two levels for this task. It routinely ran only to the observational hole on the second level while it had to cover a much longer route on the first level. This is because the rat only has access to the experimental space framed by the guiding walls on the second level and the short walls on the first level. Additionally, the experimental space available to the rats only has analogous and not identical layouts between the two levels. It is advised that future studies should utilize arenas with identical layouts across levels to test subiculum neurons' sensitivity to elevation.

Moving forward, we are most interested in cell 5 (Fig. 4B). On the second level, this neuron shows the most activity at the observational hole where the animal looks down to check the location of the blinking landmark. On the first level, this neuron fires the most at the right target area. We believe that this cell's activity is associated with the top-down perspective. We plan to keep recording this cell's activity to see if its firing is predictive of right-turning behavior. Additionally, we plan to label our current behavioral recording so the timescales of behavior and neural activity are better matched. A lot of the firing fields we have observed can be influenced by both spatial and non-spatial cues. The hippocampus cells can exhibit conjunctive coding for spatial location and odor, auditory stimuli, and items (Barry & Doeller 2010). It would be

enlightening to examine the conjunctive properties of our subiculum neurons and find out why some cells exhibit firing fields that satisfy patterns in all three categories.

The ability to relate the two perspectives might be an emergent behavior that's beyond single-neuron activities. A computational neuroscience study suggests that a top-down view to first-person view transformation requires more latent variables correlated with distance to landmarks and place fields, and fewer latent variables sensitive to head direction than a first-person view to top-down view transformation (Xing et al. 2022). This might mean that distance cues to the landmarks play a more important role in our task than previously thought. Landmarks that show salient single-point perspective projection to aid depth sensing might ease perspective transformation in rats.

For supplementary information, please refer to [honors presentation](#), [honors graphics](#), [thesis graphics](#), and [behavioral data](#).

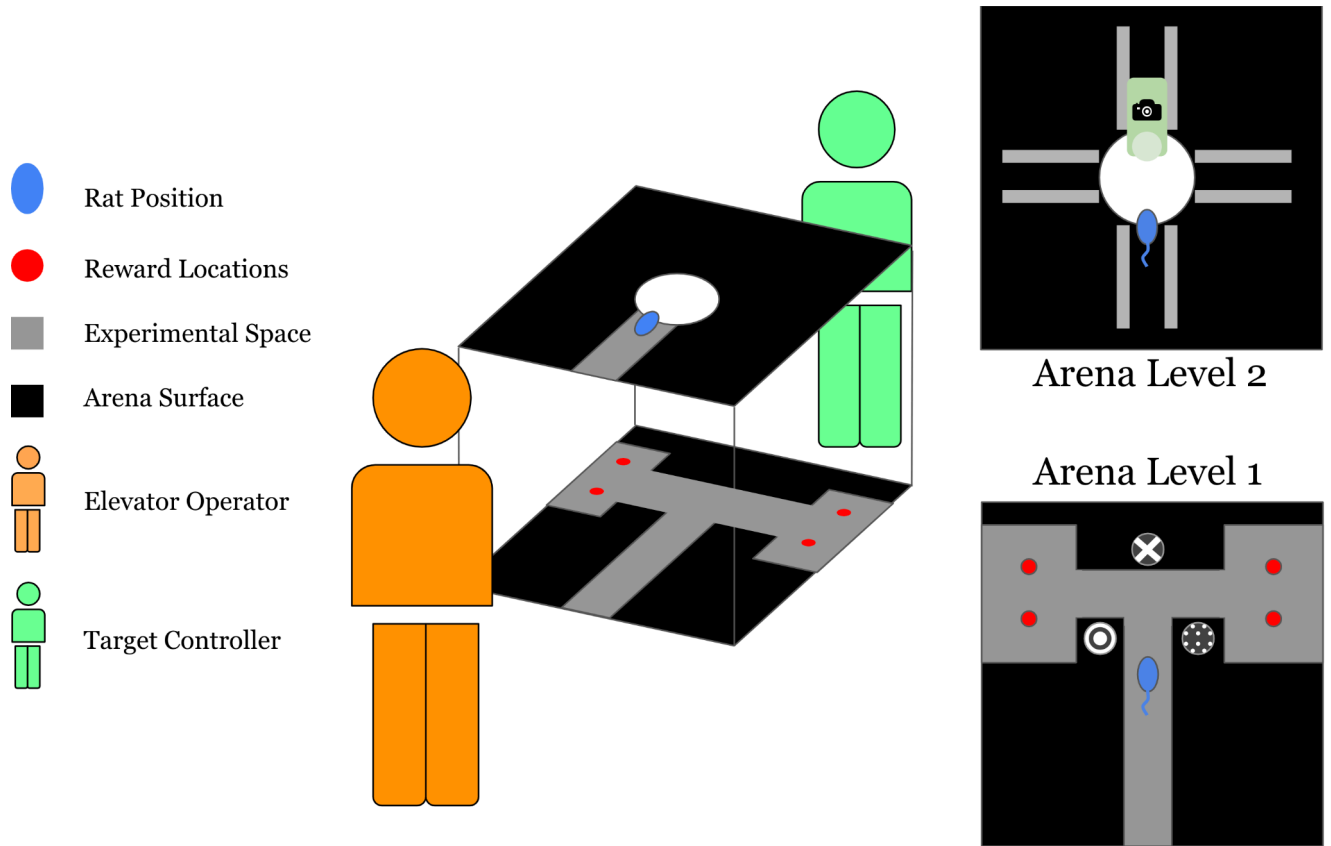


Fig. 1. The elevator operator is responsible for transporting the rats across the levels. The target controller is in charge of moving the blinking landmark and providing auditory cues (tapping) to attract the rats' attention. Landmark patterns are identical from both the top-down and first-person views.

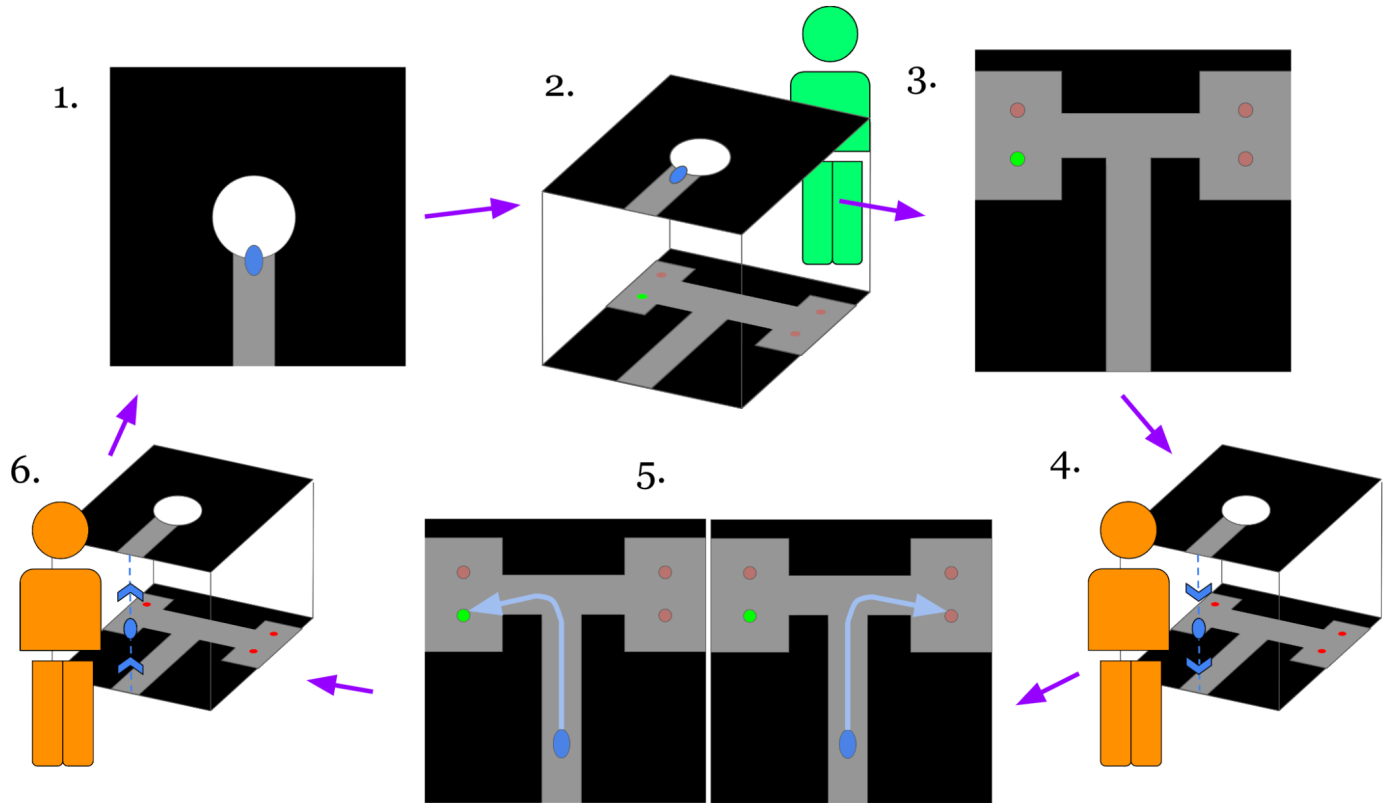


Fig. 2. Successful trial running requires rapport between rats and human operators. Before the rat gets to the second level, the target controller moves the blinking landmark to one of four reward locations. A random sequence of locations was generated before each session. After the landmark is placed, the elevator is docked and the animal is allowed to run to the observational hole. The target controller taps near the highlighted reward location to attract the animal's attention. We hope that the use of both visual and auditory cues makes the landmark more salient to the animals. The animal then runs back to the elevator and is transported to the first level. It runs on the straight track and makes a turn at the end to arrive at one of the target areas, marking the trial either successful or unsuccessful. Running a successful trial earns the rat a half piece of Cheerio as a reward. Running an unsuccessful trial earns the rat no reward.

Results: Behavioral Data

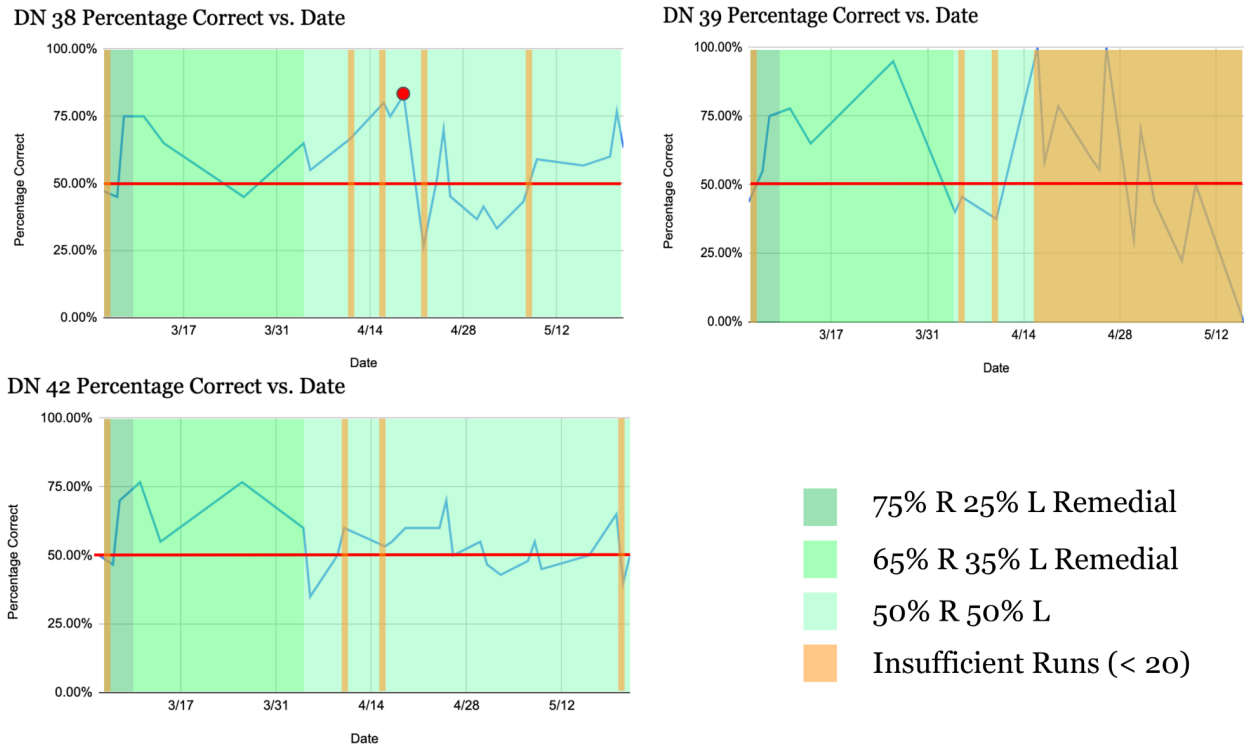


Fig. 3. Percentage correct statistics were collected and compiled (n = 25 for DN 38, n = 21 for DN 39, n = 26 for DN 42). From April 16th to May 16th, DN 39 demonstrated the behavior of not running sufficient trials (< 20 per session) and was moved off the task.

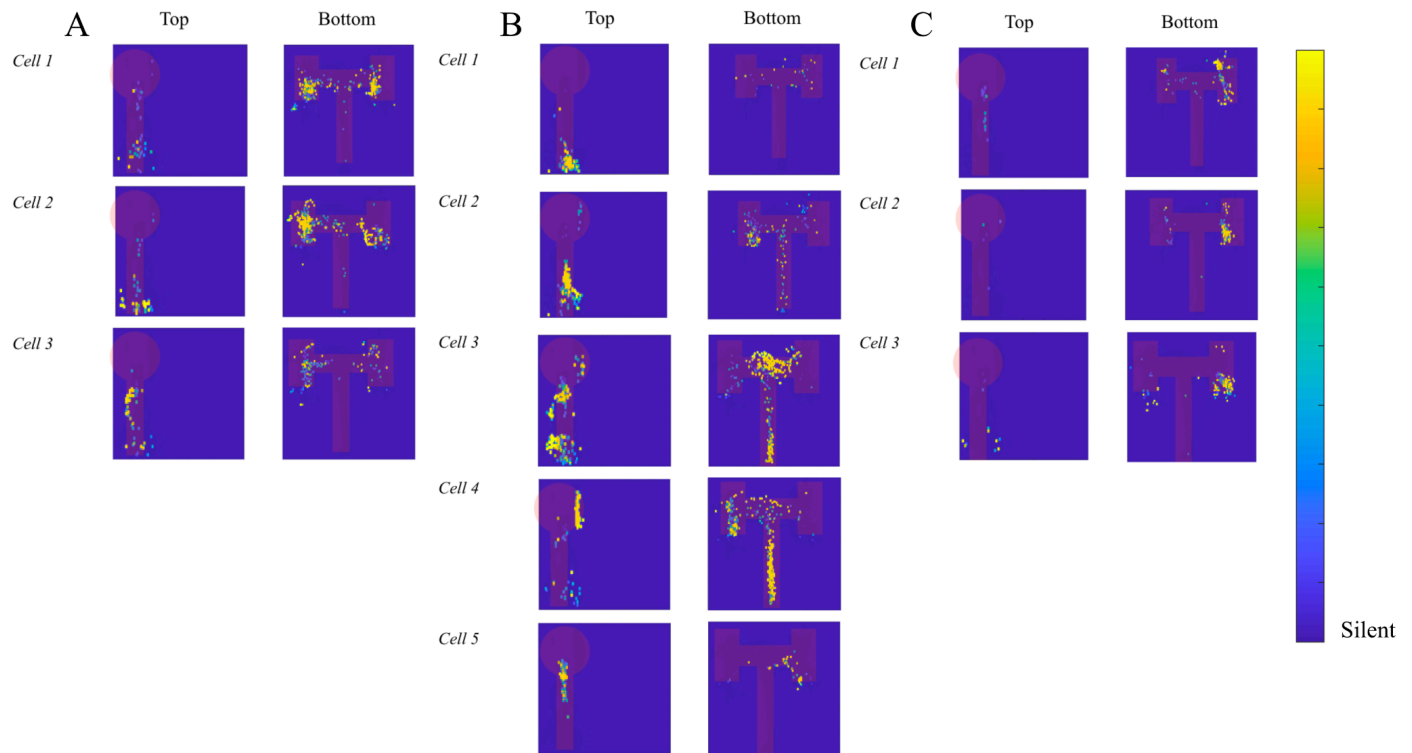


Fig. 4. Purple outlines show estimations of the experimental space on the top and bottom levels. (A) Subiculum neurons with different firing fields on different levels. While the neurons shown in this category are the most representative, most other cells (B and C) shown here can fit in this category. (B) Task-phase-specific subiculum neurons. Due to the recording angle of the overhead camera, cell 4's activities on the bottom level are shown on the top-level rate map. This means cell 4 is relatively quiet on the top level. (C) Subiculum Neurons with a directional preference. The c-axes of all the rate maps are set to 0 to 5.

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