Neurons and Navigation: How Single Neurons in the Brain Map our Environments

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Abstract

A dynamic understanding of pathways, their intersections, and orientation in a larger environment is essential for successful navigation, specifically in regularly patterned path networks. In contrast to cells in CA1, which encode for individual locations in an environment, cells in the subiculum have been found to encode multiple locations that compartmentalizes the environment into segments that bear analogy. In this work, we sought to understand navigation behaviors of rats in a patterned grid network in relation to their neural firing, to investigate the activity of subiculum neurons as the rats did tasks. Our behavioral results indicate that rats are able to learn a task that requires an understanding of the grid system and its directionality in the larger environment. Additionally, two subicular neurons were found to encode analogous segments along the grid network, adding to a growing body of evidence that the subiculum is tuning to the structural organization of the environment by encoding spatial relationships.

1. Introduction

Humans move throughout the world in pathways. Efficient traversal of paths within structured environments demands the flexible understanding of the pathways and headings possible within the space. The goal of this project is to understand and model this behavior in rats in a regularly patterned environment, with specific focus on activity in the subiculum.

Before navigational and spatial mapping research arrived at the subiculum, it began with the hippocampus, with place cells (CA1 neurons) being found to have a preference for individual locations in an environment in rats (O'Keefe & Dostrovsky, 1971). Spatial mapping research continued on to find more types of neurons in rats important for spatial navigation, notably head direction cells in the postsubiculum (Taube, Muller, & Ranck et al., 1990), grid cells in the entorhinal cortex (Hafting et al., 2005), and cells in the entorhinal cortex that detect geometric borders (Solstad et al., 2008).

Aside from head direction cells found in the postsubiculum, a 'unique role' of the subiculum in spatial navigation has not been found (Olson et al., 2021). Despite this, many neurons relevant to spatial navigation have been discovered in the subiculum in rats, likely due to its many afferents that are important for cognitive mapping, including the anterior thalamus, presubiculum, medial and lateral entorhinal cortex, and CA1 in the hippocampus (Olson et al., 2021, p. 2). Boundary vector cells that detect boundaries in the environment have been found

(Lever et al., 2009), as have cells that 'place-specific' firing that is broader than the firing patterns of place cells (Kim, Ganguli, & Frank, 2012) and bimodal axis tuned neurons (Olson, Tongprasearth, & Nitz 2017). These findings allude to the subiculum's tendency to encode for *features* of an environment, rather than specific locations. Of specific interest to this experiment is the discovery of neurons in the dorsal subiculum that encode for locations in an environment analogous in their structure and function (Olson et al., 2021), a finding that sheds light on how regularly patterned environments with multiple possible routes are cognitively mapped and reliably navigated, based on the shared features of locations in the environment rather than environmental boundaries or individual locations.

This finding was found as rats navigated a variation of the Triple-T Maze, a maze structure where the animal makes its way through a repeating and regular path with choice points. Because this maze was symmetrical, in that both sides of the maze are mirror images of each other, small segments of the path on one side of the maze became analogous to the same segment on the opposite side (Olson et al., 2021). When considering large path networks that are regular, for example the grid systems of cities like Barcelona and Manhattan, a similar spatial phenomena emerges. In contrast to the triple-t maze, which is made up of two identical mirrored halves, grid patterned path networks are made up of identical blocks. These blocks, being identical, thus contain segments that are analogous to the other blocks in the grid system. In the triple-t-maze where there is one pathway in order to get to a goal location, in a regular grid system, the rat can take multiple pathways to reach the same goal, thus making their navigation more naturalistic.

The intention of this experiment is to investigate the activity of cells in the dorsal subiculum that encode for analogous locations. In order to expand on the findings by Olson et al. 2021, we created a 4x4 grid patterned path network consisting of 16 identical square blocks. Rats performed trials on this grid consisting of runs out and back from a home base, while single neurons in the subiculum were recorded, in order to investigate subiculum activity in a larger path network consisting of a multitude of analogous segments. Behavioral data gathered from 3 rats and neural data from 1 rat allowed us to preliminarily conclude that firstly the rats learned the task, and consistent with Olson et al., 2021, neurons from the subiculum encode analogous locations in path networks.

2. Methods

Subjects

Subjects were adult male Sprague-Dawley rats (N = 3). Behavioral data was recorded from all rats, data from two are discussed in this paper. A total of 17 neural recordings were recorded from one rat. Rats were housed individually and kept on a 12-h light/dark cycle. Prior to experimentation, animals were habituated to the colony room and handled for 1–2 weeks. During training and experimentation, rats were food restricted and weights were maintained at

85–95% of free-fed weight with water available continuously. Rats were required to reach a minimum weight of 350 g (5–10 months of age) before surgery and subsequent experimentation. All experimental protocols adhered to AALAC guidelines and were approved by the IACUC and the UCSD Animal Care Program.

Apparatus

All behavioral tasks were conducted on the 4x4 square grid patterned path network. The grid is custom built, consisting of tracks made from wood that has been painted black (represented in gray, in Figure 1a). The grid is approximately 72in long by 72in wide, and was elevated approximately 4in off the ground. The tracks are approximately 4in wide. In the center of each square (where the rat was unable to traverse) there was a green LED light positioned at the rat's eye level. These were connected with wires under the tracks to an arduino, connected to a computer. Control of the lights was through a custom program. Each square was labeled with numbers 1-16, which the lights corresponded to. The room in which the grid patterned path network was located contained a different image on each of the walls of the room, allowing the rat to distinguish his direction, and the direction of other objects in the room.
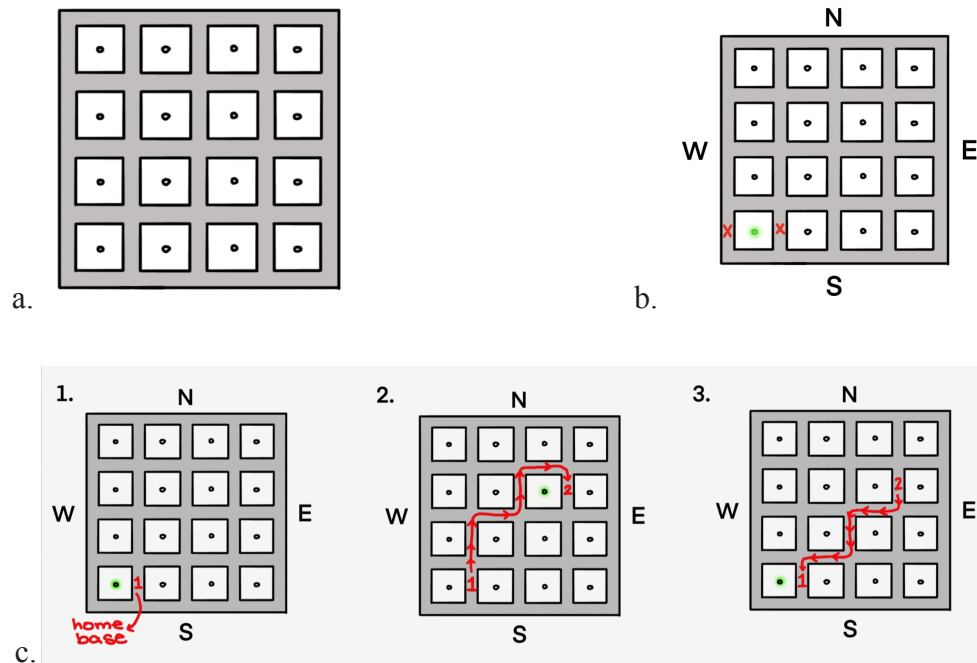

a.

b.

c.

Figure 1.
Shows the grid patterned path network. a. The 4x4 grid patterned path network where the rats were trained and recorded doing the task. The gray areas are the paths that the rats were able to traverse, and the circles in the middle of the squares are green LEDs that were able to be turned on remotely. b. The grid patterned path network with cardinal

directions indicated. The green light at the bottom indicates block 13, where home base was located, at either its west or east segment (indicated by the red X's). c. An example of a run to a goal site, and back to home base, where the goal site and home base was located on the east segment of the block.

Behavior

Rat behavior consisted of runs out from a home base to a goal site, and back from the goal site to the home base. The home base would always be on the 13th block, indicated during the task by a lit LED (Figure 1b). For a whole trial, the rat will receive a reward only on a segment of the 13th block in a specific direction, which will also inform the direction of the goal site (Figure 1c). The goal site is the segment of the block around the lit LED that is in the same direction as the home base. The reward—half a cheerio—is placed on the goal site/home base when the rat is distracted, so that the rat will go to the goal/home base via the cue of the light, rather than the experimenter placing the reward.

A sequence of goal sites is created before the recording via a random number generator. The rat would begin at home base, run to a goal site, return to home base, run to a different goal site, run back to home base, etc (Figure 1c). The rat would always return to home base between goal sites. An example sequence for a trial with 12 goal sites and 25 total runs would be:

13 7 13 8 13 10 13 15 13 11 13 9 13 4 13 16 13 12 13 3 13 14 13 5 13

Rats were trained on the task five days a week for 32 goal sites a day (64 runs). Recording days consisted of approximately 100 goal sites (200 runs). Animals were first trained on the grid network to associate reward with a green light (using a green laser pointer), then were trained on the full task.

Scoring Task Behavior for Data Analysis

When scoring the task behavior in our custom scoring program on MATLAB, we considered a successful run to be a run directly to the goal site/home base without checking any of the other segments of the block before reaching the reward, or veering off course. Data from successful runs (or "clean runs") was used for ratemapping, and data from unsuccessful runs ("dirty runs") was omitted from the ratemaps.

Rats were considered to be "checking" an incorrect segment of the block for a reward when they sniffed for the cheerio/stopped, or took a route to the reward site that took them through the other segments of the block. For example, an unsuccessful run/dirty run is shown in Figure 1.c.2, where the rat traverses the west side of the block before going to the goal site on the east side. A successful run/clean run is shown in Figure 1.c.3, where the rat runs from the goal

site directly (without stopping) to home base without checking any other segments of the block where home base is located. Emphasis was placed on the successful run being a direct, continuous path from the goal site to home base without checking any of the other locations, rather than the rat taking the most efficient path, as they often took different pathways to the same location.

Surgery

After exhibiting the ability to systematically retrieve rewards from the environmental paradigm, rats were surgically implanted with tetrode (twisted sets of four 12 micrometer polyimide-insulated tungsten wire) arrays integrated into a custom microdrive. Each microdrive held 16 tetrodes. Under isofluorane anesthesia, animals were positioned in a sterotaxic device (Kopf Instruments). Following craniotomy and resection of dura mater, the microdrive was implanted relative to bregma with targeting coordinates consistent across animals. CA1: A/P -3.24 mm, M/L + 1.8 mm

Neural and Behavioral Recordings

Following a week for recovery from surgery, animals were retrained for at least two weeks before the start of recording, ensuring adequate behavior and running ability with the new weight of the implant (~25 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' position were tracked during neural recordings using a camera located 2.6m above the recording room floor. 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 time point, position and orientation were determined using the average location of the two lights and orientation of the vector between the lights. All animal movement data such as location, head direction, and derivatives are calculated from these values.

The data presented here putatively characterizes a select of 2 neurons from the subiculum from a span of 17 recordings. We concluded that these two neurons are subicular neurons due to their neurophysiological signatures in the form of theta rhythms and the approximate depth of the tetrodes. Histology will be needed to confirm the location of these neurons.

2D Positional Firing Ratemaps

To assess activity as a function of 2D space, individual neurons' positional firing rates were calculated by dividing the total number of spikes at each location by the total occupancy time at that location. If only showing identified routes, only data identified as during successful runs (clean runs) was used. Ratemaps were velocity filtered to only include data when the rat was in motion. Positional firing maps were smoothed using a 2D convolution with a Gaussian filter with s.d. of 1cm that also accounts for bins with no occupancy. Ratemaps were additionally made for runs out (runs from home base to the goal site) and runs in (runs from the goal site to home base).

3. Results

Demonstrated Learning of the Task

Behavioral data was obtained from 2 rats over two days. On the first day (Figure 2, Figure 4), the home base was positioned at the east segment of the home block (ref Figure 1c). On this day both rats ran between 113 and 115 runs. DN 44 showed an approximately 11% increase in successful runs (Figure 2) from the first half of the runs (63.16% of 57) to the second half of runs (74.14% of 58). DN 45 showed an approximately 5.67% increase in successful runs (Figure 4) from the first half of the runs (76.79% of 56) to the second half of runs (82.46% of 57). Both rats showed an increase in successful runs over time. Statistical tests will be needed to reach concrete conclusions, but we preliminarily conclude from this data that the rats did demonstrate learning on the task due to their marked increase in successful runs.

The second day (Figure 3, Figure 5) the home base was positioned on the west segment of the home block. On this day both rats ran approximately 60 runs. DN 44 showed an approximately 34.71% increase in successful runs (Figure 3) from the first half of the runs (58.62% of 29) to the second half of runs (93.33% of 30). DN 44 showed an approximately 26.67% increase in successful runs (Figure 5) from the first half of the runs (53.33% of 30) to the second half of runs (80% of 30). Both rats showed an increase in successful runs over time. Statistical tests will be needed to reach concrete conclusions, but we preliminarily conclude also from this data that the rats did demonstrate learning on the task due to their marked increase in successful runs.

DN 44 showed a larger second half success rate on the second day (home base on the west side) than the first day (home base on the east side), a 19.19% difference. DN 45 showed a larger second half success rate on the first day (home base on the east side) than the second day (home base on the west side), a 2.46% difference. Both rats showed much larger differences in success rate between the first half and last half of runs on the second day than the first day.

Dynamic analysis of learning will be performed in the future in order to reach concrete conclusions (see methods in Smith et al., 2004), but preliminarily, we conclude that the rats

learned and understood the task, thus demonstrating their understanding of directionality in the larger space.
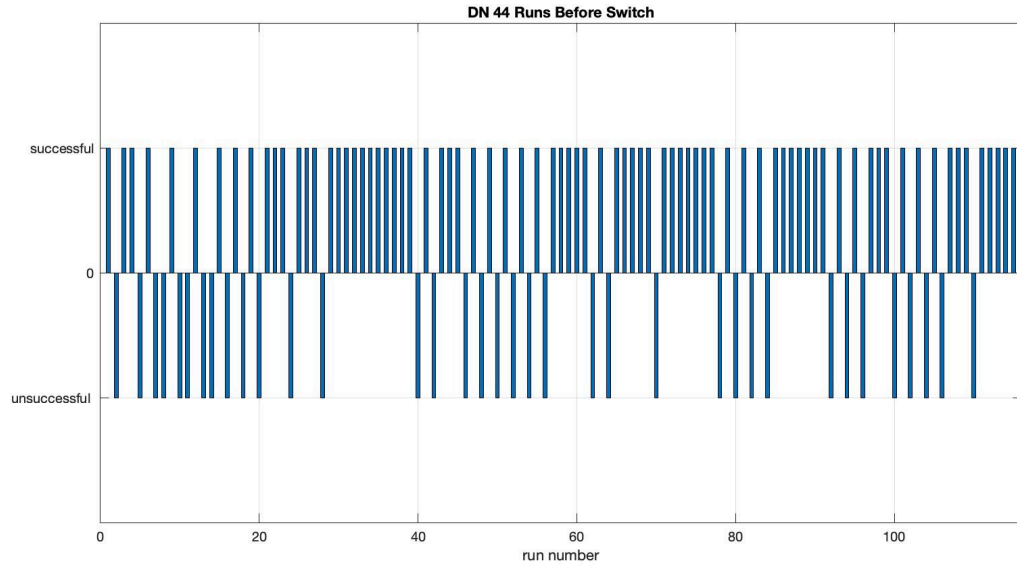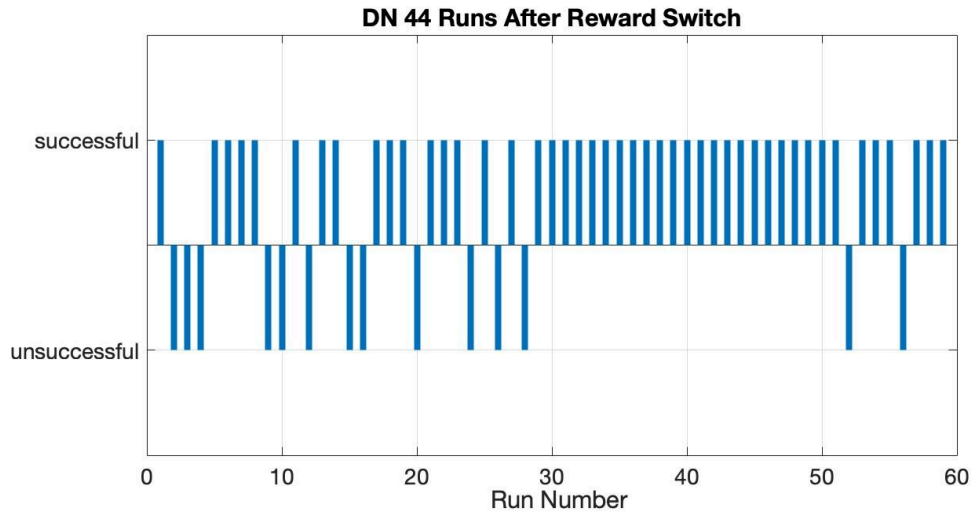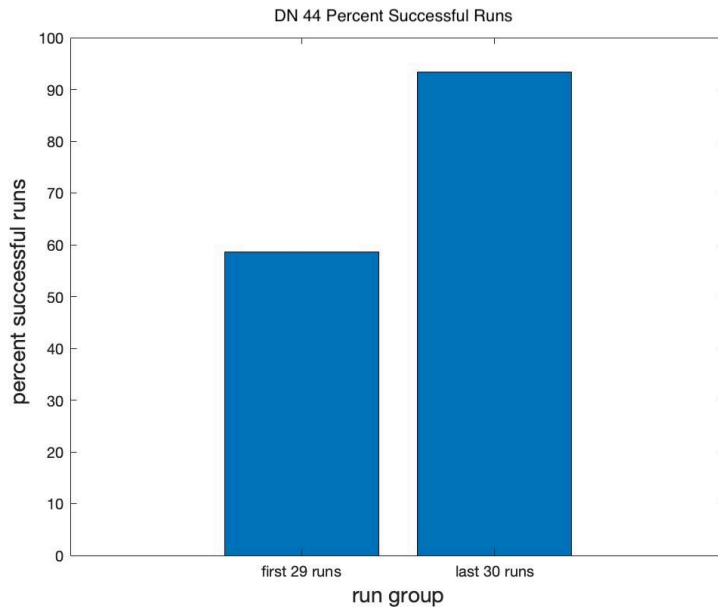

a.
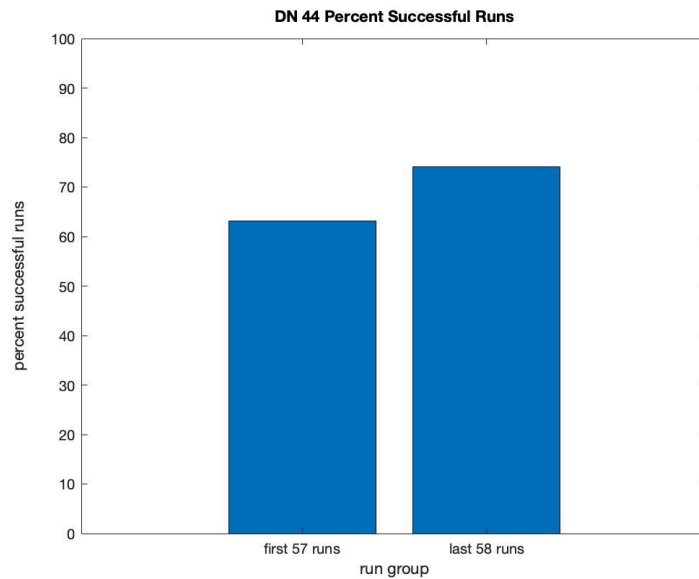
b.

Figure 2.
DN 44's successful vs unsuccessful runs, on day **one** where the home base and goal site were on the **east** segment of their respective blocks. a. The total runs, marked as unsuccessful or successful based on whether or not the rat ran directly to the goal site/home base. Total of 155 runs on this day. b. Shows DN 44's percentage of successful

runs in the first 57 runs, and the last 58 runs. In the first 57 he had a 63.16% success rate, and in the last 58 runs he had a 74.14% success rate.
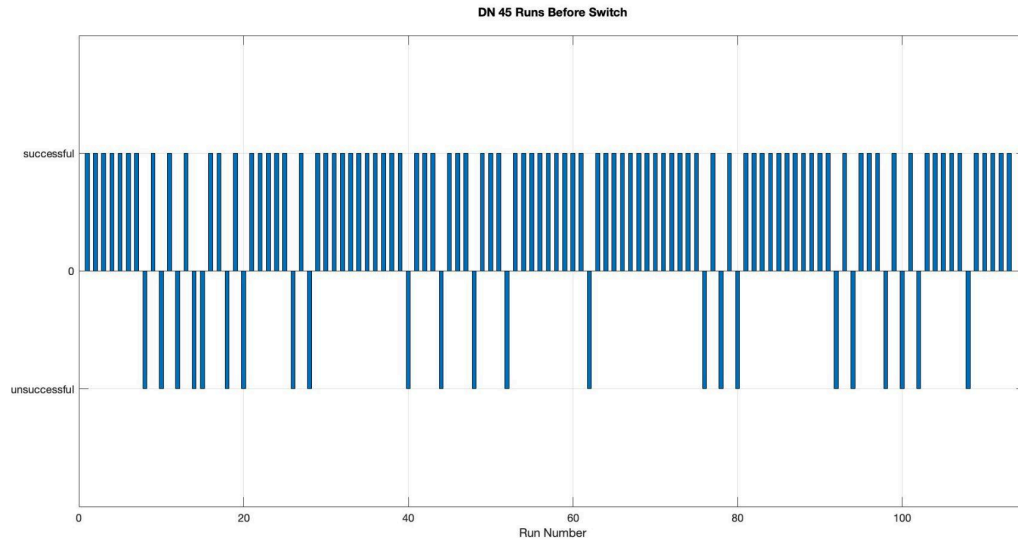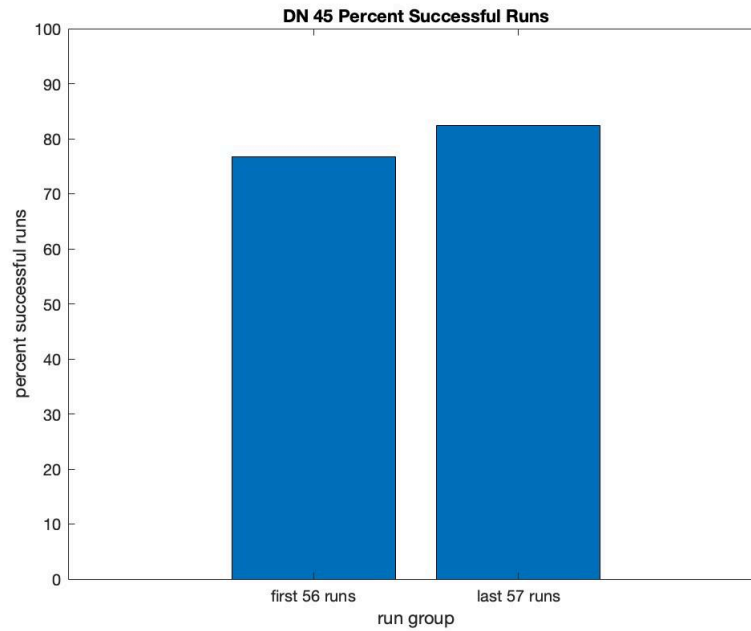

a.

b.

Figure 3.
DN 44's successful vs unsuccessful runs, on day **two** where the home base and goal site were on the **west** segment of their respective blocks. a. The total runs, marked as unsuccessful or successful based on whether or not the rat ran directly to the goal site/home base. Total of 59 runs on this day. b. Shows DN 44's percentage of successful runs in the first 29 runs, and the last 30 runs. In the first 29 he had a 58.62% success rate, and in the last 58 runs he had a 93.33% success rate.
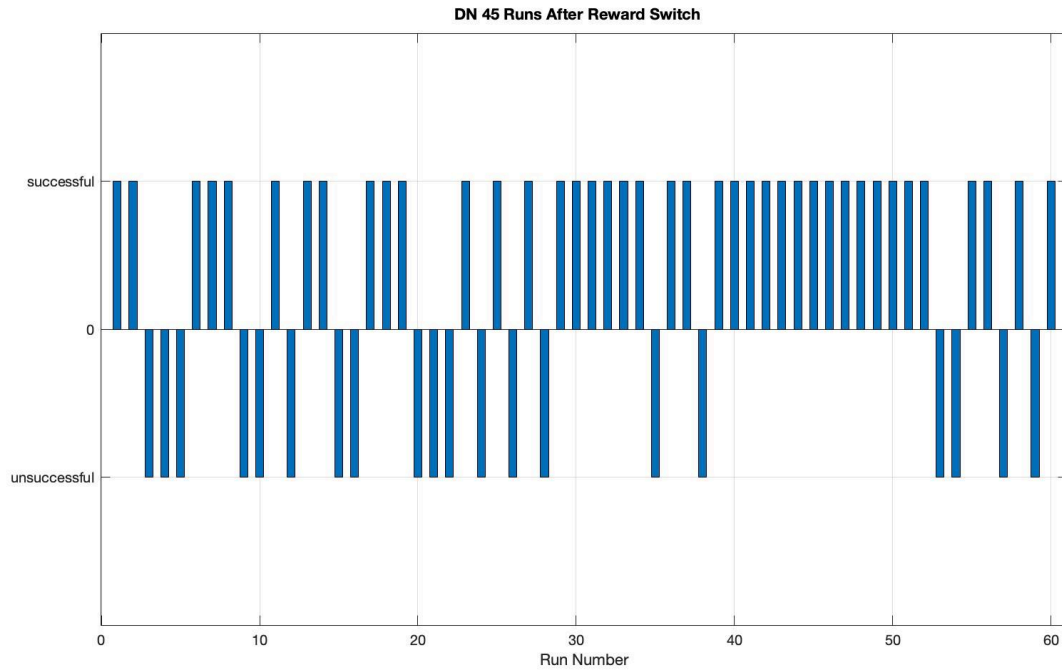
a.

b.

Figure 4.

DN 45's successful vs unsuccessful runs, on day **one** where the home base and goal site were on the **east** segment of their respective blocks. a. The total runs, marked as unsuccessful or successful based on whether or not the rat ran directly to the goal site/home base. Total of 113 runs on this day. b. Shows DN 45's percentage of successful runs in the first 56 runs, and the last 57 runs. In the first 56 he had a 76.79% success rate, and in the last 57 runs he had a 82.46% success rate.
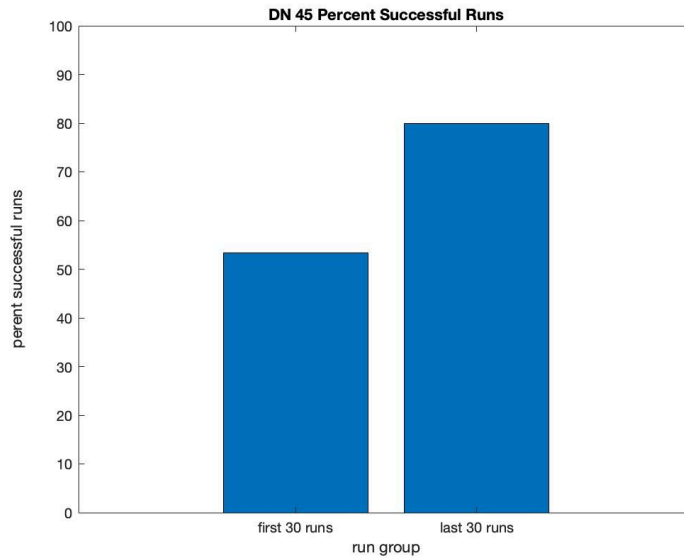
a.

b.

Figure 5.

DN 45's successful vs unsuccessful runs, on day **two** where the home base and goal site were on the **west** segment of their respective blocks. a. The total runs, marked as unsuccessful or successful based on whether or not the rat ran directly to the goal site/home base. Total of 60 runs on this day. b. Shows DN 45's percentage of successful runs in the first 30 runs, and the last 30 runs. In the first 30 he had a 53.33% success rate, and in the last 30 runs he had a 80% success rate.

Subiculum Neurons Encode for Analogous Locations

Over the course of the 17 neural recordings from DN 35, two specific neurons of interest were identified (Figure 7, Figure 8), recorded during recording 16. During recording 16, 168 runs were recorded with the home base at the west side of block 13, and the last 57 runs were with the home base at the east side. For this data, only the first 168 runs with the home base on the west side were considered, due to the larger amount of data available. All ratemaps from this recording referenced in this work will be from these first 168 runs, and will only include data from successful runs.

During the full recording, the rat visited all points on the grid (Figure 6). The spiking data from the two neurons (during the successful runs of first 168 runs of the recording) was combined with the rat's location (during the successful runs of the first 168 runs of the recording), thus producing two ratemaps (Figure 7, Figure 8). Additional rate maps were created for runs out and runs in (Figure 7, Figure 8), where runs out were runs from home base to a goal site, and runs in were runs from a goal site to home base. These ratemaps are the same orientation as the grid patterned path network shown in Figure 1b, with home base being on the west. The cardinal directions pictured in Figure 1b will be referenced in discussion of the ratemaps in Figures 7 and 8.

Neuron 1 (Figure 7) has a preference for the southeast corner of several blocks on the grid. This is most evident in the ratemap for Runs Out, but is replicated to a lesser degree in Runs In. When considering each square of the grid being an individual identical block, Neuron 1 is firing for the southeast corner of most blocks. Because the blocks are identical and the grid patterned path network is a regular grid, the southeast corner of each block is analogous to one another. Thus, we conclude that this neuron is firing for analogous locations, consistent with previous findings (Olson et al., 2021). Statistical tests will be needed to confirm this finding.

Neuron 2 (Figure 8) features a lower rate of firing over the general grid than Neuron 1, and an extremely different pattern of firing for Runs Out versus Runs In. For Runs Out, the neuron is firing at the entire west side of the grid, and more sparsely for the west segments of blocks immediately adjacent (Figure 8). As the rat traversed this area of the grid, he would be heading toward a goal site and away from home base, and thus going generally north (Figure 8b). On Runs In, the neuron is firing for parallel segments of the grid where the rat would be heading west, coming from a goal site toward home base (Figure 8c). The parallel segments in Runs Out are: 1. Parallel, 2. Straight, and 3. Pointing north (Figure 1b). As they are the same in structure and pointing in the same direction, they can be considered analogous. Similarly, the parallel segments seen in Runs In are the same in structure and direction, and can be considered analogous (Figure 8c). Thus, Neuron 2 is firing for long, parallel pathways that are analogous to each other in their structure and direction. Again, statistical tests will be needed to confirm this finding.
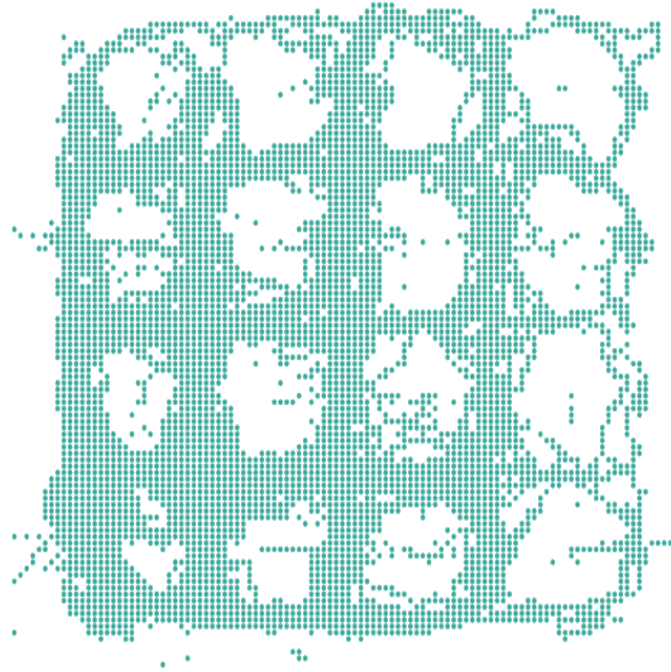
Figure 6.

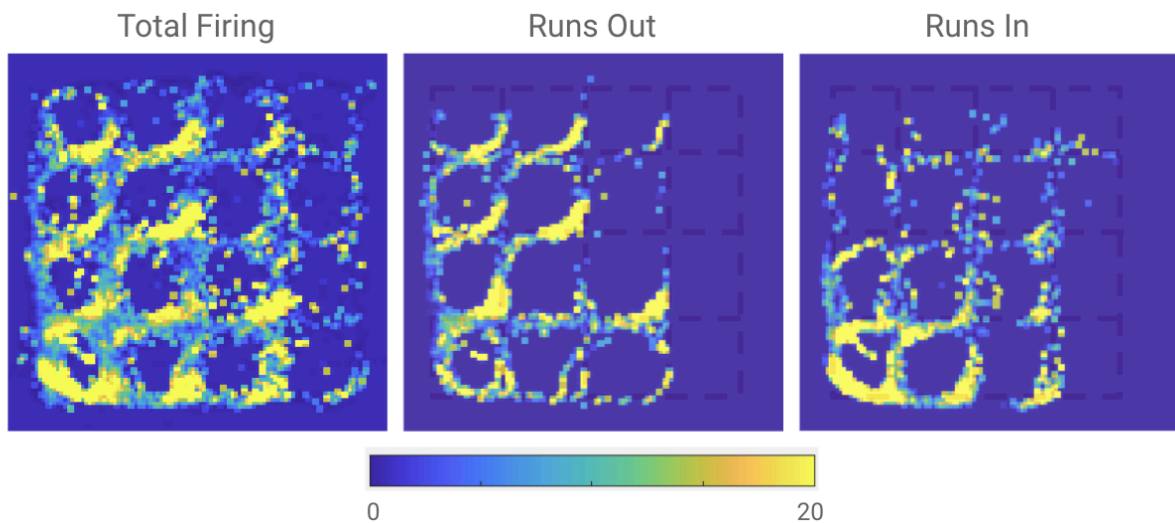Shows the occupancy map for the entirety of DN 35's recording 16.

Figure 7.

The ratemap for **Neuron 1**, identified during recording 16 in rat DN 35. The first image is the total firing of Neuron 1 during the recording. The home base for this recording is located on the **west** segment of block 13 (the block on the bottom left corner). The second image is the firing of the neuron during Runs Out (runs from the home base toward a goal site), and the third image is the firing of the neuron during Runs In (runs from the goal site back to home base).
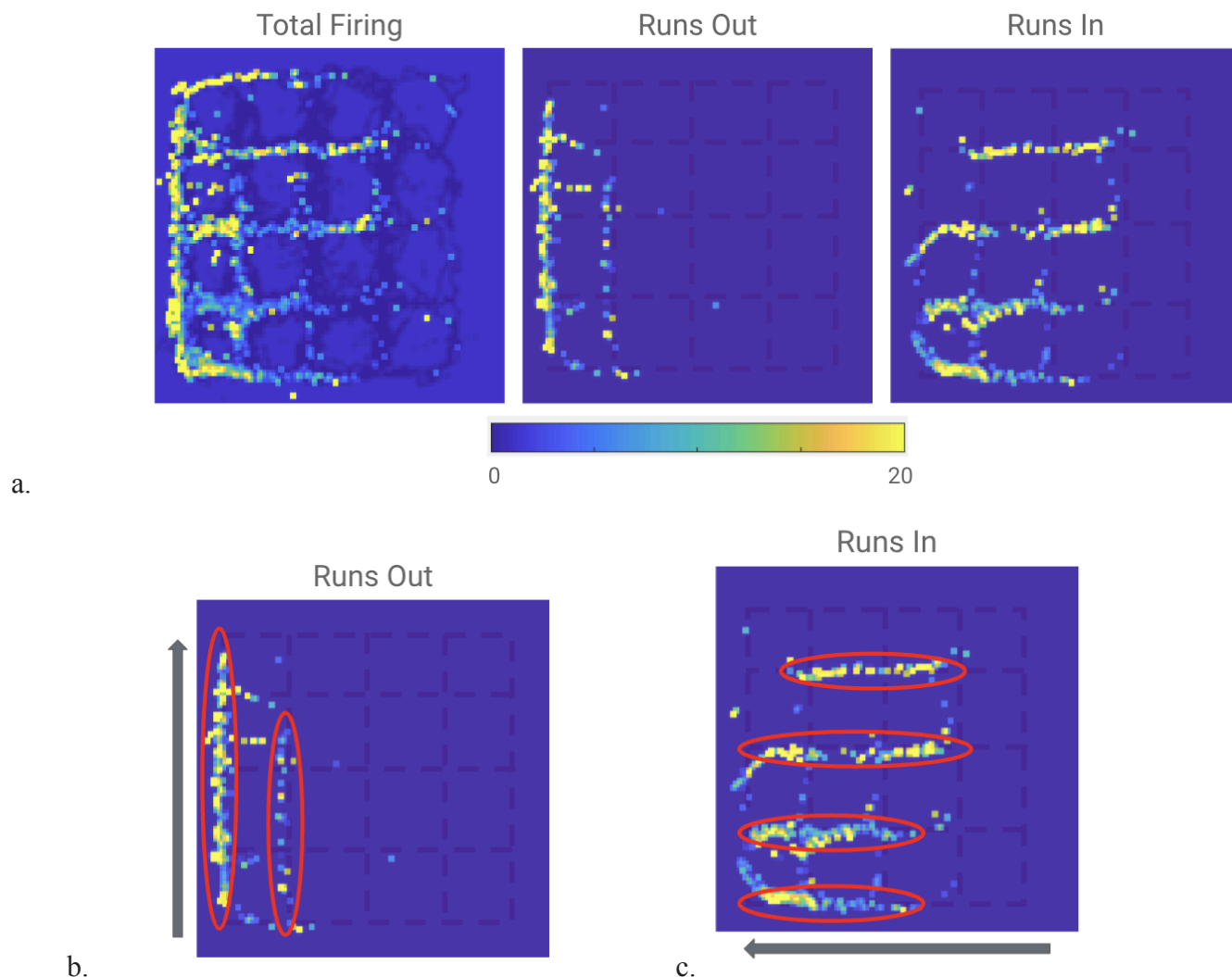
Figure 8.

The ratemap for **Neuron 2**, identified during recording 16 in rat DN 35. a. The first image is the total firing of Neuron 1 during the recording. The home base for this recording is located on the **west** segment of block 13 (the block on the bottom left corner). The second image is the firing of the neuron during Runs Out (runs from the home base toward a goal site), and the third image is the firing of the neuron during Runs In (runs from the goal site back to home base). b. Runs Out, with the firing pattern circled in red, and the arrow indicating the general direction (north) of the rat during his runs out. c. Runs In, with the firing pattern circles in red, and the arrow indicating the general direction (west) of the rat during his runs in.

4. Discussion

In this experiment, we sought to gain a greater understanding of how rats navigate in a regularly patterned environment and investigate the activity of subicular neurons in this environment. Through training rats on tasks that require an understanding of directionality on a 4x4 grid patterned path network, we found that two rats whose behavior we analyzed did indeed learn the task. Through this finding, we are able to conclude that the rats had an understanding of directionality in the environment and the structure of the grid network, which allowed them to perform the task successfully. Most importantly, we identified two subicular neurons through neural recordings in one rat that are encoding analogous locations in the grid network. One neuron encoded for the southeast corner of individual blocks in the grid, while the other encoded for parallel pathways in the direction of the rat's general trajectory. From this we can hypothesize that rather than mapping out individual points in an environment in the manner that place cells do (O'Keefe & Dostrovsky, 1971), subiculum neurons map the environment through identifying analogous segments, which in regularly patterned environments could allow for the inference of the entire structure. To expand further, this information could be further generalized to allow for easy navigation in other environments that are organized similarly. Future research investigating these hypotheses will be necessary to form concrete conclusions.

Rats Demonstrate Understanding of Directionality

Through the behavioral data we have gained from two rats, DN 44 and DN 45, we can conclude that the rats did indeed learn the task, and thus demonstrated understanding of directionality. Both rats increased the number of successful runs over time, both when the goal site was on the west segment and when the goal site was on the east segment, indicating that they understood where the goal site was going to be and were able to differentiate that site from the other segments of the block. Due to the rat's ability to differentiate between the segments of blocks—the segments being different because of their direction in relation to the green LED in the center of the block and in the larger context of the room—we can conclude that the rats did understand the concept of directionality.

It is pertinent to note that the rats, after many months of training, eventually developed a "process of elimination" behavior. During trials, we typically only put the reward on the west or the east side of the 13th block. Because of this, the rats eventually learned that the goal site was either going to the on the west or east side of the block where the green light was turned on. Since they pass the west side of the block first before reaching the east side of the block, when the goal site was on the east side, they would stop at the west side first, sniff for the cheerio, turn around, and then proceed to the east side. This additionally implies that when the reward was on the west side and the rats reached the goal site first, it is difficult to determine whether the rat actually knew the goal site was on the west side, or was simply doing the "process of elimination" behavior. Although this is indeed an issue with our data, from it we can still conclude two things: 1. The rats, even if they weren't remembering the specific location of the goal site, still maintained understanding of directionality. This is because the rats only stopped

and sniffed on the west segment or the east segment. If we were to assume the rats had no knowledge of directionality, we would expect them to circle around the block with the lit LED, sniffing at every segment until they found the cheerio. Instead, they only stopped and sniffed at the west and east segments of the block, demonstrating that they understood that the goal site would be on either segment in the two opposite directions, thus meaning that they had an understanding of directionality. 2. Despite this behavior, the rat's success rate still increased over time in all trials mentioned in this study. Thus, there must have been some learning, even if it was not exactly the learning that the task was designed to encourage. For future recordings, the experimental task will be amended to control for this behavior and make our data more robust (see Further Directions).

Subiculum Neurons Encode for Analogous Locations in a Grid

Through 17 recordings of one rat, we found two neurons that are encoding for analogous locations, consistent with the findings from Olson et al. in 2021. Neuron 1 has a preference for the southeast corner of individual blocks in the grid, all of which are analogous to each other because they are identical and in a regularly patterned grid path network (Figure 7). Expanding on this idea, we can hypothesize that this neuron is breaking up the grid into blocks. Because these blocks are identical and constitute the entire grid, the information gained by mapping out a few individual blocks could hypothetically be used to infer the structure of the larger grid without the need of having to map every location in the environment individually.

In contrast, rather than firing at the same corner in different blocks, Neuron 2 is firing for analogous parallel pathways, which are analogous in their structure and their direction (Figure 8). The direction of these parallel pathways seems to coincide with the general direction in which the rat is heading, as can been seen in the change in the neuron's firing in Runs Out compared to Runs In (Figure 8b, 8c). Rather than breaking the grid patterned path network into individual blocks, this neuron may instead map analogous pathways in order to infer the structure of the larger environment. More neural data will be needed to confirm and expand upon these findings, and provide further insight into how subicular neurons are mapping our grid patterned path network.

5. **Further directions**

- DN 44 and DN 45 will be undergoing surgery and will be recorded doing the task once they have recovered. Through this we will be able to get data from more subiculum neurons and investigate as to whether they show consistent firing for analogous locations. More behavioral data will additionally be collected from these two rats and dynamic analysis of learning will be calculated to ensure that they are learning the task.

- Histology will be performed on DN 35's brain in order to confirm the depth of the electrodes and whether or not they reached the subiculum.
- The task will be changed so that rather than the reward being placed on the maze directly, thus allowing for the "process of elimination" behavior, the rat will have to reach the goal site, stop, and wait to be handed a reward. We hypothesize that this will fix the "process of elimination" behavior, as it makes waiting at the correct goal site the most efficient option, rather than waiting at the incorrect site then proceeding to the correct one.

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