Memory Enhances Search Strategies During Odor-Guided Foraging

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Abstract

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Odor-guided searches are notoriously difficult due to the sparse and intermittent nature of odor plumes. However, rodents can adaptively modify their search strategy using internal representations of their dynamic environment. This allows for selecting the optimal strategy for making use of complex sensory cues to increase the effectiveness of odor-guided searches. To investigate this we constructed a large (2.5m x 1m) fully-automated open field arena that allowed us to distribute food pellets at precise locations throughout the arena without being restrained to defined reward locations. Using this system we precisely monitored search behavior while controlling the amount of information each animal had about possible pellet locations. To simulate nocturnal conditions Long-Evans rats foraged for sucrose pellets under far red light, which they cannot see, forcing them to rely upon olfactory cues to navigate. Rats were divided into two groups and were either trained on predictable or unpredictable pellet locations. Within a few days of training, all rats were able to complete the task quicker by decreasing their distance traveled and/or by increasing their velocity. Animals trained on the predictable, fixed condition had an increased number of efficient, stereotyped trajectories that persisted in the absence of pellets. To analyze phases of search, we sectioned trajectories by distance traveled into sequential 300cm bins. Animals trained on fixed distributions had significantly more correlated trajectories during the first bin compared to animals trained on random distributions. However, animals trained on fixed distributions were significantly impaired in navigating efficiently towards pellets located in slightly unpredictable areas, whereas animals trained on random distributions were only impaired when navigating to the most unpredictable pellets. Efficient performance recovered for all animals when they were about 40cm away from target pellet locations, suggesting this is the distance at which odor cues offer a directional benefit. Animals were then trained to forage for banana-scented sucrose pellets. When navigating to unpredictable pellets from a medium distance (20-80cm), animals had a significantly narrower angle of approach for banana-scented pellets compared to regular sucrose pellets, consistent with more intense odor cues guiding animals from a greater distance. These results suggest that rats form distinct foraging strategies based on learned probabilities of resource locations. Further, they can adaptively switch strategies during a single foraging bout, changing from a memory-based strategy to a strategy that relies on olfactory cues when resources are in unpredictable locations.

Introduction

Animals must learn to attend to salient stimuli and disregard background noise in order to successfully interact with their environment. Animals may follow a sensory-driven strategy when sensory cues are abundant and relate to task performance. For example, a cat may track a mouse by visually following its movements through the grass. However, there are times when sensory cues are sparse, unhelpful, or lose significance in relation to a task. This leads to memory gaining a more important role in the strategy that animals may use. Examples of this could be when animals have been overtrained on a simple task, or when they methodically visit areas known to contain food.

Many labs are moving towards studying sensory and memory processes during naturalistic foraging paradigms. Kim et al. (2015) developed a semi-naturalistic foraging task where rats need to procure food pellets while under the threat of danger from a robotic predator, the Robogator. They found that dangerous foraging areas can lead to unstable hippocampal place fields, suggesting a neurophysiological basis for altering foraging behavior when in risky situations. Using more naturalistic foraging tasks allows for better generalizability when compared to more traditional laboratory tasks, such as the cheeseboard (Gilbert & Kesner, 2002). Being able to get rid of defined food locations, or being able to add “predators” to a foraging environment, allows for the monitoring of behavior that more closely mimics what is happening in nature. For instance, polar bears can sense and locate seals and seal carcasses from kilometers away, suggesting a not yet understood mechanism for long-range odor localizations (Brown, 1993). Developing naturalistic foraging paradigms will allow for elucidating the processes behind behaviors such as these.

Rodents have mediocre vision and rely on olfaction as their main mode of interacting with their environment, making them efficient foragers during nocturnal conditions. Olfaction has the essential function of allowing organisms to locate resources, avoid predators, and communicate with conspecifics. While odor-guided navigation is observed in both vertebrates and invertebrates, odor-guided searches are notoriously difficult due to odor plumes being sparse and intermittent. The turbulent nature of odor plumes places many limitations on the ability of animals to navigate using these plumes (Vickers et al., 2000). Odorants in turbulent media mainly offer navigational cues in certain situations, such as when casting in an environment containing a large concentration of odor (Gire et al., 2016) or when flicking antennae to increase odorant encounter rates (Koehl et al., 2006; Moore et al., 1991). While there have been examples of animals using odor cues to navigate over long distances, such as polar bears traveling many kilometers to locate a seal carcass, the mechanism underlying this ability is unknown. Additionally, animals navigate in environments where there are multiple odorants present and must find a way to attend to only the salient cues (Schroeder et al., 2008; Wajnberg et al., 2008). Current research shows that background odors are able to alter the neuronal representation of target odors and impact tracking of plumes in moths (Riffell et al., 2014). We aim to characterize how rats form a strategy to combat noisy environments and make use of sparse odor cues in order to navigate efficiently.

There is a wealth of previous studies detailing the ability of animals to track odor trails. Researchers painted a chocolate odor trail on a moving treadmill and tracked rats' ability to follow the scent (Khan et al., 2012). The trail of the rat overlapped nicely with the trail of the chocolate odor. When experimenters would place a chocolate piece on the track the rat would display a casting behavior in order to find the trail again after eating the pellet. Researchers have also looked into more naturalistic settings and found that humans were able to track odor trails in an open grass field (Porter et al., 2007). They even observed improvements in performance as training increased. Occluding one nostril or impeding inter-nostril comparisons led to impairments in performance, suggesting that humans use differences in odor concentrations between nostrils to localize a source.

Recent experiments have suggested that bees are able to form an associative memory between scents and locations where those scents were encountered. Reinhard et al. (2004) trained marked honeybees to navigate to nectar-filled planters scented with either lemon or almond odorants. During the testing phase, researchers emptied out the nectar and removed the scent from the feeders. They then blew almond/lemon scent into the hive and monitored which planters the honeybees would visit. The bees significantly visited the planter that was associated with the scent being blown into the hive. This was not due to following olfactory cues given off from the feeder due to the removal of the scent from it. This effect was also not due to bees doing their dance to signal how to get to feeder; since bees were not rewarded at the feeder during the test phase, they had no incentive to perform the dance and signal the other bees. The study concluded that the scent of the feeder generated a visual image of its location that the honeybees then used to navigate.

Furthermore, whether or not rodents are able to navigate using odor plumes had yet to be confirmed until very recently. Current research has shown that mice are able to use plumes to navigate towards odor sources, with a strategy that matches gradient-ascent algorithms (Gire et al., 2016). Additionally, it has been shown that bats are able to make use of odorants in the air to determine which possible food source location will provide the highest quality food (Zhang et al., 2014). We sought to investigate how rats use sparse odor cues to navigate to food locations in the absence of other sensory input.

Since rodents forage using mostly olfaction, they must develop complex strategies for locating resources that make use of odor cues. Generally, they can either use sensory cues to navigate toward a source, use memorized possibilities of where that source could be, or a combination of both. There is a chief dichotomy in the literature between sensory-driven and habitual strategies (Dolan & Dayan, 2013). Sensory-driven behaviors are appropriate under conditions of uncertainty when the increased cognitive demand of the strategy is offset by the need to flexibly interact with the environment. Habitual strategies consume relatively less cognitive capacity, yet result in behaviors that are not readily adaptable to changing contingencies in the environment. Animals must maintain cognitive flexibility while foraging in their natural environment in order to execute the most efficient behaviors required for food procurement.

The ability of rodents to form internal representations of their environment could allow them to apply learned spatial information to dynamic environments, creating a map that would act to lessen the cognitive load required to use the complex sensory cues in odor plumes and greatly increase the effectiveness of odor-guided searches (Slotnick, 2001; Zhang et al., 2015). The present study aims to investigate how animals use their memory of the environment, in addition to sensory cues, to find food during a naturalistic foraging task. We develop a novel, fully-automated open field arena we are able to have complete control over the foraging environment and create multiple probability distributions of where food rewards may be located. We found that rats are able to increase their foraging efficiency when they have more knowledge of an environment, even when odor cues are sparse. We demonstrate that rats form an increasingly stereotyped trajectory as their familiarity with the open field increases. Additionally, we find that the probability of rats taking a direct trajectory to food locations increases as locations become more predictable. Our data also suggests that rats can navigate more directly to faraway pellets in unpredictable locations when these pellets emit a stronger odor cue. These results allowed us to create a model that details the behavioral strategies that rats use as they navigate towards food locations. Mainly, from farther distances rats utilize a memory-based strategy to travel to locations where they remember finding food, but as distance decreases they switch to a sensory-based strategy to find the exact location.

Materials and Methods

Experimental Subjects

The experiments in this study were performed on 12 male Long-Evans rats, purchased from Charles River Labs and housed individually. All animals were maintained on a 12-hour reverse light-dark schedule (lights off at 7:00am) with *ad libitum* access to water. After a weeklong habituation to the animal housing facility, all animals were then sustained at 85% of their free-feeding body weight in order to maintain motivation. All tests were performed between 9:00am and 6:00pm. All experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Washington.

Odor Environment

The cap was removed from an ethanol sensor in order to make it fast-sensing. It was then placed in a fixed location and liquid ethanol was placed at various distances away from the sensor. A USB-powered donut humidifier emitted water molecules while a blue light sheet laser (450nm, 100mW) scanned the output. Overhead cameras monitored the projection of the laser interacting with the airborne water molecules. A custom LabVIEW program was used to record the signals collected.

Testing Apparatus

The foraging arena was a large, fully enclosed open-field measuring 3m in length, 1m in width, and 1m in height. The sides of the arena were constructed from 1.27cm thick clear acrylic, while the ceiling was 0.635cm. The floor was a sheet of 0.0635cm opaque white acrylic. The ends of the arena were made from a wire mesh to allow for air to circulate throughout. Two synchronized high-speed cameras (The Imaging Source; DMK 23UP1300; frame rate 120 per second) were used to track the movement of the animals. An automated pellet dispenser was used to bait the arena with 45mg sucrose pellets or 45mg banana-scented pellets (Bio-Serv). An Arduino Uno controlled the movement of the motors running the pellet dispenser, allowing movement in the x- and y-coordinate plane.

Behavioral Paradigm

Before testing, animals from both the fixed and random groups were habituated to the animal facility for 1 week. Animals then spent 2 days habituating to the attached waiting cage for ~15 minutes at a time. In order to motivate animals to return to the waiting cage, sucrose pellets were placed in the cage every 2 minutes when a 1 second, 1000Hz tone was played. They were then granted access to the test arena and were given 2-3 days to habituate to it. Animals were considered to have reached criterion when they were able to make 3 transitions between the waiting cage and test arena within 30 minutes.

Animals were placed into the waiting cage at the beginning of each testing session. Rats completed 1 session a day of 3 trials each. Before each trial, the automated pellet dispenser baited the arena with sucrose pellets organized into 3 clusters of 3 pellets each. Procedures differed only through the testing phase, when animals were assigned to either the fixed or random groups. The fixed group of rats (n=8) were overtrained on a single distribution of pellet locations that stayed consistent across trials and sessions. The random group of rats (n=4) were trained on unpredictable pellet distributions that changed across trials. All rats were given a maximum of 30 minutes to eat all of the sucrose pellets during the session. The entire testing period lasted for 30-35 days (~5 sessions a week).

Data Collection and Statistical Analysis

All behavioral data was collected using a custom LabVIEW data acquisition program. Animal position data was sampled at 120Hz via two overhead high-speed cameras that tracked head position and center of mass. All analyses were conducted using custom MATLAB programs (MathWorks). No explicit power analysis was conducted in order to determine sample sizes. However, the number of animals used is consistent with experiments in the current literature (Gire et al, 2016).

Results

Characterizing Odor Environment

Signals collected from the ethanol sensor were increasingly sparse and intermittent as the distance between the source and the sensor increased **(Fig. 1a, c-d)**. This details how odorants in the air move turbulently and often don't offer directional cues.

A blue light sheet laser (450nm, 100mW) scanned the output from a USB-powered donut humidifier that was placed in the arena, detailing an almost normal-distribution of molecular output radiating from the center of the source **(Fig. 1b)**. Warmer colors indicate a stronger signal, whereas cooler colors indicate a weaker signal. This graphic details the small area where odor cues can emanate around a source.

Predictability of Pellets

Pellets for animals in both the fixed and random distributions were categorized into different levels of predictability, based on the probability of being found in certain areas of the arena **(Fig. 6a)**. Pellets that often landed in the same area of the arena were deemed most predictable and took up an area of about 0-2.5% of the total arena. The remaining levels of predictability took up 2.5-5%, 5-10%, and at least 10% of the arena’s total area, respectively. Note, pellets placed in fixed distributions had three patches from which to determine predictability while pellets placed in random distributions only had one. Additionally, different predictability levels did not contain equal numbers of pellets.

Task Performance

All animals increased their foraging efficiency as they became more experienced with the task. A Wilcoxon rank-sum test revealed that animals trained on the fixed distribution completed the foraging task in 2.92 ± 1.42sec, which is significantly faster than when they first began training (**Fig. 3a;** Z = 3.20, p = 0.00031). Animals trained on the random distribution were also able to significantly decrease the amount of time it took to procure all of the pellets (Mean = 3.52 ± 1.34sec; Z = 2.17, p = 0.029). Average velocity after training for animals in the fixed condition was 40.32 ± 6.10cm/s, which was significantly faster than in the beginning of training (**Fig. 3b;** Z = -3.31, p = 0.00016). Likewise, animals trained on the random distribution were also able to significantly increase their velocity after training on the task (Mean = 37.18 ± 1.99cm/s; Z = -2.17, p = 0.029). Animals trained on the fixed distribution significantly decreased the distance they traveled to procure all of the pellets, reducing from 221.31 ± 53.06cm to 100.37 ± 36.82cm (**Fig. 3c;** Z = 3.31, p = 0.00016). In contrast, animals trained on the random distribution were unable to significantly decrease their distance traveled, implying less efficiency in the foraging task.

Task performance measures detailed above were analyzed based on predictability level of target pellets **(Fig. 6d)**. A multi-factor ANOVA with the factors of predictability and distribution (fixed vs. random) revealed a significant effect of both predictability (F = 23.11, p = 0) and distribution (F = 8.93, p = 0.0059) on the distance traveled to procure the pellets. Additionally, both predictability (F = 19.46, p = 0) and distribution (F = 7.01, p = 0.0134) had significant effects on the amount of time it took to procure all of the pellets. These results suggest that animals trained on fixed distributions traveled significantly further distances as pellets became successively less predictable. Similarly, these animals took significantly longer to complete the task as pellets decreased in predictability. Animals trained on the random distributions only had significant increases in distance traveled and time to complete the task once they were navigating to pellets located in the most unpredictable areas of the arena. For animals in the fixed condition, a plurality of the pellets were located in the most predictable areas of the arena, whereas the pellets were more evenly distributed for animals in the random condition.

Trajectories

Animals trained on the fixed distribution spent significantly more time in areas that had a high probability of containing pellets, whereas animals trained on the random distributions spent more time in the center of the arena **(Fig. 4a)**. The trajectories the rats took to procure all of the pellets were then mapped and analyzed, with their correlations rank-ordered across trials **(Fig. 4b)**. Trajectories were developed by tracking the center of mass for the rats as they navigated through the arena. Animals in the fixed distribution were found to have many more trajectories that were highly correlated with each other across an animal’s entire history, suggesting they took the same path to procure the pellets.

To understand what role sensory cues may play in the trajectory of overtrained animals, rats underwent blank trials where no pellets were placed in the arena **(Fig. 5a-b)**. Animals that were trained on the same fixed distribution had trajectories that overlapped with each other. In comparison, animals trained on the same random distributions did not have overlapping trajectories.

To analyze the phases of search, trajectories were sectioned by distance traveled into sequential 300cm bins **(Fig. 4c-e)**. Animals trained on fixed distributions had trajectories that were significantly more correlated during days 5-10 compared to days 0-5 ($Z = 2.36$, $p < 0.015$). This increase in correlated trajectories stayed significant until the end of training. However, animals trained on random distributions did not have significantly correlated trajectories during days 5-10 ($Z = 1.299$, $p < 0.2$) or during any later stage of training. Trajectories were not significantly correlated for either condition when analyzing the second or final 300cm bins.

Probability of Approach

The probability that animals would move toward or away from a pellet was analyzed **(Fig. 6b)**. Frames were analyzed sequentially and noted for whether the animal moved closer to or further away from a target pellet. Only trajectories that ended with pellet procurement were included for analysis. Animals trained on the fixed distributions had a lower probability of navigating towards a pellet at all predictability levels outside of the most predictable 0-2.5% of the arena. Their performance began to recover when they were ~40cm away from a target pellet. Animals trained on the random distributions performed well at the majority of predictability levels, but their probability of moving towards a pellet decreased when the pellet was located in the most unpredictable area of the arena. Note, trajectories from distances of greater than 90cm had high probabilities of moving towards a pellet due to the starting location of each trial being fixed relative to where pellets were located in the arena.

Angle of Approach

To fully characterize how animals were navigating towards pellets, the angle of approach was also quantified **(Fig. 6c)**. Only trajectories towards pellets that were located in the most predictable and most unpredictable areas of the arena were included for analysis. Animals trained on fixed distributions navigating towards pellets in the most predictable areas of the arena consistently had a narrow angle of approach and traveled directly towards pellets. However, their angle of approach was significantly wider when navigating towards pellets that were located in unpredictable locations. In contrast, animals trained on random distributions had similar angles of approach regardless of navigating towards pellets in predictable or unpredictable locations. Pellets were then grouped into close (<20cm away) and far (20-80cm away) distances and angle of approach was quantified. Animals navigating towards far pellets had a significantly wider angle of approach regardless of whether the pellets were in predictable or unpredictable locations. Animals were able to decrease their angle of approach when they were about ~40cm away from target pellets.

Performance with Odorized Pellets

In order to test whether odor-intensity had an effect on foraging, animals were trained to forage for banana-scented sucrose pellets **(Fig. 7a-b)**. A multi-factor ANOVA with the factors of distance (close and far) and predictability (predictable and unpredictable) revealed a significant effect of both distance (F = 17.16, p = 0.003) and predictability (F = 19.69, p = 0.001) on angle of approach when navigating to regular-scented (control) pellets. However, there was no significant effect of distance (F = 0.06, p = 0.8093) nor predictability (F = 2.65, p = 0.1142) when navigating to banana-scented pellets. These results suggest that an increase in odor cues from the banana pellets increased performance by narrowing the angle of approach regardless of distance and predictability.

Discussion

This study shows that rats form distinct strategies based on learned probabilities of resource locations in order to optimize open-field foraging. After overtraining on the task, rats rely on a memory-based strategy in order to locate all of the pellets in the arena. This strategy develops whether the animals are trained on the fixed or random distributions. However, there is a switch from a memory-based strategy to a strategy that relies on olfactory cues when animals are navigating to pellets in unpredictable locations. Animals were significantly impaired when navigating to pellets in unpredictable locations until they were ~40cm away from the pellet, suggesting that this is the distance where the odorants coming from the pellet offer a directional cue. This recovery in performance from ~40cm away was found for animals trained on both the fixed and random distributions. This suggests that the timing of this switch is odor-intensity dependent due to animals significantly narrowing their angle of approach from further away when they were navigating towards banana-scented pellets.

Animals trained on fixed distributions performed significantly worse at the task as pellets became increasing less predictable. However, their performance improving overall was most likely due to a plurality of their pellets ending up in the most predictable locations of the arena. These animals had more experience with pellets in predictable locations, leading to the development of a strategy that relied more on memory of pellet locations. Animals in the fixed condition developed stereotyped trajectories throughout the task, suggesting that a memory-based strategy is the main strategy used once a trial begins. These animals would initially visit the same areas of the arena trial after trial, leading to the impairments found in our task when pellets were not located in these predictable areas. Sectioning their trajectories into 300cm bins further supports the idea that animals are initially navigating by memory. Animals develop highly correlated trajectories during the first 300cm when navigating through locations where pellets are most likely to be found, then their paths become uncorrelated once they begin to move through areas where pellets are less commonly found. This suggests that animals in the fixed condition are developing more stereotyped trajectories based on a global understanding of an environment where food is likely to be found in the same locations.

In contrast, pellets for animals trained on the random distribution were more evenly spread across all predictability levels, leading to trajectories which were not correlated across trials. These animals did not have significant impairments in task performance until they were navigating to pellets in the most unpredictable locations. Additionally, these animals do not develop correlated trajectories during any point of their search. This suggests that animals trained on the random distribution rely on olfactory cues earlier when foraging compared to animals trained on the fixed distribution.

Mice switching from an odor-guided strategy to one based on memory during a foraging task has been previously reported (Gire et al., 2016), however the olfactory cues in this task were generated by immense odor plumes that were blown out of fixed reward ports. This led to odor cues being pervasive throughout the arena, making it difficult for mice to get out of the plume. Our current task makes use of sparse, intermittent odor cues that offer a navigational cue when animals are ~40cm away from the target, helping to better mimic naturalistic foraging.

Additionally, the data from the experiments where rats foraged for banana-scented pellets gives support to the idea that rats can use odor plumes to aid in navigation. We found that animals are able to navigate more directly to pellets that emit stronger odor cues. Future studies will completely eliminate odor cues through intranasal application of zinc sulfate (ZnSO4), which results in full anosmia. This will explore the extent that performance on the foraging task depends upon the predictability of reward locations.

Using this novel arena for studying spatial navigation allows for a separation of memory vs. sensory processing while animals complete an odor-guided foraging task. Using this system, search behavior was precisely monitored while controlling the amount of information that each animal had about possible pellet locations. Additionally, this allows for the distribution of food pellets at precise locations throughout the arena without being restricted to defined reward locations. The ability to quickly create any reward distribution is a step forward for the field of naturalistic foraging, creating a paradigm that can be used to study many animal models of human disorders.

Future studies will aim to elucidate the neural correlates behind this dynamic and adaptive shift in search strategies. The hippocampus is a main target for electrophysiological recordings due to long being implicated in navigation-based behaviors (Morris et al., 1982; Mizumori et al., 1999). Place cells found in the hippocampus fire when rodents are located in specific areas, and have even been found to form based on odorants in the environment. Place cell formation in an open field has yet to be studied during a probabilistic foraging task. Place fields may develop differently depending on whether animals are trained on fixed or random distributions, possibly even remapping when odor cues offer more/less of a directional cue once scented pellets are used. Based on this, it would also be prudent to record from the olfactory bulb as well (Mori et al., 1999). Activity from this structure will allow for the precise tracking of when animals encounter odors and can be related to task performance.

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