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Ryan Troha
ryan.troha@uconn.edu

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Observational Learning Of A Changing Goal Location In Rats

Ryan Troha

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APPROVAL PAGE

Masters of Science Thesis

Observational Learning Of A Changing Goal Location In Rats

Presented by

Ryan Troha, B.S.

Major Advisor: Etan Markus, PhD

Associate Advisor: John Salamone, PhD

Associate Advisor: Ian Stevenson, PhD

University of Connecticut

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Authors: Ryan Troha, B.S., Danni Dong, Etan Markus, Ph.D.

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“Observational learning of a changing goal location in rats”

Introduction

Observational learning is a beneficial skill for an organism to survive in its environment. An organism which can learn through observation has a much greater chance of surviving in its environment than one which can only learn through direct experience. This paper will discuss some of the history of social learning research in animals, difficulties in classifying observational learning, issues with studying the neurobiology of observational learning, and the development of a new behavioral paradigm to assess observational learning in animals.

Social learning is essential to the adaptive success of humans, providing a readily available source of information about the environment. In fact, researchers have long discussed the striking ability of humans to learn through observing each other (Bandura, 1977; Meltzoff & Moore, 1977; Piaget 1962). Research also suggests a deficit in observational learning in children diagnosed with Autism Spectrum Disorder (ASD) (Varni et al., 1979). One perspective is that ASD, in part, manifests as a social learning disorder. Furthermore, these social learning deficits may arise through a general impairment in stimulus salience detection (Ahearn et al., 2015). That is, humans or other animals displaying symptoms of ASD might not learn in a social manner as well as a typically-developing peer.

In addition to humans, observational learning is seen in other primates such as chimpanzees (Hayes & Hayes, 1952; Hayashi et al., 2005; Marshall-Pescini & Whiten, 2008; Sumita et al., 1985). The classic study by Hayes & Hayes (1952) documents the imitative

behaviors of home-raised chimpanzees. These reports show that chimpanzees will spontaneously imitate human behaviors. In their report, Hayes and Hayes describe one chimpanzee, Viki, in particular. At 16 months of age, Viki began imitating common household behaviors such as washing dishes and clothes or dusting furniture. These initial imitations were quite crude and disorganized. However, around 2 years of age, Viki's actions became much more complex and human-like. For example, she applied lipstick accurately to her lips using a mirror and even smoothed the lipstick by pressing her lips together as a human would. These initial reports were merely descriptive, so researchers then moved to a more experimental approach to determine the extent of Viki's observational learning abilities. Viki was trained to imitate an action when experimenters told her "Do this" before demonstrating a variety of different actions, some simple (e.g. patting the head) and others more complex (e.g. opening a padlock using a key). After some initial difficulties with a few of the more complex actions, Viki was eventually able to imitate 55 out of 70 of the actions demonstrated to her.

Although Viki appeared to provide convincing evidence of observational learning in chimpanzees, more experimentation was needed to confirm the presence of observational learning in chimpanzees. Stronger evidence for social learning in chimpanzees comes from experiments showing observational learning of nut-cracking using stone tools. These studies demonstrate that chimpanzees can learn how to use tools to open nuts by observing conspecifics doing so (Sumita et al., 1985; Hayashi et al., 2005). Marshall-Pescini and Whiten (2008) built on these experiments by using a larger sample size. An important aspect of their study is the use of a "no observation" control group which could be compared to a group which was allowed to observe an experimenter demonstrating the nut-cracking behaviors. Results from this study show that the animals were more likely to acquire the nut cracking behavior after observing

experimenters do so. Their results are also consistent with previous work (Inoue-Nakamura & Matsuzawa, 1997) showing that, compared to younger chimpanzees (mean of 2.6 years), older chimpanzees (mean of 4.4 years) are more likely to acquire the proper nut-cracking technique through observation. Although only a small fraction of evidence for social learning in chimpanzees is covered here, there is a large body of literature to support this form of learning in chimpanzees (Whiten et al., 2004; Whiten, 2017).

Although social learning in chimpanzees is well-established, the degree to which non-primate animals learn by observation, as well as the manner in which this learning might be achieved, is more complex. When designing a behavioral paradigm to assess observational learning, one must consider ways in which an animal could learn without observing the demonstrator animal. One way this could occur is through *stimulus enhancement*, or the association of an outcome with a stimulus other than the demonstrating animal. For example, consider a task in which an animal observes another animal press a lever in order to obtain a food reward. Stimulus enhancement might occur by the observing animal associating the food reward with the lever rather than the collective actions of the demonstrator animal moving to the lever and pressing the lever. Another way this could occur is through *local enhancement*, or the association of an outcome with a location. Consider again the previous lever-pressing paradigm. Local enhancement might occur in this scenario if the observing animal associates the food reward with the location of the lever. That is, the observing animal would see the demonstrator animal move to the location of the lever rather than observe the demonstrator pressing the lever and obtaining the food reward (Zentall, 2012).

Tolman (1964) describes another phenomenon termed *social facilitation*. Tolman found that chickens which had already eaten would begin eating again when introduced to a hungry

chicken which begins eating. Zajonc (1965) describes several similar experiments and suggests that social facilitation occurs through a heightened state of arousal, therefore increasing activity and repetitive behavior of the animal. Thus, it appears that in some animals, a natural behavior can be produced simply by the presence of another animal performing the behavior. This introduces yet another obstacle to consider when trying to achieve true observational learning.

Another explanation of learning seen in social situations can come from a phenomenon termed *discriminative following*. In this scenario, an animal may be reinforced for simply following a conspecific. For example, Haruki and Tsuzuki (1967) showed that rats can learn to follow a demonstrator rat to the arm of a T-maze which contains a food reward. Here, the observer animal may simply be using the demonstrator animal as a discriminative stimulus which indicates which arm of the T-maze contains a food reward. Therefore, as explained in Zentall (2012), similar results might be achieved by simply dragging a piece of wood attached to a string to the correct arm or otherwise providing a discriminative stimulus for the observing animal to learn from.

Attempts have been made at reducing the possibility of these confounding sources of learning. For example, Simons and Lejeune (1997) used observational learning of tone duration discrimination. In this experiment, demonstrator rats were trained to press either a left or right lever in response to a short (1s) or long (8s) tone. That is, the animal had to learn to press the left lever after a short tone and the right lever after a long tone (or vice versa depending on the group). Here, stimulus enhancement is less likely to occur because duration, or time, is not a physical item such as a lever. Thus, learning cannot simply be explained by the attraction of the animal to a manipulandum associated with a reward. Similarly, it is unlikely that the observer animal learned through local enhancement as animals had to learn to associate a tone duration

with the correct lever and could not simply associate one location with reward. Social facilitation is also an unlikely explanation of learning because the rewarded behavior is complex and not naturally occurring.

Dawson and Foss (1965) used clever experimental methodology in an attempt to achieve true imitation by teaching budgerigars to access a food dish using three different motor actions. Observer animals watched trained demonstrators obtain the food reward using one of three different motor movements. Interestingly, the experimenters found that animals used the same motor movements as the animals they observed. For example, an observer animal that watched a demonstrator animal use its foot to access a food dish would also use its foot. This methodology provides a means to more accurately measure *true* imitation and elucidates any ambiguity as to what the observer animal is actually learning. However, an attempt at replicating this experiment (Galef et al., 1986) yielded weaker results. Experimenters found that differentiating between two of the three motor movements used by the budgerigars in Dawson and Foss (1965) was difficult. Thus, the experimenters decided to replicate the experiment using only two of the original motor movements which were easily distinguishable. The results showed only marginal significance and limited duration of learning, indicating that training animals to learn specific motor movements by observation is more difficult than originally thought. Although the results of Dawson and Foss' experiment are inconsistent and difficult to achieve, this experiment still provides an ideal observational learning model.

In most observational learning experiments, observer animals are exposed to many demonstrator trials in which they see the same behavior many times over the course of many days (Haruki & Tsuzuki, 1967; Del Russo, 1975; Heyes et al., 1994; Simon and Lejeune, 1997; Leggio et al., 2003). For example, in Del Russo (1975) rats observed a demonstrator press a

lever 55 times each day for up to 7 days. Each day after observational trials, the animals were tested. Thus, because there are so many observational trials occurring over several days, it is very difficult to determine when and how an animal is learning through observation. This poses as a limitation for both the amount of data that can be generated and the number of parameters that can be assessed because the observation is of a fixed behavior over many days and trials.

Additionally, what seems to be observational learning in experiments such as these might largely be explained by stimulus or local enhancement. Repeated interaction of a demonstrator animal with a certain physical item (e.g. a lever) and in a specific location increases the likelihood or stimulus or local enhancement.

Haruki and Tsuzuki (1967) exposed rats to 10 observational trials per day for 15 days and tested animals on the same behavior each day. Simons and Lejeune (1997) presented observer rats with 30 observational trials each day for 14 days. After observing each day, observer animals were tested. In both of these studies, because there are many observational trials and the focus is on the acquisition of learning over many days, it is difficult to determine the exact point at which observational learning is occurring. In most cases, observer animals acquire the behavior faster than a naïve control group in these experiments. However, this gives little information about when or how an animal is learning through observation. From a behavioral standpoint, these experiments may work to determine whether or not an animal *can* learn through observation. However, trying to determine *how* an animal learns through observation from a neurobiological perspective would be difficult. A behavioral paradigm where one can determine the neurophysiology of an observing animal would be quite useful. Recent work by Omer et al. (2018) tested bats in an observational learning paradigm using these methods. Bats were trained to observe conspecifics flying to a goal location to obtain a food reward. Here, researchers were

able to do single-unit recordings in the brain to determine the neurophysiology of the bat while it observed a conspecific. A similar behavioral paradigm as this, but with rats, could be extremely useful for researchers.

Therefore, the current study focuses on a behavioral paradigm which embraces a foraging task where the goal location changes pseudo randomly across testing sessions. Animals are trained to run on a T-maze where the food is found in either the left or right arm. Observer animals must pay attention to the demonstrator animal each day afresh to learn the location of the food reward before being put on the maze. Using this working memory task, one can measure both the animals' learning curve (i.e. rate of acquisition across days), as well as determine which variables affect observation on a given day (performance on the first trial of each day).

This design allows for a more detailed look at the period in which observational learning occurs. This is possible because the goal location changes across days and animals can only learn through observation during a specific frame of time on each testing day. That is, observational learning must occur from the time the demonstrator animal is placed on the maze to the time the demonstrator animal is taken off of the maze. This working memory design also allows for repeated experimental manipulations (e.g. brain inactivations) across days. In contrast, traditional observational learning experiments would only allow for one manipulation before the observer testing period.

Here we describe a series of four experiments in which the number of observations presented to observer animals was manipulated. An additional experiment was included for control purposes. First, we hypothesized that as observers were exposed to more observations on a given day, the performance of these animals would improve. Second, we hypothesized that animals would perform better if the observed animal made no mistakes compared to when the

observed animal made one or more mistakes. Lastly, we hypothesized that familiarity with the observed animal would enhance observational learning.

Methods

Subjects

Ten Fischer's F-344 female rats (Harlan, IN) approximately ten months old were used for these experiments. Eight animals were used as observer rats and two animals were used as demonstrator rats. All animals were singly housed and food-restricted to 85% of their *ad libitum* body weight. All animals were kept in a temperature and humidity-controlled animal room. The research protocol was approved by the University of Connecticut IACUC.

Apparatus

The maze room consisted of a plastic T-maze, a metal shelf used for holding observer animals at the distal location, and a small platform placed directly in front of the maze in order to hold observer animals at the proximal location. Figure 1B shows the general layout of the maze room. Figure 1A shows the dimensions of the maze and its position relative to the metal shelving and small platform. The maze room was 270 cm x 430 cm x 270 cm (length x width x height). The metal shelf used to hold the animals at the distal location was 45 cm x 130 cm x 165 cm. The platform used to hold the animals at the proximal location was 45 cm x 55 cm x 75 cm. Animals were placed in a small tube placed in a small cage with a wire mesh opening (Figure 1C). The cages used were 20 cm x 25 cm x 15 cm and the tubes used to hold each animal were 10 cm in diameter and 20 cm in length. The room lights were turned off and small desk lamps were turned on facing the back off the room so that light levels were low. During the testing session, the maze was cleaned with 30% EtOH between rats.

Procedures

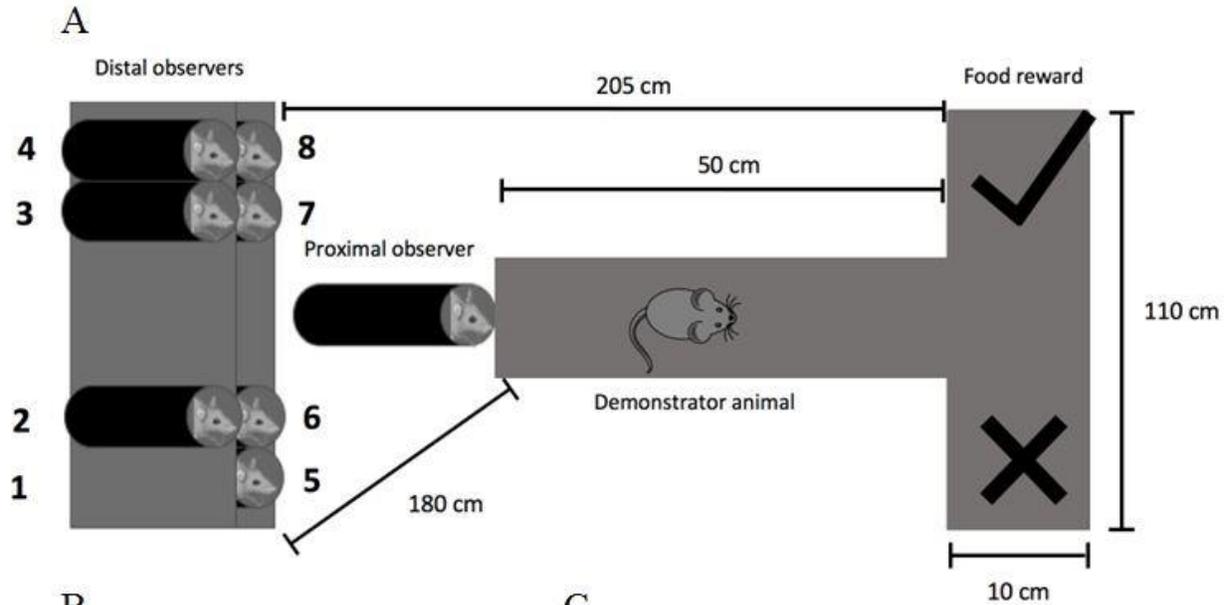


Figure 1: A, Schematic of the maze room layout. Testing order positions at the distal location are labeled 1-8. Maze dimensions are shown, as well as the distance of the distal locations relative to the maze. Note that in this picture, the first rat in the testing order is in the proximal position in order to observe a demonstrator animal. Animals in the testing positions 2-8 would then be placed in the proximal position to observe the animal before them in the testing order. B, Picture of the maze room. C, Close up picture of animal in observation tube.

Experiments 1-4

Animals were trained to navigate a T-maze in order to find a small food reward consisting of chocolate sprinkles. Demonstrator animals were each trained to run to one goal arm (left or right respectively). Animals underwent one testing session each day with each session consisting of either three, five, or ten trials according to the respective experiment. If the animal went to the correct goal arm, it ate the reward and then returned back to the start arm for an additional reward, which then began the next trial. If the animal went to the incorrect goal arm, it

was blocked off in that arm, immediately picked up by the experimenter, and placed back in the start arm to begin the next trial. Observer animals were placed in both a position far (distal) from the maze and a position close (proximal) to the maze behind the start arm. At the distal location, the actual location on the rack and testing order shifted in a systematic manner with each new daily session. For example, an animal would observe from position 1 on day 1, position 2 on day 2, and would return to its original testing position after 8 days (see Figure 1). From the proximal location, each animal observed only the immediately preceding animal. The first observer animal to be tested each day observed a trained demonstrator animal. Therefore, a rat starting in distal position 1 would not get to watch any other animals from the distance before being placed in the proximal position; a rat starting in distal position 8 would get to observe both the demonstrator animal and all seven other animals preceding it that day.

Four experiments were performed in which the number of trials that animals performed was manipulated. This in turn changed the number of observations available to each observer rat. Experiment 1 consisted of three daily trials, Experiment 2 five trials, Experiment 3 ten trials, and Experiment 4 consisted again of three trials. Experiment 1 was run for many weeks; the last 20 days were used for analysis. Experiments 2-4 were run for 20 days each.

Prior to each daily testing session, observer animals were placed in a cage with another animal for approximately 10 minutes. The partner was fixed, resulting in each rat being quite familiar with one other animal in the group. Every eight days (i.e. after all animals were tested in each position), the order of testing switched such that for one week a given rat was tested after a familiar demonstrator and on the following week it followed a non-familiar (i.e. non-paired) animals. This design allowed for assessment of any effect of familiarity with the observed animal on the performance of the observing animal.

Experiment 5

A control experiment was included to ensure that animals were not learning by following a scent trail from the previous animal, smelling the food, or watching the experimenter. An opaque plastic flap was attached to the front of each cage to block the view of the observer animal. This procedure was identical to Experiment 2 in that five trials were used. The sole difference was that the maze view of the observer animals was either blocked or unblocked on alternative days. Importantly, the line of view of animals was only blocked when at the proximal position and not at the distal position. The flap was closed to block the observer animals' vision immediately before the demonstrator animal was placed on the maze. The flap was then reopened as soon as the demonstrator animal was taken off of the maze. Thus, this ensured that each observer animal could see every aspect of the testing session (e.g. baiting the goal arm, cleaning the maze between animals, experimenter movements, etc.) except for the demonstrator animal moving on the maze.

Results

Mean performance of observer animals (Experiments 1-4)

The average percent of trials in which the animal chose the correct arm is shown in Figure 2. The data are separated into trial 1, trial 2, and remaining trials. On trial 1, deviation from chance would indicate observational learning because the animal had not been tested on the maze yet for that testing session. That is, an animal performing significantly better than 50% chance on trial 1 must be using observational learning to learn the goal location. Trial 2 and the remaining trials measure adherence to the “win-stay/lose-shift” rule (i.e. using feedback from the first trial).

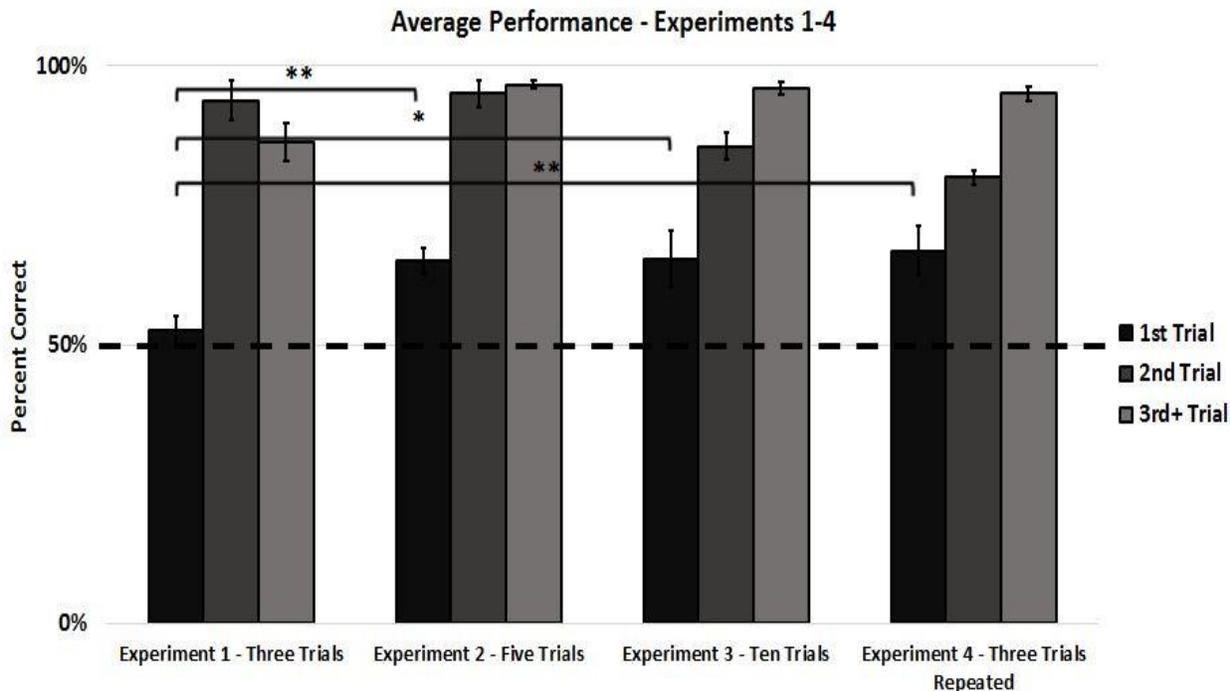


Figure 2: Average performance of observer animals in each trial in experiments 1-4. Average performance of observer animals on the first trial improved significantly after experiment 1. One-sample t-test significance levels are indicated on the inside of bars: ** indicates $p < 0.01$, *** indicates $p < 0.001$. Paired-samples t-test significance levels are indicated above bars: * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$.

Experiment 1: When observing another rat from close proximity for 3 trials, observer animals did not perform significantly different than 50% chance on the first trial ($t(7) = -0.935$, $p > 0.10$). However, one-sample t-tests show that observer animals did perform significantly better than 50% chance on the second ($t(7) = 8.485$, $p < 0.001$) and third ($t(7) = 10.744$, $p < 0.001$) trials. This indicates that animals were not learning by observation before being tested, but did understand the “win-stay, lose-shift” task in general.

Experiment 2: When observing another rat at close proximity for 5 trials, observer animals performed significantly better on the first trial compared to 50% chance ($t(7) = 6.481$, $p < 0.001$). This indicates that animals began learning the location of the goal arm before being put on the maze. In addition, observer animals continued to perform significantly better than 50% chance on the second ($t(7) = 19.442$, $p < 0.001$) and trials 3-5 ($t(7) = 66.26$, $p < 0.001$). Paired-

samples t-tests show that the performance of animals on the first trial was significantly better than in Experiment 1 ($t(7) = 0.584, p < 0.001$).

Experiments 3: When observing another rat at close proximity for 10 trials, observer animals continued to perform significantly better than chance on the first ($t(7) = 3.071, p < 0.01$) second ($t(7) = 14.934, p < 0.001$) and remaining ($t(7) = 44.341, p < 0.001$) trials. Paired-samples t-tests show that the performance of animals on the first trial ($t(7) = -2.623, p < 0.05$) was significantly better than in Experiment 1.

Experiment 4: The animals were returned to a situation identical to Experiment 1 where they observed 3 trials at close proximity. However, this time observer animals performed significantly better than chance on the first trial ($t(7) = 3.68, p < 0.001$). This was also true for the second ($t(7) = 35, p < 0.001$), and third ($t(7) = 33.675, p < 0.001$) trials. Paired-samples t-tests show that the performance of animals on the first trial ($t(7) = -2.862, p < 0.05$) was significantly better than in Experiment 1.

Effect of previous animal's performance (experiments 1-4)

The rats observed the maze first from a distance and then again from a proximal location right before being placed on the maze (see Figure 1). Figure 3 illustrates the performance of observer animals according to how the animal tested before them each day performed (i.e. the animal observed from the proximal position). In Experiment 1, the performance of observer animals was significantly better than 50% chance when the observed animal made no mistakes ($t(7) = 2.274, p < 0.05$) and significantly worse than chance when the observed animal made one or more mistakes ($t(7) = -3.416, p < 0.01$). In Experiment 2, the observer animals performed better than 50% chance both when the observed animal made no mistakes ($t(7) = 4.158, p < 0.01$) and when the observed animal made one or more mistakes ($t(7) = 2.354, p < 0.05$). In

Experiment 3, observer animals performed better than chance both when the observed animal made no mistakes ($t(7) = 2.644, p < 0.05$) and when the observed animal made one or more mistakes ($t(7) = 3.33, p < 0.01$). Lastly, in Experiment 4, when animals once again were given 3 proximal observations, the animals performed significantly better than chance when the observed animal made no mistakes ($t(7) = -11.314, p < 0.01$), but not when the observed animal made one or more mistakes ($t(7) = 0.141, p > 0.10$). A repeated-measure ANOVA reveals a main effect of the number of observations ($F(3, 21) = 4.758, p < 0.05$), a main effect of the performance of the observed animal ($F(1, 7) = 9.537, p < 0.05$), and an interaction between these two variables ($F(3, 21) = 4.633, p < 0.05$). This indicates that a mistake by the observed animal only worsened observer performance when only three observations were seen, but not when five or ten observations were seen.

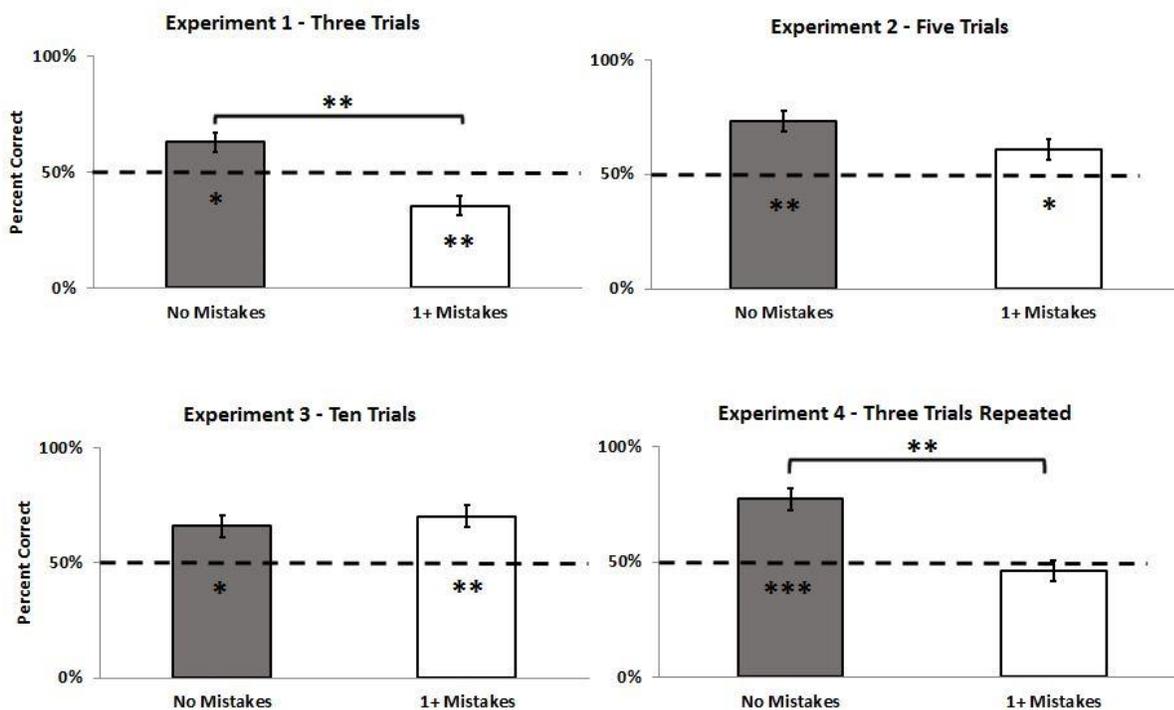


Figure 3: Average performance of observer animals based on the observed animal's performance. Note that in experiments 1 and 3, the animal performed significantly better when the observed animal made no mistakes compared to when the observed animal made one or more mistakes. One-sample t-test significance levels are indicated on the inside of bars: ** indicates $p < 0.01$, *** indicates $p < 0.001$. Paired-samples t-test significance levels are indicated above bars: * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$.

No effect of distal observations (Experiments 1-4)

If animals were able to see from the distal location and learn by observation, one would expect animals later in the testing order to perform significantly better than animals earlier in the testing order. Furthermore, some distal positions were either closer (i.e. positions 6 and 7) to the maze or had a better view (i.e. 1 and 4). Figure 4 illustrates the performance of observer animals according to the order of testing during each experiment. Significance values for all one-sample tests are indicated in each graph. No consistent significant differences were seen in the performance of animals across experiments with regard to the order of testing. This suggests that animals did not benefit from observation from the distal location.

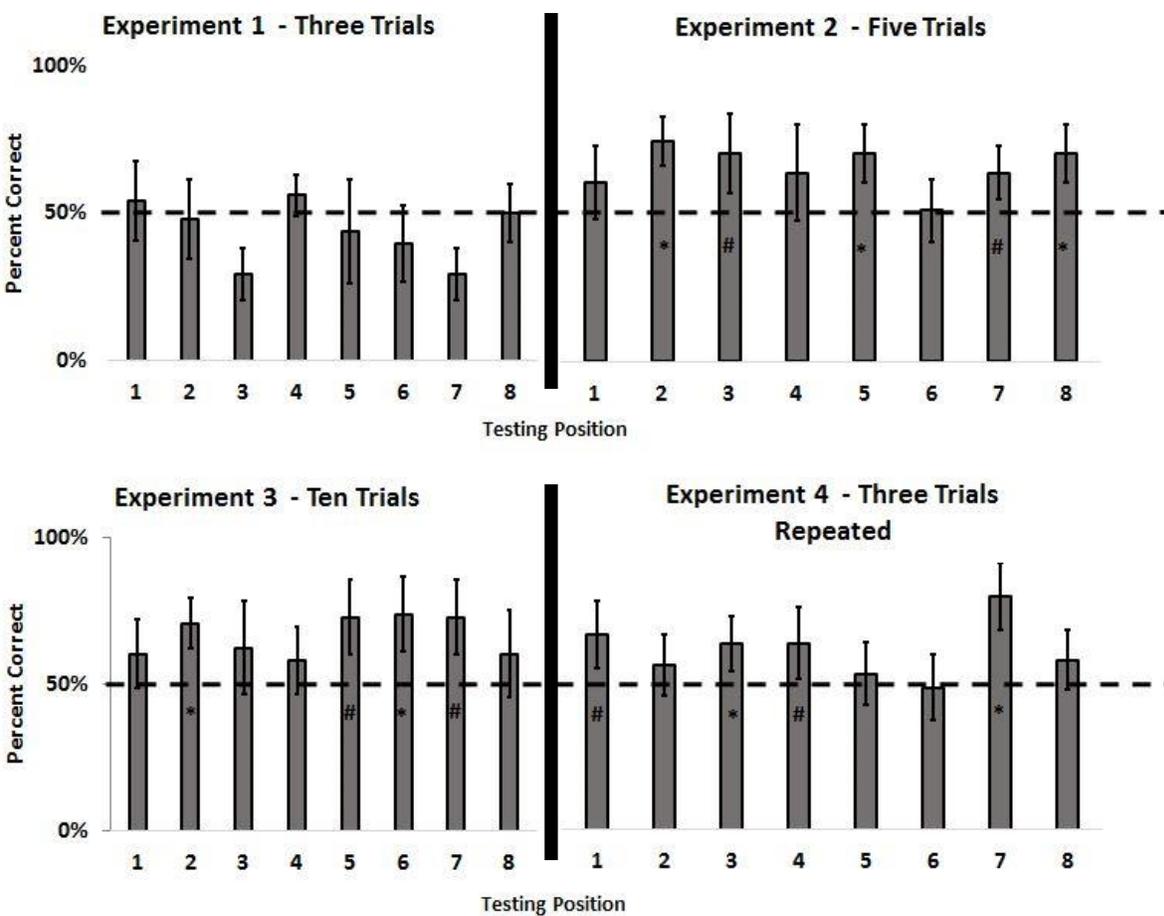


Figure 4: Average performance of observer animals in each experiment according to testing order. No consistent significant differences were found across experiments. One-sample t-test significance levels are indicated on the inside of bars: ** indicates $p < 0.01$, *** indicates $p < 0.001$, # indicates $0.05 < p < 0.1$.

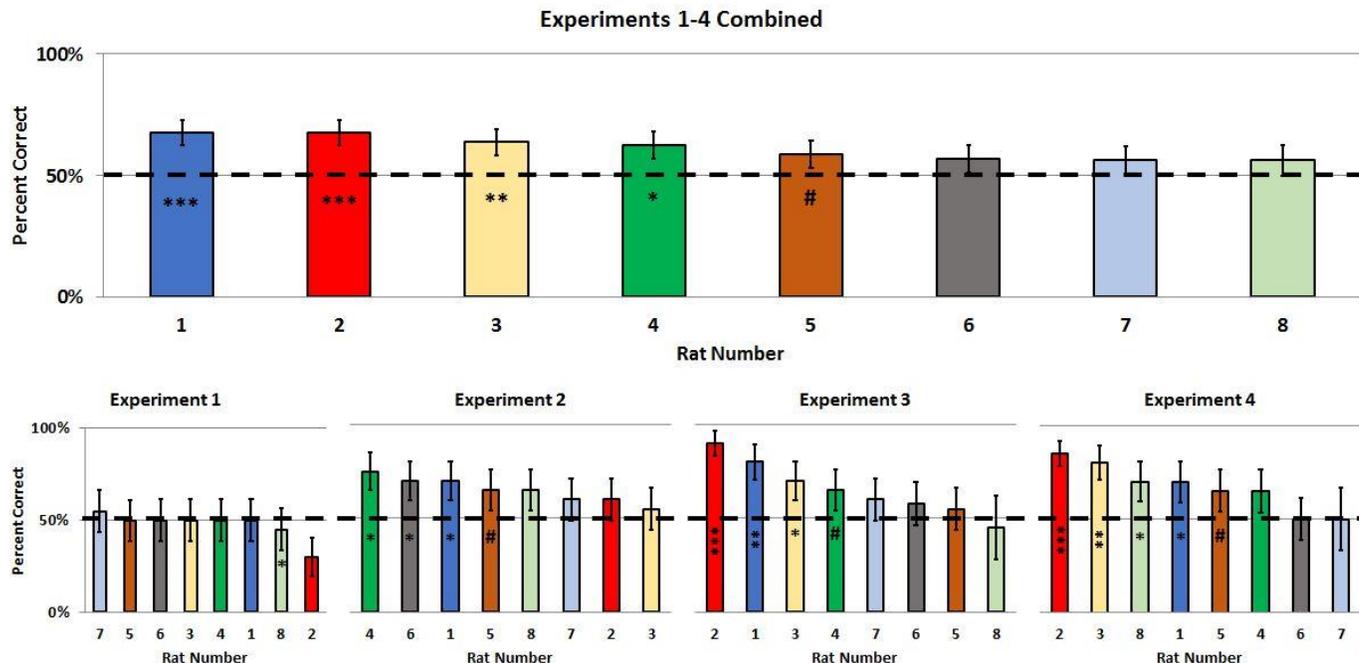


Figure 5: Mean performance of individual animals on the first trial. A, Mean performance of animals combined for experiments 1-4. B, Mean performance of individual animals for each experiment. Note the variability in the performance of some animals across experiments. One-sample t-test significance levels are indicated on the inside of bars: ** indicates $p < 0.01$, *** indicates $p < 0.001$, # indicates $0.05 < p < 0.1$.

Individual differences in performance (Experiments 1-4)

Differences in performance were seen in individual animals across each experiment.

Figure 5 shows the performance of individual animals across all experiments and in each separate experiment. Significance values for all one-sample t-tests are indicated in each graph. Note that several animals performed significantly better than chance in some experiments, but not in others.

No effect of demonstrator familiarity (Experiments 1-4)

Prior to each daily testing session, observer animals were placed in a cage with another animal for approximately 10 minutes. The partner was fixed, resulting in each rat being quite familiar with one other animal in the group. Across all four experiments, there were no consistent significant differences in the performance of observer animals when observing a

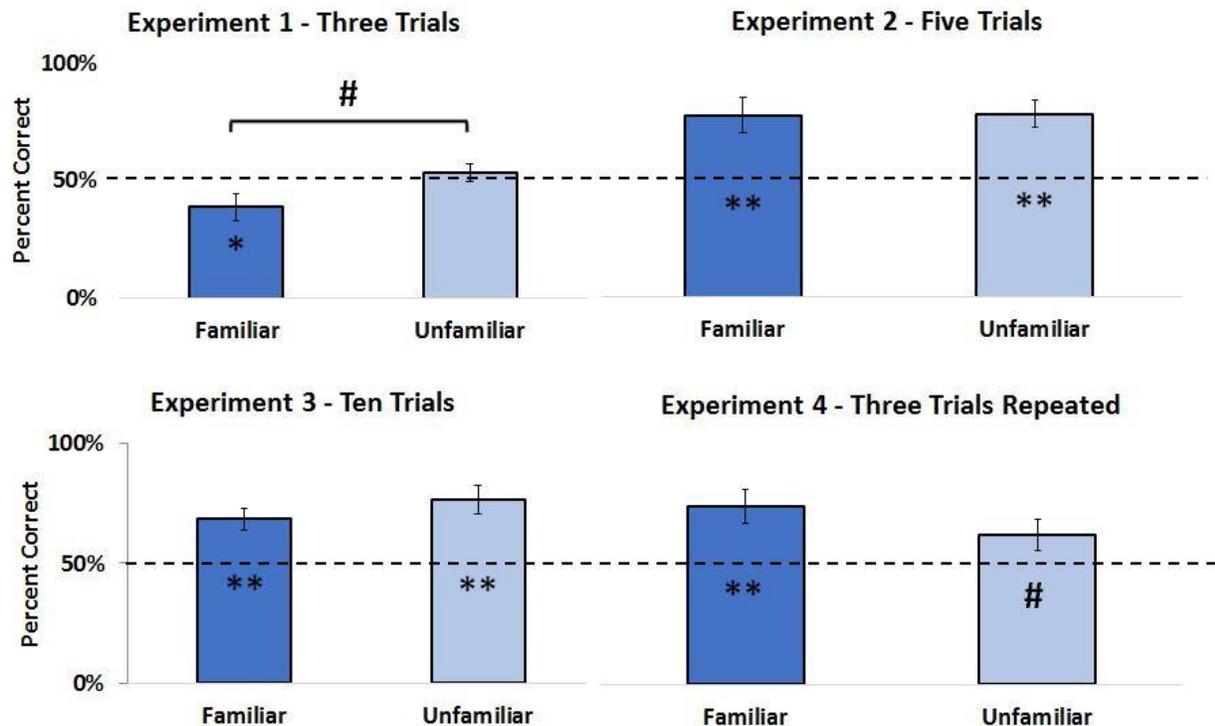


Figure 5: Average performance of observer animals on the first trial in each experiment based on familiarity with the observed animal. No consistent significant differences were found across experiments. One-sample t-test significance levels are indicated on the inside of bars: ** indicates $p < 0.01$, *** indicates $p < 0.001$. Paired-samples t-test significance levels are indicated above bars: * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$, # indicates $0.05 < p < 0.1$.

familiar animal compared to an unfamiliar animal (Figure 6). Although a paired-samples t-test showed that there was a trend towards better performance when observing an unfamiliar rat in experiment 1 ($t(7) = -1.83$, $p = 0.055$), this difference was not seen in experiments 2-4 (all $p > 0.10$).

Experiment 5

Experiment 5 examined the difference between the performance of animals in testing sessions during which their vision was blocked at the proximal position compared to testing sessions during which vision was unblocked. Figure 7 illustrates the mean performance of observer animals on the first trial under each condition. Animals performed better than 50% chance when the observed animal made no mistakes, in sessions during which observation was

allowed ($t(7) = -2.128, p < 0.05$). Importantly, this significant difference was only seen in sessions where observation was allowed and not when observation was blocked ($t(7) = 0.471, p = 0.326$). In both conditions, there was no significant difference from 50% chance when the observed rat made a mistake (both $p > 0.10$). Paired-sample t-tests show that in sessions where observation was allowed, there was also a trend for better performance on the first

trial when the observed rat made no mistakes compared to when the observed rat made one or more mistakes ($t(7) = -1.854, p = 0.053$). Collectively, these data suggest that only when the observer rat could actually see the previous animal performing the task did they benefit from this information.

Discussion

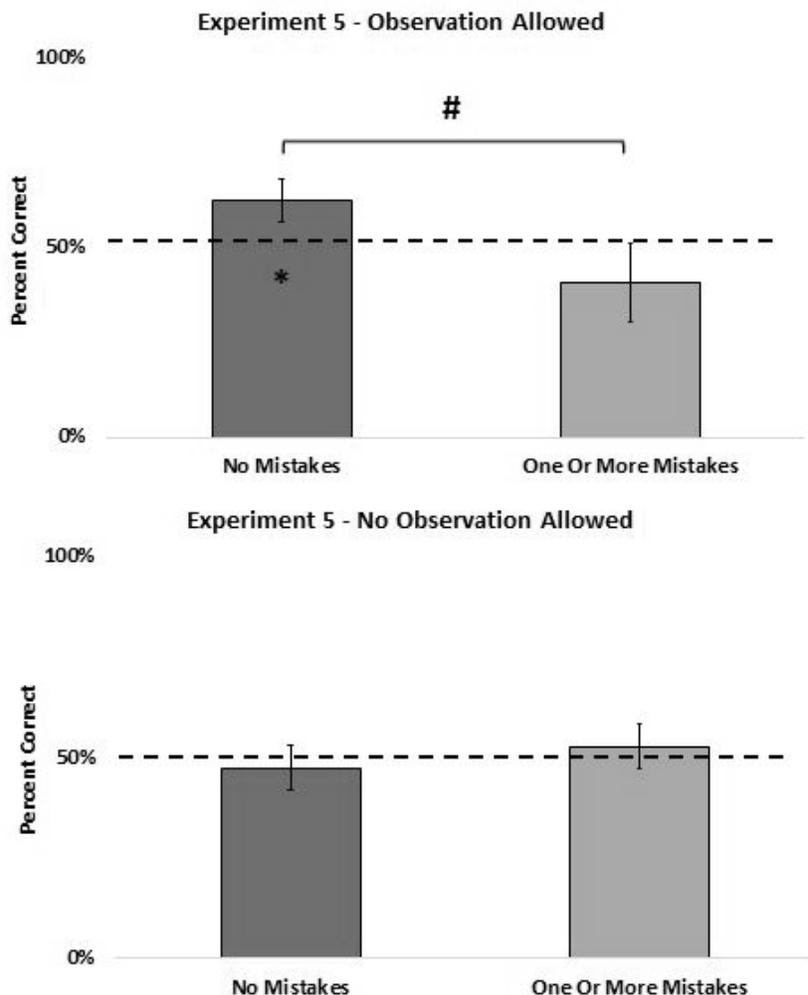


Figure 7: Average performance on the first trial based on the performance of the observed animal. Top, performance when observation was allowed. Bottom, performance when observation was blocked. One-sample t-test significance levels are indicated on the inside of bars: * indicates $p < 0.05$. Paired-samples t-test significance levels are indicated above bar: # indicates $0.05 < p < 0.1$.

The purpose of the current experiments was to assess the ability of rats to use observational learning in a working memory task. Previous observational learning tasks measure the ability of animals to observe one behavior over many trials. However, this makes it difficult for researchers to investigate the neural circuitry underlying observational learning, as observer animals can only be tested once on this single behavior. The current behavioral paradigm employs the working memory of animals and therefore creates a new observational learning opportunity with each new testing session.

These results suggest that rats have the ability to learn the goal location of a food reward on a T-maze by observing conspecifics. Experiment 1 shows that initially, animals were not using observation to learn the goal location, but did gain this ability in Experiment 2 and onwards. Therefore, these data suggest that animals *learned to observe* the animals before them in order to determine the location of the food before being placed on the maze.

In addition, observer animals did not appear to learn from the distal location, as performance did not change according to the location or order of testing in sessions. This is also supported by the fact that observer animals were sensitive to the performance of the animal observed from the proximal position. Interestingly, in Experiments 2 and 3, the performance of the animals was still significantly better than chance even when the observed animal made a mistake. However, this was not seen in Experiments 1 and 4. Therefore, it appears that the observer animals benefitted from the increased number of observations in Experiments 2 and 3. That is, with less observations available (i.e. Experiments 1 and 4), animals were affected when the observed animal made a mistake.

Previous work (Saggerson & Honey, 2006) showed that observer rats are more likely to display demonstrator-consistent behavior when the demonstrating rat is of a different strain. This

suggests a role for demonstrator familiarity in the facilitation of observational learning. However, other studies show conflicting results with respect to how demonstrator familiarity might influence observational learning (Ray et al., 2000; Reed et al., 1996). Our results are consistent with the idea that demonstrator familiarity does not influence observer behavior. While our “familiar” rats were very familiar with each other after being paired together for 10 minutes every day, the extent to which “unfamiliar” rats were truly unfamiliar in the current study could be debated. All animals were housed in the same animal room and holding racks and over time, may have gained familiarity with one another through odor, vocalization, or other stimuli. Future studies should consider these variables when assessing the role of demonstrator familiarity.

Experiment 5 helps ensure that observer animals were not learning through odor cues, as the effect of the observed animal’s performance was only seen when the observer animal’s vision was unimpaired.

Previous work in our lab focuses heavily on the behavioral correlates of the hippocampus and connected brain areas (Jacobson et al., 2013; Jacobson et al., 2015; Schmidt et al., 2012; Schmidt et al., 2013a; Schmidt et al., 2013b). In addition, research from other labs suggests a role for the hippocampus in mediating social memory (Hitti & Siegelbaum, 2014; Okuyama et al., 2016; Stevenson & Caldwell, 2014) and observational fear learning (Jones & Monfils, 2016). Therefore, our lab is interested in further investigating the relationship between the hippocampus and social learning. Specifically, our interest lies in how the spatial information of others may be represented in the hippocampus. Recent work (Danjo et al., 2018) appears to have achieved just this. Here, rats learned to follow a demonstrator animal to either the same goal arm or go to the arm opposite of the demonstrator animal to find a food reward. In vivo electrophysiology was

then used to monitor single-unit activity in the hippocampus to demonstrate the firing of cells in response to another rat's movement through specific locations on a maze. However, because the observing animal follows its conspecific in close proximity, the firing seen for the other's location could be related to the use of the other rat as a discriminative stimulus as described previously. Perhaps the other rat is coded by the observer rat not in a social manner, but rather as a discriminative stimulus by which the rat knows how to obtain the food reward. That is, perhaps an inanimate object (e.g. a block of wood) making the same movements along the maze would evoke the same hippocampal activity in the observer rat. Our behavioral paradigm in which the observing rat is stationary throughout the entire observational could help clarify the issues with these experiments.

In addition, all cells recorded by Danjo et al. (2018) were located in the dorsal region of the hippocampus and of the cells recorded, only 13% were found to significantly code for the location of the "other" rat. As previously mentioned, the ventral hippocampus has been shown to play a role in social memory and may therefore contain a higher percentage of cells which code for the location of others.

Most previous observational learning studies have been purely behavioral and have not sought to determine the neurobiology behind this form of learning. Thus, past experiments have not been designed in ways where observation learning can be easily monitored or manipulated. Observer animals in these studies observed many trials over long periods of time and were typically tested in ways where it is difficult to determine when observation is truly occurring.

The current working memory approach offers several advantages. First, daily testing sessions allow the observational learning ability of animals to be assessed many times. Second, because each daily session presents a new observational learning experience, experimental

manipulations can be made freely. Lastly, because this is a working memory task, future studies can examine the contribution of the hippocampus and related brain areas in this form of social learning.

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