THE HOMING PIGEON HIPPOCAMPUS AND THE SPATIAL OR FEATURE ENCODING OF REWARD PROBABILITY AND RISK

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ABSTRACT

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The current study examined reward probability associative learning to either spatial or feature information in homing pigeons in an open-field, laboratory setting. Additionally, the role of the avian hippocampal formation (HF) was examined in the current study by using both control sham-lesioned and hippocampal-lesioned animals in spatial or feature contexts in which rewarded goals varied in differential risk-reward properties. Homing pigeons were divided into two main experimental conditions, space or feature, and were then divided again into two brain manipulation groups, control sham-lesioned or hippocampal-lesioned. Animals were trained to locate three specific risk-reward (High-Variable 75%, Low-Variable 25%, and Constant 100%) dependent food sites (based on locations or colors) in an open-field environment. It was hypothesized that control sham-lesioned homing pigeons would develop a stronger risk-reward association with spatial information than with feature information. Additionally, it was hypothesized that control sham-lesioned and hippocampal-lesioned homing pigeons trained to feature information would perform similarly on a risk-reward based discrimination. Furthermore, it was hypothesized that control sham-lesioned homing pigeons trained to spatial information would perform differently from hippocampal-lesioned homing pigeons on a risk-reward discrimination based on space.

Results indicated that homing pigeons that were provided with feature information were more likely to choose the riskier outcome during High-Variable trials, the constant outcome during Low-Variable trials, and made fewer incorrect choices in comparison to homing pigeons that were only provided spatial information. Control sham-lesioned and hippocampal-lesioned homing pigeons trained to feature both learned to seek out risk-reward outcomes and there were no significant differences in performance. By contrast, performances of control sham-lesioned and hippocampal-lesioned homing pigeons trained to space were significantly different. Hippocampal-lesioned space birds made many more first choices to incorrect bowls and were less likely to choose both variable bowls in comparison to control sham-lesioned space homing pigeons, suggesting a development of risk-aversion.

This dissertation is lovingly dedicated to my nephew, Kegan, and my feline friend, Mocha.

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INTRODUCTION

In birds, the dorsomedial telencephalon area of the brain, is known as the avian hippocampal formation (HF). This brain structure is thought to be homologous to the mammalian hippocampus (e.g., Colombo & Broadbent, 2000; Herold, Coppola, & Bingman, 2015). Over the past several decades, there has been a plethora of research dedicated to better understanding how the avian HF may be involved in a variety of tasks including: spatial cognition (Cheng et al., 2006), homing (e.g, Gagliardo et al., 2020), food-storing (e.g., Sherry & Vaccarino, 1989; Clayton, 1998), brood parasitism (e.g, Sherry & Guigueno, 2019) and migration (e.g, Bingman & MacDougall-Shackleton, 2017). Early work in songbirds suggested that the avian HF was involved in spatial cognition (e.g, Shettleworth, 1995). Food-storing birds also rely more heavily on spatial environmental information in comparison to nonspatial information (Brodbeck, 1994; Clayton & Krebs, 1994). Initial hippocampal-lesion studies conducted in food-storing birds demonstrated that without an accessible HF, birds were unable to remember goal locations but could rely on goal color information (e.g., Sherry & Vaccarino, 1989).

Homing pigeons, while not food-storers, are well known for their navigational abilities and have been extensively used in open-field laboratory settings over the past several decades (Cheng et al., 2006; Colombo & Broadbent, 2000; Spetch & Edwards, 1986). Past research indicates that pigeons have been generally found to develop preferences for spatial rather than nonspatial cues in open-field tasks, but can also rely on nonspatial cues (Bingman et al., 2006; Nardi & Bingman, 2007; Strasser & Bingman, 1996). However, during goal localization tasks, when the avian HF is damaged in pigeons, they experience impairments in their ability to use spatial information but can utilize nonspatial cues to find goals (Bingman & Jones, 1994;

Coppola et al., 2014; Kahn & Bingman, 2009; Strasser & Bingman, 1997; Vargas, Petruso, & Bingman, 2004).

Over the past several years, there have been some new developments in single-unit recordings electrophysiology research involving homing pigeons and reward locations (Hough & Bingman, 2004, 2008; Kahn et al., 2008; Siegel, Nitz, & Bingman, 2002, 2005). Siegel et al. (2005) demonstrated that at the end of maze arms, where food rewards were located, some avian hippocampal cells had increased activity (firing rates), thus indicating some association between reward and place (goal locations). Stemming from Siegel et al.'s work (2005), Kahn and Bingman (2009) investigated the role of the avian HF in an open-field, goal-location task where intact and hippocampal-lesioned homing pigeons were used. Pigeons were trained with spatial and nonspatial cues simultaneously and provided different rewards (food) based on goal quality (preferred or non-preferred food items). Results indicated that the control pigeons, with an intact hippocampus, developed preferences for spatial rather than nonspatial cues and were able to discriminate between goal locations of preferred and non-preferred outcomes. By contrast, hippocampal-lesioned pigeons relied more on nonspatial information and could not discriminate between goal locations of preferred or non-preferred outcomes. Similar to Siegel et al. (2005), Kahn and Bingman's (2009) findings also suggest some interaction between the avian HF and goal/reward quality. These two studies were influential in providing the initial development for the current dissertation project. While Coppola et al. (2014) provided a nonspatial follow-up study to Kahn and Bingman (2009), the current dissertation project aimed to provide more experimental evidence of the relationship between the avian HF and the qualitative representations of goals, specifically that of probability-based values of reward outcomes.

Differential Reward Outcomes and Probability Learning

Animal behavior is typically understood to be driven by reward outcomes, or that animals make certain behavioral choices to access a specific reward. One lens through which this topic has been studied is foraging behavior, or how animals access food or resources. Because food availability may vary daily, animals must contend with either constant/predictable or variable/unpredictable rewards (Mazur, 1988, 1989, 2004). Researchers have long sought to understand how these varying reward outcomes contribute to foraging behavior and have thus developed several theories on how animals seek out food sites (Kamil & Roitblat, 1985; Stephens, 2008). Optimal foraging theory (Charnov, 1976; Kamil, 1983; Pyke et al., 1977), for example, posits that animals should seek out optimal food sites, namely those that provide high caloric output and require minimal time to access. Within this framework, animals would not have any preferences for specific food sites if they were all equally optimal and provided the same outcome (Krebs et al., 1981; Stephens & Krebs, 1986).

Research suggests, however, that optimal foraging theory may fail to account for the full range of animal behavior when risk or uncertainty is involved (Caraco, 1981; Caraco et al., 1980; Caraco et al., 1990). Studies indicate that animals may vary in their decision-making, with some being more prone to choosing food sources with variable or unpredictable reward outcomes rather than those with constant or predictable outcomes. The risk-sensitive foraging theory accounts for this range in behavior by suggesting a continuum of risk-averse to risk-prone tendencies (Bateson, 2002; Kacelnik & Bateson, 1996; Kacelnik & El Mouden, 2013). Animals who preferentially choose predictable or constant food options would be considered risk-averse. In contrast, risk-prone animals preferentially choose food sources that offer the possibility of a greater reward even if the outcome is variable or unpredictable in comparison to constant food options. These animals appear willing to take a risk as long as the possibility and ultimate periodic result of receiving a greater reward or a higher payout exists (Mazur, 1988, 2004; Craft, 2016).

Research indicates that pigeons can display risk indifference, risk-averse or risk-prone behaviors in studies when provided with constant and variable food reward schedules. Staddon and Innis (1966), for example, found that pigeons tended to respond equally to constant or variable durations of food hopper presentations as long as the mean quantity of reward (seconds) did not vary; they were neither risk-averse nor risk-prone when food hopper presentations averaged three seconds. Similarly, Young (1981) demonstrated that pigeons were either more risk-prone or risk-indifferent when given the option of either constant or a variable number of food pellets. Pigeons pecked more often at operant keys associated with variable reinforcements when they were equal in expected value to constant reinforcers and were indifferent to any key when the expected value of the certain reinforcer was greater than the uncertain reinforcer (Young, 1981).

Essock and Reese (1974) demonstrated that the majority of pigeons pecked at variable-outcome operant keys (access to food ranging from 2-8, 2-10, 3-10, and 4-10 seconds) more often than fixed-outcome keys (5 seconds of food access), that is pigeons were more likely to be categorized as risk-prone rather than risk-averse. In a different study conducted by Lagorio and Hackenburg (2012), they found evidence of risk-prone behaviors in pigeons. Birds were found to prefer variable over constant options in a token economy paradigm in relation to seconds of food hopper access; the majority of birds preferred the variable option of 0-12 tokens more often than the constant option of 2, 4, 6, or 8 tokens during trials in which the constant option provided equal or greater numbers of tokens than the variable alternative (Lagorio & Hackenberg, 2012).

By contrast, some research also suggests that pigeons may develop more risk-averse behaviors. For example, Menlove, Inden, and Madden (1979) found that the majority of pigeons developed preferences for constant (4 seconds) rather than variable (0 or 8 seconds) access to food hoppers. Similarly, Hamm and Shettleworth (1987) also demonstrated that pigeons were more likely to choose operant keys associated with constant outcomes (2 or 8 pellets) in comparison to variable keys (0-4 pellets, mean 2 pellets; 0-16 pellets, mean 8 pellets; 2-14 pellets, mean 6 pellets). Taken together, these results suggest that pigeons may display risk-indifference, risk-prone, or risk-averse behaviors depending on factors such as the quantity of food available and the length of time it is accessible.

Outside of operant training paradigms, risk preferences in pigeons have also been examined in more natural, foraging settings. Roberts (1988) trained pigeons on an open-field experiment with a patchy distribution of food locations. In the first experiment, all of the feeders in three out of the four patches were baited, and the number of pellets placed in the feeders varied. Patch 1 feeders were baited with 10 pellets and patch 2 feeders were baited with five pellets. By contrast, patch 3 feeders contained only 1 pellet and patch 4 feeders were not baited with food. Pigeons were found to visit patches where feeders were baited with a larger number of pellets more often than other patch sites. In the second experiment, food reinforcement probability of individual patches was manipulated, while the quantity of food per feeder remained constant. Two feeders were baited in patch 1(25% reinforcement), four in patch 2 (50% reinforcement), six in patch 3 (75% reinforcement), and 8 feeders in patch 4 (100% reinforcement). Results suggested that pigeons spent more time in patch 2, patch 3, and patch 4 in comparison to patch 1, thus suggesting that pigeons seek out reward sites that have more, rather than less, food in patchy environments (Roberts, 1988).

Recent evidence suggests that pigeons increase their risk-taking behavior when discriminating between large variable and small constant reward outcomes. Ludvig et al. (2014) trained pigeons to discriminate between safe (3 or 1 food cups) or risky (50% chance of a better or worse reward: 2 or 4 food cups; 0 or 2 food cups) options within high or low reward levels. Results suggested that pigeons became more risk-prone towards large, rather than small rewards. In a different study, a similar finding was observed with visual cues associated with variable large rewards, but not constant small rewards, increased risk-seeking behavior towards large rewards in pigeons even when the probability of loss increased (Smith et al., 2017). Rose and colleagues (Rose et al., 2009; Rose et al., 2013) revealed that pigeons learned large-reward (4 seconds of food access) discriminations more readily than small-reward (1.5 seconds of food access) discriminations. In summary, in experimental protocols where pigeons are required to discriminate between variable stimuli associated with larger outcomes and constant stimuli associated with smaller outcomes, pigeons develop risk-prone tendencies.

Additionally, pigeons studied in operant experimental settings have been found to explicitly probability-match, or select outcomes associated with specific percentages of reinforcement (Bullock & Bitterman, 1962; Graf et al., 1964; Roberts et al., 2015; Roberts et al., 2018; Scarf et al., 2014). In one such study, pigeons varied their pecking behavior in response to visual cues (triangles, command, and plus stimuli) that were associated with 40%, 70% or 100% reinforcement probabilities in touch-screen operant tasks (Scarf et al., 2014). Similarly, pigeons in another research study were found to discriminate between specific keys associated with either 75 % or 25% reinforcement and pecked more often at larger reward keys, even when the total number of reward quantities of either key were matched (Roberts et al., 2018).

In summary, pigeons seem to be more risk-prone towards large variable-based reward outcomes, preferring them to small constant-based reward outcomes in various experimental conditions. Additionally, pigeons readily discriminate between differential reinforcement-probabilities, favoring larger, rather than smaller, rewards based on the probability of reinforcement.

Reward-Related Decision-Making

Animals engaging in goal-directed behavior are influenced by both motivational factors and navigational abilities. If an animal encounters something rewarding, it is typically able to assign some type of salience or importance to the event. This motivational process is largely regulated by areas of the basal ganglia, mainly the striatum. The striatum is known to be involved in controlling stimulus-response behavior and procedural memories or "habits" (Barnes & Glimcher, 2005; Meyers et al., 2003; Pennartz et al., 2011; Yin & Knowlton, 2006). Additionally, it would be advantageous for animals to remember specific contextual elements of a rewarded event, including its spatial location. The hippocampal system is associated with episodic declarative memory, contextual-based memory, and spatial navigation (Meyers et al., 2003; O'Keefe & Nadel, 1978; Pennartz et al., 2011; Sutherland et al., 1989; Tulving & Markowitsch, 1998; Yin & Knowlton, 2006). Highlighting the divergent functional profiles of the basal ganglia and hippocampus, the basal ganglia have been suggested to be involved in simple associative learning, while the hippocampus is sensitized to detect contextual changes and process events separated in time (Buzsaki, 2005; Eacott & Norman, 2004; Mizumori et al., 2007; Myers et al., 2003; O'Keefe and Nadel, 1978; Rawlins, 1985; Redish et al., 2000). Moreover, while the striatal system is reward-based and engaged more during habitual behaviors that are "inflexible" to new contextual or environmental changes, the hippocampal system is able to update or modify memory representations of environments and goals in a more “flexible” manner (Packard & McGaugh, 1996; Palombo et al., 2015; Johnson et al., 2007; Yin & Knowlton, 2004). Based on this information, it has been proposed that the hippocampus and the striatum work in competition and are parallel memory systems, in that each system is associated with controlling different types of learning and memory processes.

Evidence of the competition theory between the hippocampus and the striatum has been demonstrated over the past few decades. Rodent behavior, for example, has been found to be more habitual when the hippocampus is damaged or unavailable (Hirsch, 1974). If an animal experiences stable rewards in its environment, an animal's repeated actions or behaviors that lead to such rewards are thought to gradually transition into automated, stereotypical behavior that is under striatal control (Regier et al., 2015). In tasks that engage both the hippocampus and striatum, it has been found that during the initial learning of a task, rats develop place strategies, which is under hippocampal control, but by the end of training, they often switch to a stimulus-response strategy, which relies on the dorsolateral striatum (Packard, 1999; Packard & McGaugh, 1996; Tolman et al., 1946). These results suggest that the hippocampus dominates initial learning, and after repeated training, neural control is shifted to the striatal system, thus providing evidence for a competitive relationship between both areas.

Although previous research suggests that the hippocampus and basal ganglia may be in competition with each other, there is a suggestive body of evidence that supports a cooperative relationship between the hippocampal memory and the striatal motivation systems, especially in navigation-based tasks (Mizumori & Tyron, 2015; Mizumori et al., 2004; Mizumori et al., 2009; Penner & Mizumori, 2012; Retailleau et al., 2012). For example, rats with both dorsal hippocampal and dorsolateral striatal lesions were severely impaired during both non-cued and cued water mazes (Miyoski et al., 2012). In mice, dorsal hippocampal lesions slightly impaired star-maze performance, while dorsomedial striatal lesions resulted in no learning of the star-maze (Fouqet et al., 2013). Jacobson, Gruenbaum, and Markus (2012) demonstrated that in rats, hippocampal lesions impaired performance on place, but not response trials. However, dorsolateral striatum lesions resulted in more errors during both place and response trials (Jacobson et al., 2012). Recently, Rice, Wallace, and Hamilton (2015) discovered that rats with hippocampal lesions had distorted initial trajectories towards escape platforms at the beginning of trials, whereas dorsolateral striatal lesions impaired swim trajectories at the end of trials. In summary, these studies suggest that, at least in mammals, there is also evidence of a cooperative relationship between the striatum and the hippocampus. In other words, a functional hippocampus and striatum enable optimal performance and learning during navigation-based tasks. However, damage to the striatum can also produce negative consequences for spatial-based information, thus indicating some type of link between the mammalian hippocampus and striatum.

In addition to the previously described lesion studies, electrophysiological research reveals a cooperative relationship between the striatum and the hippocampus in mammals; both brain areas have been found to be highly involved during navigation-based tasks. Wiener was one of the first to discover that rat striatal neurons were active during spatial navigation (Wiener, 1993). In rodents and primates, hippocampal neurons fire more often during rewarded than unrewarded trials (Hölscher et al., 2003; Rolls & Xiang, 2005). Mizumori and colleagues (2004) found that hippocampal and striatal neurons fired similarly during spatial and response maze tasks. In this study, many place fields of hippocampal and striatal neurons were similarly affected by changes to the visual and reward properties of the experimental setting. However, the authors suggested that the striatum may be more sensitive to changes in reward values in comparison to the hippocampus (Mizumori et al., 2004).

Tyron and colleagues (2017) discovered that in a maze-based, probability-discounting task with two reward options, rats preferred the riskier option when the probability of obtaining a large reward was high and shifted their behavior towards the safer alternative as the probability of the high reward decreased. Hippocampal place cells showed strong location-specific firing around goal locations, and firing patterns were influenced by reward probabilities (Tryon et al., 2017). Hippocampal neurons have also been found to store concurrent context reward value; place fields encode both spatial and location-specific reward valence information (Mamad et al., 2017).

Findings from Mamad et al. (2017)'s study compare well to Sosa and Giocomo's review article (2021) that showcases recent experimental evidence of how the mammalian hippocampus may encode and use reward information during navigation. Jeong et al. (2018) found that in mice, the mammalian hippocampus area of CA1, but not CA2, CA3, or the dentate gyrus (DG) was involved in a dynamic foraging task in a T-maze that involved probabilities of high (72%) and low (12%) rewarded blocks. Additionally, Jung et al. (2018) also posit that the mammalian hippocampus conveys reward value information and contributes to reward-based learning in navigational tasks. Jin and Lee (2021) found that intermediate, rather than dorsal, hippocampal place cells in rats were heavily influenced by the motivational significance of high-value or low-value locations in a V-shaped environment. Taken together, these studies provide experimental evidence that the mammalian hippocampus is responsive to spatial-based reward values and is involved during reward-based tasks.

While the majority of electrophysiology research discussed thus far has focused on mammals, similar experimental investigations involving homing pigeons have also been conducted (Hough & Bingman, 2004, 2008; Siegel et al., 2002, 2005; Kahn et al., 2008). Homing pigeon hippocampal formation neurons display a disproportionate number of increased firing fields at stable reward locations (Hough & Bingman, 2004; Siegel et al., 2005). In conditions with unstable goal locations, where food was randomly available, avian hippocampal place cells did not fire as often in comparison to other experimental protocols (Kahn et al., 2008). In summary, these studies suggest that the avian hippocampus is responsive to variation in reward properties and how spatial representations are affected by reward locations.

Spatial Cognition and the Avian Hippocampal Formation

In locating and recognizing goals that may be specific to food, mates, or shelter, animals may use a variety of different environmental information to assist them during goal-directed behaviors. Generally, researchers identify two major categories of such environmental information: spatial (also used interchangeably with space) and non-spatial stimuli. Spatial characteristics supporting goal recognition may be allocentrically-based, and many animals may develop a "cognitive map" of landmarks, objects, and their relationship to each other within a spatial environment (O’Keefe & Nadel, 1978). The spatial representation of a goal location within an environment can be defined by global or distal cues, local or position-based information, as well as overall environmental shape (Cheng, 1986; Cheng & Newcombe, 2005; Cheng et al., 2013; Doeller & Burgess, 2008; Gallistel, 1990; O’Keefe & Nadel, 1978; Sutton, 2009). By contrast, non-spatial environmental information, such as object colors, odors, textures, and other features, can define a goal independent of their position in space. These cues provide object or feature-based information that animals may use to guide beacon- or recognition-like, goal-directed behavior (Cheng et al., 2006; Cheng et al., 2013; Columbo & Broadbent, 2000).

Many animals, including birds, have been found to rely on various types of environmental cues during goal localization. Among songbirds, preferences for spatial and non-spatial cues during memory tasks are typically dependent upon the food-storing capability of each species. Food-storing songbirds engage in both foraging and caching behaviors and have been found to have larger hippocampi, a brain area dedicated to spatial cognition and memory, than non-food storers (e.g., Krebs et al., 1989; Sherry et al., 1989). Consistent with their larger hippocampus, food-storing birds tend to rely more on spatial cues than non-spatial, feature cues when locating a goal (Brodbeck, 1994; Brodbeck & Shettleworth, 1995; Clayton & Krebs, 1994; Gould-Beierle & Kamil, 1996; Sherry et al., 1992). Non-storing songbirds in contrast, have been found to use both spatial and non-spatial cues equally (Brodbeck, 1994; Brodbeck & Shettleworth, 1995; Clayton & Krebs, 1994; Herborn et al., 2011).

However, in some other animal species (for reviews see Cheng & Newcombe, 2005; Tyman & Newcombe, 2010), such as fox squirrels (Waisman & Jacobs, 2008), tiger salamanders (Kundey & Phillips, 2019), and bumblebees (Sovrano et al., 2013), preferences for non-spatial, feature-based information have been observed during discrimination tasks involving rewarded goals. Similarly, preferences for feature-based information have also been found in some birds including mountain chickadees (LaDage et al., 2009) and domestic chicks (Morandi-Raikova et al., 2020; Vallortigara et al., 1990). In summary, while spatial preferences may be more common in food-storing songbirds, many non-storing songbirds may equally rely on space and color/feature cues. By contrast, other animal species, including some birds, have been found to rely more on color information in comparison to spatial cues.

In both laboratory studies and field settings, the avian hippocampal formation (HF) has been found to be an important brain area during landmark-based navigation, homing, and the performance of spatial memory tasks (e.g., Bingman, 1992; Bingman & Able, 2002; Bingman et al., 2003; Columbo & Broadbent, 2000; Gagliardo et al., 1999; Pravosudov & Smulders, 2010; Sherry et al., 1989; Smulders, 2006). Past research involving hippocampal-lesions in several food-storing birds has indicated memory deficits in relation to location, but not object-centered, goal information (Clayton & Krebs, 1995; Columbo & Broadbent, 2000; Hampton & Shettleworth, 1996; Shiflett et al., 2003). Additionally, evidence from Immediate Early Gene (IEG) studies (c-Fos expression) involving birds further demonstrates the overall importance of the avian HF for space-based memory in both food-storing and non-storing avian species (Bischof et al., 2006; Coppola & Bingman, 2020; Mayer & Biscof, 2012; Mayer et al., 2010; Mayer et al., 2016; Mayer et al., 2018; Smulders & DeVoogd, 2000). In summary, in many birds, the avian HF is a critical brain area involved in spatial-based cognitive tasks, and damage to this neural structure can cause spatial-based memory deficits during goal localization tasks.

Homing pigeons, which are neither migratory nor food-storing, have also been found to rely on environmental stimuli, such as spatial and non-spatial cues, to identify reward sites (Colombo & Broadbent, 2000; Herold et al., 2015). Homing pigeons are well known for their extraordinary spatial abilities to navigate across great distances and return to their home lofts (Wallraff, 2005; Wiltschko & Wiltschko, 2003). While homing pigeons can use both spatial and feature environmental information during memory tasks, birds with intact hippocampi have been found to develop preferences for space-based rather than feature-based cues in open-field laboratory settings or outdoor field studies (Bingman et al., 2006; Gagliardo et al., 1996; Kahn & Bingman, 2009; Nardi & Bingman, 2007; Strasser & Bingman, 1996, 1999; Vargas et al., 2004), although there are some inconsistencies (Coppola et al., 2015; Kelly et al., 1998; Maury et al., 2010; Strasser & Bingman, 1996). By contrast, damage to the avian hippocampus generally produces spatial memory deficits. However, even though spatial cues may not be available due to an inaccessible avian HF, feature-based cues can be used by some hippocampal-lesioned nonstoring birds to identify goal sites, including Japanese quail (Lormant et al., 2020) and homing pigeons (Bingman & Jones, 1994; Bingman et al., 2006; Coppola et al., 2014; Gagliardo et al., 1996; Kahn & Bingman, 2009; Nardi & Bingman, 2007; Strasser & Bingman, 1997, 1999; Vargas et al., 2004). In summary, similar to food-storing birds, homing pigeons have been found to develop preferences for spatial rather than feature cues in open-field tasks. Additionally, when the avian HF is inaccessible, homing pigeons and other nonstoring birds can rely on non-spatial information, such as features, when identifying goal sites.

Based on the provided literature review so far, I have discussed past research involving risk, reward-probabilities, selected brain areas relevant to risk-based decision making, and spatial cognition and cue use in birds. The following two experimental studies (Kahn & Bingman, 2009; Coppola et al., 2014) were the primary inspiration for the current dissertation project. In one study, Kahn and Bingman (2009) investigated the role of the avian HF for the discrimination of different goal qualities, preferred or non-preferred food, in an open-field, memory task where both spatial and feature cues were simultaneously available. Control birds successfully found rewarded bowls, could discriminate between bowls with different goal qualities, and relied more on spatial information in comparison to feature cues. Similar to the control birds, hippocampal-lesioned birds were able to locate rewarded bowls. However, they relied more on color than space, and they did not seek out bowls baited with their preferred food first in comparison to bowls baited with their non-preferred food items. The contributions of this study were important for further developing a broader perspective of what constitutes content qualities of goal sites, with spatial or feature based information in association with different types of food items (preferred or nonpreferred food) and how the avian HF enabled specific goal qualities to be remembered (Kahn & Bingman, 2009).

Coppola et al. (2014) conducted a follow-up study to Kahn and Bingman (2009) with homing pigeons that investigated the role of the avian HF in feature-quality and feature-quantity discrimination tasks. This study utilized an unique experimental design in which spatial information was irrelevant for the open-field, memory task. Birds were trained to associate specific colored bowls with either preferred or non-preferred food and different quantities of pigeon chow. For both tasks, control and hippocampal-lesioned birds learned to seek out bowls that were baited with food, chose preferred over non-preferred food items, and could discriminate between bowls with high and low amounts of the same food. In contrast to the simultaneous spatial and feature study of Kahn and Bingman (2009) described above, this study highlights that the avian HF was not required during feature-quality or feature-quantity discrimination tasks (Coppola et al., 2014). Taken together, results from Kahn and Bingman (2009) and Coppola et al. (2014) provide experimental evidence to suggest that in spatial, rather than nonspatial contexts, the avian hippocampus is required for homing pigeons to remember information about rewarded goal qualities, such as preferred compared to non-preferred food items. Based on the finding from the two previously mentioned studies, the current dissertation project was developed to further examine the role of the avian hippocampus in relation to goal qualities based on probabilistic reward values.

The Present Study. The current dissertation project had two main goals: 1) to assess reward-based discriminations involving reinforcement probabilities in either spatial or feature experimental conditions and 2) to assess reward-based discriminations involving reinforcement probabilities in either spatial or feature conditions in homing pigeons with intact or damaged hippocampi. These goals are discussed in further detail below.

Research demonstrates that homing pigeons are capable of using both spatial and feature cues in an open-field memory task (Bingman et al., 2006; Kahn & Bingman, 2009; Nardi & Bingman, 2007; Strasser & Bingman, 1996, 1999; Vargas et al., 2004). Few research studies on this topic, however, have compared spatial-based and feature-based memory performance among experimental situations in which different sources of environmental information (spatial or feature) are presented in a noncompetitive format in homing pigeons. One of the few existing studies to do so found that homing pigeons trained in a time-of-day associative memory task provided only with spatial cues outperformed pigeons provided only with feature cues (Sizemore & Bingman, 2016). Thus, one of the goals of the present study was to determine whether space or feature information would yield better memory performance in an experimental setting where goal locations were associated with different degrees of risk or variable outcomes. Given that space is more often preferred over feature cues in supporting goal memory in homing pigeons, I predicted that variable-outcome or risk-associated memory performance based on spatial information would exceed memory performance based on feature information.

Risk-associated memories and reward probability learning in homing pigeons have also been investigated in more traditional operant-based testing protocols. As previously discussed, the literature does not provide a singular answer regarding homing pigeons and risk-based decision-making. The birds may range from behaving in a manner that is risk-prone, risk-averse, or indifferent to risk (Essock & Reese, 1974; Hamm & Shettleworth, 1987; Lagorio & Hackenburg, 2012; Ludvig et al., 2014; Menlove et al., 1979; Smith et al., 2017; Staddon &

Innis, 1966; Young, 1981). Homing pigeons have also been found to discriminate cues based on reinforcement probabilities during goal-seeking behavior in operant tasks (Bullock & Bitterman, 1962; Graf et al., 1964; Roberts et al., 2015; Roberts et al., 2018; Scarf et al., 2014). In contrast to controls, homing pigeons with hippocampal-lesions were impaired during differential reinforcement probabilities operant tasks (Scarf et al., 2014). However, this finding has not been replicated in mammals (Abela & Chudasama, 2013). As such, it was another interest for the current study to determine if pigeons with intact hippocampi or hippocampal-lesions would demonstrate differences in their first-choices to a constant reward (small amount of food always available) or to a riskier, variable reward (large amount of food available based on high or low probabilities) using either spatial or feature cues independently, not concurrently.

In order to address the goals of the present study, a specific set of experimental conditions were developed and will be briefly explained (also see Methods). There were two types of training conditions, Space and Feature. Homing pigeons were considered as part of the spatial group if they were trained to locate goal locations defined by unique spatial locations in the Space training condition. By contrast, homing pigeons were considered part of the feature group if they were trained to locate goal sites defined by unique colors in the Feature training condition. There were two categories of four behavioral trial types, High-Variable and Low-Variable, that all homing pigeons experienced. During High-Variable trials, there was one 75% High-Variable goal site or location where food rewards were available for three out of four High-Variable trials. During Low-Variable trials, there was one 25% Low-Variable goal site or location where food rewards were available for one out of four Low-Variable trials. For both High-Variable and Low-Variable trials, there was one 100% Constant goal site or location where food rewards were available for every trial.

Predictions. As past research suggests (Mamad et al., 2017; Mizumori et al., 2004; Mizumori et al., 2009; Mizumori & Tyron, 2015; Penner & Mizumori, 2012; Retailleau et al., 2012; Tyron et al., 2017; Wiener, 1993), animals with functional and interactive hippocampal memory and striatal motivation systems are able to preferentially shift or change their navigation-based behavior towards goals that are represented by unique locations in space and reward-based values. If pigeons were rational agents that chose goal outcomes associated with higher overall food gain per training session, then during 75% High-Variable trials, I expected sham-lesioned spatial birds to preferentially choose the 75% High-Variable rewarded goal location in comparison to the 100% Constant rewarded goal location (Budaev et al., 2019; Hurly & Oseen, 1999; Simonson & Tversky, 1992; Zentall, 2017). If pigeons were rational agents that chose goal outcomes associated with higher overall food gain per training session, then during 25% Low-Variable trials, I expected sham-lesioned spatial birds to preferentially choose the 100% constant rewarded goal location rather than the 25% Low-Variable rewarded goal location (Budaev et al., 2019; Hurly & Oseen, 1999; Simonson & Tversky, 1992; Zentall, 2017).

By contrast, in predicting the performance of hippocampal-lesioned spatial birds, previous mammalian (Fouquet et al., 2013; Jacobson et al., 2012; McHugh et al., 2008; Miyoski et al., 2012; Rice et al., 2015) and avian (Bingman & Jones, 1994; Bingman et al., 2006; Coppola et al., 2014; Kahn & Bingman, 2009; Nardi & Bingman, 2007; Strasser & Bingman, 1997, 1999; Vargas et al., 2004) research demonstrates that animals with hippocampal damage experience deficits regarding their ability to preferentially shift or change their navigation-based behavior towards goal locations defined by space based on differential reward values. However, due to the intact striatal motivation system, one could argue that animals may still perceive reliable or stable goal outcomes in space, based on reward-values that remain constant and do not change

(Mizumori et al., 2004; Mizumori et al., 2009; Mizumori & Tyron, 2015; Wiener, 1993). Based on this information, I predicted that spatial hippocampal-lesioned pigeons would not behave as rational agents, instead, they would develop risk-averse behaviors and would preferentially choose the 100% Constant Location during both High-Variable and Low-Variable trials. Hippocampal-lesioned spatial birds would not be able to remember either variable-bowl location without a functioning hippocampus in a risk-based spatial memory task, but due to their intact striatum, they should be able to remember a stable location with constant food rewards. In summary, I anticipated that the spatial control sham-lesioned group would perform as rational agents and choose goal outcomes associated with higher overall food gain per session, whereas pigeons with hippocampal-lesions would choose goals associated with constant outcomes regardless of session type and would develop risk-averse tendencies during risk-based spatial discrimination tasks.

It has been reported that some birds may rely on non-spatial, feature-based information, such as color cues during discrimination tasks involving rewarded goals (Coppola et al., 2015; Kelly et al., 1998; LaDage et al., 2009; Maury et al., 2010; Strasser & Bingman, 1996). Homing pigeons with hippocampal-lesions are still able to rely on object-centered information regarding specific goals (Bingman & Jones, 1994; Bingman et al., 2006; Coppola et al., 2014; Kahn & Bingman, 2009; Nardi & Bingman, 2007; Strasser & Bingman, 1997, 1999; Vargas et al., 2004). Therefore, in the presumptive, non-hippocampal dependent, feature-based probability task of the current study, I anticipated both feature sham-lesioned and feature hippocampal-lesioned homing pigeons would behave as rational agents (Budaev et al., 2019; Hurly & Oseen, 1999; Simonson & Tversky, 1992; Zentall, 2017) during High-Variable and Low-Variable trials and that no effect of hippocampal-lesions was expected (Coppola et al., 2014). Both groups would be able to preferentially shift or change their goal-seeking behaviors based on trial parameters towards goal sites that offered the most food overall and were defined by unique colors and reward-based values I predicted that both sham-lesioned and hippocampal-lesioned feature birds would preferentially choose the 75% High-Variable rewarded goal color in comparison to the 100% Constant rewarded goal color. Additionally, during 25% Low-Variable trials, I expected both sham-lesioned and hippocampal-lesioned feature birds would preferentially choose the 100% Constant rewarded goal color more than the 25% Low-Variable rewarded goal color.

METHODS

Subjects

Thirty-two unsexed adult homing pigeons (*Columba livia*) were obtained from local racing hobbyists. One pigeon died due to natural causes unrelated to the experiment before testing began. Birds were individually housed in metal cages (56 x 38 x 31 cm) in a temperature and humidity-controlled colony-housing room with a 14/10 light-dark cycle. Lights were turned on at 8:00 local time and turned off at 22:00 local time. Birds were food-restricted to no less than 80% of their free-feeding weights, had access to food during training, and were supplementally fed in their home cages to maintain weight. Water was provided *ad libitum*. All procedures were approved by the Bowling Green State University Institutional Animal Care and Use Committee. Pigeons were randomly assigned to one of four experimental conditions and were trained at the same time: Space control sham-lesion group (Space C, *n* = 8), Space hippocampal-lesion group (Space HF, *n* = 8), Feature control sham-lesion group (Feature C, *n* = 8), or Feature hippocampal-lesion group (Feature HF, *n* = 7).

Hippocampal Formation Electrolytic Lesion Surgery

Homing pigeons were food-deprived 18 to 24 hours prior to surgery. Anesthesia was induced in a small plastic chamber using isoflurane gas. Animals remained in the induction chamber until the anesthetic took full effect, as evidenced by a lack of response to a toe pinch, shallow breathing, and depression of pulse and blood pressure. Once anesthetized, the feathers covering the ear openings and the top of the head were clipped. Pigeons were transferred to a stereotaxic apparatus with an attached nose cone that continued to deliver gas anesthetic throughout the surgery. The skin covering the skull was cut with a scalpel and held open with hemostats. Using stereotaxic methods, six target coordinates for bilateral hippocampal-lesions were located. A portion of the skull was removed with a high-speed drill, and an electrode (stainless steel pin insulated with Epoxylite) was inserted horizontally (parallel to the anterior-posterior axis of a pigeon's head) into the brain. The sixteen sham-lesioned control animals underwent the same procedure, except they did not have electrodes inserted into their brains.

For the fifteen bilateral HF-lesioned pigeons, the target lesion coordinates for each brain hemisphere (Lesion 1 = A 3.8, L ± 0.3, V 12.2; Lesion 2 = A 3.8, L ± 0.5, V 13.3; Lesion 3 = A 3.5, L ± 1.0, just ventral to the surface of the brain) were determined according to the pigeon atlas of Karten and Hodos (1967). At each of these locations, 3.0 µA of current was applied for 15 (Lesion 1) or 20 (Lesions 2 and 3) seconds, using a 5 mm exposed electrode tip. Following the lesions, electrodes were removed from the brain, and the skin over the skull was closed with sterile wound clips. All pigeons were placed in a recovery chamber until they regained consciousness, at which time they returned to their original cage. After between one and two weeks of recovery time, the wound clips were removed from all animals, and behavioral training began.

Feature Task Training Environment

The experimental room was rich in 2-D visual cues attached to the walls and 3-D landmark objects, and its dimensions were 3.38 m x 4.28 m with eight fluorescent lights mounted on the ceiling (Figure 1). Observers stood outside of the room behind a door with a one-way mirror during pretraining and training. In the Feature Task, five colored bowls (green, red, yellow, blue, brown) were positioned in a centered, linear array approximately 100 cm from two parallel walls. The linear array setup could be vertical (as depicted in Figure 1) or horizontal (not shown) with 32 cm between each bowl. Colored bowls were pseudo-randomly shifted to various locations within the linear arrays of either orientation (horizontal or vertical) between trials and sessions, with the constraint that the same colored bowl could not be placed at the same location within the linear array more than three times per session (8 trials/session). The location of the bowls changed across trials or sessions depending on the orientation of the linear array deployed, and randomly assigned candidate food reward sites were always associated with the same three colored bowls (e.g., blue, red, green), although the color of a bowl at each site continually changed. Again, only four bowls were available during any trial. Birds were pseudo-randomly released from each of the four release sites twice per session determined via a dice roll (1 – North wall, 2 – South wall, 3 – West wall, 4 – East wall), relative to the observer. Looking at Figure 1, E/W wall release sites (depicted with Xs) were used during horizontal array orientations (not shown), and N/S release sites were used during vertical array orientations.

Spatial Task Training Environment

The Space Task's experimental room floor dimensions were 3.38 m x 4.28 m with eight fluorescent lights mounted on the ceiling (same room used in Feature Task). The room was rich in 2-D visual cues attached to the walls and 3-D landmark objects. Observers stood outside of the room behind a door with a one-way mirror during pretraining and training. For the Space Task, five bowls differing only in color, with approximately 135 cm between each bowl, were positioned at five distinct, constant spatial locations in the experimental room (Figure 2). Colored bowls were pseudo-randomly shifted to any of the five locations between trials and sessions, with the constraint that the same-colored bowl could not be placed at any one location more than three times per session (8 trials/session). The bowls' relative room location did not change across trials or sessions, and the three randomly assigned candidate food reward sites were baited at the same location and remained stable for each bird throughout training, although the bowl color (green, red, yellow, blue, brown) at each site regularly changed. Only four bowls were deployed during any trial (see below). Birds were pseudo-randomly released from each of the four release sites (depicted with Xs) that were determined via a dice roll (1 – North wall, 2 – South wall, 3 – West wall, 4 – East wall) twice per session, relative to the observer.

Pretraining

All birds were trained in the same room for both pretraining and the behavioral experimental tasks. During pretraining, birds were gradually introduced to the empty (no 2-D visual cues or landmark objects, see above) experimental environment over the course of several days. At this stage, birds were randomly placed on the floor in different locations in the room with four white bowls filled with grit; the position of the bowls on the floor changed daily. Initially, the room's lights were turned off, but once a bird was on the floor of the room and the researcher was behind the entrance door, the lights were turned on for the entire duration of a pretraining trial. Lights turned off again at the end of the trial. In the beginning, food was scattered across the floor and placed on the top of each bowl. Once a bird became more familiar with the room and ate all the food off the floor, food availability was gradually reduced until all food was buried under grit in each bowl. Pretraining trials continued until a bird found buried food in all four bowls within five minutes.

Feature Task Procedure

Pigeons were trained six days per week and sessions consisted of eight trials (one session/day). On any trial, two bowls could have contained food, and pigeons were presented with two different types of trials: four High-Variable and four Low-Variable. For both trial types, there was a specific colored bowl (e.g., blue) designated as the constant reward color and baited with food (2 pellets) for each pigeon. For every trial (four of each different type per session), this same rewarded color bowl contained food, resulting in 8 possible pellets (2 pellets X 4 trials) per session for each trial type (combined total of 16 pellets per eight trials/session: 2 pellets X 8 trials overall).

On High-Variable trials, during 75% of the four trials/session (three of four trials), the colored bowl (e.g., red) designated as High-Variable color was baited with 5 pellets; for the remaining trial, no food was present in the bowl (0 pellets) (Figure 1). If during the four High-Variable trials of a session a pigeon preferentially chose the High-Variable bowl, they would obtain 15 total pellets (5 pellets X 3 trials), exceeding the return from the Constant bowl by seven pellets (15 – 8 = 7). By contrast, during Low-Variable trials, on 25% of the four trials/session (one of four trials), the colored bowl (e.g., green) designated as Low-Variable color was baited with 5 pellets; for the three remaining trials, no food was present in the bowl (0 pellets), (Figure 1). If during the four Low-Variable trials of a session a pigeon preferentially chose the Low-Variable bowl, they would obtain 5 total pellets (5 pellets X 1 trial), a net loss of three pellets compared to the Constant bowl across the four trials (5 – 8 = -3). Importantly, on High-Variable trials, the Low-Variable bowl from the Low-Variable trials was not present, and on Low-Variable trials, the High-Variable bowl from the High-Variable trials was not present (that is why only four bowls were present on any given trial, which included two bowls of never baited colors (e.g., brown, yellow).

In order to reduce the possible use of path integration to locate a goal, Feature pigeons were slowly rotated (approximately 10-12 rotations per minute) while in a covered pet carrier on a swivel chair in a room adjacent to the experimental room for one minute before the start of every trial (see Coppola et al., 2014; Kahn & Bingman, 2009; Vargas et al., 2004). Each trial began inside the darkened experimental room as a pigeon was pseudo-randomly released from one of the four possible release positions with the constraint that each release position could not be used more than twice per session. Once a pigeon was placed at the release position on the floor of the experimental room, the researcher shut the room's door, turned on the lights, and recorded a pigeon's food bowl choices through a one-way glass window in the door. A pigeon was allowed to search for food for five minutes until it pecked into both *potentially* correct/rewarded colored bowls; the Constant bowl that was always baited (e.g., blue) and the possibly baited High-Variable (e.g., red) or Low-Variable (e.g., green) bowls.

A choice was defined as a peck into a bowl, and a pigeon had to move away from a bowl, defined as walking approximately 15 cm away from the bowl in any direction, and return in order for a second choice to be recorded for the same bowl. Bowl choices and latencies were recorded. However, I am only reporting the first-choice data, which were the most revealing. Once a pigeon pecked into both candidate baited/correct bowls or did not choose at all after five minutes, the lights were turned off, and the pigeon was removed from the room. If a pigeon did not choose a bowl after five minutes, the trial was terminated. Terminated trials were repeated until a pigeon completed the trial. There was a three-minute inter-trial interval in which a pigeon was placed in a covered pet carrier in the room adjacent to the experimental room. During this interval, the researcher cleaned the experimental room's floor of debris, changed the arrangement of the colored bowls, and re-baited the appropriate bowls. Pigeons in the Feature Task were trained for 16 sessions.

Spatial Task Procedure

Pigeons were trained six days per week and sessions consisted of eight trials (one session/day). On any trial, there were two bowl locations that could have contained food, and pigeons were presented with two different types of trials: four High-Variable and four Low-Variable. For both trial types, there was a specific bowl location (e.g., Location 1) designated as the constant reward site baited with food (2 pellets X 4 trials) for each pigeon. For every trial (four of each of the two types per session), this same rewarded bowl location contained food, resulting in 8 possible pellets per trial type (combined total of 16 pellets per eight trials/session: 2 pellets X 8 trials overall).

On High-Variable trials, during 75% of the four trials/session (three of four trials), the spatial location (e.g., Location 3) designated as High-Variable was baited with 5 pellets; for the remaining trial, no food was present in the bowl at that location (0 pellets), (Figure 2). If during the four High-Variable trials of a session a pigeon preferentially chose the High-Variable bowl, they would obtain 15 total pellets (5 pellets X 3 trials), exceeding the return from the Constant bowl by seven pellets (15 – 8 = 7). By contrast, during Low-Variable trials, on 25% of the four trials/session (one of four trials), the bowl's spatial location (e.g., Location 5) designated as Low-Variable was baited with 5 pellets; for the three remaining trials, no food was present in the bowl (0 pellets), (Figure 2). If during the four Low-Variable trials of a session a pigeon preferentially chose the Low-Variable bowl's spatial location, they would obtain 5 total pellets (5 pellets X 1 trial), a net loss of three pellets compared to the Constant bowl's spatial location on all four trials (5 – 8 = -3). Importantly, on High-Variable trials, the Low-Variable spatial location from the Low-Variable trials was not present, and on Low-Variable trials, the High-Variable spatial location from the High-Variable trials was not present (that is why only four bowl sites were present on any given trial, which included two bowls of never baited spatial locations (e.g., Location 2, Location 4).

In order to reduce the possible use of path integration to locate a goal, which was especially important for the Space Task, pigeons were slowly rotated (approximately 10-12 rotations per minute) while in a covered pet carrier on a swivel chair in a room adjacent to the experimental room for one minute before the start of every trial (see Coppola et al., 2014; Kahn & Bingman, 2009; Vargas et al., 2004). Each trial began inside the darkened experimental room as a pigeon was pseudo-randomly released from one of the four possible release positions with the constraint that each release position could not be used more than twice per session. Once a pigeon was placed at the release position on the floor of the experimental room, the researcher shut the room's door, turned on the lights, and recorded a pigeon's food bowl choices through a one-way glass window in the door. A pigeon was allowed to search for food for five minutes until it pecked into both *potentially* correct bowls' spatial locations; the Constant bowl that was always baited (e.g., Location 1) and the possibly baited High-Variable (e.g., Location 3) or Low-Variable (e.g., Location 5) bowl sites.

A choice was defined as a peck into a bowl, and a pigeon had to move away from a bowl, defined as walking approximately 15 cm away from the bowl in any direction, and return in order for a second choice to be recorded for the same bowl. Bowl choices and latencies were recorded. However, I am only reporting the first-choice data, which were the most revealing. Once a pigeon pecked into both candidate baited/correct bowls or did not choose at all after five minutes, the lights were turned off, and the pigeon was removed from the room. If a pigeon did not choose a bowl after five minutes, the trial was terminated. Terminated trials were repeated until a pigeon completed the trial. There was a three-minute inter-trial interval in which a pigeon was placed in a covered pet carrier in the room adjacent to the experimental room. During this interval, the researcher cleaned the experimental room's floor of debris, changed the arrangement of the colored bowls, and re-baited the appropriate bowls.

Although all Space birds were trained for 16 sessions, data from the first three Space Control sham-lesioned and hippocampal-lesioned birds didn't reach asymptotic performance at

Session 16. Therefore, I chose to continue running all the remaining Space birds for four more sessions, to session 20. However, due to experimental constraints, I could only do so for the last 5 pigeons per group (Space C $n = 5$ and Space HF $n = 5$). Note also that the data from the first 16 sessions of all eight Space C pigeons (used for the Space versus Feature Contrast) included the three pigeons that were not included in the Space Task's Results (Hippocampal-lesion Effect) section.

Histology and Lesion Reconstructions

After completion of the experimental study, the fifteen HF-lesioned pigeons were injected with a lethal dose of sodium pentobarbital (100 mg/ kg intramuscularly) and perfused intracardially with 0.9% saline followed by a fixative solution (10% formalin). Brains were harvested and placed in 10% formalin for 24 hours. The brains were embedded in a 30% sucrose solution in phosphate buffer saline (PBS) for 48-96 hours for cryoprotection. They were sliced into 50 µm thick sections on a freezing microtome. Every fourth section was mounted on a gel-coated slide, stained with Cresyl violet, and coverslipped. The extent of the lesion damage was examined using a Micromaster Fisher Scientific microscope. Lesions were reconstructed on standard coronal sections adapted from the pigeon atlas (Karten & Hodos, 1967).

Data Analyses

In order to compare the Feature Control sham-lesion ($n = 8$) and the Space Control sham-lesion ($n = 8$) pigeons on the risk-reward memory task, the total number of correct first choices across the training sessions were assessed using 2 (group: Feature, Space) x 4 (sessions 1-4, 5-8, 9-12, 13-16) mixed-model ANOVAs. Given the novel nature of the current study, where goal sites were based on different reward probabilities via spatial or nonspatial cues independently rather than simultaneously presented in a traditional competitive format, exploratory *post-hoc* tests were conducted using independent samples *t*-tests to examine between-group differences in learning performance at the end of training when a significant main effect or interaction was found. The criterion for statistical significance was $p \leq 0.05$.

In order to compare the Feature Control sham-lesion ($n = 8$) and the Feature hippocampal-lesion ($n = 7$) pigeons on the feature-based, risk-reward memory task, the total number of correct first choices across the training sessions were assessed using 2 (group: Control, HF) x 4 (sessions 1-4, 5-8, 9-12, 13-16) mixed-model ANOVAs. The criterion for statistical significance was $p \leq 0.05$.

In order to compare the Space Control sham-lesion ($n = 5$) and the Space hippocampal-lesion ($n = 5$) pigeons on the spatial-based, risk-reward memory task, the total number of correct choices across the training sessions were assessed using 2 (group: Control, HF) x 5 (sessions 1-4, 5-8, 9-12, 13-16, 17-20) mixed model ANOVAs. Given the uniqueness of the current spatial study in relation to reward probability discrimination and the role of the avian hippocampal-formation in an open-field environment, rather than the standard operant protocol, with smaller than anticipated sample sizes, exploratory *post-hoc* tests were conducted using independent samples *t*-tests to examine between-group differences in learning performance at the beginning or end of training when a significant main effect or interaction was found by lowering alpha from $p \leq 0.05$ to $p \leq 0.10$ Analyses were performed using SPSS Statistics, Version 26.0 (Armonk, NY, USA; IBM).

RESULTS

Space Controls versus Feature Controls

First-Choices to High-Variable and Constant Bowls during HV Trials. Across an experimental session, first-choices to the High-Variable 75% food bowl would yield a greater food gain (fifteen pellets across the four trials of a session) than first choices to the Constant 100% bowl (eight pellets across the four trials of a session), and I expected that the pigeons would preferentially learn to direct their first choices to the High-Variable 75% bowl. Examination of Figure 3A reveals this to be true for both the Feature and Space conditions. Overall, there was a main effect of blocked sessions, $F(3,42) = 6.34$, $p = 0.001$ and group $F(1, 14) = 13.45$, $p = 0.003$. Additionally, there was not a significant interaction between blocked sessions and group, $F(3,42) = 0.22$, $p = 0.885$. With main effects of both blocked sessions and group, a *post-hoc* analysis demonstrated a significant between group difference at the end of training during BLOCK 4 (Space $n = 8$, $M = 47.66$, $SEM = 5.66$; Feature $n = 8$, $M = 67.97$, $SEM = 6.73$, $t\,(14) = -2.31$, $p = 0.04$). Both types of experimental conditions yielded an increase in the number of first-choices to the 75% bowl across training, and performance on Feature trials exceeded performance on Space trials.

In contrast to the High-Variable 75% trials, no change in the number of first-choices to the Constant 100% bowl was found across training on both Feature and Space trials (Figure 3B), with the number of first choices/session staying at or slightly above chance levels. There were no main effects of blocked sessions, $F\,(3,42) = 1.41$, $p = 0.26$ or group $F\,(1, 14) = 0.29$, $p = 0.60$. Additionally, there was not a significant interaction between blocked sessions and group, $F\,(3,42) = 1.46$, $p = 0.24$.

First-Choices to Low-Variable and Constant Bowls during LV Trials. Across an experimental session, choices to the Constant 100% food bowl would yield a greater food gain (eight pellets across the four trials of a session) than choices to the Low-Variable 25% bowl (five pellets across the four trials of a session), and here it was expected that the pigeons would preferentially learn to direct their first choices to the Constant 100% bowl. Assessment of Figure 3D reveals this to be true for both the Feature and Space trials. For the analysis of the data, Mauchly's test indicated that the assumption of sphericity had been violated $\chi^2(5) = 11.03$, p = 0.05, therefore, the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity (e = 0.625). Overall, for the Low-Variable 25% sessions, no change in first-choices to the Low-Variable 25% bowl across training was found, with the probability of a first choice to the Low-Variable 25% bowl remaining at close to chance levels for both Feature and Space trials (Figure 3C). There was no main effect of blocked sessions, F (1.88, 26.26) = 0.79, p = 0.46 nor group F(1, 14) = 1.09, p = 0.31. Additionally, there was not a significant interaction between blocked sessions and group, F (1.88, 26.26) = 0.39, p = 0.67.

By contrast, and as expected, first-choices to the Constant 100% bowl increased across training for both the Feature and Space conditions during Low-Variable sessions. Both types of experimental conditions yielded an increase in the number of first-choices to the Constant 100% bowl across training, and again, performance on Feature trials exceeded performance on Space trials (Figure 3D). There were main effects of blocked sessions, F (3,42) = 6.60, p = 0.001 and group F (1, 14) = 12.47, p = 0.003. Additionally, there was not a significant interaction between blocked sessions and group, F (3,42) = 0.87, p = 0.46. With main effects of both blocked sessions and group, a *post-hoc* analysis demonstrated that there was a significant between group difference at the of training during BLOCK 4 (Space n = 8, M = 52.34, SEM = 10.76; Feature n =

8, $M = 83.59$, $SEM = 4.86$; $t\ (14) = -2.65$, $p = 0.019$). Again, the Feature group preferentially chose the Constant 100% bowl first more often the Space group during Low-Variable trials.

First-Choice Errors. The Feature and Space pigeons both behaved as rational agents in the distribution of their first-choices, preferentially choosing the High-Variable 75% bowl and the Constant 100% bowl on Low-Variable trials. However, learning performance was significantly better for the pigeons trained to Feature compared to the pigeons trained to Space. To explore this observation further, I examined the change in error-first responses, in other words, choices to a bowl that never contained food (incorrect bowls), across training. Examination of Figure 3E readily reveals that even though both groups reduced the number of their first-choice errors across training, the Feature pigeons clearly made fewer errors, explaining a good part of their more rational first-choice performance, as illustrated in Figure 4. There was a main effect of blocked sessions, $F\ (3,42) = 20.23$, $p = 0.001$ and group $F\ (1, 14) = 17.50$, $p = 0.001$. Additionally, there was not a significant interaction between blocked sessions and group, $F\ (3,42) = 1.10$, $p = 0.36$. With found main effects of blocked sessions and group, a *post-hoc* analysis revealed a significant between-group difference at the end of training during BLOCK 4 (Space $n = 8$, $M = 19.53$, $SEM = 4.79$; Feature $n = 8$, $M = 0.39$, $SEM = 0.39$; $t\ (14) = 3.98$, $p < 0.001$). At the end of training, Feature birds hardly made errors, whereas this was not the case for Space birds.

Although session latencies for first-choices were recorded for all birds, there were no significant between-group differences during High-Variable sessions or Low-Variable sessions, $p > 0.05$ for all comparisons. As such, the data are not presented.

In summary, both the pigeons trained to feature and the pigeons trained to space performed as rational agents during the learning of the probability discrimination. However, what was unexpected is that the pigeons trained to Feature clearly outperformed the pigeons trained to Space (see Discussion). At the end of training, the Feature birds preferentially chose the High-Variable 75% bowl and the Constant 100% bowl during Low-Variable trials significantly more often than Space birds, while the Space birds made more errors throughout training.

The previous section provided an examination of first-choice performance differences between control sham-lesioned pigeons trained to Space (unique goal sties based on location information) or Feature (unique goal sites based on color information) discriminative stimuli in a reward-probability memory task. The next two sections will focus on the secondary goal of the dissertation, to further investigate the role of the avian hippocampal formation in a reward-probability memory task with feature or spatial cues in a noncompetitive format. The results of the Feature Task designed to investigate the role of the avian hippocampal formation (first-choice performance of sham-lesioned pigeons compared to hippocampal-lesion pigeons) in a reward-probability discrimination task involving feature cues (unique goal sites based on color information) is presented first. The results of the Space Task designed to investigate the role of the avian hippocampal formation (first-choice performance of sham-lesioned pigeons compared to hippocampal-lesion pigeons) in a reward-probability discrimination task involving spatial cues (unique goal sites based on location information) is presented last.

The Effect of HF-lesions in the Feature Task

First-Choices to High-Variable and Constant Bowls during HV Trials. Assessment of Figure 4A reveals that both the Feature C (*n* = 8, same control sham-lesioned feature pigeons from the Feature and Space contrasts) and Feature HF pigeons (*n* = 7) were rational decision-makers, similarly learning to preferentially choose first the High-Variable 75% bowl compared to the Constant 100% bowl. There was a main effect of blocked sessions $F(3,39) = 6.74$, $p = 0.001$, but not for group $F(1, 13) = 2.20$, $p = 0.16$. Additionally, there was not a significant interaction between blocked sessions and group $F(3,39) = 0.75$, $p = 0.53$. Also, across training, both the Feature C and Feature HF pigeons showed little change in the number of first choices to the Constant 100% bowl, with first-choices to the Constant 100% bowl occurring on about 40% of the trials (Figure 4B). There was no main effect of blocked sessions $F(3,39) = 41.08$, $p = 0.34$, nor group $F(1,13) = 2.60$, $p = 0.13$. Additionally, there was not a significant interaction between blocked sessions and group $F(3,39) = 0.60$, $p = 0.62$.

First-Choices to Low-Variable and Constant Bowls during LV Trials. The High-Variable trials revealed no difference between the Feature C and Feature HF pigeons in their ability to learn to choose first the High-Variable 75% bowl when Feature was used as the discriminative stimulus. A similar lack of difference was also found for first-choices during the Low-Variable trials (Figure 4C). There was a main effect of blocked sessions, $F(3,39) = 3.00$, $p = 0.04$, reflecting fewer first-choices to the Low-Variable 25% bowl across training, but more importantly, there was no main effect for group $F(1,13) = 0.37$, $p = 0.55$. Additionally, there was not a significant interaction between blocked session and group, $F(3,39) = 1.30$, $p = 0.29$. By contrast, both groups displayed an increase in the number of first-choices to the Constant 100% bowl as training progressed (Figure 4D). There was a main effect of blocked sessions *F*

(3,39) = 11.08, $p < 0.001$, but not for group F (1,13) = 0.04, $p = 0.85$. Additionally, there was not a significant interaction between blocked sessions and group, F (3,39) = 1.12, $p = 0.35$.

Although session latencies for first-choices were recorded for all birds, there were no significant between-group differences during High-Variable sessions or Low-Variable sessions, $p > 0.05$ for all comparisons. As such, the data are not presented.

In summary, by preferring the High-Variable 75% bowl on High-Variable trials and the Constant 100% bowl on Low-Variable trials, both the Feature C and Feature HF pigeons performed as rational agents during the learning of the probability discrimination based on the color features of the goals. What is notable about the data is how similar the Feature C and Feature HF pigeons performed; there was no hint of a learning difference. The results are consistent with a similar study that did not include a risk/variable element in choice outcomes (Coppola et al. 2014) and is overall consistent with the literature (see Discussion), suggesting little effect of HF-lesions when pigeons learn and remember feature properties to represent a goal.

The Effect of HF-lesions in the Spatial Task

First-Choices to High-Variable and Constant Locations during HV Trials. As explained previously (see *Data Analysis* and *Space Task Procedure*), due to the initial poor performance of both Space Groups (Control sham-lesioned and HF) and experimental constraints, a smaller number of Space birds (Space Control sham-lesioned $n = 5$, Space HF $n = 5$) received an extension in the number of training sessions, from Session 16 to Session 20.

Visual inspection of Figures 5A suggests that, as expected, HF-lesions impaired the spatial-positional learning of directing first-choices to the High-Variable 75% bowl, and some of the statistical contrasts supported this visual impression. Reflecting the overall poorer performance of C pigeons on the Space task, there was no main effect of blocked sessions, *F* (4,32) = 1.70, *p* = 0.17. Importantly, there was a main effect of group, *F* (1, 8) = 3.38, *p* = 0.09. Additionally, there was not a significant interaction between blocked sessions and group, *F* (4,32) = 1.11, *p* = 0.37. Due to the main effect of group, a *post-hoc* analysis indicated that at the end training the Space C pigeons significantly outperformed (more High-Variable 75% first choices) the Space HF pigeons (BLOCK 5, C *n* = 5, *M* = 53.75, *SEM* = 5.45; HF *n* =5, *M* = 23.75, *SEM* = 8.00; *t* (8) = 3.10, *p* = 0.015). By contrast, no group effect could be detected with respect to first choices to the Constant 100% bowl, *F* (1, 8) = 0.007, *p* = 0.94; Figure 5B). However, there was a main effect of blocked sessions as there seemed to be a modest increase in Constant 100% bowl first-choices across training, *F* (4,32) = 2.43, *p* = 0.07. Because a main effect of blocked sessions was found, a *post-hoc* analysis was conducted. There was not a significant between-group difference at the end of training during BLOCK 5 for first-choices directed towards the Constant 100% bowl during High-Variable trials (C *M* = 37.50, *SEM* = 5.59; HF *M* = 43.75, *SEM* = 14.66; *t* (8) = -0.40, *p* = 0.70). Additionally, there was not a significant interaction between blocked sessions and group *F*(4,32) = 0.36, *p* = 0.83.

First-Choices to Low-Variable and Constant Locations during LV Trials. Examination of Figure 5C also suggests a notable difference between the Space C and Space HF pigeons, but here it was the Space C pigeons who were more likely to initially choose the less rational Low-Variable 25% bowl and change (decrease) their first choices to the Low-Variable 25% bowl across training. Mauchly’s test indicated that the assumption of sphericity had been violated χ^2 (9) = 21.47, *p* = 0.01, therefore degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity (*e* = 0.49). There was no main effect of blocked sessions, *F* (1.95, 15.62) = 0.42, *p* = 0.66, but importantly, there was a robust main effect for group, *F* (1, 8) = 14.16, *p* =

0.006. Additionally, there was not a significant interaction between blocked sessions and group, *F* (1.95, 15.62) = 0.61, *p* = 0.56. The HF-lesion effect was already present early in training as a *post-hoc* analysis (conducted due to the main effect of group) revealed a significant between-group difference during BLOCK 1 (C *n* = 5, *M* = 43.75, *SEM* = 7.13; HF *n* = 5, *M* = 11.25, *SEM* = 2.34; *t* (8) = 4.33, *p* = 0.003).

As with the High-Variable trials, visual inspection of Figure 5D suggests that there was no effect of HF-lesions on first-choices to the Constant 100% bowl during Low-Variable trials. There was a main effect of blocked sessions, *F* (4,32) = 3.82, *p* = 0.01, as the pigeons increased their first-choices to the Constant 100% bowl across training. However, there was no main effect for group, *F* (1, 8) = 0.04, *p* = 0.84 nor a significant interaction between blocked sessions and group, *F* (4,32) = 1.07, *p* = 0.39. There was not a significant between-group difference at the end of training, during BLOCK 5, as indicated by a *post-hoc* test conducted due to the main effect of blocked sessions (C *M* = 61.25, *SEM* = 10.90; HF *M* = 49.15, *SEM* = 12.99; *t* (8) = 0.71, *p* = 0.50).

Although statistically underpowered by the relatively small sample sizes (Space C *n* = 5, Space HF *n* = 5), the data presented in Figure 5 suggests that the HF-lesions affected the choice performance of the pigeons. There appear to be two effects of the lesions that were subsequently examined in greater detail. First, the data appear to reveal that the HF pigeons committed more Space errors during training. Second, independent of High-Variable and Low-Variable trials, the HF pigeons appeared to make fewer choices to the food bowls associated with a variable outcome (75% or 25%), in other words, they seemed more risk-averse.

First-Choice Errors during HV and LV Combined Trials. As suggested above, a visual assessment of Figure 5E supports the observation that across training, the Space HF pigeons made more first-choice errors by selecting a bowl location that never contained food (incorrect bowls). There was a significant main effect of blocked sessions, F (4, 32) = 7.30, $p < 0.001$, as all Space pigeons made fewer errors across training. Importantly, there was a main effect of group, F (1,8) = 4.57, $p = 0.07$. There was no interaction effect between blocked sessions and group, F (4, 32) = 1.05, $p = 0.40$. With a found main effect of group, a *post-hoc* test indicated that at the end of training the Space HF pigeons were making more first-choice errors than Space C pigeons as there was a significant between-group difference during BLOCK 5 (C $n = 5$, $M = 9.38$, $SEM = 4.64$; HF $n = 5$, $M = 35.43$, $SEM = 10.12$; t (8) = -2.34, $p = 0.047$). The significant group difference during Block 5 suggests a perhaps unsurprising spatial memory impairment following HF-lesions; Space HF pigeons chose incorrect bowls significantly more often than Space C birds independent of High or Low Variable trial types.

Pooled First-Choices to High and Low Variable Locations. As suggested above, a visual inspection of Figure 5F further supports the observation that across training the Space HF pigeons, compared to the Space C birds, were less likely to preferentially select riskier food bowls (75% or 25% variable outcomes) as their first-choice in comparison to bowl locations associated with a constant outcome (100%). There was no significant main effect of blocked sessions, F (4, 32) =0.84, $p = 0.51$. Importantly, there was a robust main effect for group, F (1,8) = 12.17, $p = 0.008$, as the Space HF pigeons made fewer overall first-choices to a variable (75% or 25%) reward food bowl. There was not a significant interaction between blocked sessions and group F(4, 32) = 0.50, $p = 0.74$. Because of the found main effect of group, a *post-hoc* analysis demonstrated that at the end of training there was a significant between-group difference in first-choices to either of the variable goal locations (BLOCK 5, C $n = 5$, $M = 41.25$, $SEM = 6.43$; HF $n = 5$, $M = 18.13$, $SEM = 5.54$; $t(8) = 2.72$, $p = 0.03$). Space C pigeons were much more likely to choose a variable outcome first in comparison to Space HF pigeons.

In summary, the analyses on the number of errors and the number of variable food bowl first-choices suggest that the HF-lesions resulted in impaired spatial learning, and as expected, a shift away from choosing food bowls with variable outcomes. As originally predicted, the Space HF pigeons seemed to become more risk-averse and directed their first-choices more to the 100% constant goal location in comparison to the other variable goal locations (75% and 25% bowls).

Although session latencies for first-choices were recorded for all birds, there were no significant between-group differences during High-Variable sessions or Low-Variable sessions, $p > 0.05$ for all comparisons. As such, the data are not presented.

HF-lesions Reconstruction Summary

Figure 6 (Feature) and Figure 7 (Space) summarizes the bilateral electrolytic lesion damage sustained by the HF-lesioned birds. All pigeons (Feature $n = 7$, Space $n = 5$) sustained extensive damage to the hippocampus proper (HP), with less damage to the neighboring parahippocampus (APH). Some animals also sustained minor damage to the adjacent hyperpallium apicale and mesopallium (M) on both sides.

DISCUSSION

The present dissertation investigated the role of the avian hippocampal formation in both spatial and feature risk-reward discriminations in homing pigeons. This study used an open-field experimental design that enabled noncompetitive spatial and feature training conditions in which three different goal sites varied in reward outcomes based on specific probabilities of 100%, 25%, or 75% reinforcement. Over the duration of either 16 or 20 experimental sessions, four different groups of homing pigeons, 1) Space control sham-lesioned, 2) Space hippocampal-lesioned, 3) Feature control sham-lesioned, and 4) Feature hippocampal-lesioned birds were trained on two different types of trial categories, High-Variable and Low-Variable. Overall, results provide insights into differences regarding memory performance for risk-reward discriminations based on either space or feature information and evidence of memory impairments due to hippocampal-lesion effects in spatial, but not feature contexts.

Comparison of Pigeons in Space or Feature Reward-Probability Tasks

Typically, in animals, spatial and feature cues have been investigated simultaneously in competitive behavioral training paradigms (Brodbeck, 1994; Cheng & Newcombe, 2005; Kahn & Bingman, 2009; Strasser & Bingman, 1996; Tyman & Newcombe, 2010) and comparative investigations of non-competitive environmental cue use in homing pigeons has been relatively understudied (Coppola et al., 2014; Sizemore & Bingman, 2016). One of the goals of the current study was to test the prediction that risk-based learning with respect to spatial cues would be in some way better than risk-based learning with respect to feature cues.

Contrary to the original prediction, the Spatial group (control sham-lesioned animals) did not out outperform the Feature group (control sham-lesioned animals) during either High-Variable or Low-Variable training sessions. Surprisingly, the Feature group developed stronger preferences than the Space group for both 75% High-Variable goal sites during High-Variable trials and 100% Constant goal sites during Low-Variable trials. As revealed in Figures 3A and 3D from the Space versus Feature Contrasts, in comparison to the Space group, the Feature group acted as rational agents and was better able to maximize food acquisition on their first-choices by preferring the 75% High-Variable colored bowl and the 100% Constant colored bowl when the 25% Low-Variable colored bowl was present. Additionally, as Figure 3E suggests, throughout training, the Feature group made significantly fewer errors than the Space group. During the last session block, a significant between-group difference emerged, the Feature group hardly made any incorrect first-choices, whereas this was not found for the Space group.

These findings are surprising because in food-storing birds (Brodbeck, 1994; Brodbeck & Shettleworth, 1995; Clayton & Krebs, 1994; Sherry et al., 1992) and homing pigeons (Bingman et al., 2006; Nardi & Bingman, 2007; Vargas et al., 2004), there is typically a preference for spatial cues during goal localization or recognition, but not always (see Coppola et al., 2015; Kelly et al., 1998; LaDage et al., 2009; Maury et al., 2010; Strasser & Bingman, 1996). As previously mentioned, there are relatively few studies (Coppola et al., 2014; Sizemore & Bingman, 2016) that have specifically examined memory performance of spatial or nonspatial discriminative stimuli on open-field experimental protocols in a non-competitive format. However, there is one study conducted by Kahn and Bingman (2004) that may provide indirect support for the observed differences between the space and feature groups in the current study. Results from Kahn and Bingman’s (2004) brain lateralization study demonstrated that in control pigeons with intact hippocampi, when trained to criterion, birds only trained with feature information advanced at a faster rate (4.89 sessions on average) in comparison to pigeons only trained to spatial information (17.88 sessions on average). However, this finding should be taken with some caution because the researchers did not explicitly compare the groups in their study (Kahn & Bingman, 2004). However, this indirect evidence is also inconsistent with the spatial advantage that Sizemore and Bingman (2016) found in a time-of-day associative learning study in homing pigeons.

This leads to the question, why did space yield worse performance? One potential solution may stem from a possibly more difficult space task where animals had to associate three different locations with various reinforcement probabilities rather than uniquely colored food bowls. Based on the experimental design of the current study, in the Space Task, pigeons were trained to find goal locations based on spatial properties of the experimental room, bowl color information was made irrelevant by not being consistently associated with food rewards based on specific colors. Whereas in the Feature Task, spatial information was made irrelevant due to the design of the linear array of bowls (horizontal or vertical) that changed position between trials. However, in both Space and Feature tasks, five different colored bowls were interchangeably used throughout training. This methodology approach could have been problematic for Space birds by way of interference of previously rewarded bowl color cues on the spatial task (Tello-Ramos et al., 2019). While the current study ensured that at the end of training, all Space birds had an equal number of bowl color experiences at each goal location, Space birds, unlike Feature birds, had to learn to associate stable goal locations with reward outcomes while simultaneously needing to forget previously learned outcomes associated with specific bowl colors. The cognitive load of the task for the Space birds was perhaps higher than that of the Feature birds and thus, resulted in more errors and learning differences between the groups (Tello-Ramos et al., 2019). If replicated, the present study suggests that a uniform bowl color should be used throughout training on a Space-only task rather than multiple bowl colors. This could potentially decrease the cognitive demands of the task and ensure that pigeons are only using provided spatial information rather than also trying to associate color cues with goal locations.

Additionally, if the Space task, rather than the Feature task, was in part controlled by the avian HF, as some previous research suggests (Columbo & Broadbent, 2000; Coppola et al., 2014; Herold et al., 2015; Kahn & Bingman, 2009; Vargas et al., 2004), stress associated with the task may have had negative consequences on hippocampal function (mammals – Kim & Leem, 2016; Sandi, 2013, Sousa et al., 2000; Japanese quail - Lormant et al., 2021) perhaps explaining in part the poorer performance of the Space birds. In other studies, stress effects between training conditions or groups have been demonstrated via latency differences (e.g., Lormant et al., 2020). However, in the current study, there were no significant group differences between Space control sham-lesioned and Feature control sham-lesioned birds regarding latencies at any point in the study. Stress effects in birds may also be characterized by a wide variety of distressed behaviors such as freezing, increased fecal droppings, loss of body weight, and overgrooming (e.g., Kastelic et al., 2021). In the current study, Space birds remained as motivated as the Feature birds to find food, and none of the animals were removed from the study due to health concerns. One common bioindicator of stress levels in birds is measured via corticosterone levels, or CORT derived from blood samples (Calandreau et al., 2011; Jones et al., 2016; Kastelic et al., 2021). It would be advantageous for future follow-up studies to measure CORT levels in homing pigeons at the beginning and end of training to determine if stress levels were significantly different between Space-only and Feature-only groups and to examine how those differences in CORT levels may correlate with potential differences in learning performance between groups.

Alternatively, the poorer performance of the Space pigeons may reflect more exploratory behavior on the part of birds when discriminating goal locations using spatial compared to feature information. In other words, the poorer performance of the Space birds was not a consequence of a less robust memory representation, but rather, a greater propensity to sample all sites periodically, perhaps to buffer against a change in the spatial location of food rewards (Lester, 1984). This is also consistent with recent ideas proposed by Anselme and Güntürkün (2019) in such that motivation increases foraging behavior when uncertainty is involved as a way to deter starvation. In the Space task of the current dissertation study, perhaps pigeons experienced an increase in motivation to continuously seek out all food goal locations for the potential chance that unexperienced rewards may be found, whereas with the Feature task, birds did not have the motivation to explore other goal sites based on nonrewarded colors (Campbell et al., 2018).

Although the current dissertation examined noncompetitive training conditions of spatial and feature cues, follow-up projects should also investigate potential preferences for space or color information while simultaneously available in relation to reward probabilities. By providing both spatial and feature information for pigeons during a probability-based task in an open-field, this could minimize the potential effect of stress on memory performance. While the current study did not investigate probe trials, this is very common in other competitive training formats (Columbo & Broadbent, 2000), and could provide more consistent results showcasing preferences rather than performance differences during training. Specifically, it would be illuminating to determine if the spatial preference found so often in previous work (Kahn & Bingman, 2009; Nardi & Bingman, 2007; Strasser and Bingman, 1997) would develop more for spatial-goals based on variations in probabilistic rewards rather than what was found in the current study with feature-based goals in homing pigeons. This rationale could also benefit the avian cue use literature by demonstrating if the proposed interference effect of the current Space task would emerge during future studies where both spatial and feature cues were used simultaneously.

Overall, results of the current dissertation project suggest that homing pigeons can associate goal sites based on colors (features) or locations (space) (Figures 3, 4, and 5) with three different reward-based outcomes of 100%, 75%, and 25% reinforcement probabilities. This aligns well with past research indicating that homing pigeons can discriminate between differential reinforcement probabilities during operant tasks (Bullock & Bitterman, 1962; Graf et al., 1964; Roberts et al., 2015; Scarf et al., 2014). In terms of future research, it would be useful to extend the findings of this dissertation project by further investigating how homing pigeons may form associations with goal sites based on color or spatial cues that provide additional variations in reinforcement probabilities, such as 100%, 80%, 75%, 60% 50%, 40, 25%, 12.5%, 5%, and 0%, similar to what is typically found in reward-based operant testing protocols (Bullock & Bitterman, 1962; Roberts et al., 2015; Scarf et al., 2014; Zentall, 2017; Zentall & Laude, 2013). By using different reinforcement percentages as discriminative stimuli in future studies, more insights could be provided as to how pigeons may engage with different goal sites based on color or location cues on a wider spectrum of values beyond what the current dissertation study used (100%, 25%, and 75%), thus granting more comparative analyses between standard operant and open-field testing protocols. This would also allow for further development of how pigeons may use matching law, maximize choices, perform suboptimally, and establish biases in relation to unpredictable reward values associated with spatial or feature cues (e.g., Houston, Trimmer, & McNamara, 2021; Vonder Haar; Zentall, 2017).

In summary, the results of the current dissertation project provide evidence that homing pigeons can form associations influenced by differential reward outcomes based on probabilities in an open field environment using either spatial or feature discriminative stimuli. Birds in the feature condition outperformed spatial birds during probability-reinforcement associative learning.

The Effect of HF-lesions in Feature or Space Reward-Probability Tasks

The second goal of the current study was to determine what role, if any, the avian hippocampal formation may have in a risk-based reward-probability discrimination task involving spatial or feature cues.

Examination of Figure 4 reveals that the Feature Control sham-lesioned pigeons, as well as the HF-lesioned pigeons when tested with feature, generally behaved as rational agents as previously predicted. This is reflected in their preference for the High-Variable 75% goal site over the Constant 100% reward site, and the Constant 100% goal site over the Low-Variable 25% reward site. This finding compares well with previous avian work suggesting no evidence for HF-control of non-spatial behavior (Coppola et al., 2014; Fremouw et al., 1997; Hampton & Shettleworth, 1996; Kahn & Bingman, 2009). Under the feature conditions of this dissertation, both Control sham-lesioned and HF-lesioned pigeons acted as rational agents when reward discrimination was based on feature. This result directly contrasts other operant studies involving visual cues that suggest pigeons behave in a more risk-averse (Hamm & Shettleworth, 1987; Menlove et al., 1979) or risk-prone manner (Essock & Reese, 1974; Lagorio & Hackenburg, 2012; Smith et al., 2017; Young, 1981). Follow-up studies should investigate how changing the feature-quality of specific goal sites, such as different food items, would impact variable or constant reward discriminations in homing pigeons (Coppola et al., 2014; Kahn & Bingman, 2009). While the current dissertation study did not use preferred or non-preferred food items, these reward qualities could be determined for individual birds and used during future follow-up studies. This additional characteristic of goals would enable a deeper understanding of how the avian hippocampal formation may encode feature-quality of food rewards that are unpredictably available. Based on work from Zentall's lab (e.g., Zentall, 2017), I would expect pigeons to perform suboptimally and not as rational agents when making risk-based discriminations based on their preferred or non-preferred food items.

Results of the current study provide strong evidence to support a significant effect of HF lesions on the Space task. Displaying results from the end of training, as originally predicted, Figure 5A demonstrates a significant difference in 75% High-Variable first choices between Control sham-lesioned and HF-lesioned spatial birds. Compared to the 100% Constant bowl (Figure 5B), Space Control sham-lesioned birds were more likely to choose the longer-term, more rewarding, but riskier variable option, while Space HF-lesioned animals were not. Additionally, Figure 5E also showcases a significant difference between Space Control sham-lesioned and Space HF-lesioned birds regarding incorrect first-choices. Space Control sham-lesioned animals were more likely to choose correct locations, whereas Space HF-lesioned pigeons made many more errors. This finding is not surprising and is consistent with many bird studies that show HF-lesion, spatial-learning deficits in remembering the location of food goals (Clayton & Krebs, 1995; Colombo & Broadbent, 2000; Hampton & Shettleworth, 1996; Lormant et al., 2020; Shiflett et al., 2003; Smulders & DeVoogd, 2000; Strasser & Bingman, 1999).

As predicted, results emerging from Figure 5 suggest that the Space HF-lesioned birds were less likely to choose variable-bowls (75% and 25%) overall in comparison to Space Control sham-lesioned pigeons. The data of Figure 5F, along with Figure 5A, suggest that the Space HF pigeons were less likely to direct their choices toward the riskier/variable options in comparison to the Space Control sham-lesioned pigeons. This result compares well with Scarf et al.'s (2014) study that demonstrated that hippocampal-lesioned pigeons, unlike intact pigeons, were impaired in their ability to use reward-outcomes based on specific probabilities in an operant task. These results are also consistent with previous studies related to goal-directed, spatial behavior that suggested rodents with inactivated hippocampi routinely seek out stable, reliable, and constant reward-related outcomes compared to variable or risker options, a choice presumably supported by the striatum (Mizumori et al., 2004; Mizumori et al., 2009; Mizumori & Tyron, 2015; Wiener, 1993). Previous mammalian studies have shown that when the hippocampus in rodents is damaged, more habitual behaviors that are "inflexible" to new information emerge (Hirsch, 1974; Johnson et al., 2007; Packard & McGaugh, 1996; Palombo et al., 2015; Regier et al., 2015; Yin & Knowlton, 2004) and that the striatum is sensitive to reward values (Mizumori et al., 2004). However, recent developments also suggest that the mammalian (Jeong et al., 2018; Jin & Lee, 2021; Jung et al., 2018; Sosa and Giocomo, 2021; Wood et al., 2000) and avian hippocampus (e.g, Kahn & Bingman, 2009; Siegel et al., 2005) may be sensitive to reward properties within a spatial environment as well.

Past research also indicates that striatal lesions negatively impact spatial navigational abilities in rodents (Fouqet et al., 2013; Jacobson et al., 2012; Miyoski et al., 2012), and one immediate early gene (IEG) study conducted in domestic chicks found increased c-Fos expression in the medial striatum in birds trained to feature rather than spatial information (Mayer et al., 2016). In order to determine what role the avian striatum may play in reward values within a spatial context and to better understand the importance of the avian hippocampal formation in risk-reward discriminations, future studies should perform striatal lesions in homing pigeons in tasks similar to the current study, to offer a comparative analysis of what role each brain area may play regarding reward-based values in either spatial or nonspatial conditions. Due to the current study demonstrating that without an accessible avian HF it is difficult for pigeons to form differential risk-based associations based on spatial locations, additional studies are required to investigate how striatal lesions are involved in a similar task as the current study and to provide additional insight regarding the relationship between the hippocampus and the basal ganglia overall (Johnson et al., 2007; Mizumori et al., 2004; Mizumori et al., 2009; Mizumori & Tyron, 2015; Packard & McGaugh, 1996; Palombo et al., 2015; Penner & Mizumori, 2012; Retailleau et al., 2012; Yin & Knowlton, 2004).

In summary, in the non-spatial feature task, a functional avian hippocampus was not necessary to preferentially shift goal-directed behavior to differential reward sites based on outcome probability. By contrast, the avian hippocampus was clearly recruited in the spatial task, enabling fewer errors and more adaptive but riskier first choices. Additionally, the current study offers the important finding that in homing pigeons, spatial memory that captures the risk and reward properties of locations in an environment, and the decisions made based on that memory, involves the hippocampus, similar to what is seen in young children (Paulsen et al., 2012). These findings open some new areas of investigation into real-world goal-based decision-making where humans and other animals have to balance risk with reward in their behaviors (Sosa & Giocomo, 2021;Vonder Haar, 2020).

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APPENDIX A. FIGURES

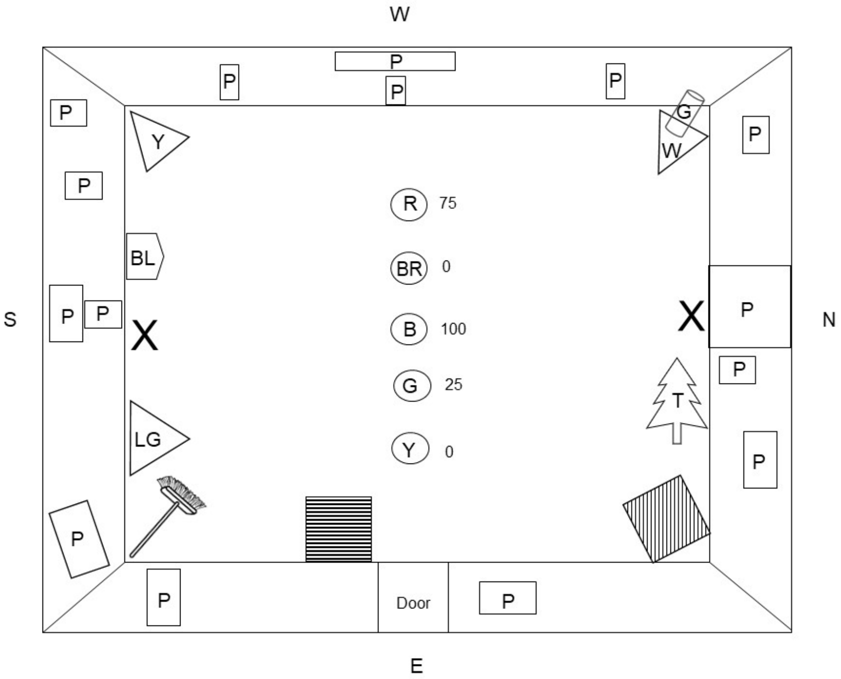


Figure 1. Feature Task Environment (vertical alignment depicted, horizontal alignment not shown). Two release sites (X) were used per alignment. Five bowls (B, blue; Y, yellow; BR, brown; R, red; G, green) were positioned in a vertical alignment in the center of the room. The vertical alignment position of any given bowl changed across sessions. Different probabilities of reward reinforcement were associated with specific colors: Constant - 100% (2 pellets X 4 trials per each trial type = 8 pellets available; combined total of 16 pellets available per session overall: 2 pellets X 8 trials), 0% (0 pellets), 0% (0 pellets), High-Variable – 75% (5 pellets X 3 trials = 15 pellets available), or Low-Variable – 25% (5 pellets X 1 trial = 5 pellets available). The two colors associated with variable outcomes were never presented together. Two-dimensional wall posters (P), various three-dimensional objects (broom; T, artificial tree; BL, black cone; G, green garbage can), three wooden triangles (LG, light green; Y, yellow; W, white), and two striped boards (black and white) provided a robust visuospatial environment.

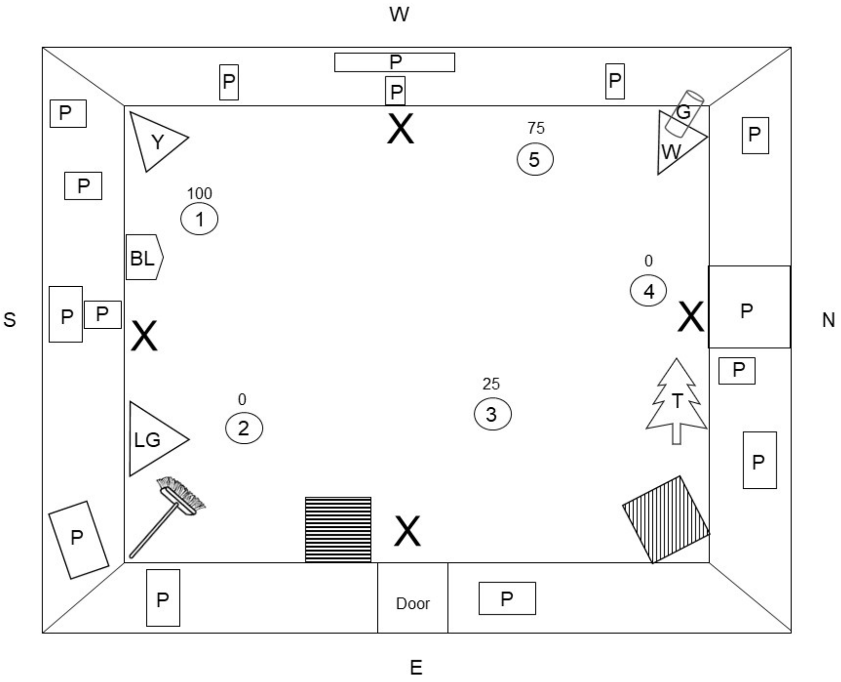
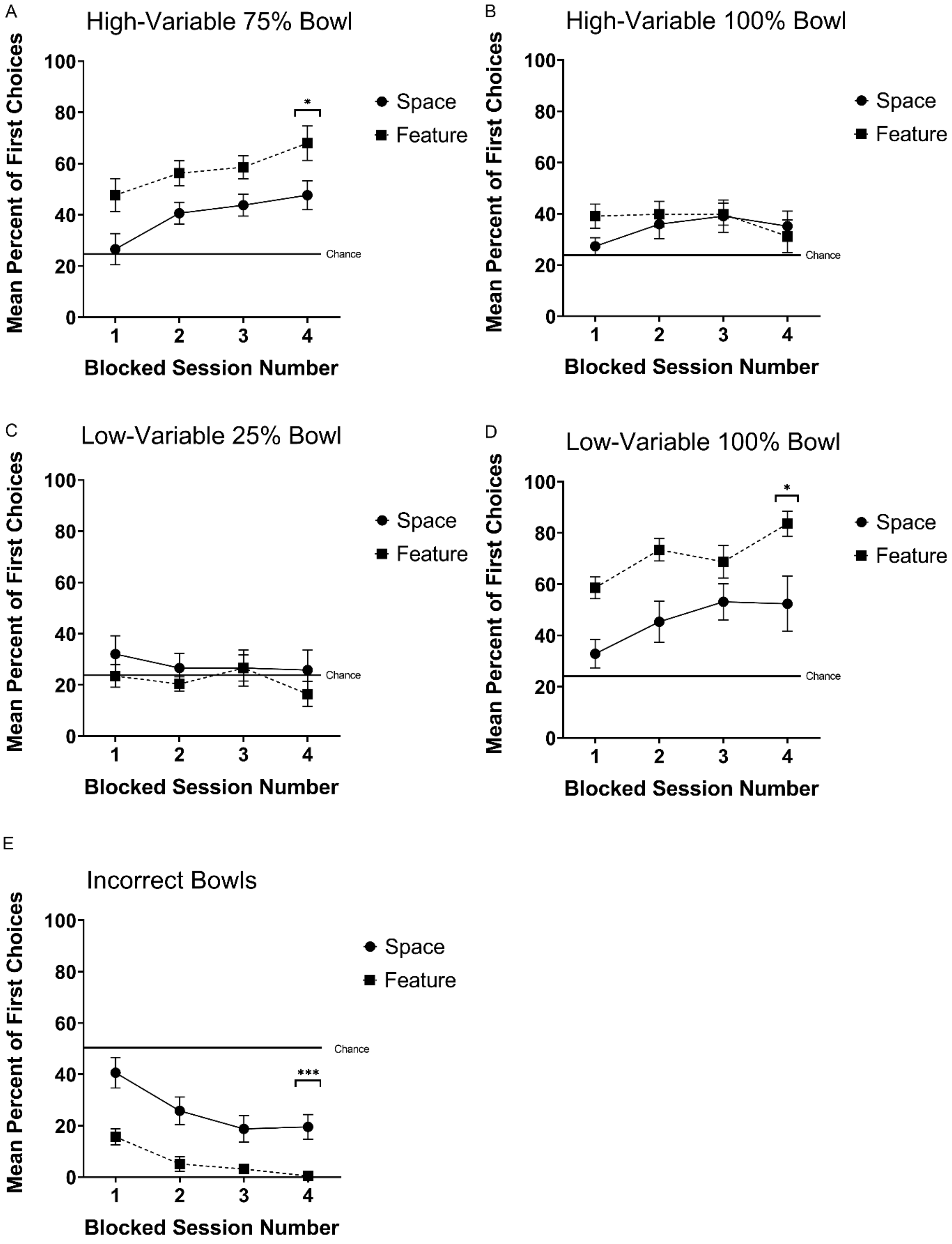


Figure 2. Space Task Environment. Four release sites (X) were used. Five different colored (blue, green, red, yellow, brown) bowls were positioned at distinct spatial locations (1, 2, 4, 5). Bowls changed position across sessions. Different probabilities of reward reinforcement were associated with specific spatial locations: Constant - 100% (2 pellets X 4 trials per each trial type = 8 pellets available; combined total of 16 pellets available per session overall: 2 pellets X 8 trials), 0% (0 pellets), 0% (0 pellets), High-Variable – 75% (5 pellets X 3 trials = 15 pellets available) or Low-Variable – 25% (5 pellets X 1 trial = 5 pellets available). The two variable goal locations were never available together. Two-dimensional wall posters (P), various three-dimensional objects (broom; T, artificial tree; BL, black cone; G, green garbage can), three wooden triangles (LG, light green; Y, yellow; W, white), and two striped boards (black and white) provided a robust visuospatial environment.


A
High-Variable 75% Bowl
Mean Percent of First Choices
Blocked Session Number
0
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60
80
100
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2
3
4
*
Chance
Space
Feature
B
High-Variable 100% Bowl
Mean Percent of First Choices
Blocked Session Number
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20
40
60
80
100
1
2
3
4
Chance
Space
Feature
C
Low-Variable 25% Bowl
Mean Percent of First Choices
Blocked Session Number
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Chance
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D
Low-Variable 100% Bowl
Mean Percent of First Choices
Blocked Session Number
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Chance
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Feature
E
Incorrect Bowls
Mean Percent of First Choices
Blocked Session Number
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60
80
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1
2
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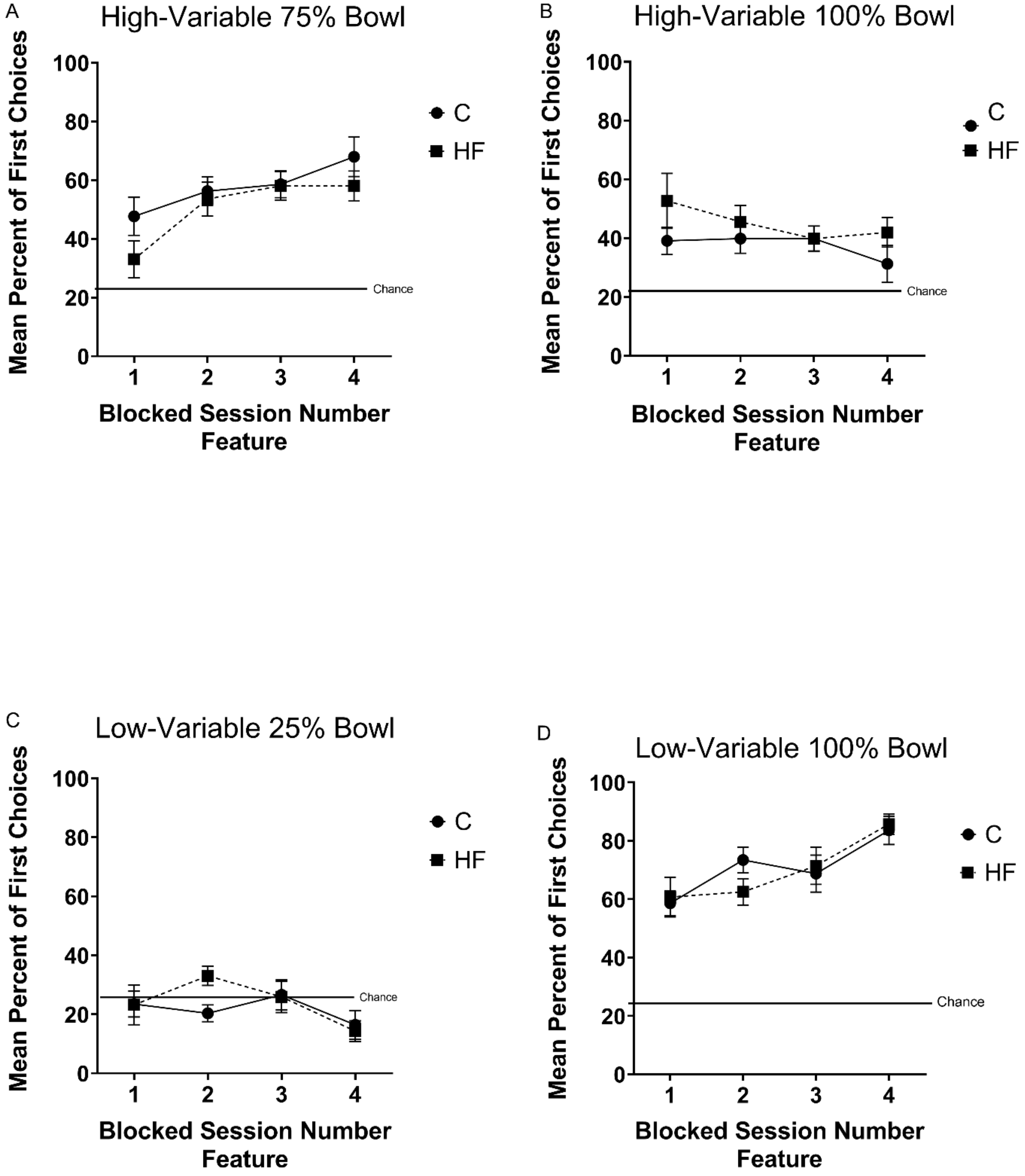
4
***
Chance
Space
Feature

Figure 3. Learning progressions of the probability discrimination task by Space (*n* = 8) and Feature (*n* = 8) control sham-lesioned birds. A) Mean percent of first choices to High-Variable 75% bowls during High-Variable sessions across four training blocks (Sessions 1-16), significant effect of group throughout training, * $p < 0.05$; Chance level was 25%. B) Mean percent of first choices to 100% Constant bowls during High-Variable sessions across four training blocks; Chance level was 25%. C) Mean percent of first choices to Low-Variable 25% bowls during Low-Variable sessions across four training blocks; Chance level was 25%. D) Mean percent of first choices to Constant 100% bowls during Low- Variable session across four training blocks, significant effect of group throughout training, * $p < 0.05$; Chance level was 25%. E). Incorrect learning progression of the probability discrimination task by Space and Feature birds. Mean percent of first choices to Incorrect bowls (colors or locations) during both High-Variable and Low-Variable sessions across four training blocks, significant group difference at the end of training, *** $p < 0.001$; Chance level was 50%. Error bars indicate *SEM*.


A
High-Variable 75% Bowl
Mean Percent of First Choices
100
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60
40
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4
Blocked Session Number
Feature
Chance
C
HF
B
High-Variable 100% Bowl
Mean Percent of First Choices
100
80
60
40
20
0
1
2
3
4
Blocked Session Number
Feature
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C
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C
Low-Variable 25% Bowl
Mean Percent of First Choices
100
80
60
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4
Blocked Session Number
Feature
Chance
C
HF
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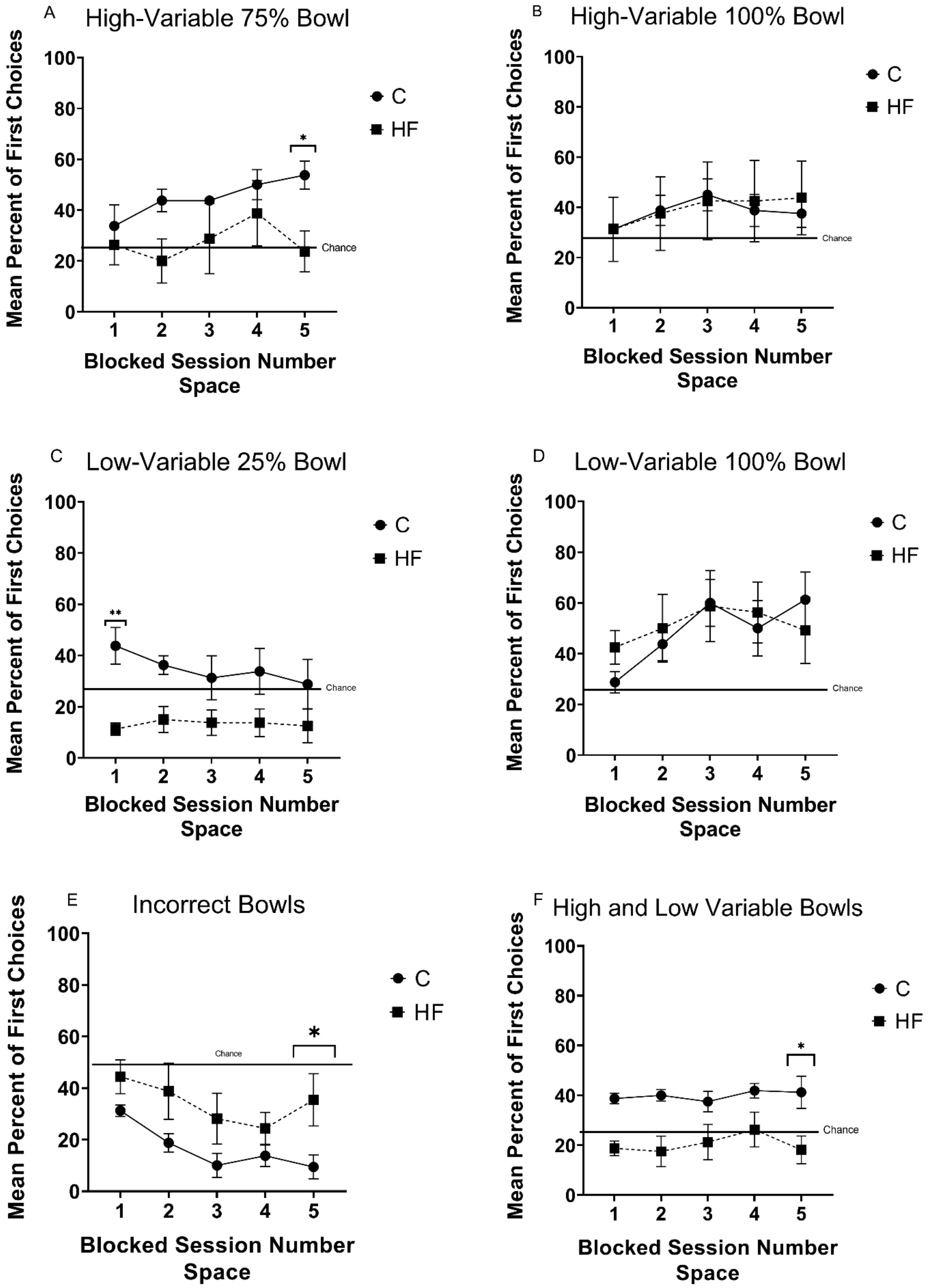
Low-Variable 100% Bowl
Mean Percent of First Choices
100
80
60
40
20
0
1
2
3
4
Blocked Session Number
Feature
Chance
C
HF

Figure 4. Learning progressions of the probability discrimination task by C (*n* = 8) and HF (*n* = 7) Feature birds. A) Mean percent of first choices to High-Variable 75% color bowls during High-Variable sessions across four training blocks (Sessions 1-16). B) Mean percent of first choices to Constant 100% color bowls during High-Variable sessions across four training blocks. C) Mean percent of first choices to Low-Variable 25% color bowls during Low-Variable sessions across four training blocks. D) Mean percent of first choices to Constant 100% color bowls during Low-Variable sessions across four training blocks. Chance level was 25% for all graphs. Error bars indicate *SEM*.


A
High-Variable 75% Bowl
B
High-Variable 100% Bowl
C
Low-Variable 25% Bowl
D
Low-Variable 100% Bowl
E
Incorrect Bowls
F
High and Low Variable Bowls
Mean Percent of First Choices
Blocked Session Number
Space
0
20
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1
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■ HF
Chance
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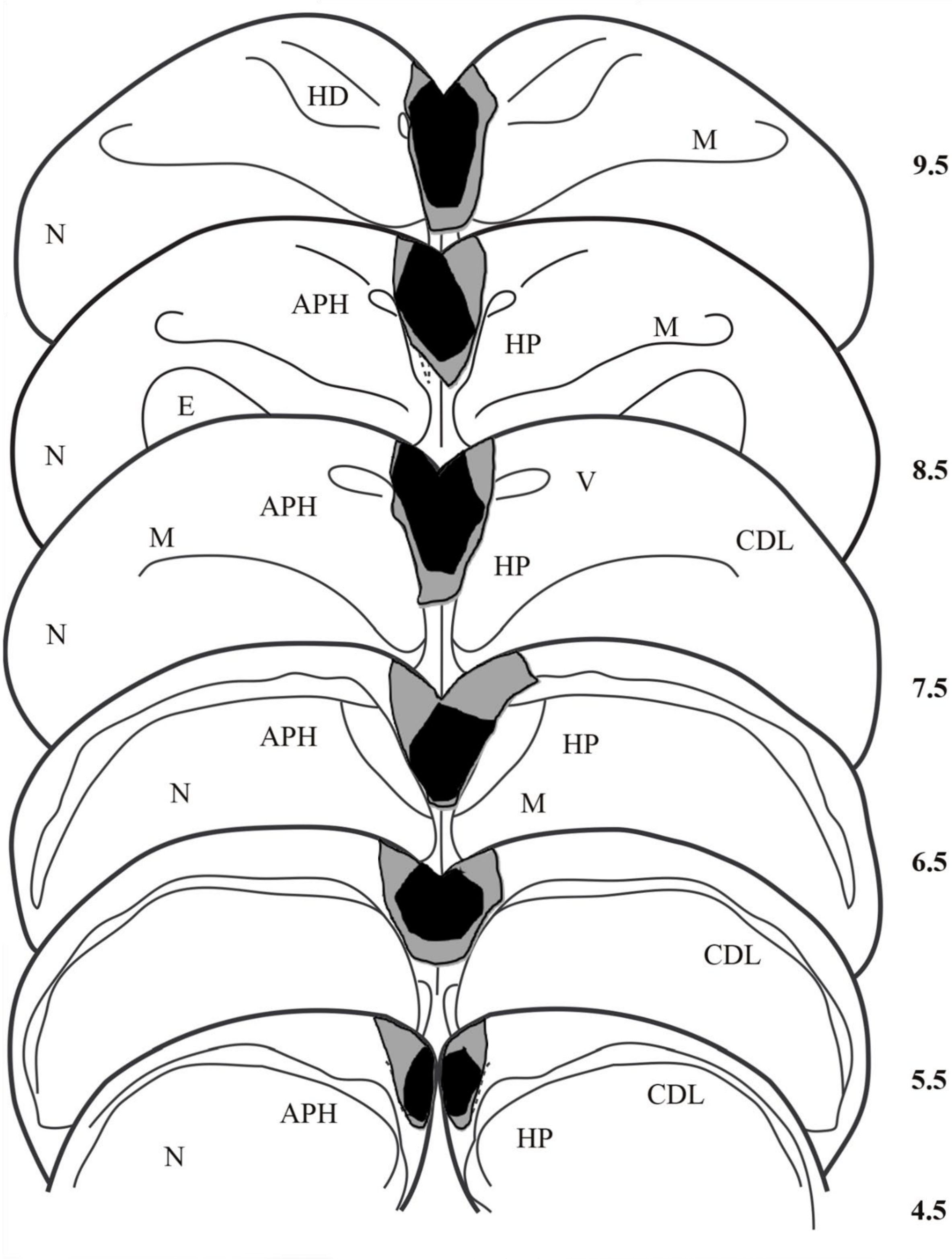
Figure 5. Learning progressions of the probability discrimination task by C ($n = 5$) and HF ($n = 5$) Space birds. A) Mean percent of first choices to High-Variable 75% bowl locations during High-Variable sessions across five training blocks (Sessions 1-20), significant group difference at the end of training, * $p < 0.05$; Chance level was 25%. B) Mean percent of first choices to Constant 100% bowl locations during High-Variable sessions across five training blocks; Chance level was 25%. C) Mean percent of first choices to Low-Variable 25% bowl locations during Low-Variable sessions across five training blocks, significant group difference at the beginning of training, ** $p < 0.01$; Chance level was 25%. D) Mean percent of first choices to Constant 100% bowl locations during Low-Variable sessions across five training blocks; Chance level was 25%. E) Mean percent of first choices to Incorrect bowl locations during both High-Variable and Low-Variable sessions across five training blocks, significant group difference at the end of training, * $p < 0.05$; Chance level was 50%. F) Mean percent of first choices to both High-Variable 75% bowl locations and Low-Variable 25% bowl locations overall across five training blocks, significant group difference at the end of training, * $p < 0.05$; Chance level was 25%. Error bars indicate *SEM*.


HD
M
9.5
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CDL
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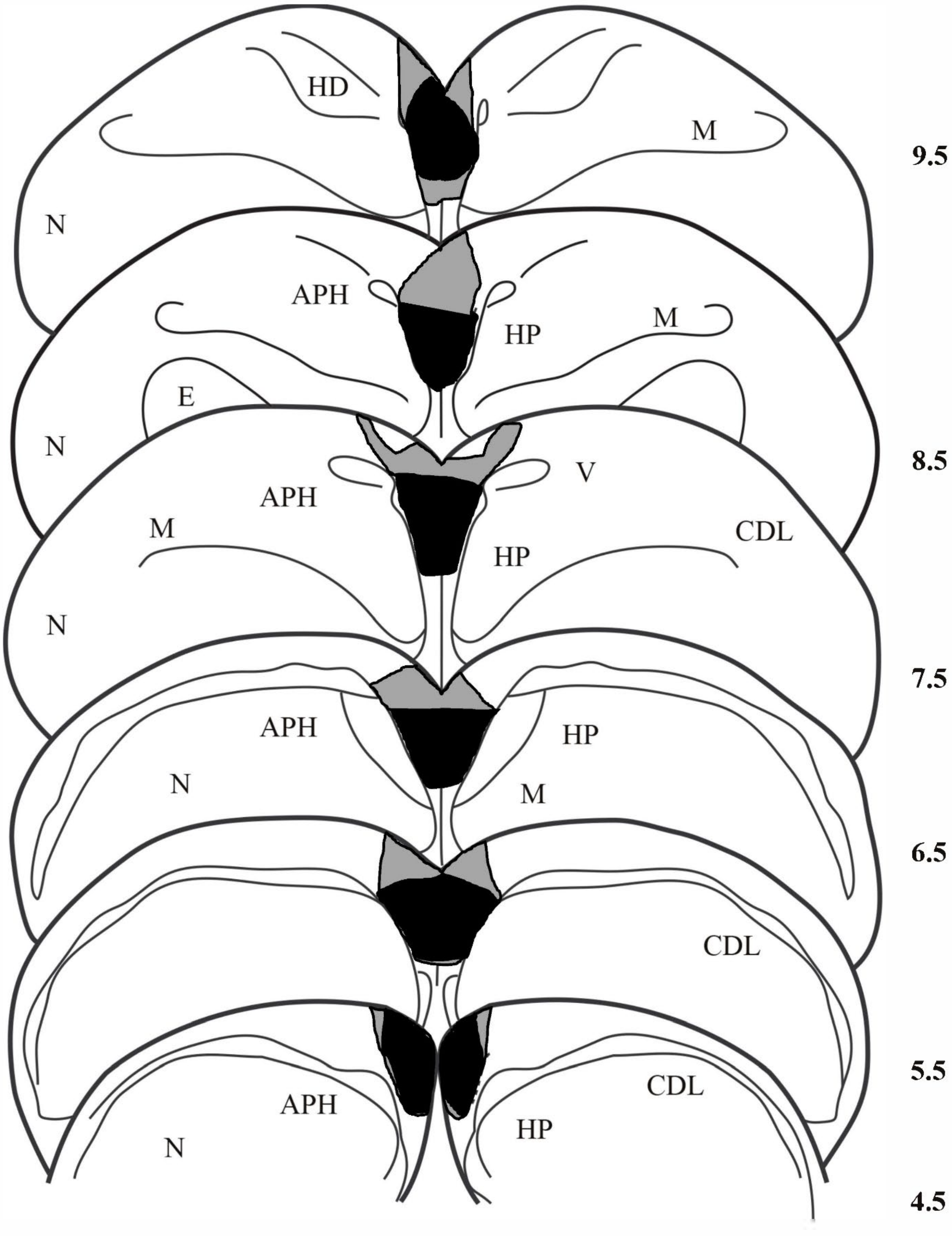
HP
N
M
6.5
CDL
5.5
CDL
APH
HP
N
4.5

Figure 6. Schematic coronal sections of the lesion reconstructions at 1.0 mm intervals from anterior (A 9.5) to posterior (A 4.5) according to the atlas of Karten and Hodos (1967), labeled according to the revised nomenclature (Reiner et al., 2004). A) Lesion reconstructions for HF-lesioned Feature birds. The black areas represent damage seen in at least six of the seven pigeons with bilateral HF-lesions. Gray areas represent damage seen in at least three of the seven pigeons with bilateral HF-lesions. Pigeons sustained extensive damage to the hippocampus. *APH* parahippocampus. *CDL* corticoid; *E* entopallium; *HD* hyperpallium densocellulare; *HP* hippocampus; *M* mesopallium; *N* nidopallium; *V* ventriculus.


HD
M
9.5
N
APH
HP
M
E
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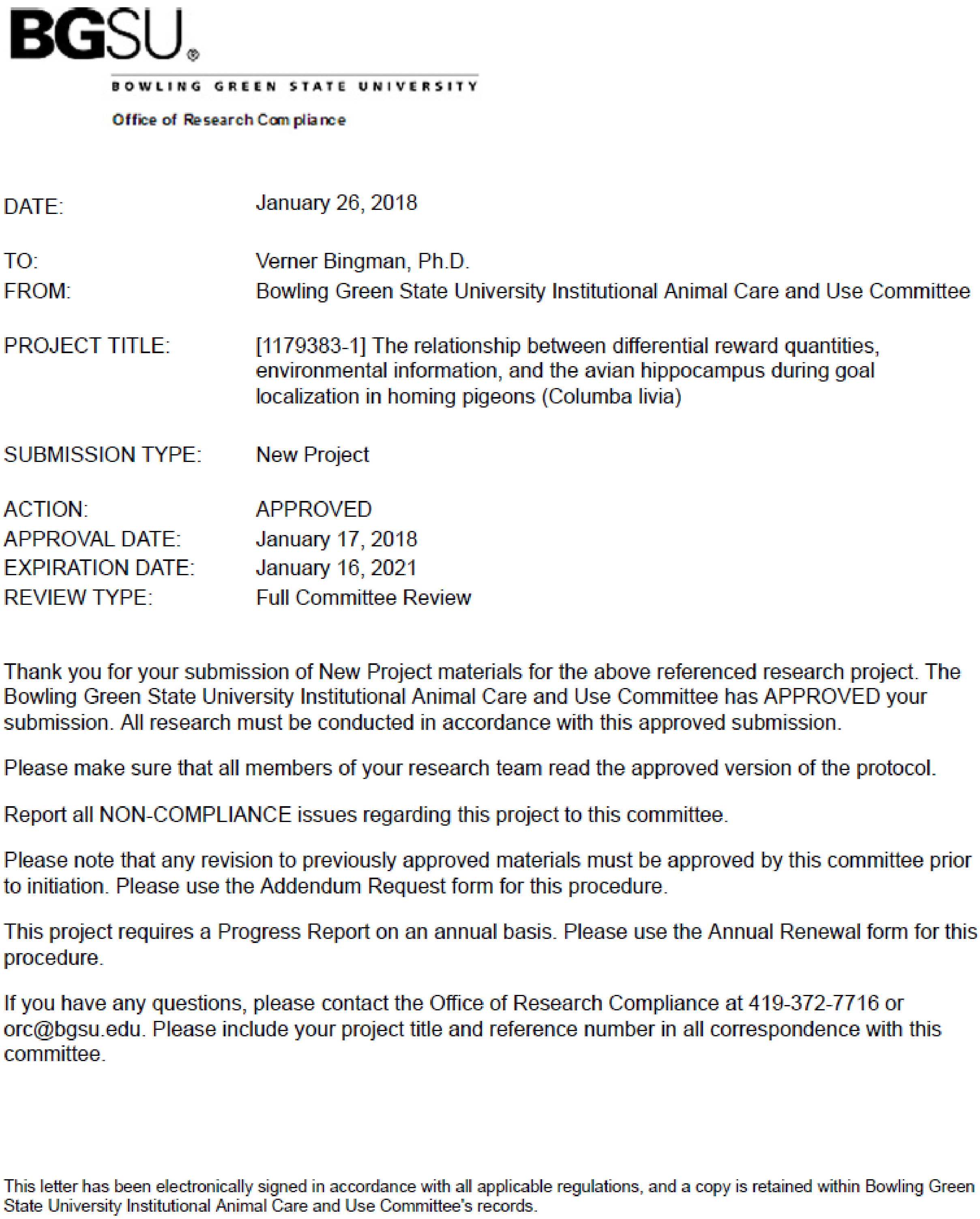
8.5
V
APH
M
CDL
HP
N
7.5
APH
HP
N
M
6.5
CDL
5.5
CDL
APH
HP
N
4.5

Figure 7. Schematic coronal sections of the lesion reconstructions at 1.0 mm intervals from anterior (A 9.5) to posterior (A 4.5) according to the atlas of Karten and Hodos (1967), labeled according to the revised nomenclature (Reiner et al., 2004). Lesion reconstructions for HF-lesioned Space birds. The black areas represent damage seen in at least four of the five pigeons with bilateral-HF lesions. Gray areas represent damage seen in at least two of the five pigeons with bilateral-HF lesions. Pigeons sustained extensive damage to the hippocampus. *APH* parahippocampus; *CDL* corticoid; *E* entopallium; *HD* hyperpallium densocellulare; *HP* hippocampus; *M* mesopallium; *N* nidopallium; *V* ventriculus.

APPENDIX B. IACUC APPROVAL LETTER



BGSU.
BOWLING GREEN STATE UNIVERSITY
Office of Research Compliance

DATE:	January 26, 2018
TO:	Verner Bingman, Ph.D.
FROM:	Bowling Green State University Institutional Animal Care and Use Committee
PROJECT TITLE:	[1179383-1] The relationship between differential reward quantities, environmental information, and the avian hippocampus during goal localization in homing pigeons (Columba livia)
SUBMISSION TYPE:	New Project
ACTION:	APPROVED
APPROVAL DATE:	January 17, 2018
EXPIRATION DATE:	January 16, 2021
REVIEW TYPE:	Full Committee Review

Thank you for your submission of New Project materials for the above referenced research project. The Bowling Green State University Institutional Animal Care and Use Committee has APPROVED your submission. All research must be conducted in accordance with this approved submission.

Please make sure that all members of your research team read the approved version of the protocol.

Report all NON-COMPLIANCE issues regarding this project to this committee.

Please note that any revision to previously approved materials must be approved by this committee prior to initiation. Please use the Addendum Request form for this procedure.

This project requires a Progress Report on an annual basis. Please use the Annual Renewal form for this procedure.

If you have any questions, please contact the Office of Research Compliance at 419-372-7716 or orc@bgsu.edu. Please include your project title and reference number in all correspondence with this committee.

This letter has been electronically signed in accordance with all applicable regulations, and a copy is retained within Bowling Green State University Institutional Animal Care and Use Committee's records.