The Neural Bases of Avian Visual Perception: Effects of Brain Lesions on Motion and Static Processing in Pigeons (*Columba livia*)

An honors thesis for the Department of Psychology

Gabriel R. Rothman

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Abstract

Previous research in pigeons has indicated that there might be functional segregations in visual processing between the anterior and posterior regions of the entopallium. We chose to investigate how these regions differentially process moving (dynamic) and non-moving (static) presentations of two human actions, Indian dance and martial arts. Six pigeons learned a go/no-go action categorization task, with reinforcement being conditional upon the presentation type. Three subjects received lesions to the posterior entopallium and three received lesions to the anterior entopallium. Posterior lesions impaired performance on both dynamic and static presentations, whereas anterior lesions had little, if any effect on performance in either presentation type. These results, along with prior studies, suggest that motion information is almost exclusively routed through the posterior entopallium, whereas static information is more widely distributed between both the anterior and posterior entopallium. Additionally, neither lesion had any detectable effect on categorization of these actions, which reveals that the entopallium as a whole is not critical for maintaining conceptual knowledge and is more important for building a percept of incoming visual information.

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Introduction

Birds have quite remarkable visual capabilities, as the need to evaluate far-off landscapes while flying requires high visual acuity. Mammals also possess powerful visual systems, and both classes rely heavily on the visual modality to navigate through their respective environments. There are marked differences between the brains of birds and mammals that make them neurally distinguishable, yet both are able to accomplish many of the same tasks. Therefore it is important to examine neurocognition in birds to better understand how different neural networks can solve the same problem, which can further our understanding of neural processing as a whole.

In the mammalian visual system, there are two parallel streams of visual processing that converge in the occipital lobe: the ventral stream predominantly processes static information, and the dorsal stream predominately processes motion information, which we will refer to as "dynamic" (Milner & Goodale, 1995). While there are a number of differences in the organization of mammalian and avian brains, some research has suggested that a similar system of parallel processing exists in birds. Pigeons (*Columba livia*) have been a popular model organism in cognition since the origins of behaviorism, and their visual capabilities are well characterized in a large body of literature, making them an ideal choice for studies of avian neurocognition.

Shimizu, Patton, and Husband (2010) reviewed a number of studies on avian neural organization, and their synthesis is highlighted here. The avian telencephalon is generally organized in clusters of neuronal nuclei, whereas the mammalian telencephalon is organized in a laminar cortex; however, avian neuronal nuclei are arranged in columns within the telencephalon, which mimics laminar processing to some degree. The primary visual processing route in birds is

the tectofugal pathway, which travels through the telencephalon from the retina to the optic tectum, nucleus rotundus (located in the thalamus), and finally the entopallium (the entopallium then projects to higher-level processing structures). Because the entopallium is a major point of convergence in the tectofugal pathway, it is an interesting target for examining visual processing.

Experiments investigating neural connectivity in the pigeon tectofugal pathway have found topographical projections that are highly conserved from lower- to higher-order structures. The nucleus rotundus contains a number of subdivisions that receive spatially distinct and parallel inputs from the optic tectum (Hellmann & Güntürkün, 2001), and these parallel projections are maintained even further in the entopallium (Benowitz & Karten, 1976). For example, projections originating in the most anterior portions of the optic tectum connect to the most anterior portions of the nucleus rotundus, which then connect to the most anterior portions of the entopallium (Fig. 1). This suggests that visual information might also be processed in distinct parallel pathways, with advances through structures representing higher-level processing of the individual streams (Fredes, Tapia, Letelier, Marín, & Mpodozis, 2010).

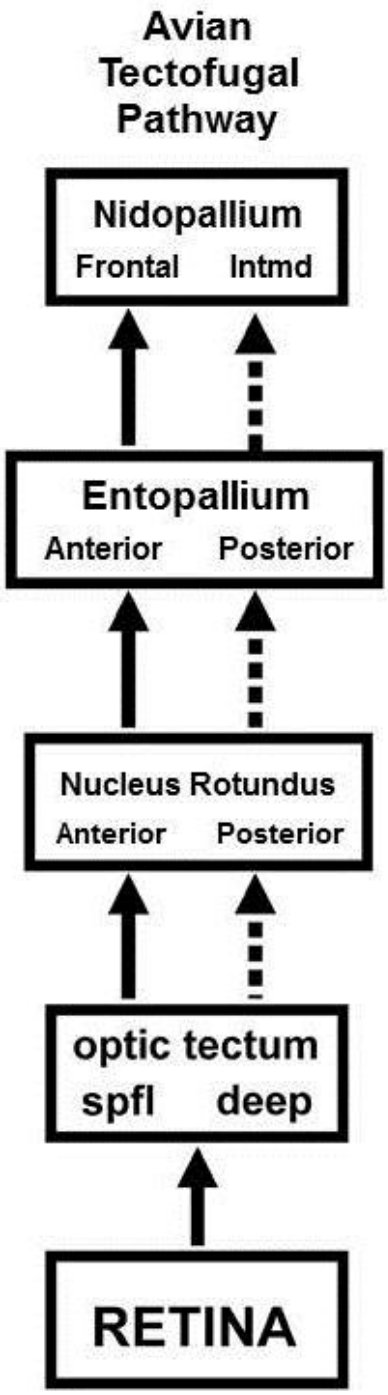

Figure 1: Adapted from Ngueyn et al. (2004) using updated terminology. A schematic representing segregated connectivity and functionality in the avian tectofugal pathway. Connectivity studies show highly conserved topographical projection, and it has been hypothesized that this spatial layout brings about parallel processing. Here, the arrows represent information passing through the pathway, with solid lines representing static information and dotted lines representing motion information. Spfl, Superficial; Intmd, Intermediate.

There are a number of cue subtypes that make up the larger categories of motion and static information. Motion information includes changes in edge position and shading, and static information includes form/shape (these terms can be used interchangeably as they characterize the same type of cue but tend to semantically match different types of stimuli better), color, and brightness. To understand which specific cues are processed in the tectofugal pathway, experimenters first used brain lesions to identify disruptions in perceptual processing. The first of these showed that lesions of the nucleus rotundus in pigeons caused deficits in color discrimination (Hodos, 1969), and follow-up studies showed both the nucleus rotundus and the entopallium to be necessary for processing color, pattern and brightness (Hodos & Karten, 1970; Hodos, Weiss, & Bessette, 1986; Bessette & Hodos, 1989; Watanabe, 1997)

To expand on the early lesion literature, experimenters utilized electrophysiological recordings to measure stimulus-specific responses in the pigeon brain. Wang, Jiang, and Frost (1993) recorded from individual cells in the nucleus rotundus, and found that cells in the anterior portion responded highly to manipulations of color and illumination, whereas cells in the posterior portion responded highly to motion. Additionally, Xiao, Li, and Wang (2006) took similar recordings in the entopallium and found a number of cell populations only in the posterior entopallium that respond to looming stimuli. Together, these studies suggest that there are separate anterior and posterior streams in the tectofugal pathway, with the anterior stream handling static information and the posterior stream handling motion information.

Lesions have recently resurged as a popular method in comparative cognition, although now experimenters aim for smaller targets to evaluate finer processing differences and complement the electrophysiology literature. Nguyen et al. (2004) performed selective lesions on either the anterior or posterior portion of the entopallium in a sample of pigeons, and tested all

subjects on both a dot motion task and static grading task. This study found a double dissociation: lesions in the posterior entopallium induced deficits in the motion task but not the static task, and lesions in the anterior entopallium induced deficits in the static task but not the motion task. These results reinforce the functional segregation hypothesis and suggest very strict divisions in processing. However, Cook, Patton, and Shimizu (2013) followed Ngueyn et al. by training pigeons on three complex visual tasks (target localization, object discrimination, and "where/what" identification), and found that lesions in the posterior entopallium induced deficits in portions of the tasks involving motion and static information (specifically form cues), whereas lesions in the anterior entopallium induced deficits in portions of the tasks involving static information (form and color cues). This study reveals an area of ambiguity concerning the processing of form information, which might be distributed across both the anterior and posterior portions of the entopallium.

We chose to continue this line of research by investigating form and motion in more complexity. The previous selective lesion studies used fairly simple stimuli (i.e. signals and shapes), which do not necessarily capture the richness of avian visual capabilities. Additionally, the previous stimuli tested components of visual perception, but did not capture cognitive behaviors directed at realistic representations, and therefore may not be accessing the full potential of the entopallium.

Experiments have shown avians to have an innate preference for biological motion, which seems to apply to both feature-specific point-light displays and detailed natural videos (Dittrich & Lea, 1993; Dittrich, Lea, Barrett, & Gurr, 1998; Vallortigara, Regolin, & Marconato, 2005). Early studies focused on stimuli of conspecific movement, but Asen and Cook (2012) extended the literature by showing that pigeons were highly capable of discriminating and

categorizing simple biological actions in many species. However, Asen and Cook's stimuli depicted the somewhat universal actions of walking and running, which could possibly be informed by pre-existing representations of conspecifics, so this experiment does not tap into birds' abilities to interpret entirely novel actions.

We chose to test the pigeons using stimuli and human figures performing either Indian dance or martial arts. These stimuli contain a great deal of complexity, as all four limbs of the figure are engaged in independent movements with little predictability, and they depict biological motion natural to the human body, making them an excellent set for examining more realistic processing in the pigeon entopallium. Previous research in our lab has already shown that pigeons can learn to categorize these actions (Qadri, Sayde, & Cook, 2014), so we adapted this stimulus set to be used in conjunction with a lesion procedure.

Our past research used both dynamic presentations (videos of the actions) and static presentations (still images of the actions) to train and test pigeons, and the different presentations were reinforced redundantly; the S+ action category was the same across the two presentation types, meaning that the birds didn't necessarily have to use both motion and static cues to solve the discrimination. Therefore, in the present study we made reinforcement conditional upon the presentation type, thereby requiring the birds to use both motion and static cues to solve the discrimination. We trained the birds on this discriminatory task, tested for categorization of the actions in the same manner as Qadri et al. (2014), performed selective anterior and posterior lesions, and then repeated all pre-lesion tests after the operations to evaluate lesion effects. Considering the previous research discussed above and the nature of our conditional task, we hypothesized that we would find a double dissociation; anterior lesions would disrupt

discrimination of static trials but not motion trials, and posterior lesions would disrupt discrimination of motion trials but not static trials.

Methods

Subjects

Eight adult male White Carneaux pigeons (*Columba livia*) were used in this study. The subjects are identified here by sequential numbering within their assigned lesion group (A1-4, P1-4). The birds were obtained from Palmetto Pigeon Plant (Sumter, SC), and were housed in individual cages in a colony room on a 12-h light/dark cycle. Grit and water were available ad lib in the colony room. All subjects had prior operant experience in an experiment studying object orientation, but were naïve in terms of action discrimination. The birds were maintained at 85% free-feeding weight throughout the duration of the experiment unless otherwise noted. All procedures were approved by the Tufts University Institutional Animal Care and Use Committee under the protocol M2014-62, and care was provided by the Tufts University Division of Laboratory Animal Medicine.

Apparatus

The pigeons were tested in an operant chamber equipped with a 28V overhead houselight, LCD computer monitor (NEC AccuSync LCD51VM-BK; Wooddale, IL; 1024 × 768 pixels), infrared touchscreen (Carroll Touch Systems, distributed by Tyco Electronics), and food hopper (Coulbourn Instruments, Whitehall, PA). The houselight was positioned centrally above the subject, and was constantly illuminated during behavioral sessions unless a timeout was issued. The computer monitor was placed 8 cm behind the touchscreen, and presented stimuli during sessions. The pigeons were then able to respond to the stimuli by pecking at the touchscreen. The food hopper was positioned centrally below the touch screen, and delivered mixed grain as reinforcement for correct responses.

Stimuli

The stimuli used here were originally created by Qadri, et al. (2014) and repurposed for the present experiment. They depicted either Indian dance or martial arts, and could be presented as a moving video (dynamic) or a non-moving image (static). Stimuli measured 400x400 pixels, and were presented for 20s. The actor in each stimulus was visually centered throughout the entire presentation.

Two variants of each action were initially used for acquisition, and two additional variants were introduced in the action categorization test. These variants represented the same human action, but contained different sets and combinations of poses. Additionally, each variant was rendered at 12 different perspectives, which were unique combinations of camera placement along three azimuth positions (x-axis), two altitudes (y-axis), and two distances (z-axis).

Dynamic stimuli varied continuously over an entire stimulus presentation at approximately 30 fps. Playback began at a random frame within the first 300 frames of a video, and after the 600^{th} (final) frame the video looped back to the 1^{st} frame. This method allowed us to control for any biases for specific portions of the sequence in a dynamic stimulus, while also limiting the impact of the cue that arises from the jump between the 600^{th} and 1^{st} frame. Static stimuli consisted of a single frame taken at random from any of the dynamic stimuli that were concurrently included in the stimulus set.

Session

A typical session consisted of 80 trials. Forty of these trials were assigned to dynamic presentations (20 S+/20 S-), and another 40 were assigned to static presentations (20 S+/20 S-). Within both dynamic and static presentations, subjects viewed each action variant an equal number of times, and perspectives were selected at random for each trial. 8 S+ trials in each

session were designated as nonreinforced probe trials, and thes were used to determine discrimination behavior without the interference of feeding. At some points in the experiment, double-length sessions were used to accelerate the acquisition process, and their use is specifically noted below. In these double-length sessions, the total number of trials was increased to 160, but all of the ratios between the actions, variants, presentation types, and reinforcements were maintained. Reinforcement assignment was conditional upon the presentation type: in dynamic presentations martial arts reinforced (S+) and Indian dance was punished (S-), whereas in static presentations martial arts punished and Indian dance was reinforced.

A go/no-go paradigm was used in this experiment. The pigeons initiated each trial by pecking once at ready signal (a centrally located white circle 2.5 cm in diameter). Next, one discriminative stimulus was presented for 20 s. Pecks to the touchscreen during S+ presentations were rewarded with 2.9 s of access to mixed grain via the food hopper on a VI-10 reinforcement schedule. Pecks to the touchscreen during S- presentations resulted in a variable dark timeout after the trial (0.5 s per peck). Additionally, all non-probe S+ stimuli were reinforced after the 20 s stimulus presentation and before the next stimulus to strengthen the association between discriminative stimuli and a food reward. This post-trial reinforcement always lasted 1s longer than the hopper time. Any changes to the above methods are explicitly noted in the following section.

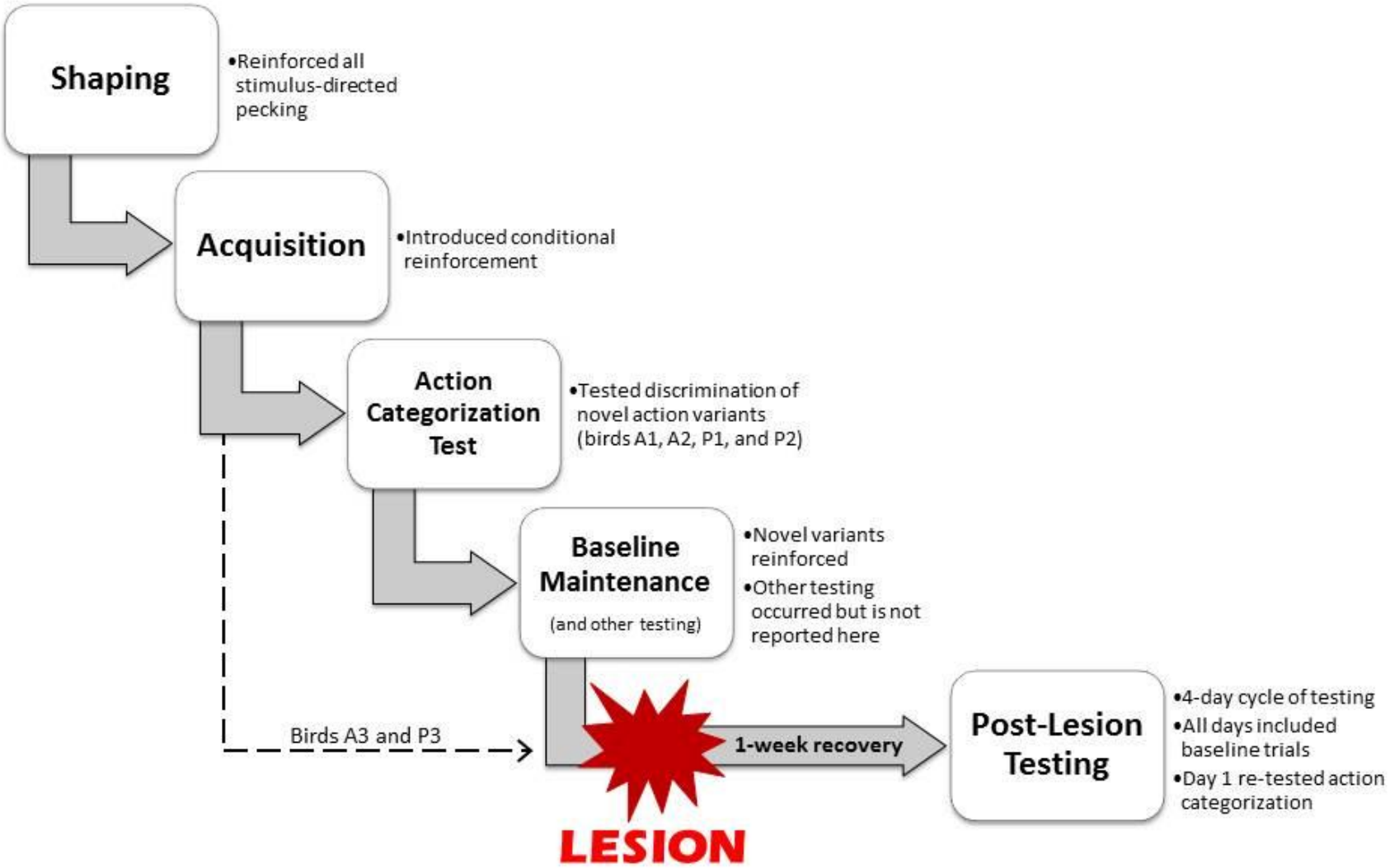

Figure 2: A visual representation of the experimental timeline. Birds were first shaped to the stimuli, and then trained on a conditional action discrimination task. Two of the birds (A3 and P3) learned the task slower than the others and were not able to be included in additional pre-lesion tests. The other four birds were tested on categorization of the action stimuli and a number of other analytical tests that are not reported here. All six birds then underwent lesion surgeries, were allowed one week to recover, and were then re-tested on all pre-lesion stimulus sets.

Experimental Timeline (Fig. 2)

Shaping

In a go/no-go task, the subject's decision is measured by the degree of response suppression (Peissig, Young, Wasserman, & Biederman, 2000); therefore, the birds were first shaped to respond to all stimulus presentations. The shaping sessions consisted of a typical set of stimuli, but all pecks to the display were reinforced. When the pigeons were judged to be pecking consistently throughout dynamic and static trials, they were moved on to acquisition.

Acquisition

In acquisition, punishment (dark timeout) was introduced on S- trials to train peck suppression. Acquisition of the discrimination was measured with Rho (ρ). Rho is a widely-accepted measure for acquisition in categorization tasks, and uses a normalized Mann-Whitney U test to determine the probability that responses to a given S+ trial are higher than responses to a given S- trial (Herrnstein, Loveland, & Cable, 1976). Rho was calculated using peck rate, a measure of all pecks over the course of a trial, and there were different Rho's for dynamic and static presentations within each behavioral session. Each bird was evaluated for acquisition individually, and was determined to have learned the task if both its dynamic and static Rho's were greater than or equal to 0.7 for the same three consecutive sessions. After meeting criteria, birds were continued on baseline sessions to maintain the discrimination or moved to other tests.

Any sessions that were not 90% completed were removed from analysis. After 50 sessions, post-trial reinforcement on S+ trials was removed to encourage more pecking during the trial. Two of the birds (A4 and P4) were unable to learn the discrimination under the conditional reinforcement setup and were removed from further analysis in the experiment. Bird P3 technically met the acquisition criteria after 55 sessions, but an examination of the underlying

peck rates revealed that this was due to erratic behavior and not systematically differential responding, so training was continued. Later in the acquisition phase, birds A3 and P3 were showing difficulty in learning the conditional discrimination, so double-length sessions were implemented beginning at session 75 to accelerate their learning. Shortly thereafter, bird A3 became inconsistent in its responding and was unable to complete full sessions, so at session 82 a number of parameters were changed for this bird only: the number of trials per session was reduced to 80, the variable dark timeout was decreased from 0.5 s per peck to 0.25 s per peck, the time of food availability was increased from 2.9 s to 3.1 s, and the post-trial reinforcement was reintroduced. These changes for bird A3 were maintained throughout the rest of the experiment.

Categorization Test

After reaching acquisition criteria, birds A1, A2, P1, and P2 were tested for their ability to categorize novel variants of the trained actions. Categorization sessions were nearly identical to acquisition, but an additional eight trials (4 S+/4 S-) were added to test for discrimination of the two variants that were not yet introduced (88 total trials). Half of these additional trials were designated to each novel variant (novel 1: 2 S+/2 S-, novel 2: 2 S+/2 S-). There were equal numbers of both dynamic and static presentations of the new variants, and all of these test trials used the most frontal, centered, and neartest visual perspective. Each bird received four sessions of categorization testing.

Next, the novel variants were integrated into baseline testing. These post-test baseline sessions were nearly identical to the acquisition sessions, except they now tested an equal number of all four variants (while maintaining equal S+/S- and dynamic/static presentations).

Additionally, all possible visual perspectives of all four variants were now tested. Other tests were conducted during this baseline period but are not reported here.

Lesion

The lesion groups were assigned based on performance during acquisition. It was reasoned that because there was such a small sample of birds and the lesion itself is a rather high-cost procedure, non-random assignment balancing task performance between the groups would be more suitable than random assignment in determining the effects of selective entopallial lesions.

The pigeons were anesthetized using ketamine (40 mg/kg of body weight) and xylazine (10 mg/kg of body weight) delivered sequentially and intramuscularly, and were then placed in a stereotaxic apparatus. Stereotaxic coordinates for the anterior and posterior entopallium were determined from the accepted stereotaxic atlas of the pigeon brain (Karten & Hodos, 1967). The anterior entopallium was targeted at A10.5, L6.0, V8.5, and the posterior entopallium was targeted at A8.5, L5.5, V10.5. A small drill was used to create precise holes in the skull, and an insulated electrode was inserted through these holes to the appropriate coordinates. A current of 1mA was then administered through the electrode for 20 seconds. Finally, the head was closed with a medical adhesive, and the birds were given one week of recovery time to ensure their health was stable before proceeding with post-lesion behavioral tests. During recovery, the pigeons had ad lib access to food for the first day of recovery, and were then reduced to a typical feeding schedule to restore 85% free-feed weight.

Post-Lesion Testing

After recovery the lesioned pigeons were tested on a four-session block. The first session in the block was identical to an action categorization session; the initial baseline variants were

tested in both reinforced trials and nonreinforced probes, and the novel variants were only tested as nonreinforced probes (88 total trials). The other three sessions in the block also tested the baseline variants as both reinforced and nonreinforced, and included other tests that will not be reported or discussed here. However, since all post-lesion trials included baseline trials, that portion of the data is reported here. Each bird received three iterations of the cycle, for a total of three categorization sessions and 12 baseline sessions post-lesion per bird. At the conclusion of post-lesion testing in the action discrimination task, the birds were moved to other tests. They will be euthanized and evaluated for brain damage via histology in the next two months.

Results

Analysis 1: Baseline performance

Acquisition

Acquisition progress for each individual bird is shown in Figure 3. Six of the eight birds trained with the conditional action discrimination were able to learn the task. Two subjects (A4 and P4; data not shown) were unable to learn the task and removed from further analyses.

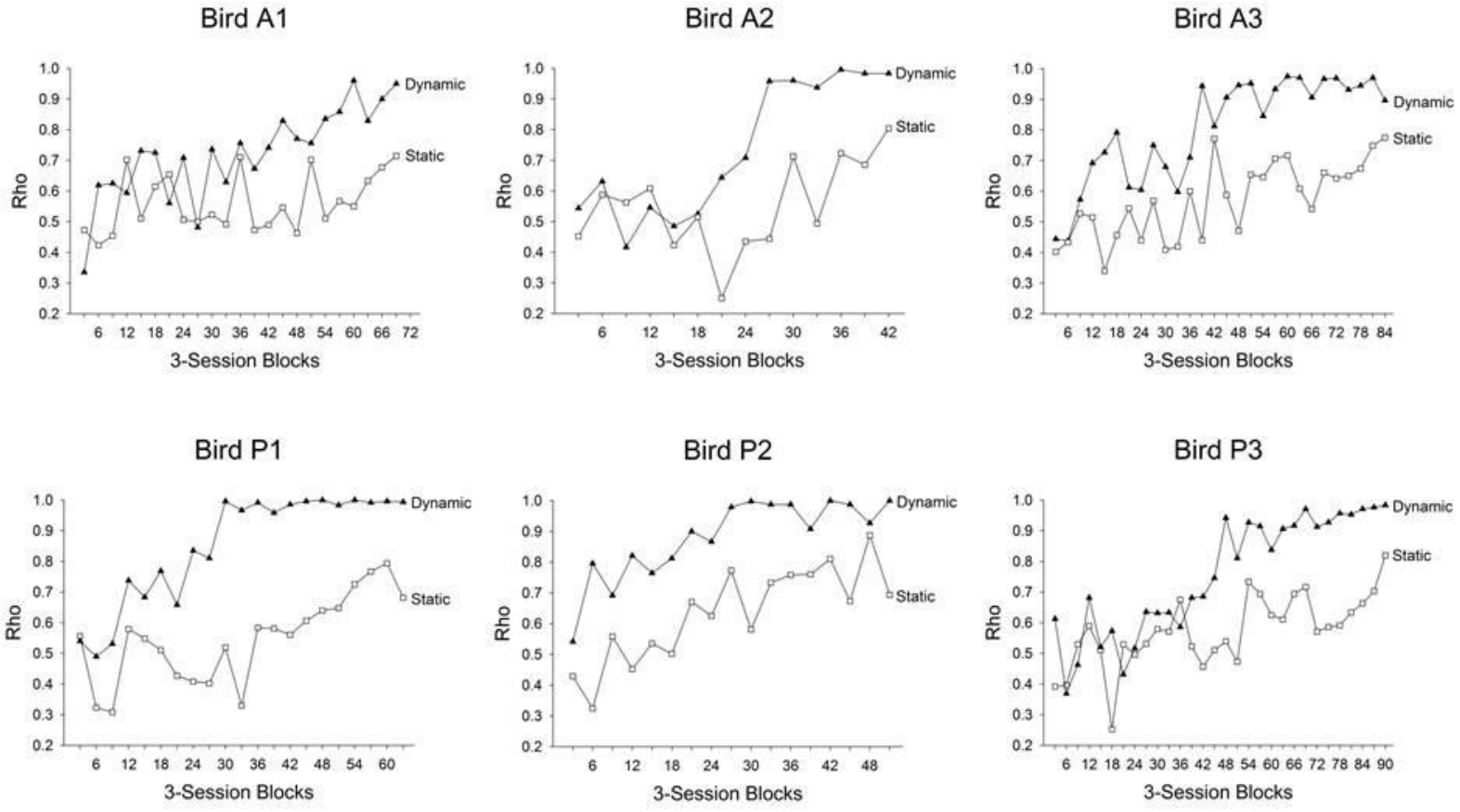

Figure 3: Acquisition progress in the six birds that learned the task. Birds assigned to the anterior lesion are in the top row, and birds assigned to the posterior lesion are in the bottom row. The session at which each bird met the acquisition criteria are as follows: A1, 67; A2, 41; A3, 83; P1, 57; P2, 48; P3, 88

Post-lesion

After the lesion, many of the birds recovered task performance quickly. Therefore, to best capture the effects of the lesion on cognitive performance, we compared only the last four sessions of pre-lesion testing to the first four sessions of post-lesion testing (equivalent to one post-lesion testing cycle). Although Rho was a suitable measure of discrimination in the larger acquisition data set, it is based upon ranked data and is therefore more likely to fall on certain values in smaller samples, so it was less ideal here. We instead used discrimination ratio (DR), which is defined as the measure of average responses on S+ trials divided by the sum of average responses on S+ and S- trials (within each session). In a large data set Rho and DR would converge, but in a smaller data set such as this, DR is a more sensitive measure and was therefore a more suitable tool for detecting lesion effects. Additionally, in an effort to better sample the pigeons' responses, here we used an adjusted peck rate to calculate DR instead of the typical peck rate used for Rho in acquisition. Responses were measured by the rate of pecking before the first reinforcement was administered (pre-reinforcement peck rate), and this effectively removed the interference of feeding on response measurements, allowing the data set to be expanded to all trials within the designated temporal range.

A mixed design ANOVA comparing lesion condition (anterior vs. posterior, between-subjects), presentation type (dynamic vs. static, within-subjects), and lesion phase (pre- vs. post-lesion, within-subjects) showed a main effect of presentation type ($F(1,4) = 32.903$, $p = 0.005$), and an interaction effect of lesion condition*lesion phase ($F(1,4) = 8.050$, $p = 0.047$).

Because we found a main effect of presentation type, we determine that our task was really a combination of two related sub-tasks, so we performed post-hoc mixed design ANOVA's within each presentation type comparing lesion condition and lesion phase. In

dynamic presentations we found an interaction effect of lesion condition*lesion phase ($F(1,4) = 27.212$, $p = 0.006$), whereas in static presentations there were no significant findings. These results indicate that the posterior lesion induces a significant decrement on dynamic trials relative to the anterior lesion, and that neither lesion has an effect on static trials. Individual t-tests were performed within each bird to examine lesion-induced decrement by presentation type but there were no significant findings.

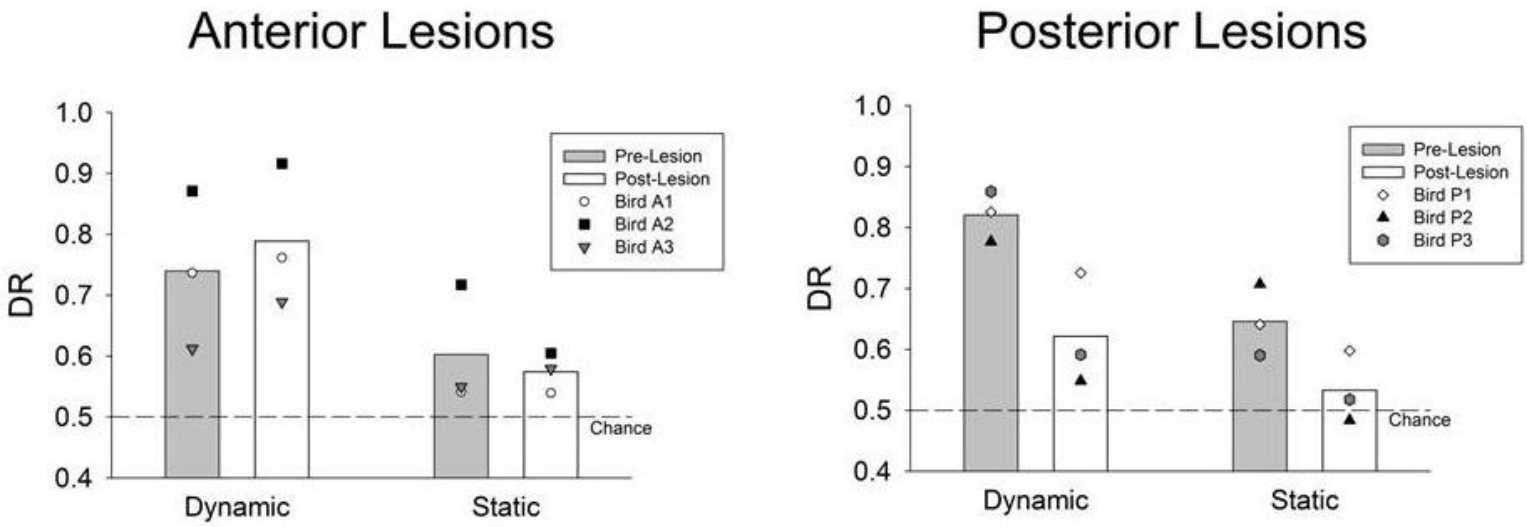

Figure 4: Effects of the lesions on discrimination of the familiar variants, comparing the last four pre-lesion sessions and the first four post-lesion sessions. Overall, the anterior lesions have no effect on performance in either presentation type. The posterior lesion does induce significant decrement in dynamic presentations (lesion condition*lesion phase interaction, $p = 0.006$). Although there is no significant effect of either lesion on static presentations, all three birds in the posterior lesion condition show numerical decrement, indicating a trending effect.

Past literature has reported that lesioned subjects recover task performance post-lesion, but authors have not reported on this phenomenon in detail, so we tracked recovery post-lesion to more fully understand the effects of entopallial lesions. It was difficult to examine this information statistically for a variety of reasons, so a recovery criterion was introduced: a bird was considered to have recovered to pre-lesion performance during post-lesion testing within a given presentation type when their DR (calculated with pre-reinforcement peck rate) was greater than 95% of their average DR over the last 10 pre-lesion sessions. In this analysis, each bird had its own individualized recovery criteria for each presentation type. Table 1 shows the post-lesion session number at which performance returned to pre-lesion levels based on these criteria.

Table 1: Session at which discrimination of baseline discrimination returned to pre-lesion levels (NR=never recovered).

a. Anterior lesion birds

	Dynamic	*Static*
A1	2	2
A2	1	10
A3	1	1

b. Posterior lesion birds

	Dynamic	*Static*
P1	4	1
P2	NR	NR
P3	NR	NR

Analysis 2: Categorization with novel exemplars

Pre-Lesion

To confirm that the pigeons were able to categorize the actions, we tested novel variants and examined transfer of performance to these unfamiliar and untrained stimuli. We used DR here because the data sets were again substantially smaller than acquisition. Additionally, because the trials of interest (categorization test trials) were non-reinforced probes, we calculated DR by total pecks/trial (peck rate). We analyzed the birds' responses to novel variants for above-chance performance (chance = 0.50 DR), and generalization decrement in comparison to nonreinforced probes of the familiar variants.

One-sample t-tests comparing performance on novel variants against chance determined that the birds were indeed performing above chance on the categorization test in both dynamic ($t(3) = 10.996$, $p = 0.002$) and static ($t(3) = 6.894$, $p = 0.006$) presentations. To analyze the presence of decrement due to generalization, we conducted a mixed design ANOVA comparing lesion condition, presentation type, and variant type (familiar vs. novel, within-subjects), and this test showed only a main effect of presentation type ($F(1,2) = 53.525$, $p = 0.018$). There was a trending main effect of variant type ($p = 0.091$), but it should be noted that a descriptive analysis of the data reveals this trend to be likely due to improved performance on the novel variants and not decrement (Fig. 5). Therefore, we concluded that the birds had learned to categorize novel action exemplars, and moved on to the next phase of the experiment.

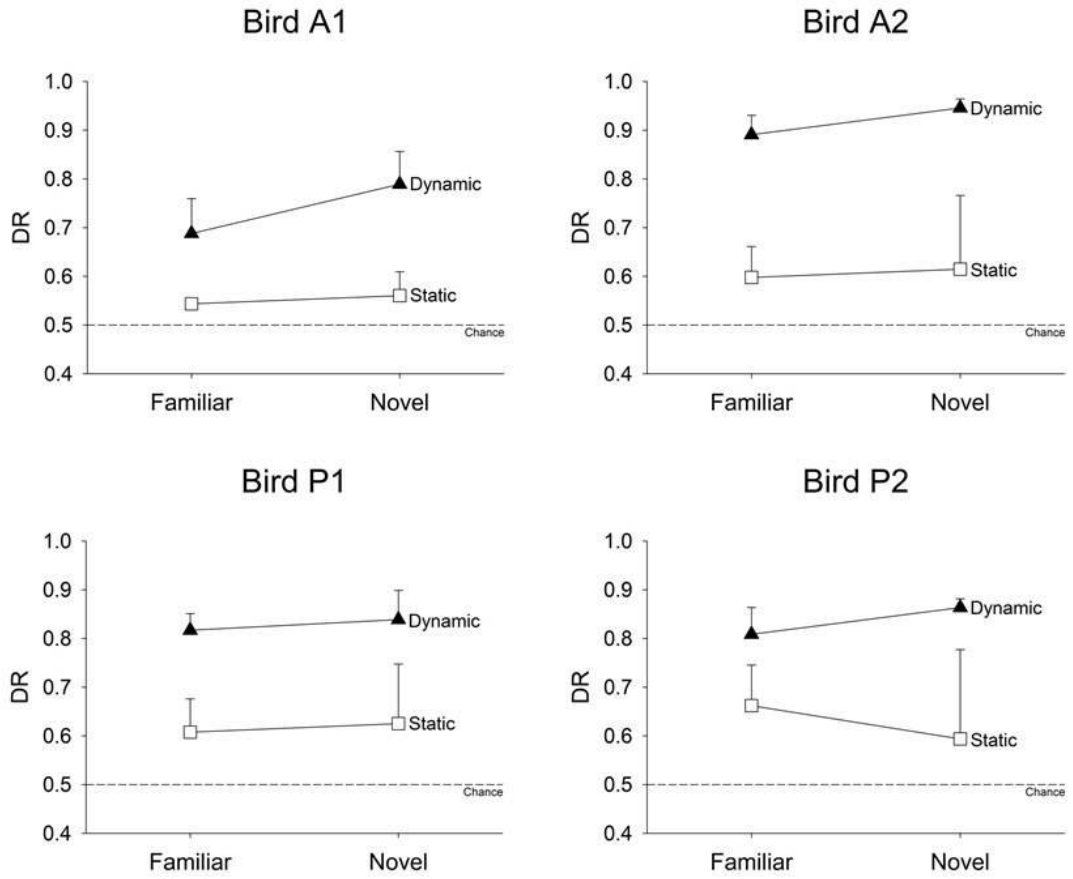

Figure 5: Transfer of task performance from familiar to novel action variants pre-lesion. No statistical analyses indicated that the birds showed any generalization decrement in transferring discrimination.

Baseline maintenance

After the categorization test, the novel variants were added to the set of reinforced trials for all sessions between the end of the categorization test and the lesion procedure. We decided after this fact and before the lesion that we would repeat the categorization test post-lesion to test lesion recovery and differential effects on perception and categorization (see below). However, if the birds showed learning of the novel variants as reinforced exemplars pre-lesion, this would affect any conclusions from this test because to the pigeons, the novel variants would be equivalent to the familiar variants for all intents and purposes. Therefore, we examined pre-lesion learning of the novel variants. Here, an increase in DR over time would indicate an increasing level of differential responding and therefore learning of the stimuli as reinforced exemplars. Since the novel variant trials were now being reinforced, DR was calculated using pre-reinforcement peck rate to best represent responding.

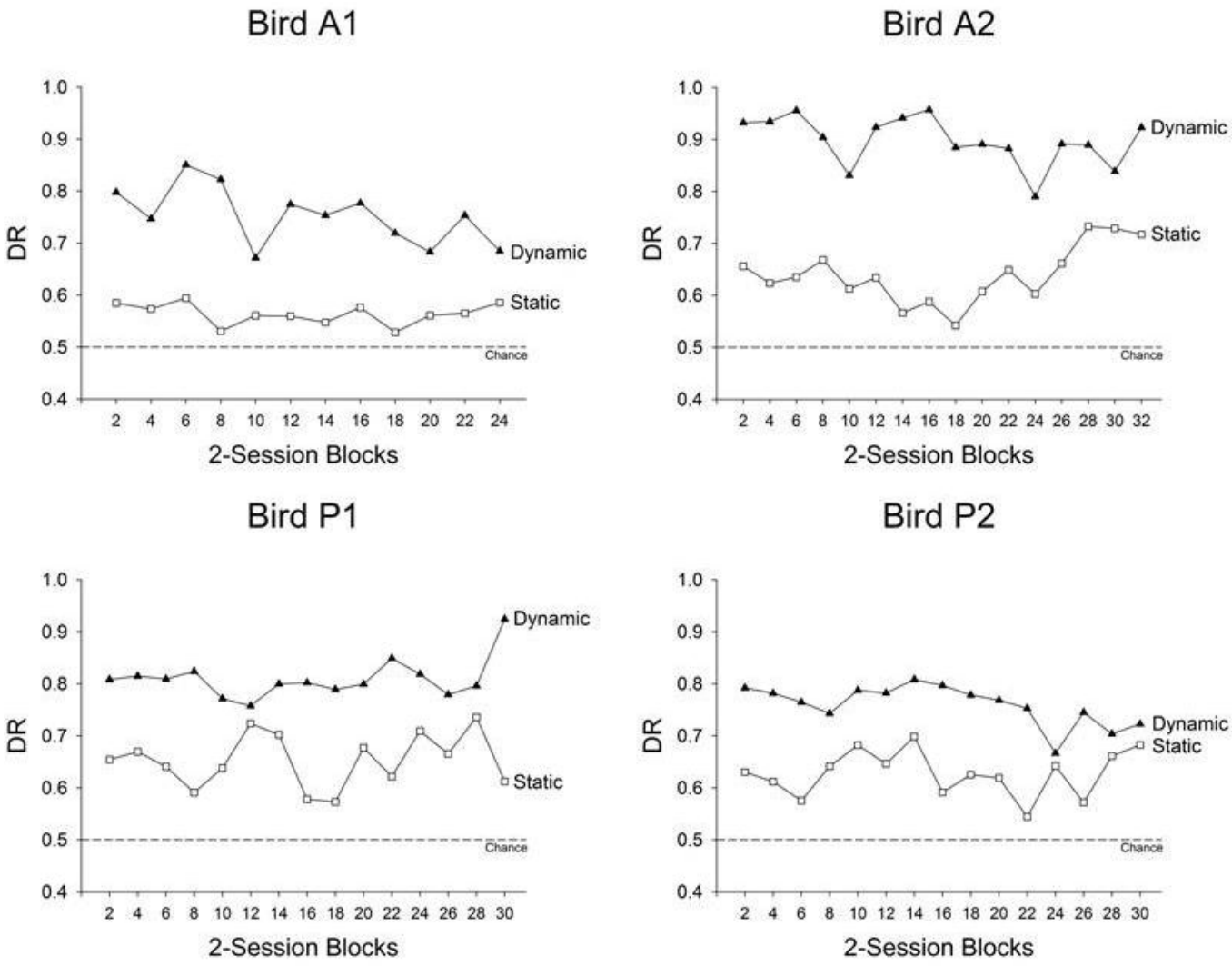

Figure 6: Performance on reinforced novel variants between the beginning of reinforcement and the lesion. Upward trends would indicate learning of the stimuli, but no such trends are clear in any of the birds. However, because there was basically no decrement during the transfer, this may have been due to a ceiling effect.

A regression analysis comparing this DR with presentation type (fixed factor), subject (random factor), and session number (covariate) showed a significant main effect of presentation type ($F(1,67.588) = 235.640$, $p < 0.001$) and a significant interaction of presentation type*session (F (1,46.068) = 14.232, $p < 0.001$). The estimate of difference due to presentation type was 0.226 ($p < 0.001$), and the estimate of difference due to the interaction was -0.003 ($p < 0.001$). The interaction effect indicates that performance on dynamic and static trials becomes mores similar over time, but this does not necessarily confirm or refute learning of the novel variants.

A descriptive analysis of the data revealed varying changes over time by bird, with no clear learning effects overall (Fig. 6). It is possible that birds A2 and P2 learned the novel variants in static presentations, since their static DRs increase slightly over time. These birds (along with A1) also showed a slight decrease in their dynamic DR, and it is less clear what might be causing this because continued reinforcement should maintain high discriminative responding. The action categorization test was reintroduced post-lesion as planned, although the uncertainty of our learning detection should be kept in mind when considering post-lesion effects on the categorization test.

Post-Lesion

We first evaluated performance on the action categorization test within only post-lesion sessions to evaluate how well the birds transferred discrimination to novel variants after the lesion. This analysis was very similar to the evaluation of the categorization pre-lesion, and DR was calculated using the standard peck rate measure. This analysis assumes that the birds did *not* learn the novel variants pre-lesion. One-sample t-tests comparing categorization performance against chance showed performance to be significantly above chance in both dynamic ($t(3) = 5.104$, $p = 0.015$) and static ($t(3) = 3.715$, $p = 0.034$) presentations. To analyze the presence of generalization decrement, we conducted a mixed design ANOVA comparing lesion condition, presentation type, and variant type and only found a significant main effect of presentation type ($F(1,2)=26.779$, $p=0.035$). Therefore there was no change in categorization behavior as a result of the lesion.

We next examined the effects of the lesion categorization performance. A mixed factors ANOVA comparing lesion condition, presentation type, lesion phase, and variant type showed a

significant main effect of presentation type (F(1,2)=39.213, p=0.025), but no other noteworthy findings.

One of the intentions of reintroducing the categorization test post-lesion was to examine performance recovery (Fig. 7). A mixed design ANOVA comparing lesion condition, presentation type, lesion phase, variant type, and session showed a significant main effect of presentation type (F(1,2)=20.025, p=0.046), but no interaction of variant type*session (p=0.962) or presentation type*variant type*session (p=0.543), both of which would have indicated differences in recovery between familiar and novel variants. Therefore it can be concluded that there is no difference between recovery rates on familiar variants and novel variants post-lesion.

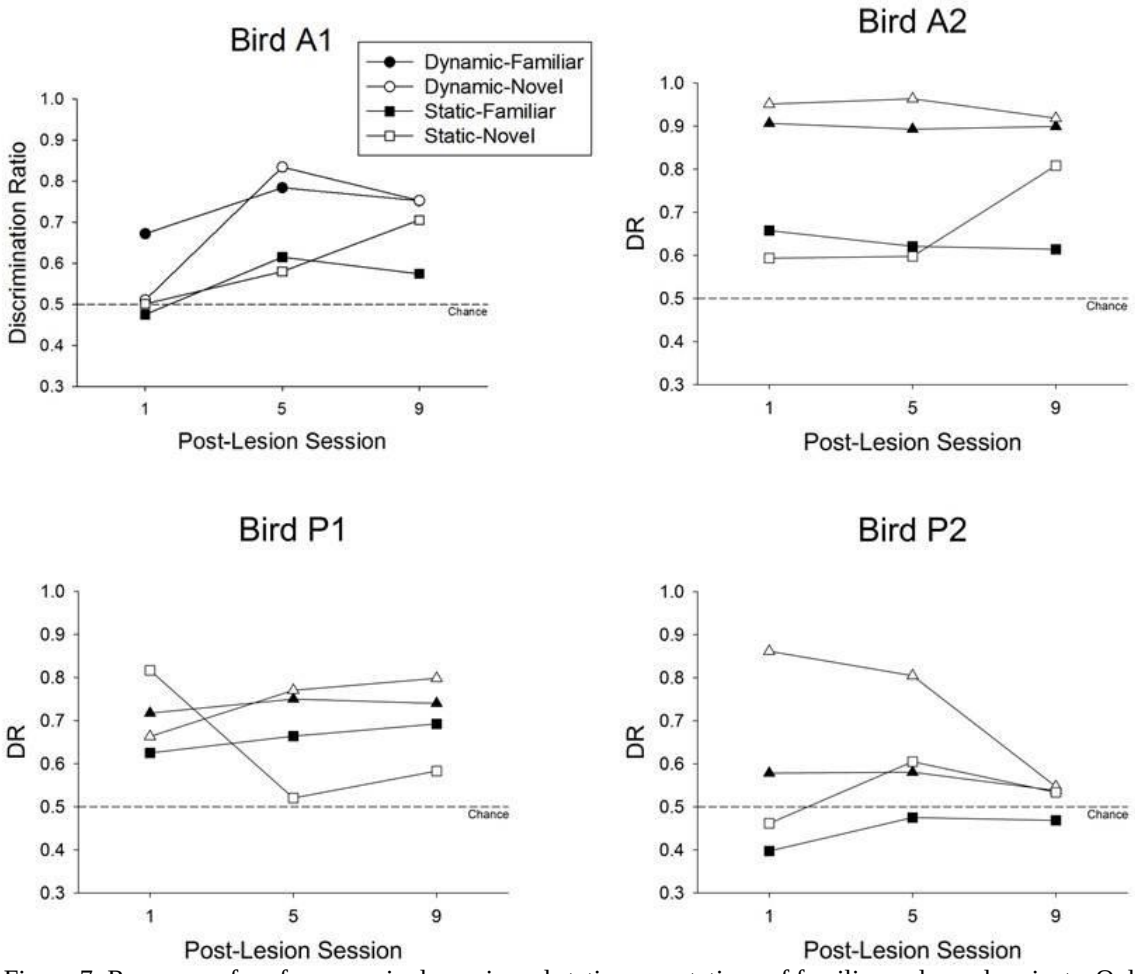

Figure 7: Recovery of performance in dynamic and static presentations of familiar and novel variants. Only the first session in each four-session cycle is represented on the x-axis, so each bird has accrued four times as many exposures to familiar stimuli as novel stimuli at each point. However, despite this difference in exposures there are no differences in patterns of recovery.

Discussion

Conditional Action Discrimination Task

Acquisition

Previous work in our lab has only tested a conditional action discrimination in birds that had first learned the task with redundant reinforcement (i.e. all Indian dance are S+, all martial arts are S-), and were subsequently given the conditional setup (unpublished results). This prior experiment is the only known study of its kind, so the acquisition portion of the experiment here was novel in that it trained a conditional action discrimination from the very beginning. With redundant training the birds learned to discriminate the actions quite well in about 12 sessions (Qadri et al., 2014), and then require approximately 30 sessions to re-learn the task with conditional reinforcement (unpublished results). However, with only conditional training the birds require 41-88 sessions to learn the task, and two of the subjects were not able to learn the task within the time constraints of our experiment. Therefore it is clear that redundant training facilitates learning of the conditional task. This is an excellent example of shaping; when subjects begin by focusing on one dimension of the task, it is easier to learn the second dimension than if both dimensions are introduced from the beginning.

Effect of Lesion on Action Discrimination

In the present study, posterior entopallium lesions were found to be generally more disruptive than anterior entopallium lesions, affecting both dynamic and static processing. Within dynamic presentations the groups do not differ pre-lesion, and there is a clear differential effect of the lesions, with the anterior birds showing no change and the posterior birds showing decrement. Within the static portion of the task, the groups again do not differ pre-lesion, and

while there are no statistically significant effects of the lesion, two of the three anterior birds show no decrement post-lesion, whereas all three of the posterior birds show some level of decrement, indicating a trending effect of the posterior lesion on static discrimination.

Our experiment builds on evidence from Nguyen et al. (2004) and Cook et al. (2013) showing a single dissociation between the anterior entopallium and processing of motion information. In all experiments to date, birds lesioned in the anterior entopallium never show any decrement on trials involving presentations of motion, and it is becoming clear that the anterior entopallium has a minimal (if any) role in motion processing. On the other hand, birds lesioned in the posterior entopallium always show decrement on dynamic presentations of many different stimuli, which establishes a strong link between this region and motion processing.

The picture of static processing in the entopallium is much less clear. There are a couple of reasons as to why there was not a significant effect in either group within the static portion of the task. Firstly, the samples were rather small, with only three birds per group. This created a limitation to statistical power, and it is possible that these findings are falling victim to a type II error due to high between-bird variability. Additionally, throughout the experiment there is a dynamic superiority effect (DSE; Qadri et al., 2014), where the birds show better discrimination on dynamic presentations than static presentations. As a result, pre-lesion static DR is not very high above chance. Given that DR, as a measure, generally bottoms out around chance (0.50), the birds did not have very much room to show decrement post-lesion, so it is possible that an effect of either lesion on static processing was masked in the statistical analysis by a floor effect. In fact, the two birds in the anterior condition that don't show decrement are barely above chance pre-lesion, and the one bird in this group that does show high static discrimination pre-lesion shows a large decrement post-lesion (Fig. 4). While we can't conclude anything definitive from

one subject's data, it is likely that there is undetectable effect of the anterior lesion on static performance, especially considering the previous literature that has repeatedly shown this brain region to be critical for static processing (Nguyen et al., 2004; Cook et al., 2013).

Despite our experiment's limitations, we can conclude that posterior lesions do have some impact on static discrimination, which builds on the results of Cook et al. (2013) and disagrees with the double dissociation found in Nguyen et al (2004). The stimuli used in Nguyen et al. were very simple dimensional stimuli that did not share any related features, specifically there were no common form cues. This was not the case in the Cook et al. experiment and in the present experiment, where there was shared form information between the dynamic and static stimuli, and this might relate to the involvement of the posterior entopallium in processing static information. Additionally, our reinforcement of dynamicity, or the presence of motion, did not seem to affect how static information was processed in the entopallium. We intended to make dynamicity a relevant cue for task performance with conditional training, but this did not produce a different result than Cook et al., which trained the dynamic and static task redundantly. Therefore it seems that attention to the presence or lack of motion does not impact which neural structures engage in visual processing, and it is more likely that cues and interactions between related features are hardwired through certain processing pathways.

There is still an unaddressed conflict in the entopallial lesion literature that our study does not address. In Cook et al. (2013), the same birds from the object discrimination were trained on a target localization task that used form as the salient cue. The localization task does not share any features with the object discrimination, so pairing this task to the object discrimination mimics the methods of Nguyen et al. (2004) in that there is a static task being tested alongside an unrelated motion task. However, Cook et al. found that posterior and anterior lesions disrupted

performance on the localization task, whereas Nguyen et al. found that only anterior lesions disrupted a static task. These results are difficult to make sense of, and our present findings do not add clarification. One possible hypothesis is that the overlap in cues within Cook et al.'s object discrimination task engaged the posterior entopallium in static form processing, which then somehow carried over to the target localization task. This would not have occurred in Nguyen et al. because there were no related cues among any of the stimulus sets. However, this hypothesis is pure speculation, and there is no component of our experiment that is comparable. Future studies should further investigate static processing in the entopallium, separating out form, color in different tasks.

Action Categorization Test

Pre-Lesion

In the pre-lesion action categorization test the birds show basically no generalization decrement, and transfer discrimination to the novel variants quite well. In fact, some of the birds even show an improvement in performance with the novel variants over the familiar variants; there is no theoretical explanation for this, and the trend is likely due to chance, but the fact that such a trend appears is an interesting marker of how well the birds performed on the categorization task.

There are a few different possibilities as to why the birds were able to transfer performance to novel variants so well. Categorization in pigeons has been shown to be dependent upon the number of trained exemplars, with more exemplars leading to less decrement (Bhatt, Wasserman, Reynolds, & Knauss, 1988). In the static task, a stimulus could be any one of 300 frames from any dynamic stimulus, meaning that there were 300 possible unique exemplars

from each viewpoint, variant, and action. This is a massive stimulus set, so it is no surprise that the birds were able to transfer to novel variants here.

In our dynamic task, there were only two variants of each action, but each variant was presented from 12 different perspectives, and these could be acting as additional, or at least partial exemplars. It is unclear whether pigeons integrate different perspectives of the same stimulus as one 3-dimensional unit; some studies have suggested that there is integration, but only when the rotation is viewer-centric (Cook & Katz, 1999; Cook, Shaw, & Blaisdell, 2001). When the rotation is object-centric, studies have shown mild, poor, and sometimes no integration, especially at farther angles from the trained viewpoint (Peissig et al., 2000; Spetch & Friedman, 2003). Our rotations were object-centric, so it is likely that the pigeons did not fully integrate all of the perspectives into one unit. However, there may have been some partial integration between similar viewpoints, so the different perspectives could be acting as partial exemplars—not entirely unique representations of the action, but different enough that they offer the bird some unique information about the action category. Additionally, it is probable that information in the static and dynamic portions of the task interacted because form cues were redundantly present, so static trials may have further strengthened dynamic discrimination, or vice versa.

Baseline Maintenance

After the action categorization test, the two novel variants were introduced into the set of reinforced stimuli. We then monitored learning of the novel variants between the beginning of novel variant reinforcement and the lesion and found mixed results. Some birds (A2, P2) showed slight upward trends in static DR, but overall there were no clear signs of learning in any of the subjects. Birds A1 and P2 also seemed to show a slight decline in dynamic DR, and it is unclear what might have led to this. It is somewhat strange that the birds don't show any signs of

learning because reinforcement typically increases differential responding to any stimulus that was previously non-reinforced. However, this finding can be explained by taking into account the complete lack of decrement in the categorization test. If the birds categorized so well that they flawlessly transferred to novel variants, they were also likely performing at their maximum discrimination level. Therefore it is likely that there was a ceiling on the DR measure, and this masked any learning of the novel variants.

Post-Lesion

After the lesion, the novel variants were removed from the set of reinforced stimuli and the action categorization test was reintroduced. Again, the birds generally showed no signs of decrement in comparison to baseline trials. Performance on all variants is very similar throughout the entire experiment, and therefore neither the posterior nor anterior entopallium is critical for categorization of human actions. This finding is important because it shows that categorization is not dependent on the entopallium, and it is more likely that the entopallium as a whole is far more important for processing incoming visual information rather than higher-level cognitive processes.

Recovery

Baseline performance

It was noted in Cook et al. (2013) that the birds recovered task performance shortly after the lesion procedure, so recovery was analyzed in more depth here to better understand how pigeons compensate for induced brain damage. In the anterior lesion group only bird A2 showed prolonged impairment, specifically in static discrimination. It could be suggested that this reveals a possible effect of the anterior lesion on static discrimination that was undetected by statistical

testing, but only one bird in the anterior group shows any issue with recovery, so if the anterior lesion did have any impact on static performance then it was mild. In the posterior lesion group, bird P1 showed brief but substantial impairment in the dynamic discrimination, and birds P2 and P3 never fully recovered in either the dynamic or static discriminations. This reinforces our conclusion that posterior lesions were overall more effective than anterior lesions in disrupting an action discrimination task.

Our recovery analysis of baseline trials is not based on statistics so it is not necessarily the most valid approach, but by using a fairly stringent criterion we were able to make reasonable approximations about how lesion effects changed over time. This analysis also circumvents some of the issues we ran into when analyzing overall post-lesion performance. As previously noted, static discrimination might be falling victim to a floor effect, making it more difficult to detect a lesion effect. However, by examining recovery we were able to show that, for some birds (notably P2 and P3), static discrimination remains consistently lower than pre-lesion performance for a prolonged period of time, and this sustained impairment suggests that there may have been a statistically undetectable effect of the posterior lesion on static discrimination.

Baseline performance compared to novel variants

Performance on the post-lesion categorization test was tracked over time and compared to baseline recovery to determine if there were differential recovery effects in these two stimulus sets. Statistical and descriptive analyses of the data show that there is no difference in recovery of performance in these two tests (Fig. 8). Even though there may have been undetectable learning of the novel variants pre-lesion, this finding shows that recovery of the task is category-wide and not stimulus specific. Over the course of post-lesion testing the birds accumulate exposures to the stimuli, and overall they receive more exposures to the baseline stimuli than the

novel variants. Therefore, if recovery was driven by re-learning of specific stimuli, then we would have seen much faster recovery in familiar variants than novel variants. However, this was not the case, and we can therefore conclude that the birds were instead recovering performance on the action discrimination task as a whole, and that categorization was the primary strategy for solving the discrimination.

General

Our results show that lesions to the posterior entopallium impair performance on an action discrimination task regardless of how the action is presented, and lesions to the anterior entopallium have a relatively mild effect. Experiments concerning entopallial lesions have now covered motion in the form of simple signal information (Nguyen et al., 2004), basic shapes (Cook et al., 2013), and complex organismal actions (present study), and all results have converged upon a functional segregation of motion processing in the entopallium, with the anterior region having no role whatsoever and the posterior region being an essential component.

Despite our contributions to the literature, static processing in the entopallium is still not well understood. This is partially because the static cues that have been studied thus far can be broken into at least two subcategories, color and form. The only selective entopallial lesion study to examine color processing found a dissociation between the anterior and posterior regions, with the anterior region being important for color processing and the posterior region being uninvolved (Cook et al., 2013), whereas there is discrepancy in the current body of research on form processing. Nguyen et al. (2004) found that, when discriminating between noise and graded patterns (systematically repeated form), the anterior region was a critical component and the posterior region was uninvolved. However, Cook et al. found in both a target localization task (also systematically repeated form when shape is the salient differentiating cue) and a shape

discrimination task that both the anterior and posterior regions of the entopallium play an important role in form processing. And finally, in the present study we found the anterior region to be relatively uninvolved, whereas the posterior region was likely involved at some level. Together, these studies indicate that form processing is widely distributed across the entopallium, and it is likely that slight differences in lesion targeting have major effects on the birds' ability to use form information.

Additionally, there are a number of nuanced differences in the tasks across these studies, and these may have a variety of effects on how the stimuli are processed in the brain. In Nguyen et al. (2004), the birds were only required to find the relevant patterns within noise, but were not required to make a decision about the nature of the patterns or differentiate between slightly different versions of the patterns. In Cook et al. (2013) and the present study, the birds were required to make a decision about the stimuli based on feature changes of the target stimuli. While these tasks attempt to evaluate the same cognitive processes, the decision making process in each is different and this may play into how particular brain regions are involved in solving the task.

In future experiments, it would be interesting to specifically investigate the interaction between dynamic and static cues. In the present study, form cues were inherently related to the dynamic cues and they likely interacted, but the directionality of this relationship is unknown. Jitsumori, Natori, and Okuyama (1999) showed that pigeons could transfer discrimination of dynamic conspecific action stimuli to still images of those same actions, so it is plausible that pigeons in our task used dynamic cues to inform static cues. A dynamic presentation is technically a sequence of still images, and all of the possible static form cues are contained within the motion information, so it is reasonable to hypothesize that form information can be

extracted from dynamic presentations, allowing dynamic trials to inform discrimination on static trials. This would also provide a logical explanation for why damage in a motion-processing center of the brain impairs performance on a static discrimination that is related to learned motion information.

In humans, there is some interesting evidence concerning transfer between motion and static information that relates to our study. A neuropsychological case study of a patient with hemianopia (partial blindness in half the field of vision) found that a lesion in the ventral extrastriate cortex selectively impaired the extraction of form information from motion information without disrupting static form perception or motion detection (Cowey & Vaina, 2000). This study is particularly interesting in the context of our experiment because the primate extrastriate cortex is thought to be analogous to the avian entopallium (Colombo, Frost, & Steedman, 2001). It is plausible that the posterior entopallium and the ventral extrastriate cortex are both responsible for bridging form and motion information, specifically in the direction of motion to static, making these regions essential centers for perceptual integration, and this comparison should be investigated.

The temporal arrangement of the experiments may also be a factor in determining which brain regions are involved in each task. Expectations have been shown to be an important component in determining neural processing (Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011), and from our observations in the lab, it is clear that pigeons are very good at forming temporal associations. In Nguyen et al. (2004), the birds were tested on the static and dynamic tasks on alternating days, so it is plausible that the birds in this study learned to predict which task they would see on a given day. These expectations may have modified how their brains handled each task, leading to a divergence in processing between the anterior and

posterior entopallium and a double dissociation. In the Cook et al. (2013) object discrimination task and the present study, all portions of the experiments were integrated in the same sessions (the pigeons saw both dynamic and static stimuli of all actions and variants in every session). Therefore there was much less predictability of presentation type on a trial-by-trial basis, and this may have contributed to the differing results, possibly by increasing engagement of the posterior entopallium.

Lesion methods are limited in that they can only show which processes are disrupted, and this disruption is used to infer something about the normal neurocognitive function of the targeted region. These procedures are useful in terms of understanding neurocognitive pathways, but do not necessarily prove that the targeted region responds to the stimuli. Other methods, such as electrophysiological readings and functional neuroimaging, can add more detail to our understanding of avian neurocognition. As noted in the Introduction, electrophysiological studies of the entopallium generally agree with the lesion literature. Neuroimaging, on the other hand, is a relatively untapped method in the realm of avian neurocognition. There are a number of studies that have used functional neuroimaging to examine songbirds concerning auditory processing and neural plasticity (Van Meir et al., 2005; Van der Linden, Van Meir, Tindemans, Verhoye, & Balthazart, 2004), but there have only been two published papers that used functional neuroimaging methods with non-songbirds, specifically crows (Marzluff, Miyaoka, Minoshima, & Cross, 2012; Cross et al., 2013). Given the wealth of information available on pigeon cognition, it would be very useful to integrate neuroimaging methods into future studies to better understand the neural bases of cognition. We are currently in the process of developing a positron emission tomography (PET) protocol, which we hope will further our understanding of

avian cognition by revealing patterns of neural activity associated with specific cognitive processes.

The present study is promising in advancing our understanding of avian neurocognition, but there are some major limitations that should be addressed. Given that our results differ from past experiments, it is possible that our task is not suitable for studying functional segregation in the entopallium. The conditional reinforcement was implemented with the goal of requiring attention to both motion and static cues, but it is possible that the pigeons only learned one set of cues, used this set to inform the other presentation type, and then learned to respond conditionally upon detection of motion in the display. This strategy would essentially erase the impact of conditional reinforcement, and we do not have a way to confirm whether or not this occurred.

Additionally, the consistently low discrimination on static presentations may make this task unsuitable for examining functional segregations in the entopallium. As mentioned previously, static discrimination was generally lower than dynamic discrimination, and this may have led to a post-lesion floor effect that masked any real decrement. Because this relatively low static discrimination is characteristic of the task, it might be that lesion effects on static processing are simply undetectable within our task, making it unfit for investigating differential processing in pigeons.

No histological analyses have been performed yet on the damaged tissue, so at this stage we cannot confirm that the lesions were administered in the intended locations, or that they were similar in their extent. This analysis is critical for finalizing the findings of the present study, and all conclusions discussed above must be considered tentative until such an analysis is completed. There was clearly a differential effect of the two attempted lesions, so our conclusions about the

differences in cognitive processing between the groups can be considered valid, but any attributions to a particular brain region or neural pathway must be considered indefinite.

However, we can draw on the literature to make some inferences about our lesions. In past entopallium lesion experiments (Hodos & Karten, 1970; Nguyen et al., 2004), there is typically a strong correlation between amount of neural damage induced and severity of performance impairment. The birds in this experiment show a variety of levels of impairment, exemplified by the wide variation in post-lesion decrement and recovery. Therefore, we can infer that the more highly impaired birds likely suffered from more neural damage, and vice versa. Again, the specificity of that damage is unknown, but the clear differential effects between the groups proves that there were two general types of lesions induced, and the damaged areas play very different roles in the perception of action.

References

Asen, Y., & Cook, R. G. (2012). Discrimination and categorization of actions by pigeons. *Psychological science*, *23*(6), 617-624.

Benowitz, L. I., & Karten, H. J. (1976). Organization of the tectofugal visual pathway in the pigeon: a retrograde transport study. *Journal of Comparative Neurology*, *167*(4), 503-520.

Bessette, B. B., & Hodos, W. (1989). Intensity, color, and pattern discrimination deficits after lesions of the core and belt regions of the ectostriatum. Visual Neuroscience, 2(01), 27-34.

Bhatt, R. S., Wasserman, E. A., Reynolds, W. F., & Knauss, K. S. (1988). Conceptual behavior in pigeons: Categorization of both familiar and novel examples from four classes of natural and artificial stimuli. Journal of Experimental Psychology: Animal Behavior Processes, 14(3), 219.

Colombo, M., Frost, N., & Steedman, W. (2001). Responses of ectostriatal neurons during delayed matching-to-sample behavior in pigeons (Columba livia). *Brain research*, *917*(1), 55-66.

Cook, R. G., & Katz, J. S. (1999). Dynamic object perception by pigeons.*Journal of Experimental Psychology: Animal Behavior Processes*, *25*(2), 194.

Cook, R. G., Patton, T. B., & Shimizu, T. (2013). Functional segregation of the entopallium in pigeons. *Philosophy (London, England)*, *130*, 59.

Cook, R. G., Shaw, R., & Blaisdell, A. P. (2001). Dynamic object perception by pigeons: Discrimination of action in video presentations. *Animal Cognition*, *4*(3-4), 137-146.

Cowey, A., & Vaina, L. M. (2000). Blindness to form from motion despite intact static form perception and motion detection. Neuropsychologia, 38(5), 566-578.

Cross, D. J., Marzluff, J. M., Palmquist, I., Minoshima, S., Shimizu, T., & Miyaoka, R. (2013). Distinct neural circuits underlie assessment of a diversity of natural dangers by American crows. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*(1765), 20131046

Dittrich, W. H., & Lea, S. E. (1993). Motion as a natural category for pigeons: Generalization and a feature-positive effect. *Journal of the experimental analysis of behavior*, *59*(1), 115-129.

Dittrich, W. H., Lea, S. E., Barrett, J., & Gurr, P. R. (1998). Categorization of natural movements by pigeons: Visual concept discrimination and biological motion. *Journal of the experimental analysis of behavior*, *70*(3), 281-299.

Fredes, F., Tapia, S., Letelier, J. C., Marín, G., & Mpodozis, J. (2010). Topographic arrangement of the rotundo-entopallial projection in the pigeon (Columba livia). *Journal of Comparative Neurology*, *518*(21), 4342-4361.

Hellmann, B., & Güntürkün, O. (2001). Structural organization of parallel information processing within the tectofugal visual system of the pigeon.*Journal of Comparative Neurology*, *429*(1), 94-112.

Herrnstein, R. J., Loveland, D. H., & Cable, C. (1976). Natural concepts in pigeons. Journal of Experimental Psychology: Animal Behavior Processes, 2(4), 285.

Hodos, W. (1969). Color discrimination deficits after lesions of the nucleus rotundus in pigeons. Brain, Behavior and Evolution, 2(3), 185-200.

Hodos, W., & Karten, H. J. (1970). Visual intensity and pattern discrimination deficits after lesions of ectostriatum in pigeons. Journal of Comparative Neurology, 140(1), 53-68.

Hodos, W., Weiss, S. R., & Bessette, B. B. (1986). Size-threshold changes after lesions of the visual telencephalon in pigeons. Behavioural brain research, 21(3), 203-214.

Jitsumori, M., Nakamura, N., & Wasserman, E. A. (2013). Discrimination of coherent and incoherent motion by pigeons: An investigation using a same-different motion discrimination task. *Behavioural processes*, *93*, 116-124.

Jitsumori, M., Natori, M., & Okuyama, K. (1999). Recognition of moving video images of conspecifics by pigeons: Effects of individuals, static and dynamic motion cues, and movement. *Animal Learning & Behavior*, *27*(3), 303-315.

Karten, H. J., & Hodos, W. (1967). Stereotaxic atlas of the brain of the pigeon (Columba livia).

Marzluff, J. M., Miyaoka, R., Minoshima, S., & Cross, D. J. (2012). Brain imaging reveals neuronal circuitry underlying the crow's perception of human faces. *Proceedings of the National Academy of Sciences*, *109*(39), 15912-15917.

Melloni, L., Schwiedrzik, C. M., Müller, N., Rodriguez, E., & Singer, W. (2011). Expectations change the signatures and timing of electrophysiological correlates of perceptual awareness. The Journal of neuroscience, 31(4), 1386-1396.

Milner, A. D., & Goodale, M. A. (1995). The visual brain in action (Vol. 27).

Nguyen, A. P., Spetch, M. L., Crowder, N. A., Winship, I. R., Hurd, P. L., & Wylie, D. R. (2004). A dissociation of motion and spatial-pattern vision in the avian telencephalon: implications for the evolution of "visual streams". *The Journal of neuroscience*, *24*(21), 4962-4970.

Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). The plastic human brain cortex. *Annual Review Neuroscience*, *28*, 377-401.

Peissig, J. J., Young, M. E., Wasserman, E. A., & Biederman, I. (2000). Seeing things from a different angle: The pigeon's recognition of single geons rotated in depth. *Journal of Experimental Psychology: Animal Behavior Processes*, *26*(2), 115.

Qadri, M. A., Sayde, J. M., & Cook, R. G. (2014). Discrimination of Complex Human Behavior by Pigeons (Columba livia) and Humans. *PloS one*, *9*(11), e112342.

Shimizu, T., Patton, T. B., & Husband, S. A. (2010). Avian visual behavior and the organization of the telencephalon. Brain, behavior and evolution, 75(3), 204.

Spetch, M. L., & Friedman, A. (2003). Recognizing rotated views of objects: Interpolation versus generalization by humans and pigeons. *Psychonomic Bulletin & Review*, *10*(1), 135-140.

Vallortigara, G., Regolin, L., & Marconato, F. (2005). Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns. *PLoS biology*, *3*(7), e208.

Van der Linden, A., Van Meir, V., Tindemans, I., Verhoye, M., & Balthazart, J. (2004). Applications of manganese-enhanced magnetic resonance imaging (MEMRI) to image brain plasticity in song birds. *NMR in biomedicine*, *17*(8), 602-612.

Van Meir, V., Boumans, T., De Groof, G., Van Audekerke, J., Smolders, A., Scheunders, P., Sijbers, J., Verhoye, M., Balthazart, J., & Van der Linden, A. (2005). Spatiotemporal properties of the BOLD response in the songbirds' auditory circuit during a variety of listening tasks. *Neuroimage*, *25*(4), 1242-1255.

Wang, Y. C., Jiang, S., & Frost, B. J. (1993). Visual processing in pigeon nucleus rotundus: luminance, color, motion, and looming subdivisions. Visual neuroscience, 10(01), 21-30.

Watanabe, S. (1997). Visual discrimination of real objects and pictures in pigeons. Animal Learning & Behavior, 25(2), 185-192.

Xiao, Q., Li, D. P., & Wang, S. R. (2006). Looming-sensitive responses and receptive field organization of telencephalic neurons in the pigeon. *Brain research bulletin*, *68*(5), 322-328.