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The Role of Object Location and Identity in Sequence Encoding in Pigeons and Humans

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The Role of Object Location and Identity in

Sequence Encoding In Pigeons and Humans

A dissertation submitted in partial satisfaction of the

requirements for the degree

Doctor of Philosophy in Psychology

by

Julia Elizabeth Schroeder

2016

ABSTRACT OF THE DISSERTATION

The Role of Object Location and Identity in

Sequence Encoding in Pigeons and Humans

by

Julia Elizabeth Schroeder

Doctor of Philosophy in Psychology

University of California, Los Angeles, 2016

Professor Aaron Paul Blaisdell, Chair

Animals and humans may learn much information when presented with a series of images at various locations. The order in which the objects appear, the order of locations in which they appear, and whether those locations vary or are stable for any given object will impact how and what the subject may learn. Encoding these patterns can allow for optimal responses in identifying objects and locations in the future. Many studies have examined object-location learning, and sequence learning in mammals. However, there is less research in other phyla. Birds offer a prime taxonomic group in which to investigate these abilities.

Though separated from mammals for 300 million years they are able to learn to perform many spatial and memory feats necessary to survive. As many of these abilities are shared with mammals, birds offer us two opportunities first, to look into our own evolutionary and possibly developmental past, and second, to investigate alternative ways of completing the same cognitive functions.

This research will focus primarily on learning through the incidental encoding of object and location sequences. Incidental encoding is the learning of relationships and functions with the explicit knowledge of what is learned. Incidental encoding is of particular interest in this research as it plays a key role in survival under changing and unpredictable conditions. Incidental learning relies on a separate encoding mechanism from explicit encoding and goes through separate aging processes (Krinsky-McHale, Kittler, Brown, Jenkins, & Devenny, 2005; Naveh-Benjamin et al., 2009; Neill, Beck, Bottalico, & Molloy, 1990; Qin et al., 2014; Smith, Urgolites, Hopkins, & Squire, 2014). As every day in the world exposes an animal to a wide variety of stimuli, it is important to understand what and how information is selected for encoding. Such selection is necessary as it would be cumbersome for the animal to remember everything it experienced., However, it is never known exactly what information will be necessary in the future. Memory processes may have been shaped to be sensitive to many aspects within a task and use such information to direct such incidental encoding.

The dissertation of Julia Elizabeth Schroeder is approved.

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University of California, Los Angeles

2016

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1. Introduction

Almost every animal, from fish to humans, has evolved methods to be able to encode relationships in their current environment and predict future events. Knowing the temporal and spatial relationships in their environment allows animals to optimize their own behavior in preparation for likely or meaningful events. This behavior might include learning that the smell of a predator is often followed by predation, or learning that after storms fresh nuts or berries are likely to be located below a tree rather than on it. This information does not need to be important or clearly useful at the time of encoding. Instead, much learning of our environment comes from incidental encoding, which is the learning of relationships and functions without the intent to learn (Reber, 1967). Understanding what cues are encoded in such incidental learning may be important for our understanding of the causes in many differences between humans, particularly those that cause disabilities.

Language is one area of research in incidental learning that is very important for our understanding of human development. Most children naturally pick up on the statistical properties of phonemes and grammar in the language environment in which they are raised, allowing them to form a basic structure into which more words and complex meanings may fit. (Markson & Bloom, 1997; Perruchet & Pacton, 2006; Reber, 1967; Saffran, Johnson, Aslin, & Newport, 1999; Saffran, Newport, Aslin, Tunick, & Barrueco, 1997). Deficits in noticing these cues are tied to many different developmental problems, including autism and dyslexia. When children fail to learn these basic statistical properties of languages it can

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become very difficult to teach language skills even through explicit, or intentional, encoding therapies (Järvinen-Pasley & Heaton, 2007; Whitehouse, Barry, & Bishop, 2008).

Implicit Learning

There is little consensus on exactly what should be categorized as implicit or incidental learning (Forkstam & Petersson, 2005). Researchers have suggested many different characteristics that could be used to categorize implicit versus explicit learning and memory. However, these definitions often use different characteristics, leading to an entire collection of types of tasks being categorized differently by different researchers. One of the most common characteristics used in these categorizations is the conscious awareness of learning, conscious intent to learn, or conscious recalling the relevant information. This definition has many drawbacks because some tasks may be learned implicitly, such as the grammar of one's first language, as well as explicitly, though a very intense English grammar class in 7th grade. Additionally, while one may be able to remember and report a pattern of locations, the speed of performance at touching those locations may increase with training (Aarts & Dijksterhuis, 2000).

Alternative methods for categorizing implicit versus explicit memories come from identifying the neurobiological systems on which each relies. The hippocampus and associated structures have been implicated in explicit memory. Human patients and animal subjects with damage to the hippocampus show impairments in the encoding of episodic-like memories and the learning of new explicit information (Squire, 1992). However, the hippocampus is also involved in many other tasks, such as spatial learning and configural learning, which do not necessarily involve explicit learning. This method for categorization is further weakened since implicit memories have not been found rely on any specific brain

structure. Instead, different forms of implicit learning and memory rely on a diffuse array of structures.

While there is little consensus on where the line should be drawn between implicit and explicit learning and memory, a few tasks have been identified which are commonly accepted as measures of implicit learning (Forkstam & Petersson, 2005). Artificial grammar learning and Serial Response Time (SRT) tasks have both been conducted in both humans and animal models. These measurement procedures have been found to correlate with many disabilities characterized, at least in part, with deficits in incidental statistical learning such as dyslexia (Howard, Howard, Japikse, & Eden, 2006). These tasks generally follow the categorization lines described above making them generally acceptable to many fields of learning and memory research.

Investigations of incidental learning often rely on pattern learning or recognition through the use of artificial grammars (Reber, 1967). These grammars create complex rule based patterns to investigate the sensitivity to pattern recognition. These types of patterns were modeled after those used in languages. To do this, most procedures create strings of letters by following rule systems such as the structure listed in figure 1-1. The resulting strings of letters can then be used in recognition or categorization procedures to investigate learning and recognition (W. T. Herbranson & Shimp, 2003, 2008). In studies with human subjects, participants were able to recognize patterns significantly above chance, despite not being able to verbalize or describe the patterns or rules. (Chomsky, 1959; Chomsky & Miller, 1958) These studies highlight the utility of artificial grammar in investigations of verbal development, while offering a simplified method for use with animal subjects.

Not all incidental learning tasks rely on the artificial grammar learning. SRT tasks focus on the utilization of the memories of past orders rather than the recognition of a pattern. These tasks cue locations in a repeating sequence such that subjects are always aware of the location of the correct response. Even after subjects can verbalize the sequence and explicit memory has been completed, response times continue to decrease as the location sequences is encoded through implicit memory. This task probes a different type of learning than the artificial grammar task, and instead looks at the increased ability to unconsciously increase performance. Much as a child can memorize the letters pattern on a keyboard but still be a slow typist, procedural learning can result in a much faster response pattern than explicit memory alone.

Although SRT and artificial grammar tasks are only two methods to measure implicit learning, they offer insight into two very different skills and the wide range and usefulness of skills, which can be learned through implicit learning. These skills offer either quicker learning (artificial grammar) or faster responding (SRT) than explicit memory alone provides. These tasks utilize a vast array of skills from object recognition, location encoding and prediction, and relational learning between one item in a string or series and the next. These all come together to offer important insights into how information can be processed outside of intent or consciousness.

Spatial Pattern Learning

Our understanding of spatial pattern learning has expanded greatly from the serial response time tasks to encompass the learning of the locations themselves and with more complex patterns. Simple patterns, such as two to the right followed by one to the left may easily be identified by both rodents and birds (Fountain, 1990; Fountain & Hulse, 1981;

Fountain & Rowan, 1995, Garlick & Blaisdell, Unpublished). When similar patterns are created with a predictable pattern violation, performance decreases on the violation element, with most errors conforming to the continuation of the pattern behavior. These studies demonstrate that the pattern itself drives the location selection as pure associative strings of behaviors would be able to encode the violation equally well. However, the pattern itself may be learned through associative mechanisms, as many associative phenomena such as temporal chunking in rats and decreases in performance when chunks were randomized in pigeons. These spatial patterns have shown a remarkable amount of generalization across spatial scales although the pattern appears rigidly learned (Garlick, Fountain, &Blaisdell Under Review).

Cognitive Maps

Tolman disagreed with the idea that learning how to reach a rewarded location could be explained by response learning alone. Rather, he championed the idea that multiple types of learning occur in animals and suggested the use of a cognitive map in spatial tasks (E. C. Tolman, Ritchie, & Kalish, 1946a, 1946b; Edward C. Tolman, 1948). He reasoned that a more integrative system was far more practical for rats outside of mazes, since having to learn every single option, without the aid of past experiences in similar tasks, would take too much time and effort for rats to get back to their nests. Instead he thought that rats were capable of integrating the information into a broader map, allowing pieces of information from one task to carry over to a new problem and guide the use of a novel route. He published three main pieces of evidence in support of the concept of a cognitive map. The three findings, latent learning, vicarious trial and error, and taking novel routes when they became options were the evidence for cognitive maps or the integrative processes. Such

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cognitive maps are of great interest for research in incidental encoding. For learning to be easily added to, transferred, and utilized when unexpectedly useful, cognitive maps and implicit memory rather than stimulus response theory offer a more concise explanation for how spatial information is initially learned.

Similar to how humans can learn the landmarks they pass on aimless dog walks, animals have been shown that they can encode general maps of their environment even without incentives to reinforce navigational behaviors. Tolman's latent learning studies demonstrated that rats would learn a maze even when there is no reward within it (E. C. Tolman et al., 1946a, 1946b; Edward C. Tolman, 1948; Edward Chace Tolman, 1930). He used three groups of rats, one which found the reward at the end of the maze from the first time they traversed it, and two groups which had either three or six days to explore the maze without the reward. After the exploration days, the reward was placed at the end of the maze. When the reward had been located once, those rats who had previously not been rewarded were able to reach the rewarded location in the same amount of time as those rats who had been rewarded from their first exposure to the maze, indicating that the maze was learned even without a goal or source of reinforcement to strengthen associations, and that the knowledge of the pathways within the maze could transfer to a foraging behavior. Additionally, the motivational state of the rats could guide them to a known food location or a known water location, suggesting that the reward at the end did not only blindly reinforce behaviors but was a deciding factor in which behavior was performed.

Tolman also demonstrated that this behavior was not simply due to a series of very thin "strip maps" which came together at known junction points. Instead this behavior is guided by an integrated map which involves the use of landmarks, and the selection of novel

routes (E. C. Tolman et al., 1946a). The first major study he published on this theory involved rats trained to reach a goal location after taking a route with three separate bends in it. Importantly, the start of the path did not leave the starting platform at an orientation heading towards the goal box. Rather it first went to the left, and then eventually cut over to the right. After rats had been trained on this task they were presented with a novel maze with 18 arms radiating out from the start platform in a half circle. Over a third of the rats went to the arm that was pointing towards the rewarded location, while less than a tenth chose the arm that was the old starting direction. However it is important to note that a light had been placed at the goal location. This could serve as a beacon for the rats to home toward. As rats would not have had as clear a view of the light while in the maze until they made the last turn, they may have used it as a stimulus which triggered a response of running towards it.

Connecting Meaning and Location Together

This early work in cognitive maps indicated that at some level animals were capable of attributing meaning to a location or stimulus. For explanations such as Tolman's cognitive maps to be feasible, spatial locations must be able to be associated with some known property. A landmark must be tied to a location to be able to offer an egocentric representation of the individual's location relative to it on a map. Additionally, the locations indicated must have properties associated with them to be of use in navigation. These properties could be as simple as being next to a wall or being a location that contains the reward. The simplest evidence for this comes from studies involving only one or two locations within a limited arena, evidence already presented in Tolman's work. However, other research has focused more clearly on how this occurs. The "peak shift phenomenon"

relies on locations forming appetitive or aversive associations, and these associations being able to be present for all locations currently available. In a typical peak shift task, one location leads to a reward while another either does not, or leads to a punishment. Responses tend to err on the side of the rewarded location away from the non-rewarded location. Cheng and Spetch tested how humans integrate appetitive and aversive outcomes with spatial locations (Cheng & Spetch, 2002). They first had subjects train with only two illuminated locations, one of which was rewarded and a second which was not. Then they were presented with a single cue, which could appear at a variety of locations and asked whether or not that location was the rewarded location in training. Overall subjects preferred to error on the side of the rewarded location further away from the non-rewarded location in training, or the peak of their responding was shifted away from the non-rewarded location. Similar results were found in pigeons (Cheng, Spetch, & Johnston, 1997). In this task, birds were trained on two locations, pecking on the rewarded location led to the presentation of food, while pecks to the non-rewarded location ended the trial and no food was made available. The birds were then tested, by presenting an array of locations, including both of the trained locations. The birds responded more to those locations on the side of the rewarded location and further from the non-rewarded location than to those locations on the side that was closer to the non-rewarded location. If the locations were sufficiently close together, the location most selected would shift off the rewarded location away from the non-rewarded side. These finding support the idea that the location itself acquires an association with either a reward or a lack of reward, and that these associations generalize around the location.

Item-Location Conflict

Beacons remove the need for a specific location to be encoded. Rather a cue (the beacon) becomes associated with the location of food. A beacon is a spatial landmark placed at the site of a reward (Etienne et al., 1998; Mittelstaedt & Mittelstaedt, 1980; Morris, 1984). This learning is distinctly different from what is encoded in most spatial tasks, as the cue, or beacon alone is sufficient for an animal to reach the goal. These differences in respect to biological mechanisms will be discussed later. Beacons allow animals to find the location they wish to reach without having to use a cognitive map of any form. That is, the physical characteristics of the beacon overshadow the location information. Additionally, they have a clear function evolutionarily. Those cues closest to the goal are often, in fact, part of the goal outside of the laboratory. A tree is itself a source of pinecones and shade, not just an arbitrary indicator of a location of shade or pinecones. And as in Mittelstaedt's studies, the smell and sounds of the nest are beacons for the nest. (1980)

Landmarks

Proximal cues, such as an array of landmarks, allow animals to more easily integrate the location of the goal (in many cases their nest). And in some cases, selecting more proximal cues provides increased control of their behaviors. More distal landmarks would require an additional skill, such as being able to properly estimate distances or triangulate the angles between multiple landmarks, methods in which small errors may greatly increase the necessary search area. More proximal landmarks do require the animal to be near the goal to be used but will then reduce the space to be searched. This simple logic also supports some of the navigational behaviors of invertebrate species such as the digger wasp (Tinbergen, 1951). Timbergen tested this with digger wasps by arranging an array of landmarks around their nest and moving the array once the wasps had left to forage. Upon

returning, the wasps searched within the array of landmarks, not at the nest location. Such use of local cues also lightens the requirements on long-term memory and experience learning. Instead of integrating a map of their surroundings over many trips, the wasps reset their map each trip by circling their nest when leaving. This allows them to easily adjust to changes in their environment from snow, leaves falling, or plants growing.

Not all species are as prone to using such local cues to guide behavior (Healy, de Kort, & Clayton, 2005). Great tits were tested for the methods they used in finding food. Though not normally a food caching species, they were able to acquire the search task readily. Every day they were presented with a grid of 48 possible locations with the rewarded location covered with a distinctly colored cloth. After 10 training trials the location of the colored cloth was moved and the birds were allowed to forage. Both sexes preferred to search at the location where the food had previously been rather than under the cloth cue. Other studies found that shiny cow birds and chickens, particularly female birds, are more guided by a beacon than by the absolute location (Tommasi & Vallortigara, 2004; Vallortigara, 1996), while Clayton and Krebs study found no preference for pattern or color cues over absolute locations (N. S. Clayton & Krebs, 1994). However these birds were trained with this procedure over many days, perhaps teaching that the color cue changed regularly and was therefore not a dependable cue.

Object-place learning

Locations can also become associated with simple landmarks, as is the case in object-location learning. Learning a location is not only controlled by rewarding or aversive outcomes, but can rather be linked to any other feature at the location (Gilbert, Kesner, & DeCoteau, 1998). Object place learning studies take advantage of many species' natural

curiosity about new or different objects. Rats can remember what objects are associated with which place and will approach and explore objects which have been moved to a novel location, even though they had previously been exposed to both the new location and the objects (Dix & Aggleton, 1999). This is different than a conditional beacon, as there is never a reward in training. Instead the object is in a simple association with a location not an outcome or attribute of the location.

The fact that landmarks can become associated with a specific location even when separated from any source of motivational force suggests that although beacon learning does not need to be guided by location learning, it may aid in the initial finding of a location or allow for the location to be linked to other more distal landmarks. Such linking could allow distal landmarks to guide an animal to the general location of its goal, then use the beacon to avoid the necessity of a carful and meticulous search.

More distal landmarks have many advantages over proximal landmarks. They may guide behavior from distances further from the goal location, allowing animals to travel much farther from the proximal landmarks and still navigate home. Additionally, they may be larger and more reliable than any source near the goal location. For example, mountains and trees are less likely to change location or be covered by snow or leaves than rocks or pinecones. However this requires an ability to associate a distant cue with the target location, encoding the cue, the target, and importantly their relationship to each other in terms of angle and distance (John O'Keefe & Nadel, 1979). Though many of the specific ideas presented by O'Keefe and Nadel have not held up under recent investigation, the influence of the idea of relational encoding has left a lasting influence in the field.

Landmark Integration and weighting

Additionally, rather than navigation being based on a single landmark, many studies have found evidence that, when possible, multiple landmarks are encoded for a single goal location. This allows for the goal to be determined by the angle and distance from all landmarks, allowing for a more directed search. One theory for how such integration occurs is the vector sum model. Landmarks are not always set by the experimenter; rather, anything in the environment can function as a landmark: the walls of the cage or other enclosure, lights, food hoppers, or any other salient feature of the environment. In the vector sum model (Collett, Cartwright, & Smith, 1986) the distance and direction between each landmark and the goal is encoded separately. When gerbils had been trained to forage for food relative to two landmarks, they seemed to encode each landmark separately, and when the landmarks were moved, they foraged at the location which had been the same distance to the goal from each landmark.

Birds do not appear to be as prone to using this system. Studies have found that many birds, including pigeons, are more likely to average across all possible cues (Cheng & Sherry, 1992; Tommasi, Gagliardo, Andrew, & Vallortigara, 2003; Tommasi & Vallortigara, 2001, 2004; Vallortigara, Pagni, & Sovrano, 2004). Black capped chickadees (Cheng & Sherry, 1992) and Clark's nutcrackers (Gould-Beierle & Kamil, 1996). Cheng found that after having been trained to forage with a single landmark, foraging did shift in the direction the landmark was shifted, however, it did not shift to the same degree. This has been interpreted as the pigeons averaging the landmark's vector with those formed from other room cues, such as the walls of the enclosure. Tommasi has carefully investigated the methods that chicks may use to determine their foraging space. After having been trained to search for food in an open enclosure the chicks were moved into larger or smaller

enclosures. Their foraging strategies appeared to use a combination of the methods above. Like the gerbils, they did search at the same distance from walls as where the reward was previously hidden, however they also searched at the geometric center, where the average vector sum would have indicated. In other manipulations, the chickens were trained with a beacon at the goal location, and when the beacon was moved, most normal chicks continued to search at the correct location, not giving the single beacon landmark much weight. Other manipulations of this study will be discussed later.

All landmarks need not be weighted equally, and many features of the environment may not control foraging behaviors at all (Herz, Zanette, & Sherry, 1994). Herz et al. found that when given the choice of proximal or distal landmarks, Black Capped Chickadees encoded the location of cache sites from the distal cues, but not the proximal cues. In their studies, wild caught chickadees were allowed to cache food within four artificial trees. Two cue types were made easily available to the birds, proximal cues, which were placed 4 cm from each of the possible cache sites, and distal cues which were placed 2 m from each artificial tree. When allowed to recover their caches hours later, the removal of proximal landmarks did not change the percentage of sites foraged that had contained a cache, however the removal of the distal landmarks significantly reduced the percentage of searched sites containing a cache. When the distal landmarks were rotated 90° the percentage of sites searched which had contained caches dropped significantly, and searching was instead increased at the cached sites relative to the landmarks. Rotations of 180° had less affect, suggesting that the rotation was extreme enough for the conflict between the distal cues and other room cues to be apparent.

These results differ from those found in studies using touch screen computers with pigeons. Many studies on touch screen computers have found that proximal landmarks are weighted more heavily than more distal landmarks (Cheng, 1989; Marcia L. Spetch, 1993; Spetch, Cheng, & Mondloch, 1992). In these studies pigeons had been trained to peck at locations on the screen relative to proximal and distil landmarks. If the landmarks were shifted, or in conflict, the peak search location was shifted in a similar direction. However this effect was greater for the more proximal landmarks. These differences in findings in the studies could be due to a variety of factors. The chicks (Tommasi et al., 2003; Tommasi & Vallortigara, 2001; Vallortigara et al., 2004) and chickadees (Herz et al., 1994) search behavior appeared to be guided by more distal landmarks, (such as walls or placed cues). However, in these studies subjects were performing far more natural behaviors within a much larger space. Additionally, locations were consistent across all training sessions for the chicks and self-determined by caching behaviors for the chickadees. Within the space allowed by the touch screen, even the most distal cues may be processed as proximal cues, as the bird's orientation to the cues is always fixed. Within a touchscreen environment, birds prefer those cues closest to the goal, even if all cues have been learned equally. This difference in touch screen procedures may indicate that the physical movement or exploration may influence how locations are encoded. Distal cues (which can guide to a general area) are often preferred over more proximal cues, which may be seen as less reliable as the subjects must be close enough to see them, and only followed when in agreement with the distal cues.

Mammals seem to follow a more complex weighting system, which may vary by sex, species, or time of year (Barkley & Jacobs, 2007; Jacobs, 1996a, 1996b; Lavenex,

Steele, & Jacobs, 2000; Waisman & Jacobs, 2008). When trained to find food in an array of 128 possible search sites in the presence of 8 landmarks, Barkley and Jacobs found two species of kangaroo rats were better able to recover hidden food when later tested in the presence of 16 landmarks than none. Females were aided most by the presence of the landmarks, suggesting that they were using these more proximal cues. Males, however, seemed to be more guided by distal enclosure-based cues and found no more target sites when landmarks were present than when they were not. As males of both species are polygamous, they are known to naturally travel further distances in search of females. Female kangaroo rats however tend to stay near their nests and only navigate to find food. If this food is too far from the nest it will be less useful nutritionally, as resources are wasted in acquiring it, making their home range necessarily smaller than those of the males. Additionally, this work found that those species that are naturally scatter hoarders were able to recover the food faster in the presence of any landmarks. In a similar study, Waisman and Jacobs provided squirrels with a stable array of four distinct objects. After they had reliably learned to go to a single object for their reward, the object's location within the array, relative to the outside world, or unique object was manipulated. It appeared that in late summer the unique feature within the array (beacon), was preferred, but the preference was not consistent between animals at other times of the year.

These studies suggest that the weighting of features and landmarks may not be fixed across all animals. Sex, and seasonal differences may have arisen as different niches were filled, and small differences in the task measured may dramatically change what strategy is implemented. In winter, more distal landmarks may be more reliable due to snowfall, but in summer there is less risk to heavily weighting the most precise proximal landmark.

Additionally, in many species males will travel further distances than females, either due to being kicked out of their home nesting ground at puberty, or voluntarily leaving to find females. Females, on the other hand, may stay closer to their nests or have a more restricted home range, allowing more proximal landmarks to be sufficient to navigate their whole range. Another factor that may lead to different strategies is that the training in touch screen tasks is far more extensive, with the landmarks moving between trials and the only accurate predictor of the goal being its relation to the landmark. When many distal cues, such as the walls of the box, were trained as unreliable indicators, the weight of more proximal methods may increase. Even though the distal landmark on the screen was just as reliable as the proximal landmark, the generalization of the lack of reliability of other distal landmarks may weaken its ability to control navigation, or change the strategies used.

How Locations are Encoded

Within the subphyla vertebrata, the hippocampus is necessary, though not always sufficient, for spatial navigation and location encoding as described in the tasks above. Loss of the hippocampal structure results in several impediments to object-location memory and spatial navigation in birds and mammals as well as in fish and reptiles. Even in tasks that do not in themselves involve navigating to new locations or integrating multiple cues, the impairments are pronounced. Mice, like rats will spend more time exploring novel objects than familiar ones, and are sensitive to their placement, and changes in their location. Murai et al. (2007) found that mice were sensitive to alterations in the location of two identical objects placed in corners of an arena, when they were moved relative to each other, to the point of entry, or to distal room cues (Murai, Okuda, Tanaka, & Ohta, 2007). However, when given scopolamine, a competitive antagonist at muscarinic acetylcholine receptors

blocking hippocampal function, the mice were no longer sensitive to either the placement of the objects relative to each other or their relation to the entry point. When all cues outside of the maze were removed by putting up a curtain, all preferences for exploring the displaced object were similarly removed. However, an acetylcholine esterase inhibitor donepezil, which decreases the breakdown of acetylcholine thereby increasing its presence and effects, increased the time spent on the displaced object. Such integration of cues between objects and locations, as well as between landmarks, seems to require hippocampal function, suggesting that this is at least part of how the hippocampus is able to aid in navigational behaviors.

It is important to note that the mice described above had little motivation to encode the location of the landmarks and were only presented with visual cues to use as landmarks. It could be entirely possible that the hippocampus is only required for visual cues, or alters the animal's intrinsic motivation to explore their environment. To test this theory, rats were trained on a series of tasks including object-location binding, scent-location binding, and object- scent pairings (Gilbert & Kesner, 2002). Before learning the task, electrolytic lesions to the hippocampus were made in one half of the rats to ensure that the hippocampus and all tracks through it could not be used in learning. Rats were then trained on two distinct object-location pairs in which each object had only one correct location in which it covered a full food well, but if the object was placed on another location relative to the other object there would be no reward. The difference in time between the rewarded trials and the non-rewarded trials did not differ between the lesioned group and the sham-lesioned group for the first block of 60 trials. However, after that the sham-lesioned animals improved significantly from both their baseline and from the hippocampal-lesioned animals. The

lesioned animals, however, never improved. The same task was performed again but instead of object cues, scents were used. While the sham-lesioned animals did take longer to learn this task than the object-based task, after training they were responding to the rewarded trials significantly faster than to the non-rewarded trials. Once again, the hippocampal-lesioned animals did not improve. This deficit from the lack of hippocampus appeared to be location-binding specific, as object-sent pairings were learned equally well by both groups, suggesting that it was not just an inability to form associations within or across modalities.

This deficit in spatial cognition does not appear to affect all forms of landmark use. In a Morris water maze task, animals with hippocampal lesions experienced only select deficits in locating the hidden platform (Save & Poucet, 2000). Save and Poucet tested animals' use of either distal room cues or beacons in locating the hidden platform. When provided with only distal landmarks, those animals that had hippocampal lesions took significantly longer to reach the platform than rats with either sham lesions or parietal cortex lesions, though those with the parietal lesions did also take longer than the sham lesioned animals. When it came to the length of their path to the platform, or how far from the platform the rats were on average, the hippocampal-lesioned animals were the only group that was further away from the platform on average than the intact animals. When the platform was removed, the hippocampal-lesioned animals showed no preference for the quadrant that had contained the platform at all. However, when trained with a beacon on the platform, all animals were able to learn the task and perform equally well. This once again suggests that the deficit was somewhat specific for spatial learning, not object-goal associations more generally.

This reliance on the hippocampus does not only occur in mammals. Hampton and Shettleworth tested chickadees and dark eyed juncos in a matching to sample task (Hampton & Shettleworth, 1996). In this task, birds were trained to recognize if a cue was either the same color displayed or placed in the same location. Lesions were made after training, separating this from the learning-based tasked outlined above. Before surgery, all the birds had acquired the task and were better at the spatial matching than the color matching. However, after surgery, those birds that had hippocampal lesions were much worse at the location task when compared to either before surgery or to the color task. Watanabe and Bischof found similar deficiencies resulting from hippocampal lesions in passerine birds (zebra finches) both before and after training on a spatial task, indicating that this deficit in birds is not only found in passerine birds (Watanabe & Bischof, 2004). Additional, evidence for the involvement of the hippocampus or similar structures in spatial tasks comes from findings that the transplantation of hippocampal tissues into a lesioned area can partially restore spatial abilities (Patel, Clayton, & Krebs, 1997).

Hippocampal Place Cells

Much about how information is encoded and integrated is still not fully understood, even in mammals. However, as mentioned above, the involvement of the hippocampus has been firmly established. Place cells, found in the CA1 region, have been of particular interest in the quest to understand how spatial locations are utilized in cognitive tasks over the past few decades, as they encode when an animal is in a specific location (Brun et al., 2002; Bures, Fenton, Kaminsky, & Zinyuk, 1997; Burgess, Donnett, Jeffery, & O'Keefe, 1997; Doeller, King, & Burgess, 2008; Gilbert & Kesner, 2002; Gilbert et al., 1998; Gustafson & Daw, 2011; Hafting, Fyhn, Molden, Moser, & Moser, 2005; Hampson,

Simeral, & Deadwyler, 1999; Hollup, Molden, Donnett, Moser, & Moser, 2001; Knierim, Kudrimoti, & McNaughton, 1995; Moser, Kropff, & Moser, 2008; J. O'Keefe & Dostrovsky, 1971).These pyramidal cells fire when an animal, though possibly only a mammal, enters the cell's place field, the spatial area for which the cell has been tuned in that environment. These cells receive this spatial information at least partially from grid cells, located in the dorsal medial entorhinal cortex (Pilly & Grossberg, 2012), Grid cells are a collection of cells which have multiple place fields around a given environment. These collections of locations form a series of equilateral triangles through the environment, a grid that may allow animals to track their own movements. Place cells seem to use this information to create their single place field within the environment, allowing for the animal to know it's current location. However, it would be completely unreasonable for animals to have a cell for every location it had ever visited. Rather than using such a single location method, place cells remap, or alter the location with which they are associated, when an animal enters a new environment (Moser, Kropff, & Moser, 2008).

Place cells appear to be the way mammals, including humans, encode spatial information. But exactly how this is done has remained unclear. Place cells fire for a specific location, but do not themselves encode any information about that location (Poucet et al., 2004). Associations between a specific location and any attributes about that location, even what locations it is near, do not appear to be encoded by the place cells system. However, the allocation of place cells is not without some environmental modification. When first placed into an environment an animal must have time to explore and learn about its environment, before the place fields become stable. Even the value of a spatial location, while perhaps not directly coded for by a specific place cell, is at times represented by

having a far greater accumulation of place cells around specific rewarded locations (Hollup et al., 2001), though this has been somewhat debated (Gilbert & Kesner, 2002; Poucet et al., 2004). However, NMDA and other cellular learning mechanisms in place cells have been found to be necessary for spatial learning (Lee & Kesner, 2002; Nakazawa, McHugh, Wilson, & Tonegawa, 2004) making at least some involvement from these cells necessary for spatial tasks. Place fields also have the interesting feature of not being set by any specific cue within the environment, and will fire stably across many environmental changes, seemingly only remapping when the environment is not recognizably the same.

There is a long literature on place cells, grid cells and head directional cells, which is not the focus of this work. Instead, these cells will be discussed in terms of how they have contributed to spatial learning research across many species. When an enclosure, maze or cue is rotated, place cells will often rotate their firing field to the same degree, and importantly, animals' behavior follows, with searching for food at the rotated angle (Cressant, Muller, & Poucet, 1997; Doeller et al., 2008; Save & Poucet, 2000; Sturz, Kelly, & Brown, 2010). This provides an excellent method to approximate what the animal knows or has noticed about its environment.

While these cells have been useful in explaining many aspects of spatial cognition, it is important to note that, despite much effort, grid cells or place cells have only been identified in mammals (Bingman & Able, 2002) despite the fact that nearly all vertebrates, and some invertebrates, are capable of navigating to and remembering information about a variety of locations. The fact that for vertebrates the hippocampus is necessary for the encoding of spatial locations is well established, but the exact role and evolutionary history of place cells is unknown.

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Place cells and head direction cells provide a framework for the visual, vestibular, kinesthetic, and other sensory information to feed into. From this input they can determine which environment they are in, where in it they are, and to set their place fields accordingly. How place fields are set by proximal and distal cues was tested by Cressant, Muller, and Poucet (Cressant et al., 1997). In their studies, rats were placed in a circular arena, which was surrounded by a drape, preventing external room cues from adding unintentional distal cues. The manipulated distal cue was a simple cue card placed on the draped arena walls. The proximal cues were three landmarks arranged in a cluster at the center of the arena. Originally, only the proximal landmarks were used, however they were insufficient to control the place fields and the distal cue card was added. When the center landmarks and the cue card were rotated +90° the firing fields were rotated nearly to the same locations relative to the cues, and even after the card was removed the fields remained stable. This suggests that the distal cue was necessary to map place fields, although internal cues were sufficient to maintain them. However, when the three proximal objects were then rotated +90° the fields rotated -60°, indicating that control of the place fields is not transferred from the distal cue to the more proximal cues. This is in line with the findings that moving objects within a scene would lead to re-exploration as the objects are detected at novel locations, not rotating or remapping which would indicate that the objects were all assumed to be in novel locations. However, when the proximal objects were moved to form a line (without the distal cue card) and positioned closely together to prevent the rats from being able to move between them, or when the objects were placed around the periphery, rotation of the proximal cues did lead to field rotations. There are many possible explanations for these findings, including that possibly encoding the angular relationship between close objects is

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particularly difficult for rats and not being able to explore between them allowed the objects to be encoded as a single large shape whose rotation was sufficient to control the place fields. Additionally, in the world of lab rats, objects within their cage are easily moved and altered, while those objects outside of the cages are fixed and relatively stable. In UCLA's vivarium, food dishes and Nyla bones are often provided, and easily moved, while the identification cards on the exterior of the cages remain stable throughout the rats' lives. This may train rats to attend to objects around the edge of their enclosures to determine their orientation.

Place Cells and Landmarks

Much as the place card was only needed to be present at the initial exposure to the arena to stabilize place fields, landmarks need only be visible for short times in order to ensure an animal can reorient and navigate home. Etienne conducted a series of experiments to determine what was encoded when animals were disoriented and then given landmarks to use in reorienting (Etienne & Jeffery, 2004; Etienne, Maurer, Boulens, Levy, & Rowe, 2004). Much as discussed earlier in this paper, hamsters were slowly rotated in order to disorient them while limiting the amount of remapping they would naturally perform. Once they reached the site of food, lights were turned on for 10 seconds while the hamster were hording, the landmarks did not only reestablish directionality, (possibly encoded through head direction cells) but they also reset their location within the maze, and the hamsters not only went the correct direction back to the nest, but on further manipulations were able to search for the nest at the correct distance from the food source.

Avian and Mammalian Hippocampi

The degree of similarity between avian and mammalian brains both in the behavioral and biological alterations with spatial tasks is particularly impressive given the differences in the mammalian and avian telencephalon. Until 2002, there was not even consensus as to which areas were homologous, and the extent of those homologies. For the purposes of this paper I have been using the agreements of the Avian Brain Nomenclature Forum held in 2002. This group agreed that the avian hippocampus, though structured differently, was a functional homolog of the mammalian hippocampus ("Avian brains and a new understanding of vertebrate brain evolution," 2005; Reiner, 2005; REINER, PERKEL, BRUCE, et al., 2004; REINER, PERKEL, MELLO, & JARVIS, 2004). This divergence may seem odd, but given 300 million years of separate evolution and ecological niches, it is not too surprising that the structures are hardly recognizably similar.

There are many aspects of the hippocampus that appear to have been preserved. Both the avian hippocampus and the mammalian hippocampus appear to develop from the same area of the telencephalon (Kallen, 1962), have pyramidal and granular neurons (Mollà, Rodriguez, Calvet, & Garcia-Verdugo, 1986), and contain similar neurotransmitters including acetylcholine, catelolamine, GABA, and serotonin peptides (Erichsen, Bingman, & Krebs, 1991). Additionally, both hippocampal structures have similar connectivity. These biological similarities, paired with the above-mentioned behavioral results of hippocampal damage or inactivation, were sufficient for the authors to agree that though not identical in structure and function, the two regions are for many practical applications, homologous.

However, these structures do have many noticeable differences as mentioned. No place cells have ever been detected in the avian hippocampus, making avian spatial encoding even more of a mystery than mammalian. The shape of the avian hippocampus is

entirely different from that of the mammalian double C layout. Instead, the avian hippocampus appears to be a simple V shape, resulting in no Trisynaptic loop between the dentate gyrus, CA1, and CA3, no ammon horn structure (Erichsen et al., 1991), and a lack of mossy fiber neurons (Bingman, 1993). Additionally, though there is a region believed to be homologous to the dentate gyrus the order of processing between the DG and CA regions appears to be inversed from that of mammals (Hough, Pang, & Bingman, 2002; Kahn, Hough, Ten Eyck, & Bingman, 2003; Mehlhorn & Rehkämper, 2009). Other internal and external connectivity differences have been found. These connectivity differences are not surprising given the differences in hippocampal placement, with the avian hippocampal structures located medially on the dorsal surface of the brain.

The extent of these differences suggests that there may be many different ways to process higher levels of spatial cognition, though the basic features were preserved even from fish (Rodríguez et al., 2002). Such strong preservation is not surprising given the importance of spatial navigation to survival for many species.

Avian and Mammalian Visual Processing

Many of the navigational cues used in these spatial cognition studies rely on the visual identification of landmarks. This simple underlying sensory input may itself be importantly different between avian and mammalian nervous systems. Visual information processing in avian eyes and brains differs significantly from that of mammals. These differences may lead to very different perceptions of the same image. Using differing numbers of foveae and cones, to extremely reduced cortical processing, the avian brain may not recreate the same representations of the world as the mammalian brain (Shimizu, Patton, & Husband, 2010). These differences may lead to changes in how visual attention is

controlled, and how different aspects of stimuli are bound and how these representations are utilized.

The avian retina has two major differences from that of mammals. First, it has two foveae, allowing for both medial and lateral areas to be processed in detail and with color (Frost, Wise, Morgan, & Bird, 1990; Moore, Pita, Tyrrell, & Fernandez-Juricic, 2015). Secondly, the avian retina morphology itself allows for a greater amount of interretinal connections (Rodieck, 1973), including a greater number of bipolar cells as well as an increase in their aborization. Both the avian and reptilian retina contain two types of horizontal cells, one of which is sensitive to specific wavelengths and another which is less selective, allowing for a greater degree of utilization of various numbers of both single and double cones present. Additionally, the density of retinal ganglion cells is in the avian retina is roughly twice that of the mammalian retina (Sillman, 1973; Thompson 1991). This, combined with the greater number of types of retinal ganglion cells allows for far more processing of information to occur within the eye itself. Because more processing can occur in the ganglion cells, the information entering the avian CNS may already be considerably different from that of mammalian representations.

Like that of mammals, the avian visual system has two main pathways for visual processing with the optic tectum (superior colliculus in primates, TeO in birds) or dorsal thalamus (OPT in birds, LGNd in primates) receiving retinal projections (Shimizu et al., 2010). From these pathways, visual perception proceeds largely though homologous pathways. A key difference in visual processing appears to be the relative weight given to these parallel pathways. In the avian brain the tectofugal pathway appears dominant while in mammalian brains the geniculo-striate system seems to be the primary system (Husband, S.

& Shimizu, T, 2001). These differences in processing streams lead to various differences in visual cognition including the ability to rotate stimuli (Hollard & Delius, 1982, but see Neiworth & Rilling, 1987), visual attention, and global and local processing and grouping (Cook, 2001; Fremouw, Herbranson, & Shimp, 2002). These differences in visual perception and processing may lead to differences in the sensitivity and utilization of visual presented sequential patterns.

Binding Features

Vision, conceptual and perceptual space, and information integration all come together to explain perceptual binding. Binding many features of a single object together is necessary to create a representation of that object as a whole (Treisman, 1998). For objects such as landmarks this is particularly important. No one single feature is sufficient to allow an association with a goal to be formed. For example, a green 1 cm cube may indicate that a reward is located nearby, but a red cube, a larger cube, or a green sphere, are unlikely to carry the same predictive value. Binding has been proposed as a mechanism for the integration of all aspects of an object. Binding assumes that attention is devoted serially to a single object at a time. While the attention is on an object, all the features at that location are bound together to create the perceptual representation of the object, allowing the object as a whole to become associated with values. Treisman and Schmidt suggested that binding between features is mediated by the features' links to a common location (Treisman & Schmidt, 1982).

In mammalian visual processing, the perceptual aspects of an object are processed through different pathways. The visual cortex maintains the spatial topographical representation of the image received by the retina with different processing pathways for

various aspects of the visual input (Nassi & Callaway, 2009). V1 and V4 for instance have cells sensitive to specific colors while the striate cortex has cells sensitive to specific orientations. These different aspects of an object must be recombined to form a complete visual object. This recombination is what we will refer to as binding.

In the avian brain, as in the mammalian brain, features of visual stimuli are processed somewhat independently (Cook, 1992; Cook, Cavoto, & Cavoto, 1996; Riley & Brown, 1991). These features of individual items then must be rebound together for higher level processing and associations. Feature binding has previously been identified in visual processing in birds (George & Pearce, 2003; Katz, Cook, & Magnotti, 2010). In these studies features such as color, shape, and orientation were trained in compound. George and Pearce created stimuli in which attending to orientation and color independently should result in a continuation of the trained behavior if the stimulus was rotated, but if the features were bound, the rotation should elicit the reverse of the trained behavior. Katz, Cook, and Magnotti (2010) chose to examine binding by looking at binding errors when stimulus presentations occurred sequentially at either the same or at novel locations. As feature binding is assumed to rely on the reintegration of multiple aspects of a visual item after separate processing, overlapping in space should result in binding errors, while appearing in novel locations should not.

While a single location may be necessary for features of an object to become bound, it is less clear that the location itself is one of the features that is bound within an object's identity in this system. While past evidence has indicated that animals, including birds, are capable of remembering where individual items were in the past, or what items were at a

given location, the inclusion of location as part of an object's identity has not been clearly shown (Nicola S. Clayton & Dickinson, 1998; Jacobs & Liman, 1991).

How the nervous system selects which bits of all of this information to learn about and later recall is one of the major goals of memory research. In order to gain a better understanding of how information is selected for encoding, simplified tasks should be developed to allow for the different aspects of our environments to be more carefully examined. The following research was designed to examine what aspects of simple repeating patterns are learned and utilized. By combining the serial response time task and a very simplified version of an artificial grammar, the differences between object and location predications will be investigated. Manipulating the predictability, interactions and exposure time, and object-location belongingness across pigeons and humans the salience of predictable stimuli can be investigated. Object and location patterns may not interact with each other and in these cases the two patterns may be learned independently and violations to one pattern or the other will have smaller effect than a violation of both patterns. If the learning of one of these patterns overshadows the learning of the other it may be seen through a greater behavioral change when that pattern is violated. However the patterns should both be learned when trained separately.
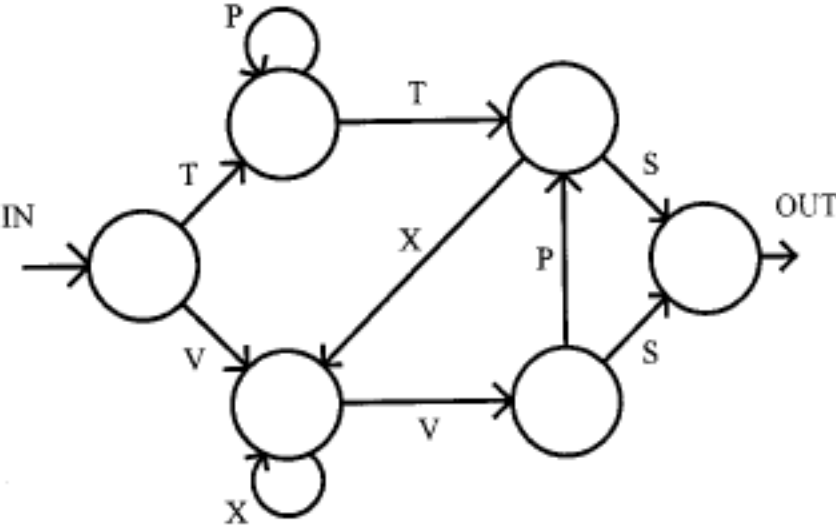
Figures

Figure 1-1 Artificial grammar

Based on W. T. Herbranson & Shimp, 2003 and Reber, 1967

2. EXPERIMENT 1

Learning of object and location sequences: Determining if incidental encoding occurs during object and location sequence presentations

Summary

In order to examine the various aspects in the learning of spatial and object base sequences, a simplified task containing only four objects and four locations was created. This allows for four different sequences to be studied utilizing the same objects and locations with the only alteration being the sequence, which could be learned. After extensive training with the sequences, the rules in the sequential presentations were altered in various ways on probe trials. Response times were measured as an indication of violations of expectancy.

Introduction

Implicit pattern learning has been demonstrated across both object and location sequences. However, how different aspects of patterns are encoded and utilized has not been

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fully explored. To better understand what information is encoded in such sequential tasks, a procedure combining both object and location patterns has been developed. This procedure allows for the independent manipulation of either aspect of the pattern to investigate how different types of information may be integrated or weighted in pattern encoding and recognition.

This procedure is a very simplified form of the artificial grammar and sequence response time tasks. Only four objects and locations will be used with different training conditions offering either randomized or consistent orders to the presentations. A single object is displayed at a time with any response to the object being categorized as correct and advancing the trial to the next presentation. To ensure that training does not bias learning of any specific aspect of the patterns there are no incorrect responses or punishments. Rewards will be given on a lean variable ratio schedule in which the number of correct responses to receive a reward will vary, to ensure that responding is rarely disrupted and all presentation types are equally reinforced. As no responses are incorrect there is no necessity for subjects to encode any aspect of the pattern. Waiting till the object appears and responding to that location is all that is required to complete the task. All learning of the task, besides how to respond to objects, is through incidental encoding.

By manipulating the object and location pattern separately the differences in what is naturally encoded may be examined. Objects and location patterns may be encoded separately or integrated. If the two patterns are integrated the learning of one may interact with the other. Each pattern type is of equal length and complexity, allowing for them to be directly compared. Probe trials in which the pattern is broken will be added after training. Probe trials will disrupt the object order, location order, or both. When the object and

location orders are both broken two different probes are used. The All probes break both the sequence and object-location binding by presenting an object out of sequence, not at its training location, and not at the location predicted by the sequence. The Both probes switch the presentation with another in the sequence, allowing the object to be presented at its training location but at a different point in the sequence. Disruption to responding will be measured through the response time to each presentation.

Experiment 1.1: Learning of object and location sequences

Rationale:

Experiment 1 was designed to identify if incidental encoding takes place when sequences of objects, locations, or both are presented. Additionally, this study allowed us to find out what information is utilized during typical task performance. Increased response time from training trials were measured as an indication of a violation of learned associations.

Methods and Materials

Subjects

The subjects were twelve pigeons (*Columba livia*). They had previously participated in a variety of open field and touchscreen experiments in which they had been reduced to 80–85% of their free-feeding weights. Pigeons were individually housed in a colony with a 12-h light–dark cycle and had free access to water and grit. Experimental procedures occurred during the light portion of the cycle.

Apparatus

Testing was conducted in a flat-black Plexiglas chamber (38 cm wide × 36 cm deep × 38 cm high). All stimuli were presented by computer on a color LCD monitor (NEC MultiSync LCD1550M) visible through a 23.2 cm × 30.5 cm viewing window in the middle of the front panel of the chamber. The bottom edge of the viewing window was 13 cm above the chamber floor. Pecks to the monitor were detected by an infrared touchscreen (Carroll Touch, Elotouch Systems, Fremont, CA) mounted on the front panel. A 28-V houselight located in the ceiling of the box was illuminated at all times, except when an incorrect choice was made. A servo driven food hopper (produced in house) was located in the center of the front panel, with its access hole flush with the floor. All experimental events were controlled and recorded with a Pentium III-class computer (Dell, Austin, TX). A video card controlled the monitor in the SVGA graphics mode (800 pixels × 600 pixels). The stimuli used in this procedure are similar to those used by Blaisdell & Cook (2005). Four 3x3cm locations on the screen were used to present stimuli. These locations were arranged 8 cm from the top, 7 cm from the sides, 4 cm from the bottom of the screen; locations were 5 cm apart. Locations were presented as white boxes on which the stimuli could be presented. See figure 2-1.

Methods

Behavioral Training

Twelve pigeons were first trained to eat grain from the food hopper (magazine training) followed by shaping through reinforcement to peck at a white circle presented at the center of the touchscreen. Following this initial training, each bird was randomly

assigned to one of four conditions. In the first stage of training, each trial consisted of the sequential presentation of four stimuli, one at a time, each in one of four quadrants on the screen. For this task four images A, B, C, and D (figure 2-1) were used and displayed in four locations (figure 2-1). Images were presented on the screen in one of the array locations, one at a time, and remained up for either 30 seconds or until pecked. Once the 30 seconds had elapsed or the image had been pecked the image was removed and the hopper was raised for 3 seconds. As the hopper was lowered, the next stimulus was presented. Which image was displayed and on which array location it appeared was dependent on condition. For subjects in group Place Consistent, each icon always appeared in the same location in the array across all trials, but the order in which the objects were presented varied randomly across trials. In group Object Consistent, objects were shown in the same order on every trial, but the location of the objects varied randomly across trials. In group Both Consistent, both object and location order were fixed across all trials; while in Neither, the location and order of icons in the array varied randomly, figure 2-2. A trial was completed after each of the four possible images had been presented. Sessions began at any point in the sequence.

Once subjects were responding to the majority of stimuli presentations the 30-second limit was lifted allowing stimuli to remain up until pecked. As peck rate increased the schedule of reinforcement became progressively leaner. Prior to testing, each subject was required to respond consistently to each trial while on a lean schedule of reinforcement such that on average every 20th presentation was rewarded. Once subjects reached a steady performance level, testing sessions were added in place of some training session.

Behavioral Testing

Testing sessions were identical to training sessions except that 20 of the 90 training

trials were replaced with non-reinforced probe trials. Four types of probe trials were used

for all birds regardless of their training condition. Object Probe trials switched the object

between two presentations within the trial without altering the sequence of locations used.

Location Probe trials switched the location between two presentations within the trial

without altering the sequence of objects used. Both Probe trials exchanged two presentations

within the trials, both their object and location. This ensured the objects were presented in

the location that they were in originally, however the sequence for both objects and location

was simultaneously disrupted. No sequence or binding probe trials (referred to as All

probes) broke all parts of the pattern and removed one presentation from the trial and

exchanged it with an object from one presentation appearing in the location used for a

different presentation. See figure 4-3 for examples of probe trials. Probe trials always had at

least 3 training trials between them and never occurred within the first ten trials of a session.

Analysis plan

To measure the response time cost for probe trials, the time to respond from when

the object was displayed until the subject pecked within the outline of the locations area was

measured. From this time a baseline response time was subtracted and that difference

divided by the baseline time. For example if the baseline time was 1 second and the probe

trial time was 1.5 seconds the response time cost would be $(1.5-1)/1 = .5 \times 100 = 50\%$.

Baseline times were gathered for each probe trial by selecting the response time from the

trial immediately preceding the probe presentation. There were a few restrictions placed on

the baseline response time. It could not be more than 2 seconds, or be within 3 presentations

in which the subject took more than 2 seconds to respond. Additionally, baseline times were

only taken from presentations in which there had been at least 3 presentations since the last

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food reward was offered. Response times on trials in which the first response was not to the goal location were not included in analysis.

Results

A mixed ANOVA was calculated on the percentage difference in the response time from baseline on the last 100 probe trials of each probe type across the four training conditions as measured in the analysis plan. A significant main effect of training group was found $F(3,8) = 4.401$, $p < 0.05$. A significant main effect of probe type was found: $F(3, 6) = 4.095$, $p < 0.05$. Additionally, there was a significant interaction between group and probe type $F(9,24) = 4.221$, $p < 0.05$. Surprisingly post-hoc testing found that in the Both Consistent training condition there was a significant difference between Both probes ($M = 4.8$, $SD = 3.16$) and the All probes ($M = 17.8$, $SD = 6.72$), with the Both probes having significantly less effect on the response time than the All probes ($F(1,4) = 41.293$, $p < 0.05)$. The Object Constant training condition did not differ significantly from the Neither Consistent training condition $F(1,8) = .107$, $p > 0.05$, with a mean response time cost of 1.6 % and a 95% confidence interval for response time cost on probe trials in which the object sequence was broken of -3.3 to 6.4%. The Location Consistent training group did not differ between probe trails which broke the location sequence and those which did not $F(1,8) = 3.675$, $p = 0.092$. See figure 2-6.

Discussion

As our group size only consisted of three subjects in each condition there is some chance that the significant increase in response time in the Both Consistent training group to probes which break the object and location binding are driven more by individual difference

than by training condition. In order to address these concerns a replication of this study was

conducted.

Experiment 1.2 Replication of Experiment 1

Rationale:

As experiment 1 had only three subjects in each condition a replication of

experiment 1 was conducted in order to ensure that results were not due to individual

differences between birds.

Methods and Materials

Subjects:

All subjects were the same as those used in Experiment 1

Apparatus:

Stimuli:

To ensure that past learning did not interfere with learning the new condition novel

images E, F, G and H were used (figure 2-5a) and locations rotated 45 degrees, see figure 2-

5b.

All other aspects of the apparatus were the same as Experiment 1

Methods
Reassignment

One subject from each condition was assigned to each of the other conditions in an

orthogonal manner. For example of the three birds originally trained in group Both

Consistent one was reassigned to group Location Consistent, one was reassigned to group

Object Consistent, and the third was assigned to group Neither Consistent. For visual

example see figure 2-4

Behavioral Training

All training was identical to that of Experiment 1

Behavioral testing

All testing was identical to that of Experiment 1

Results

Results were taken from each subject's average response time cost as a percentage of

baseline from the last 100 probe trials from each probe type. A mixed ANOVA was

calculated on the percentage difference in the response time on probe trials from baseline

across the four training conditions as measured in the analysis plan. No significant main

effect of training group was found $F(3,8) = 2.903$, $p > 0.05$. A trending effect of probe type

was found $F(3, 6) = 3.915$, $p = 0.073$. Additionally there was a significant interaction

between group and probe type $F(9,24) = 2.425$, $p < 0.05$. Post-hoc testing again found that

in the Both Consistent training condition there was a significant difference between Both

probes ($M = 2.0$, $SD = 3.85$) and the All probes ($M = 12.2$, $SD = 5.12$), with the Both probes

having significantly less effect on the response time than the All probes ($F(1,8) = 35.149$, p

$< 0.05)$. The Object Constant training condition did not differ significantly from the Neither

consistent training condition $F(1,4) = .002$, $p > 0.05$, with a mean response time cost of 1.1

% and a 95% confidence interval for response time cost on probe trials in which the object

sequence was broken of -3.5 to 5.7%. The Location Consistent training group did not differ between probe trails which broke the location sequence and those which did not $F(1,8) = 3.800$, $p = 0.087$. See figure 2-7.

As this study was a direct replication of Experiment 1 the results of the two were combined. A significant main effect of training group was found $F(3,20) = 7.801$, $p < 0.005$. A significant effect of probe type was found $F(3, 60) = 3.172$, $p < 0.05$. Additionally there was a significant interaction between training group and probe type $F(9,60) = 5.238$, $p < 0.05$. Post-hoc testing found that in the Location Consistent training condition there was a significant difference between the Object probes and all other probe types $F(9,20) = 9.015$, $p < 0.05$, and that in the Both Consistent training condition there was a significant difference between Both probes and all other probe types, with the Both probes having significantly less effect on the response time than the All probes ($F(1,20) = 30.904$, $p < 0.001$). No significant difference was found between Object Consistent training and the Neither consistent training conditions ($F(1,20) = 0.018$, $p > 0.05$) with a mean response time cost of 1.3 % and a 95% confidence interval for response time cost on probe trials in which the object sequence was broken of -1.6 to 4.2%. See figure 2-8.

Discussion

After a direct replication, many results were reliably repeated. The sequential training did result in a learning of the location pattern in both the Both Consistent and the Location Consistent training condition as evidenced by the increase in response time created by probe trials in which the location order was broken. Although the Object Consistent training group did not show evidence of encoding the sequence of objects, the violations of the object sequence did increase the response time in the Both Consistent training condition.

The Both Consistent training condition also showed a decrease in the response time cost compared to the All probes when the object and location sequences were broken, but the object was presented at its original trained location. In probes in which the object identity was the only manipulation, the response time increase was significant only for the Both Consistent subjects, the only ones for whom this object-location pairing had been consistent. This suggests that the object and location had become bound through training.

Interestingly, animals trained in the Both Consistent condition and the Location Consistent condition had very similar response time costs. The serial response time task, which is very similar to the Location Consistent condition used in this study, has been used to indicate that mammals can encode a sequence of locations and utilize a previous location's predictive ability to indicate the next goal location (Nissen & Bullemer, 1987). Pigeons have also been shown to encode sequences of locations (Froehlich, Herbranson, Loper, Wood, & Shimp, 2004; W. T. Herbranson & Stanton, 2011; W. Herbranson, Xi, & Trinh, 2014). However, in none of these previous studies were visual cues also placed on the locations. As training in the Both Consistent condition would allow the past object to become a disappearing but distinct landmark for the next location while within the Location Consistent group the locations used would be the only cue. This could indicate one of two possibilities about the encoding of the sequences. Either the location is such a salient cue that altering the objects presented does not interfere with the encoding of the location sequence, or that the training was sufficient for any such interference to have been overcome. Both explanations are possible given the previous research. Evidence from rat spatial pattern learning suggests that visual information about goal locations may not overshadow spatial relationships, although temporal phrasing cues do (Brown, Yang, &

DiGian, 2002; Stempowski, Carman, & Fountain, 1999). In avian research on chickadees, specific features or landmarks have been shown to overshadow geometric spatial encoding (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005). As our boxes provide information more similar to the geometric features used in Gray et al's work, overshadowing may have occurred but the training was sufficient to overcome any overshadowing.

These results indicate that our procedures for implicit learning were successful. Despite there being no necessity to encode any aspect of any of the sequences presented, two training conditions suffered response time costs with the violation of their training sequence. These results also suggest that there may be some conditions under which an identically predictable aspect of a stimulus may not be learned. The Object Consistent subjects showed no response time costs to any probe trials. This suggests that even if the pattern was encoded it did not impact the response. However, there is evidence that as in artificial grammar learning, object identity within a pattern can be encoded and utilized. This task did not require the learning of any aspect of the sequences. With many grammar-learning tasks subjects are either instructed to examine lists of grammar or asked to categorize grammars. The feedback provided by the categorization procedure works to reward learning the grammatical rules. This task specifically avoided such reinforcement of pattern learning by using the serial response time task in which no answer to a cued location could be incorrect. Though predicting the next object to appear from the previous one may aid in visual search, the effort to do so may have not been worth the cost with such a small display. Within this experiment the subjects trained in the Both Consistent group encoded features of the objects. Though there is not evidence that they encoded the object's position within the sequences, there is evidence that the object's location within space was learned.

This is suggestive of object-location binding, a phenomena not previously identified in birds (Lazareva & Wasserman, 2016).

Past attempts at identifying object-location binding in pigeons have used very different procedures. Lazareva and Wasserman (2016) found no evidence of object-location binding in pigeons using a change detection task. Their procedure used presentations of displays made from multiple colored lines at varying orientations. Though birds learned to classify displays as different if they contained novel orientations or colors, trials in which the lines were moved within the display while each lines other properties were maintained were treated as being the same as the original display. This was taken as evidence that the birds could not learn to bind a specific line with a specific location.

There are many possible reasons why binding may occur in the procedure used in these experiments but not in other change detection procedures. In some change detection tasks, including in Lazareva and Wasserman's (2016) procedure, the same locations within the screen may be utilized by different stimuli across different trials, although within the same context. Also, the same stimuli may appear at different locations across trials. This relocation on every trial may teach subjects that location is not fixed for any individual stimuli. As each stimuli is not fixed and may indicate many different locations across time, they cannot function as landmarks, so there is no good reason for them to be encoded. As any individual presentation of the stimuli conveys no meaningful navigational information it may not be bound to a location in the same way that more spatially stable objects are. As any single landmark may be sufficient to reset place fields within place cells (Moser et. Al, 2008) it could be of great evolutionary value to have the binding of location be a selective feature of an object to be bound.

Location binding may also be more selective due to the features of any individual place as a location. Unlike colors, which may be easily shared across many unrelated visual objects, any location can only hold one object at a given time. Any color can be bound to other visual features such as shape without affecting any other objects. Because only one object can occupy the same space there is reason for the processing of any individual object's location to contain information about other objects, specifically that they are not at the given location. The simpler explanation is that locations can become bound to objects, rather than objects becoming bound to locations. This process may be less durable or require more time, interaction, or experience to learn. While perceptual binding may tie together the features of an object, that object would only be bound to a location within the field of view, not within the more durable cognitive map.

As the Both Consistent training condition always presented each object at the same location, each object had the opportunity to become bound with a specific location. Importantly, until probe trials, no other object occupied that same location. This allowed each object to become a reliable landmark within the context and the presentation of any other object at the landmark would be misleading. The appearance of an object at a location other than its trained location on probe trials creates a conflict between the spatial location of the object and the location which that object indicated as a reward. When the binding is broken, the visual properties of the object indicate that a response should be made to a specific location relative to the landmark and a specific location within the context. When these two locations are in conflict with each other we see an increase in response time not present when the object and location binding is maintained.
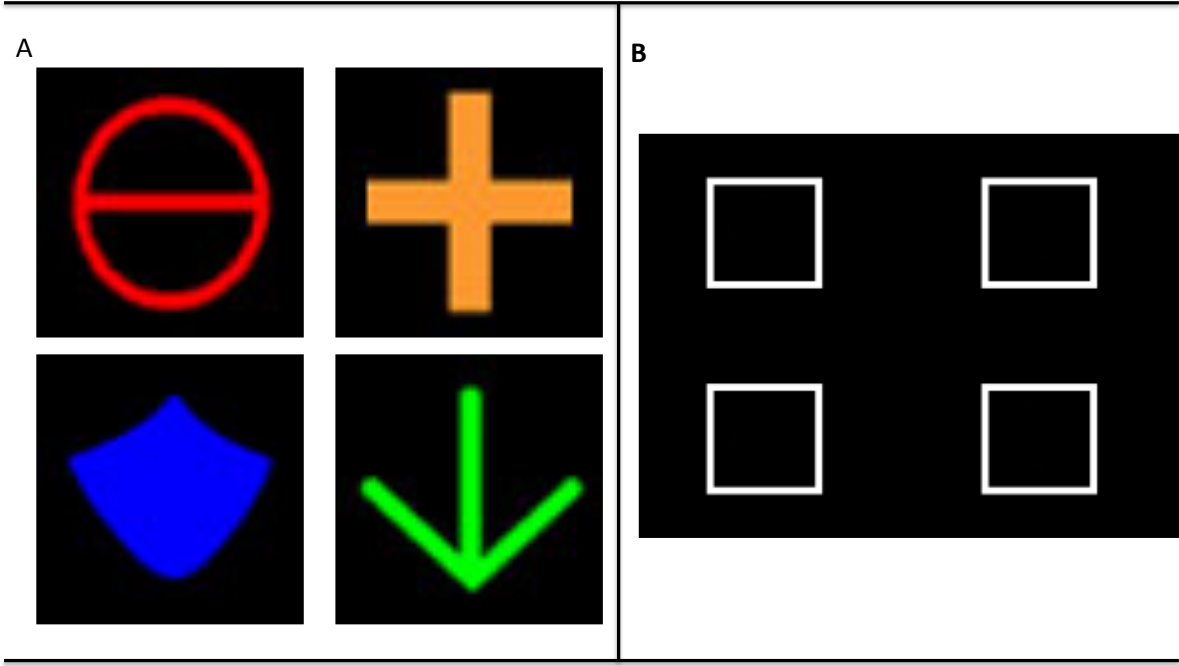
Figure 2-1 Objects and Locations used in Experiment 1.

A. These four images were used as the objects displayed for all subjects in experiment 1. B.

These were the locations of the four possible locations used in experiment 1.
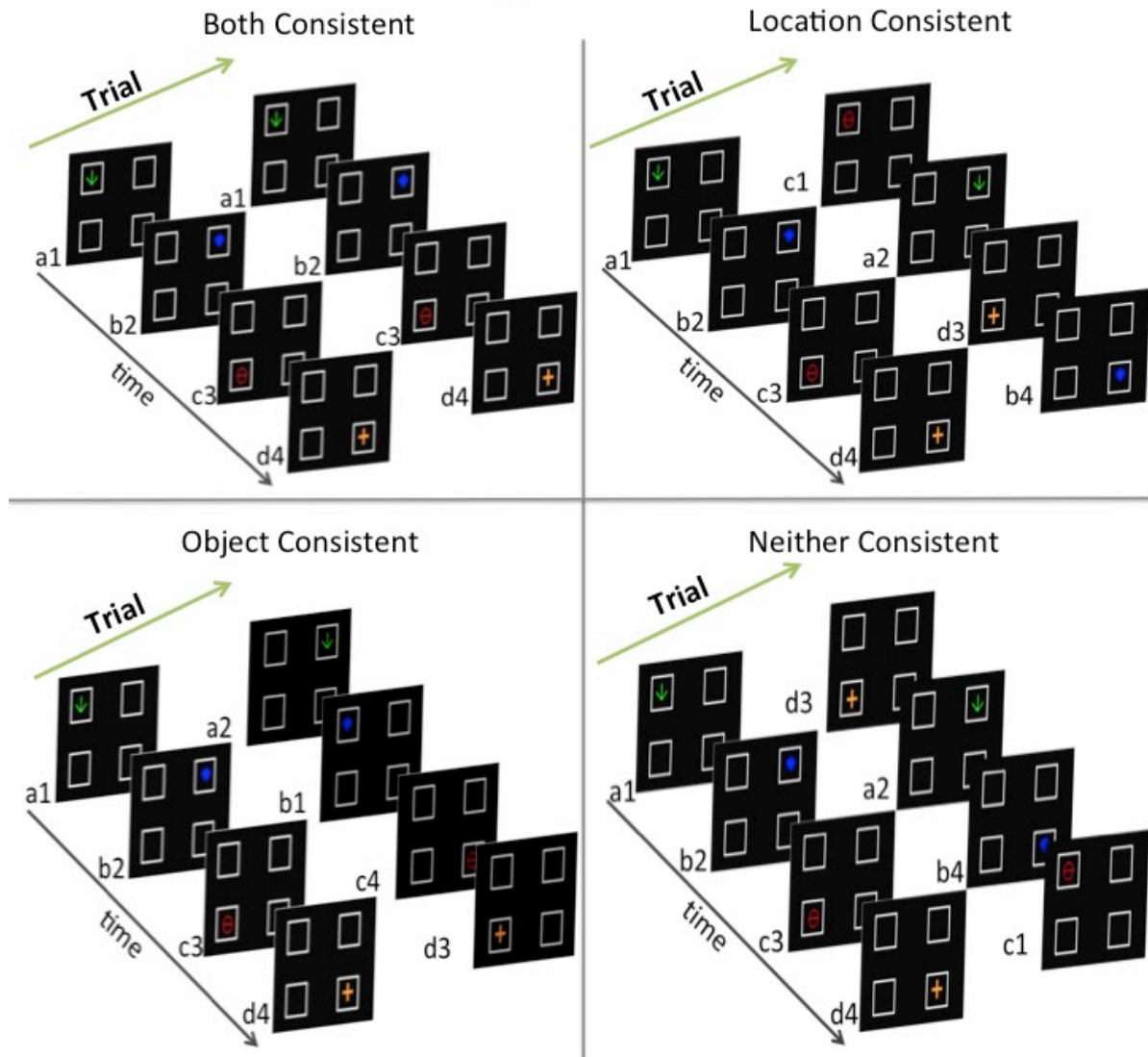
Figure 2-2 Training conditions used in all experiments.

Two trials are shown for each experiment using the objects and locations used in experiment

1.1. Objects and Locations varied across experiments though the rule for each training
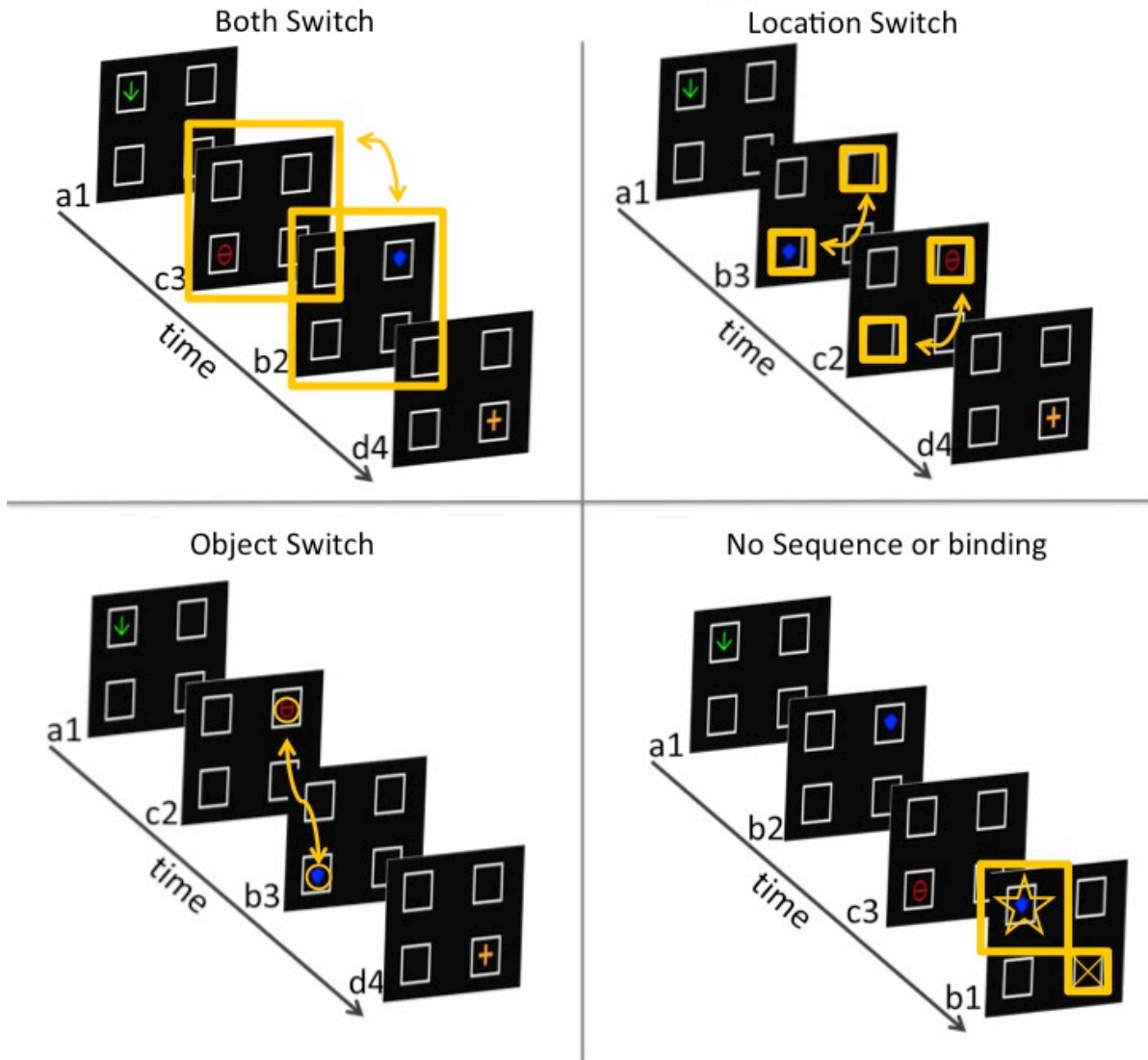
condition was maintained.

Figure 2-3 Examples of probe trials.

Probe trails for all experiments were created using the same rule for the manipulation.

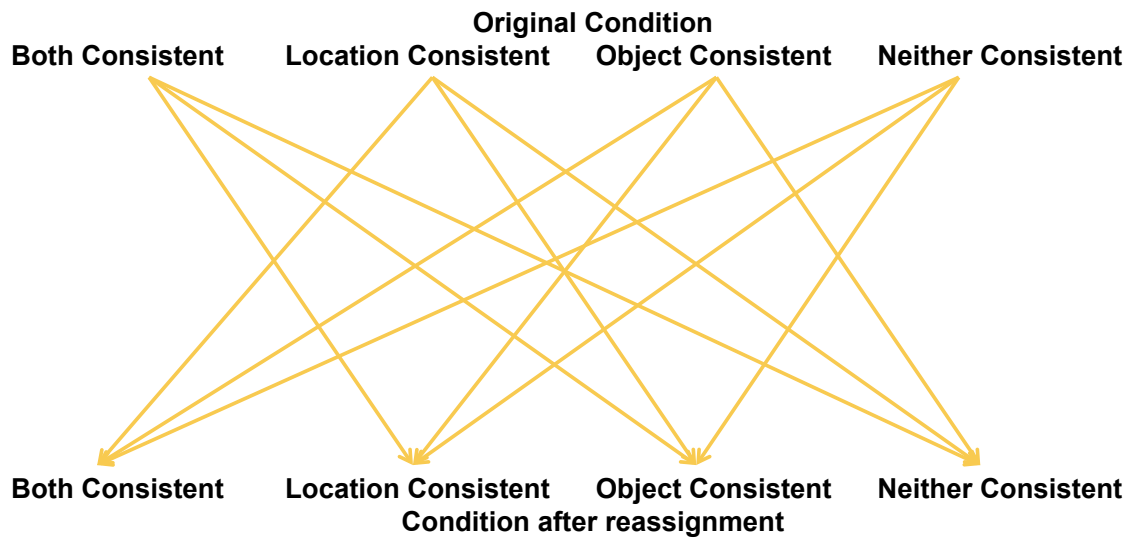Stimuli and locations used were the same as training locations and stimuli for all studies.

Original Condition

Both Consistent   **Location Consistent**   **Object Consistent**   **Neither Consistent**

Both Consistent   **Location Consistent**   **Object Consistent**   **Neither Consistent**

Condition after reassignment

Figure 2-4 Subject Reassignment

One subject from each condition was assigned to each of the other conditions in an orthogonal manner.
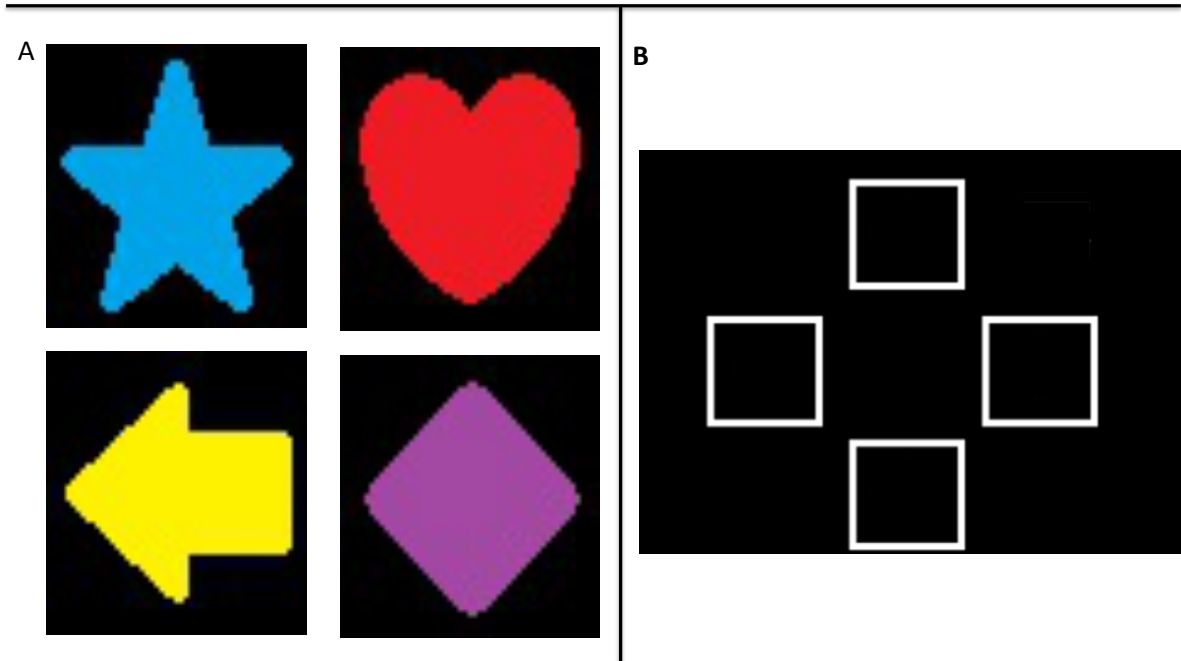
Figure 2-5 Objects and Locations in the replication of Experiment 1

A. These four images were used as the objects displayed for all subjects in Experiment 1. B.

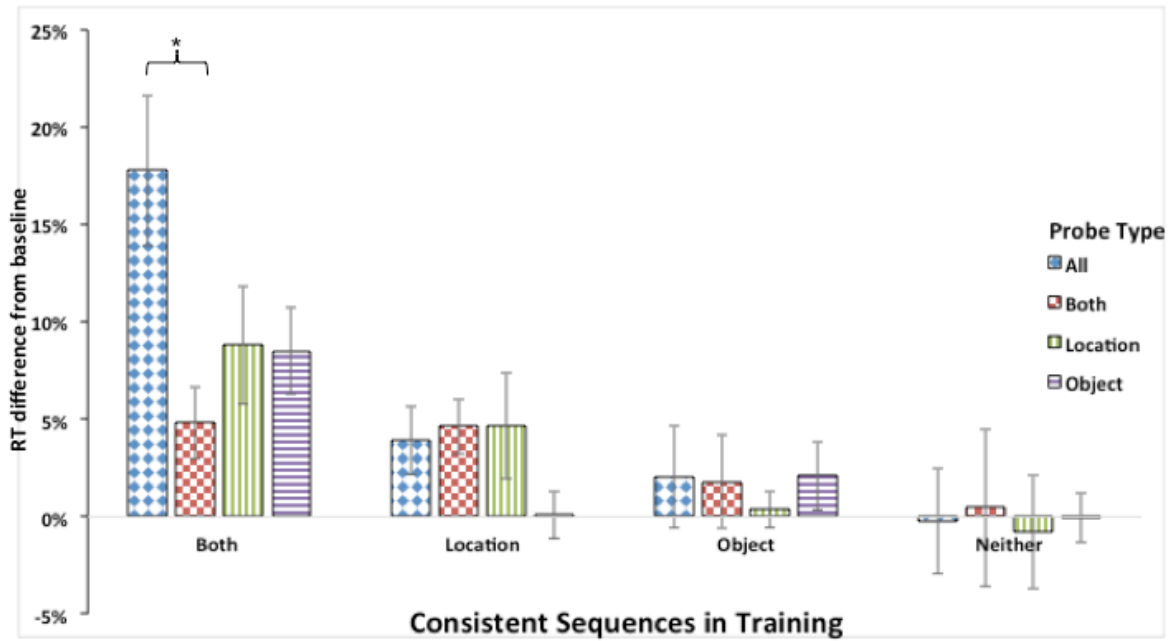These were the locations of the four possible locations used in Experiment 1.

Figure 2-6 Results of Experiment 1

Results from the first version of Experiment 1 graphed as a percent increase in response time over baseline. Error bars show the Standard Error of the Mean (SEM).
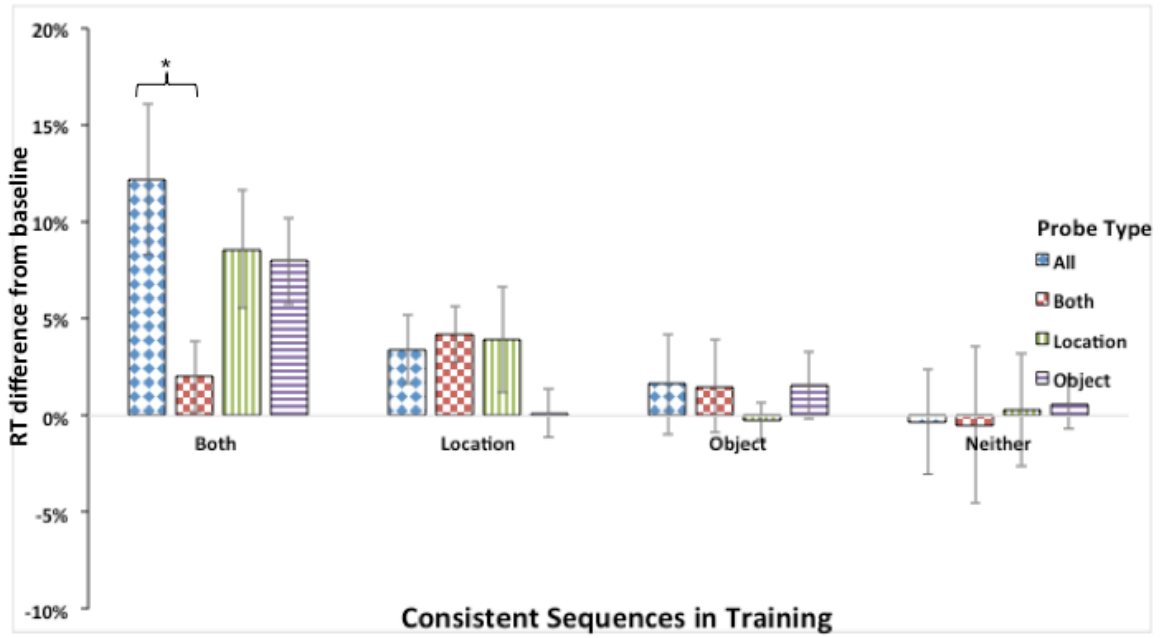
Figure 2-7 Results of the replication of Experiment 1

Results from the replication of Experiment 1, graphed as a percent increase in response time over baseline. Error bars show the Standard Error of the Mean (SEM).
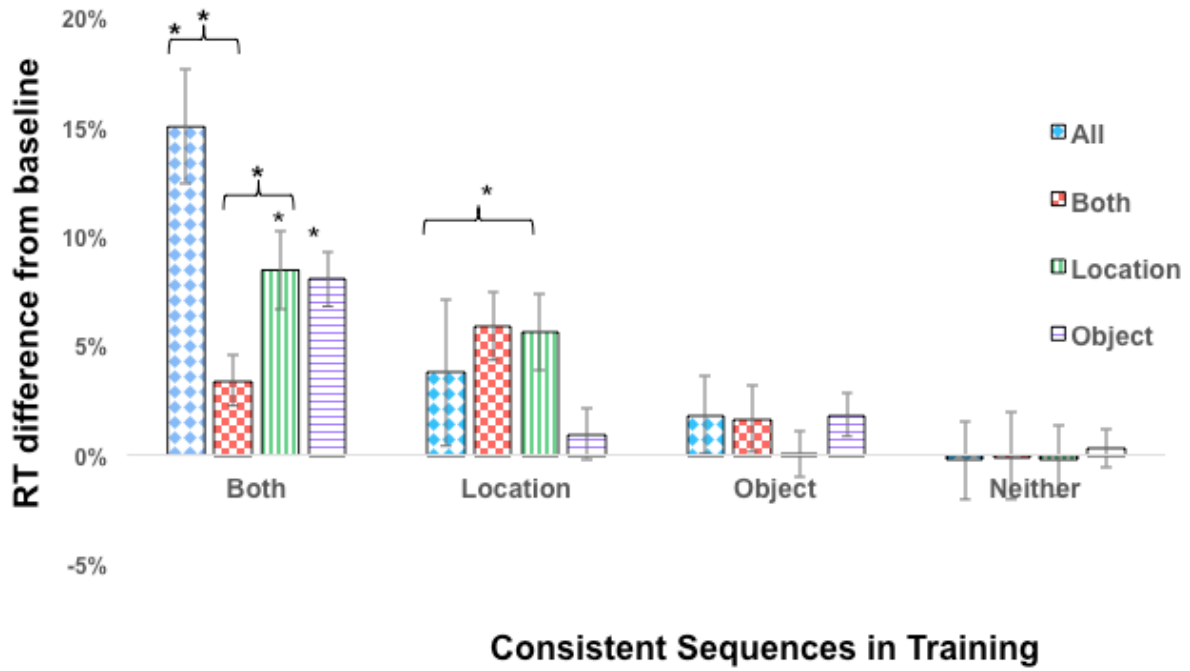
Figure 2-8 Results of the combined replications

Results from combined replications of Experiment 1, graphed as a percent increase in response time over baseline. Error bars show the Standard Error of the Mean (SEM).

3. EXPERIMENT 2

Sensitivity to Exposure Time

Introduction

Many of the explanations for the object-location binding occurring in the presence of sequential information but not with only object and location pairings are based on the increased ability to direct attention to the relevant object or location. The exposure time, or time the object was presented on the screen before being removed, to the presentation in Experiment 1 and its replication was very short after very little training. As subjects were able to respond so rapidly to the presentation, the encoding of item information may have been prevented. Object identity may have not been encoded as well as by the time the subject was in front of the image as the pigeon was probably beginning its ballistic peck behavior. Pigeons close their eyes while pecking, severely limiting their exposure to the object identity information (Ostheim, 1997). If object order is only encoded due to object-location consistency, increased exposure to task-irrelevant information, such as the object presented, should have little effect on response times when the order of objects is violated. However, an alternative account for why the object consistent training appears to have little effect could be that the subjects had too little information about the object identity due to their ability to respond so rapidly. If it is simply an awareness of the object identity that is

important for object order encoding, an increase in interaction with an object may increase the inter object associations.

An increase in the number of responses required for the advancement of each presentation will also allow for each training condition to spend more time at each location and with each object, possibly changing which aspects of the sequences are encoded. By decreasing the importance of navigation between objects and increasing the time spent at each location the location information may be encoded in a different manner. Location sequences may be more important during tasks involving a large amount of movement, though the location of any object may be less salient if the subject does not need to navigate between locations as often. Additionally, increasing the interaction with each object may allow for more processing of each object's identity. Increased interactions before a reward may increase the object's identity association with rewards, locations, or past presentations.

Experiment 2: Effect of increased Object exposure Time on Encoding

Subjects:

All subjects were the same as those used in Experiment 1.2

Apparatus:

Stimuli:

All aspects of the apparatus were the same as Experiment 1.2.

Methods

Behavioral Training:

Subjects remained in the training group to which they had been assigned for the replication of Experiment 1. After testing in the replication of Experiment 1, probe trials are discontinued while subjects receive additional training on the modified procedure. This training was identical to that of Experiment 1, with the exception of an increased number of responses required to terminate each trial. Subjects were progressively advanced from a fixed ration 1 (FR1) schedule in which each response advances the trial to the next presentation to a variable ration 5 (VR5) schedule to advance each presentation. Once subjects were responding steadily the reinforcement schedule was made progressively lean until on average only one presentation in 20 was reinforced. After 45 days of training many birds had decreased their peck rate. To ensure consistent responding the advancement schedule was dropped to be VR3.

Behavioral testing:

Probe trials were run under the same conditions as in Experiments 1 while continuing the VR3 schedule for advancement.

Results

Results were taken from each subject's average response time cost as a percentage of baseline as describe in the analysis plan from the last 50 probe trials from each probe type. A mixed ANOVA was calculated on the percentage difference in the response time on probe trials from baseline. A significant main effect of training group was found $F(3,8) = 6.536\ p < 0.05$. In this manipulation a trend towards a main effect of probe type was found $F(3,8) = 2.681, p = 0.070$. Additionally, there was not a significant interaction between group and

probe type $F(9,24) = 1.122$, $p > 0.05$. Post-hoc testing did not find significant difference in the Both Consistent training condition between Both probes ($M = 6.06$, $SD = 0. 3.89$) and the All probes ($M = 5.07$, $SD = 5.06$), ($F(1,4) = 0.434$, $p > 0.05$). The Object constant training trended towards significant differences from the Neither consistent training condition on probe trials in which the sequence of objects was broken $F(1,8) = 3.44$, $p = 0.05$, with a mean response time cost of 1.7 % and a 95% confidence interval for response time cost on probe trials in which the object sequence was broken of 0 to 3.4%. A comparison of the Object Consistent training probe data on probes for which the sequence of objects was broken and 0 (No RT cost) found a significant difference, ($t(8) = 4.811$, $p. < 0.05$). And a comparison of probe data from the Location Consistent training for which the sequence of locations was broken and 0 found a significant difference ($t(8) = 6.713$, $p. < 0.05$). The Neither Consistent training condition did not show a difference from baseline on any probes not including a novel location or object.

Discussion

The additional responding and exposure with each presentation greatly changed how subjects responded to probe trials. With the addition of the VR3 schedule of trial progression, the subjects trained in the Both Consistent condition no longer performed differently on the Both Consistent probes than on other alterations to the training sequence. Additionally, subjects in the Object Consistent condition showed an increase in response time when the order of objects was changed on probe trials indicating that the order of objects had been encoded during training. However all subjects had difficulty performing under the VR3 schedule of trial progression, and required extended training on the new reinforcement schedule before probes could be administered.

The increase in responding with each object allowed for the order of objects to be learned in the Object Consistent group. This result suggests that the object presentations in the FR1 training studies may simply not have allowed for enough time to encode the identity of each object. As increases in interaction with the object, the order of objects was encoded. Object identity may have become more salient or gained more control of behavior through this training for several reasons. The first is that subjects simply received a greater opportunity to fully examine each object on each presentation. As they did not need to fully view the object in order to respond this may have been sufficient. Pigeons close their eyes when pecking and the location from peripheral vision may have been enough to direct their pecking location without their eye even being open directly in front of the object during the training in Experiment 1. Also, even if the object was seen in the peripheral fovea, as pigeons have two, see introduction, it is still unclear if information entering through that region of the retina is processed the same as that which enters through the medial fovea. (Ortega, Stoppa, Güntürkün, & Troje, 2008).

However, the same manipulation resulted in the loss of the binding effect seen in Experiment 1. This could be due to the possible differences in fovea processing. The same object now appeared at many different locations in the visual field and the same central location was used to process all the objects for many response per presentation. Or it could be due to the increase in responding to a single object while movement to its location is not necessary. This may have allowed the locating of the goal location to become separated from the objects identity as they both developed their own part of trails. While in Experiment 1, the presentation and encoding of the location and the object occurred at the same time, in this study the location of the object was only important for the first response.

All subsequent responses could be made without attending to screen location. As the

location possibly became less salient, the object-location binding may have been broken.
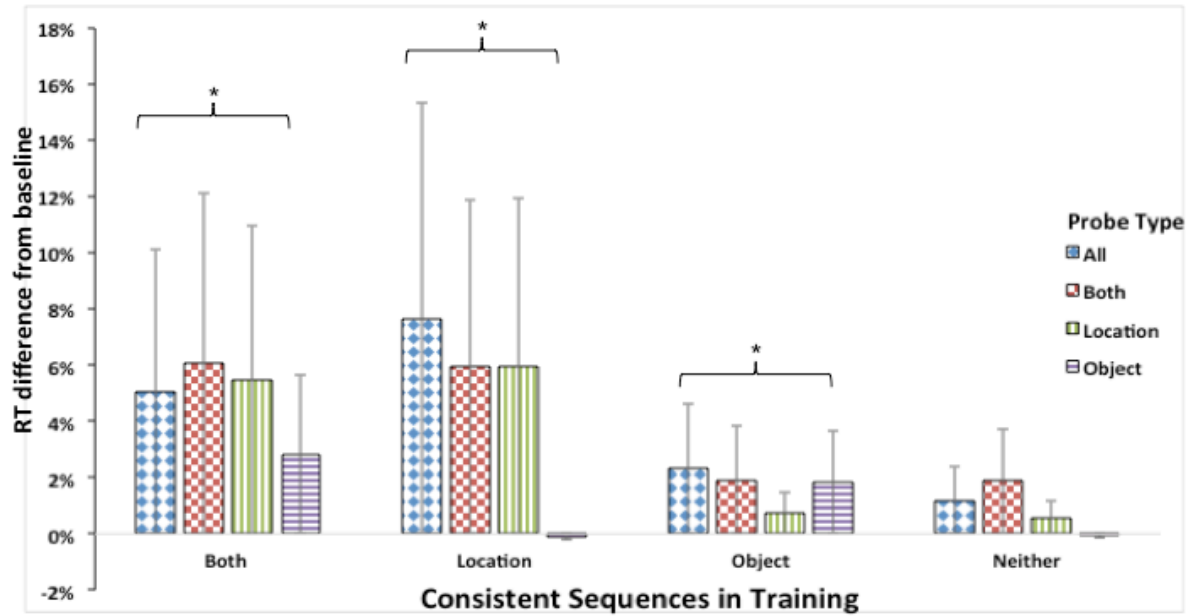
Figure 3-1 Response time cost.

The response time cost to the first response when a variable ratio of 3 responses was necessary to advance to the next presentation. Error bars show the Standard Error of the Mean (SEM).

4. EXPERIMENT 3

Effects of object location pairings without a predictable sequence

Introduction

Experiment 1 found evidence of object-location binding after sequential presentations of objects and locations when each object always appeared at the same location. While the association between a location and an object may be learned through such repeated pairings, it was not clear if such pairings are sufficient for learning of object-location associations. The sequential aspect to this task offered many additional associations to be learned which may have affected the salience of the object-location pairings or increased predictability of appearing.

While the number of pairings between two stimuli will increase or decrease their associative strength, this is not independent of other knowledge. In many different learning procedures, the associations formed between two stimuli produce cue competition which will affect what is learned or utilized in performance between either one of those stimuli and another stimuli, or how much control each individual cue will have on behavior. Two examples of this are blocking and overshadowing. In blocking, the association between a Conditioned Stimulus (CS) A and an Unconditioned Stimulus (US) X will block the learning of a second CS B to X if it is presented at the same time as A, which has already

formed an association. The Rescrola Wagnaer 1972 model explains blocking by suggesting that learning is driven by unexpectedness. If a US is unexpected, the associative strength between a predicting cue and the US will increase. However when the US is fully predicted by known CS's there is little reason to increase the associative strength between the US and any other stimuli. In this way CS A's ability to fully predict X blocks B's ability to form its own association with X. In overshadowing, multiple cues may be learned at the same time. However, the more salient cue will gain associative strength more quickly. Once all cues present predict the outcome all cues stop gaining in associative strength in continuing pairings. This results in the most salient cue being able to produce a response more effectively than less salient cues even after the same number of pairings.

As the sequences of objects, locations, or binding may alter the salience of any other aspect of training, it is important to not assume that object-location pairings alone will result in object and location associations. The learning of any aspect of the sequence may affect the learning of other aspects. Additionally, the learning of one aspect may change the salience of another. Knowledge of the next object may affect how noticeable a location is or visa versa. By presenting an equal number of object and location pairings to all subjects with some having a predictable order and others not, the importance of the sequential aspects of training may be identified.

Experiment 3: Sequential information in Object-Location Binding

Rationale:

Experiments 1.1 and 1.2 identified aspects of object and location encoding when presented with a sequence task. However with the Both consistent training group both the

object-location associations and the object and location predictability were confounded. The initial results from Experiment 1.0 suggest that objects and location can become bound through incidental encoding if they are regularly associated. If subjects were sensitive to the presentation of the object at a given location or a location being associated with a given object, the sequence should have minimal effect. On probe trials the violations of these associations did produce a larger effect than violations to the sequence in which this binding was preserved. To investigate if a predictable sequence was necessary for this encoding or if the dependable association is sufficient Experiment 2.1 presents each object at only one location and each location will be presented with only one object, although no sequence will be present in training.

Methods and Materials

Subjects:

The subjects were six pigeons (*Columba livia*) from the same colony as those used in Experiments 1.1, 1.2, and 2.1.

Apparatus:

The apparatuses used were the same as those used in Experiment 1.2 .

Methods:

Behavioral Training:

Six pigeons were first be trained to eat grain from the food hopper (magazine training) followed by shaping through reinforcement to peck at a white circle presented at the center of the touchscreen. Following this initial training, each bird was randomly

assigned to one of two conditions. In the first stage of training, each trial consisted of the sequential presentation of four stimuli, one at a time, each in one of four quadrants on the screen. For this task, images A, B, C, and D were used and displayed in four locations. Images were presented on the screen in one of the array locations one at a time and remain up for either 30 seconds or until pecked. Once the 30 seconds had elapsed or the image had been pecked, the image was removed and the hopper raised for 3 seconds. As the hopper was lowered, the next stimulus was presented. Which image was displayed and on which array location it appeared was dependent on condition. For subjects in the Both Consistent group, both object and location order were both fixed across all trials. For subjects in group Bound each object was assigned a single location and each location had only one object assigned to it (figure 4-1). These were randomly ordered on each trial though the object and location association was maintained across all trials and training sessions.

A trial was completed after each of the four possible images had been presented. Sessions may begin at any point in the sequence. Once subjects were responding to the majority of stimuli presentations the 30-second limit was lifted allowing stimuli to remain up until pecked. As peck rate increased, the schedule of reinforcement became progressively leaner. Prior to testing, each subject was required to respond consistently to each trial while on a lean schedule of reinforcement such that on average every 20th presentation was rewarded. Once subjects reached a steady performance, testing sessions were added in place of some training session.

Behavioral Testing:

Behavior test sessions were identical to those used in Experiment 1.2.

Results

Results were taken from each subject's average response time cost as a percentage of baseline as describe in the analysis plan from the last 50 probe trials from each probe type. A mixed ANOVA was calculated on the percentage difference in the response time on probe trials from baseline. A significant main effect of training group was found $F(1,4) = 8.620$, $p < 0.05$. No main effect of probe type was found $F(3,2) = 1.295$, $p > 0.050$. Additionally, there was not a significant interaction between group and probe type $F(3,2) = 0.858$, $p > 0.05$. Post-hoc testing did not find significant difference in the Both Consistent training condition between Both probes ($M = 5.08$, $SD = 02.74$) and the All probes ($M = .12.19$, $SD = 10.56$), ($F(1,4) = 0.258$, $p > 0.05$). The Binding Consistent training group showed no difference from 0 ($M = 0.3\%$) and a 95% confidence interval from -4.3% to 4.9%. See Figure 4-2.

Following these results, the Both Consistent training group was examined by subject. Two of these subjects had significant differences between the All probes and the Both probes, while one did not. The first subject, a pigeon named Darwin, had a significant difference between Both probes ($M = 4.61$, $SD = 1.47$), and the All probes ($M = 12.96$, $SD = 2.12$) ($t(76) = 20.00$, $p. < 0.05$. Additionally All ($t(40) = 39.14$, $p. < 0.05$, Location ($t(39) = 13.22$, $p. < 0.05$, and Object probes ($t(47) = 14.63$, $p. < 0.05$ were significantly different from 0. Goodall had a significant difference between Both probes ($M = 3.81$, $SD = 3.20$), and the All probes ($M = 22.35$, $SD = 3.49$) ($t(77) = 24.10$, $p. < 0.05$. Additionally All ($t(41) = 41.50$, $p. < 0.05$), Location ($t(39) = 12.57$, $p. < 0.05$), and Object probes ($t(42) = 12.12$, $p. < 0.05$) were significantly different from 0. Wilhelm only had one probe type significantly different from 0, the Both probes ($t(47) = 17.65$, $p. < 0.05$). See figure 4-3.

Discussion

The comparison between the Both Consistent and the Binding Consistent training demonstrate that the object and location pairings are not sufficient to create binding as measured by response time cost. This suggests that the presence of a sequence during learning affects how such information is encoded or utilized. Additionally, in the Both Consistent training group individual birds responded to the probes differently, though all subjects were trained with the same presentations. Such individual differences may be akin to the individual differences in humans during such implicit and incidental learning. The majority of the subjects in the Both Consistent training condition responded with the same response time cost when binding was broken as seen in Experiment 1, indicating that this is a more common method of encoding such information. However, no subjects in the Binding Consistent condition had any response time cost when the binding was broken, indicating that the sequential aspect of training altered either what was learned, the salience of different features, or how it was utilized.

The consistent sequence of locations and objects may have aided in the encoding of object-location binding in several ways. As the order was fixed within the Both Consistent training condition, the object would always appear in the same location relative to the past location. This consistency may have allowed for the location of the visual stimuli on the retina to be more consistent. By having a predictable stimuli at a predictable location both in space as well as in the visual field, location binding can be detected in avian visual processing. Also, the predictable order of locations may have allowed each object to act as a predictor for the upcoming object or location. This could allow the shifting of attention to

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the upcoming goal location before the object even appeared, or to a more directed search for the form of the expected object. By having a more efficient search strategy, the attention may have been free to encode other information within the presentation. Particularly, if the visual attention was already moved to the location where the goal object appeared, the object itself may have been better encoded. If the attention was already on the location, the object would have been the indicator that a response would be reinforced. When objects appeared in the Binding Consistent training, visual attention may not have fully shifted before the bird responded. As the location could have been sufficiently indicated through little visual processing from peripheral visual information the full image may have never even entered the fovea on many trials. Having such specific predictions confirmed with the appearance of the following stimuli may have further increased the salience the encoding of the location and the object. Simply having an object consistently occur at a given location would not have allowed for such predictions to be made.

The Binding Consistent group may have learned the object-location pairings but simply not expressed them in the same manner. As there was not an expected location to respond to on a given trial their responses may have been controlled by a different aspect of the visual presentation. Though the baseline times were not significantly different across the two training conditions this does not mean that the responding was controlled by the same mechanism. Even though the Both Consistent training group had less time cost when binding was maintained even though the sequence was broken, the ability to anticipate the next location they may have been using the location sequence to guide behavior. Just because we did not see a response time cost in the birds in the Binding Consistent condition does not mean that they did not learn the object-location associations.
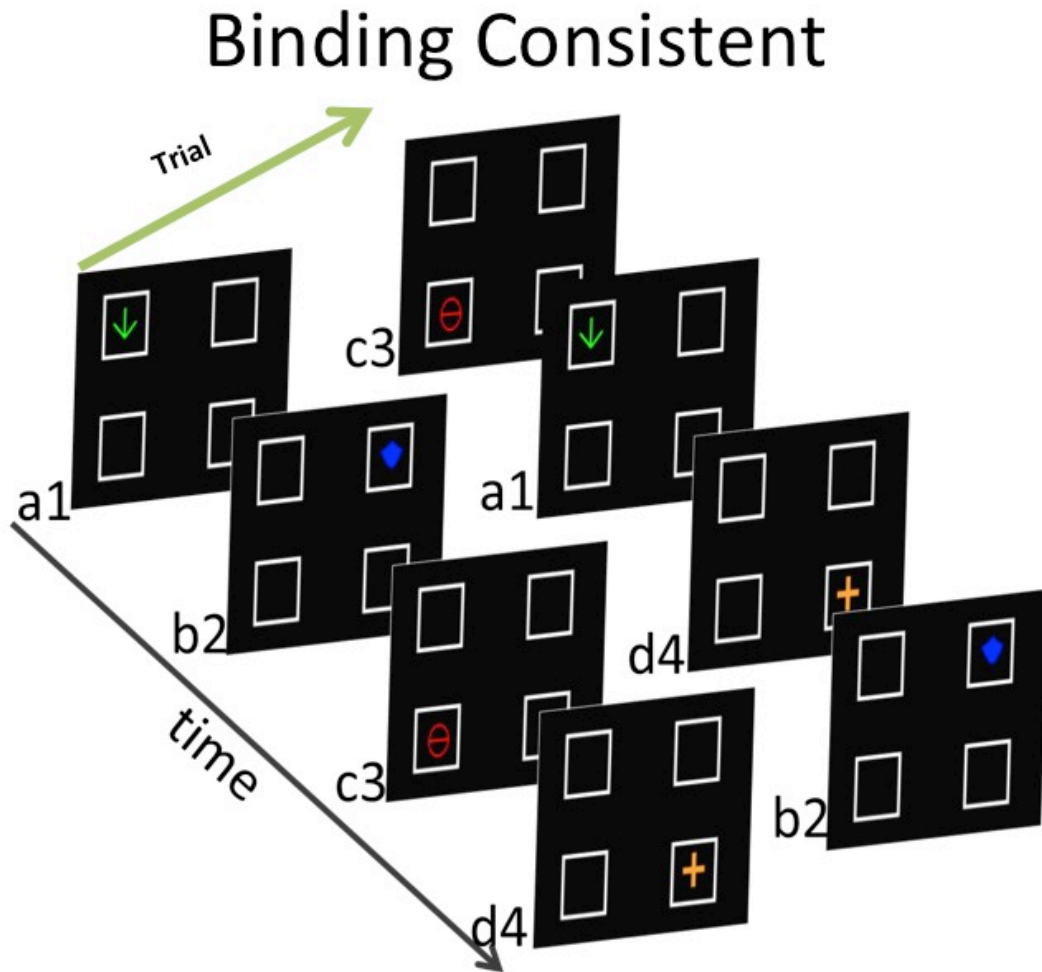
Figure 4-1 Binding consistent training trials

An example of two trials from the new training condition used in Experiment 3. The

both consistent was identical to those used in Experiment 1.
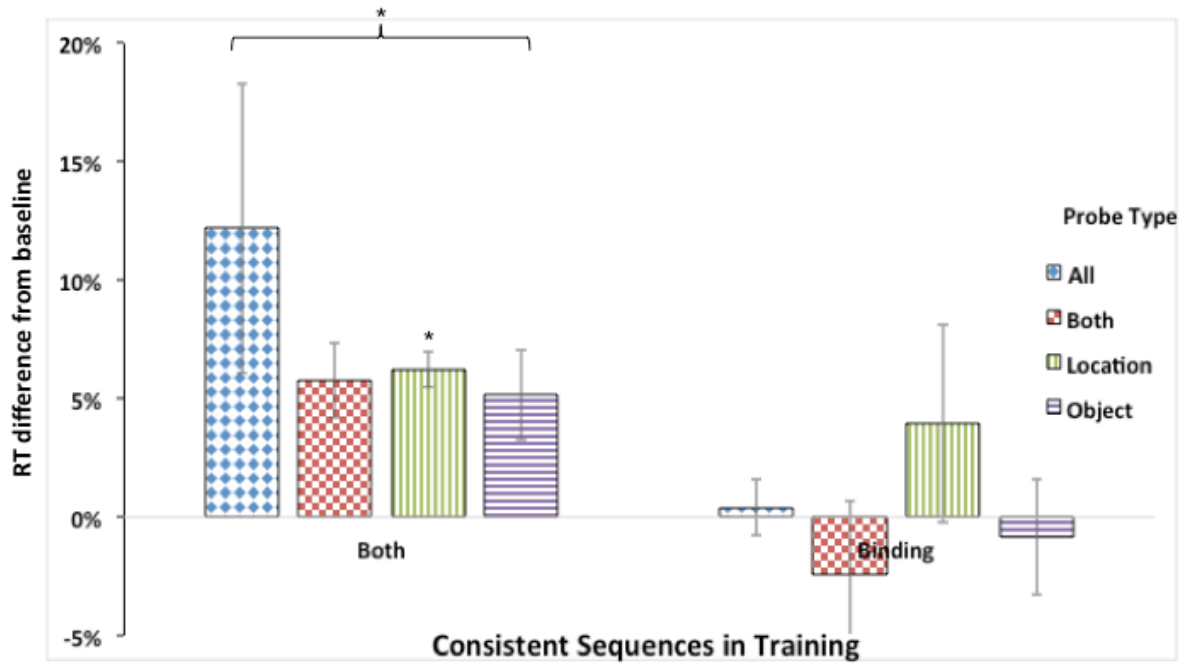
Figure 4-2 Results from all subjects

Response time costs as a percentage increase from baseline with all subjects included.

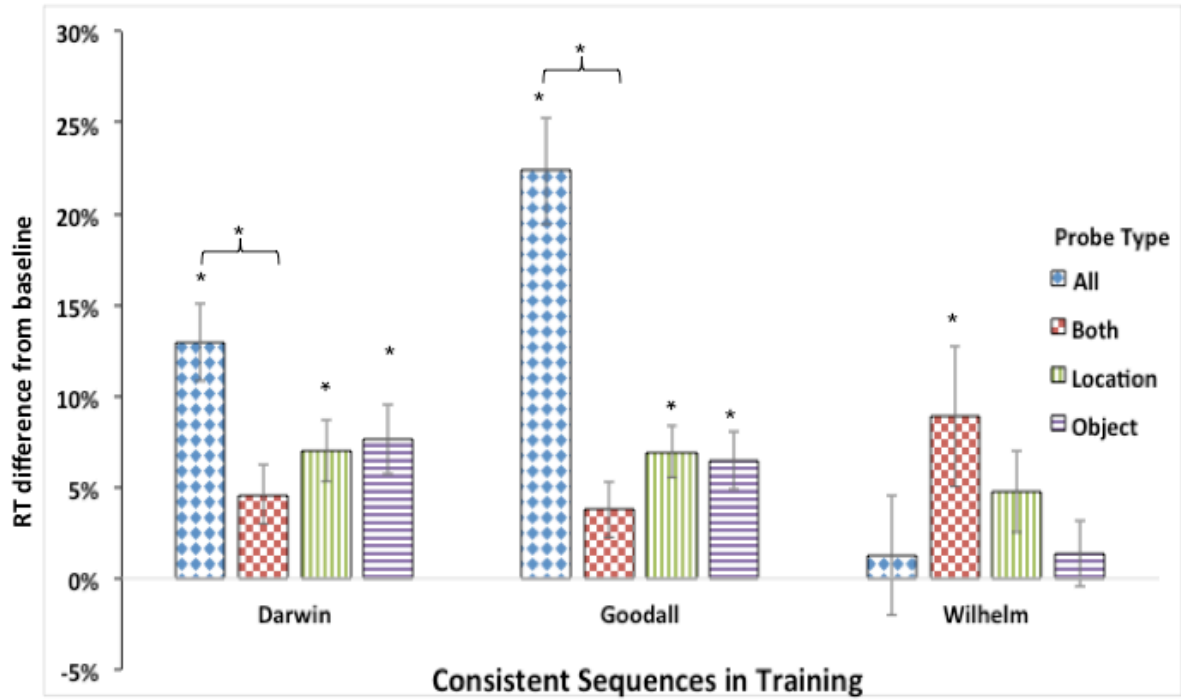Error bars show the Standard Error of the Mean (SEM).

Figure 4-3 Individual performance of subjects

The individual results from the three subjects in the Both Consistent training condition are displayed. Only two displayed evidence of the object-location binding effect. Wilhelm had a unique pattern of results. Error bars show the Standard Error of the Mean (SEM).
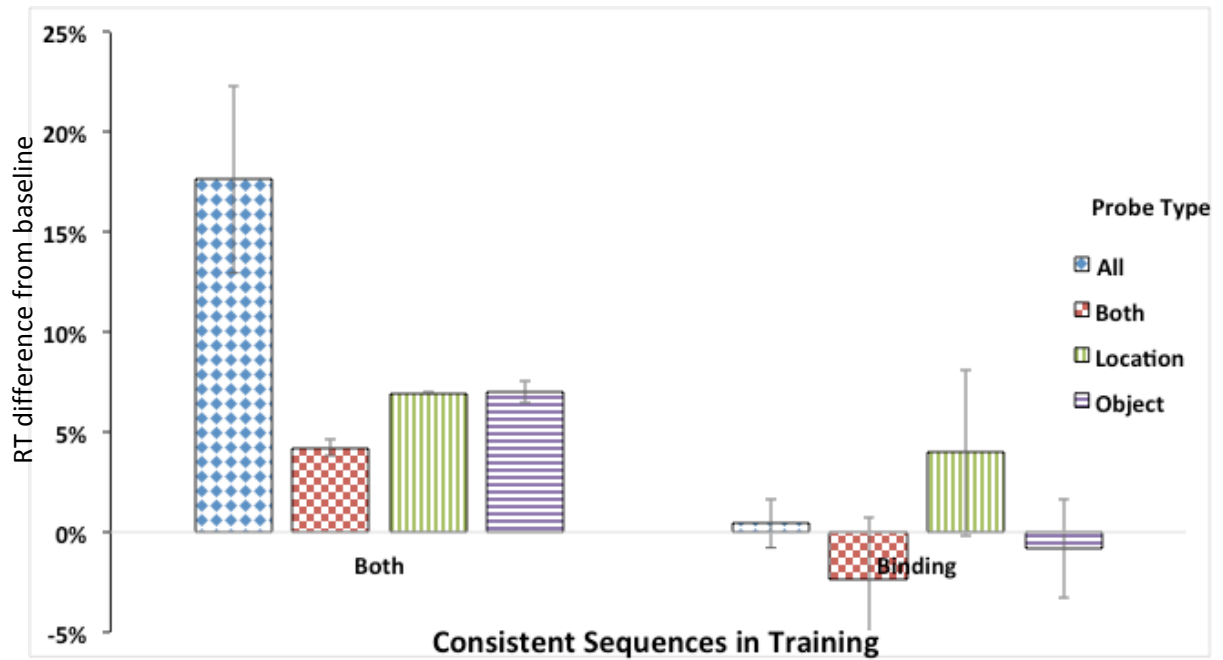
Figure 4-4 Results with one subject removed

When Wilhelm's data was removed the pattern of results in the Both Consistent training condition once again reflects evidence of object and location binding. Error bars show the Standard Error of the Mean (SEM).

5. EXPERIMENT 4

What was learned? An examination of the

location and object predictions

Introduction

While Experiments 1 through 3 showed that subjects could encode the sequences of objects, locations, and object-location binding under the right training conditions, there are many possible aspects of the sequences which could have been learned. For instance when learning the order of objects and locations is 1A->2B->3C->4D many different associations could be formed, and different training conditions may result in very different forms of associations. These different forms of associations would result in very different conflicts occurring on probe trials. While the probe trials have informed us of times in which the subjects behavior was disrupted by changes in the sequences they have not informed us of what aspect of the probe trial was unexpected.

What follows What.

One association which could be learned through training is which objects and / or

locations will follow after a specific presentation. For example 3C may inform a subject that location 4 and object D will appear next. This form of prospective coding would allow subjects to guide their visual attention towards an expected object or location. On probe trials an increase in response time would result from the probe object appearing being different from the expected object.

What followed what.

Slightly different associations would result from learning which objects followed which. For example, when location 4 is presented with object D the subject may remember that this followed object C at location 3. This retrospective coding would allow the current presentation to be placed in memory relative to past learning. On probe trials the increase in response time would be in response to the object appearing when that object or location would normally have been proceeded by a different object or location than the previous trial.

Object-Location binding

For those subjects trained in the Both Consistent condition there are even more associations which could be learned. On all probe trials in which neither the sequence nor the object and location binding is maintained the source of increased response time could come from at least four other sources of interference. The RT cost could come from the image being at a location with which it is not associated, the location where the object is presented being associated with a different object, the image being different than expected, or the location being different than that expected. In the case where the fourth presentation is image B at location 3 the possible sources of conflict would be:

Image D should have followed image C

Image B should be after image A

Location 4 should have followed location 3

Location 3 should be after Location 2

Location 3 should be image C

Image B should be at location 2 See figure 5-1 for visual explanation.

In the Location Consistent or Object Consistent training, only some of these sources of conflict would occur.

To better understand what is encoded during training novel probe types will need to be added. Studies that use novel locations and objects, and with no expected sequence order nor object-location associations, may allow for a better understanding of what aspects of a sequences are encoded. For instance, if a known object is presented at a novel location, an increase in response time would indicate that the object was expected at a different location, while a novel object at a known location increasing response time would indicate that a different object was expected at that location. Such new probe types may allow for a better understanding of the associations formed in object-location binding.

Experiment 4: What aspect of a probe trial disrupts normal responding

Rationale:

Increased response times in experiments 1.0, 1.1, 1.2, 2.1, and 2.2 may have been caused by either of two aspects of the sequence being broken. The response time may have been increased because what was presented differed from the typical sequence, because what was presented was expected at a different point in the sequence, because it was not the image expected, or because it was not the location expected. By presenting novel location,

novel object, and completely novel probe trials such differences may be separated.

Methods and Materials

Subjects:

The subjects were the same twelve pigeons (*Columba livia*) used in Experiments 1.1, 1.2, and 2.1.

Apparatus:

The apparatuses used were the same as those used in Experiment 1.2 with the addition of three novel images and three novel locations. The novel images were used only in behavior testing probe trials and not displayed in training. The novel location trials were presented on the screen for training as well as testing trials, but images only appeared at these locations in behavioral testing probe trials.

Methods:

Behavioral Training:

Twelve pigeons previously trained in Experiments 1.1, 1.2, and 2.1 will continue training in the condition they were assigned for Experiments 1.2 and 2.1. Training was identical to that in Experiment 1.2 with the exception of the three unused locations being present on the screen throughout training trials. See figure 5-2.

Behavioral Testing:

Behavior test sessions were identical to those used in Experiment 1.2 with new probe types added. Every third test day included these new probe types. The novel probe types were: Novel Image, Novel Location, and Novel Both. On Novel Image probe trials one

image was removed from the trial and replaced with one of the Novel images listed in figure 5-2. These always were placed in the location consistent with the sequence. On Novel Location probe trials the image consistent with the sequence would be presented on one of the three novel locations displayed in figure 5-2. For Novel Both trials the novel image was presented at one of the novel locations.

Results

Results were taken from each subject's average response time cost as a percentage of baseline as describe in the analysis plan from the last 20 probe trials from each probe type. A mixed ANOVA was calculated on the percentage difference in the response time on probe trials from baseline. No significant main effect of training group was found $F(3,8) = 0.18$ $p > 0.05$. A significant main effect of probe type was found $F(2,6) = 6.97$, $p < 0.05$. Additionally, there was not a significant interaction between group and probe type $F(18,42) = 0.038$, $p > 0.05$. Post-hoc testing did not find significant difference in the Both Consistent training condition between Both probes ($M = 5.0$, $SD = 2.239$) and the All probes ($M = 5.3$, $SD = 3.23$), ($F(1,7) = 0.10$, $p > 0.05$). Significant differences were found between Novel probes and those probe types previously administered for all training groups, Both Consistent ($F(1,7) = 3.72$, $p < 0.05$, Location Consistent($F(1,7) = 4.84$, $p < 0.05$, Object Consistent($F(1,7) = 8.91$, $p < 0.05$, and Neither Consistent ($F(1,7) = 17.39$, $p < 0.05$. See figure 5-3.

Discussion

The results from this experiment are difficult to interpret due to two main problems: First that any novelty in a probe presentation may have had a significant increase in

response time; second that the object-location binding effect in the Both Consistent training condition was disrupted by either the past training or by the alterations to the procedure in this experiment. However, this study did replicate the RT cost patterns in Experiment 2, with an increase in RT when a trained pattern was broken but without the evidence of object-location binding found in the Both Consistent group in Experiments 1 and 3.

The loss of the object-location binding effect, despite very similar training for subjects in the Both Consistent condition could stem from the past manipulations. Subjects in the Both Consistent group were retrained for this task after having completed the VR3 schedule of advancement in Experiment 2. During probe trials in Experiment 2, no object-location binding was detected. As discussed in Experiment 2, this could have been a result of either change in encoding or in responding on probe trials. If the increase in responding to each presentation changed what was encoded, the change would likely generalize when the training switched back to the FR1 schedule for advancement. As the same objects and locations were used, there is no reason for the information learned in training during Experiment 3 to not carry over to this experiment.

A second possible source of disruption to object-location binding may have been the addition of novel locations. These new locations may disrupt responding and encoding of location. During training for Experiment 1, each location could be reached without passingby any other location. From one presentation to the next, no locations would need to be bypassed in order to reach the next goal location. This meant that subjects never had to withhold responding to a location which was directly in front of them en route to the goal. With the three novel location being in the center of the screen, many presentations would require passing over a non- target location.

Also, these locations may have crowded the screen. If an objects appearance was only seen in peripheral vision it would have been easy to know its location in Experiment 1. With only four locations there would only be a single target location in any given direction. With the middle line contacting five possible locations, subjects needed more than just a target direction in order to begin responding to the goal location. This tracking of the goal location from the lateral fovea to the medial fovea of the eye may have resulted in a change in how the location was encoded. A pilot version of this study, using nine objects and nine locations in a 3x3 array, resulted in difficulty with subjects encoding the sequences of objects and locations. The addition of the novel locations may have resulted in similar difficulties as reported in the previous pilot study.

A more interesting possible reason for the addition of the three novel locations to affect object-location binding would be that these locations did not have objects associated with them. During the training for Experiment 1, all objects had locations, and every location had a single object. This led to no ambiguity in associations. Having three locations which were identical to those locations which had become associated with rewards, but which were never used in training may have altered how the location stimuli were encoded. First, the associative strength between the location outlines and object presentations may have been weakened. This may have increased the associative strength between objects and rewards and while weakening the associations between locations and objects. Additionally, if some locations do not have objects associated with them, the reliability between any given object and its location may become more flexible. When each location has an object and each object has a location not inconsistent presentations would break two different relationships. Now that there are locations where any object could appear without displacing

another the object-location belongingness across the whole task may have decreased.

The addition of novel objects may also have disrupted object and location binding. As in probe trials in previous experiments where each object had been extensively trained to a single location, there was little reason to remap which object should be associated with a location due to just a few probe trials. However, with novel objects being presented these objects would not have to become unassociated with another location in order to increase association with an already trained location.

Interestingly even though the Object Consistent group had a significant response time cost to probes which focused on the object sequence when multiple responses were required for advancement within a trial, there was no significant response time cost in this study. As the sequence had some control of behavior in Experiment 2 the learning would be expected to be generalized to the same object order under the FR1 schedule of advancement. This may be evidence that the FR1 schedule leads to different utilization of the sequential information than the VR3 schedule.

All training groups had significant response time costs to novel locations and objects. This is not surprising considering that both the objects and locations used had been extensively rewarded. Additionally subjects had been presented with only these same four stimuli for two years at the time that this experiment concluded. Responding to any other object or location may have been inhibited or at least not primed, after such extensive training. Unfortunately, as all novel stimuli resulted in such similar increases in response times it is difficult to extract much detail as to whether novel objects or locations were more disruptive to responding.
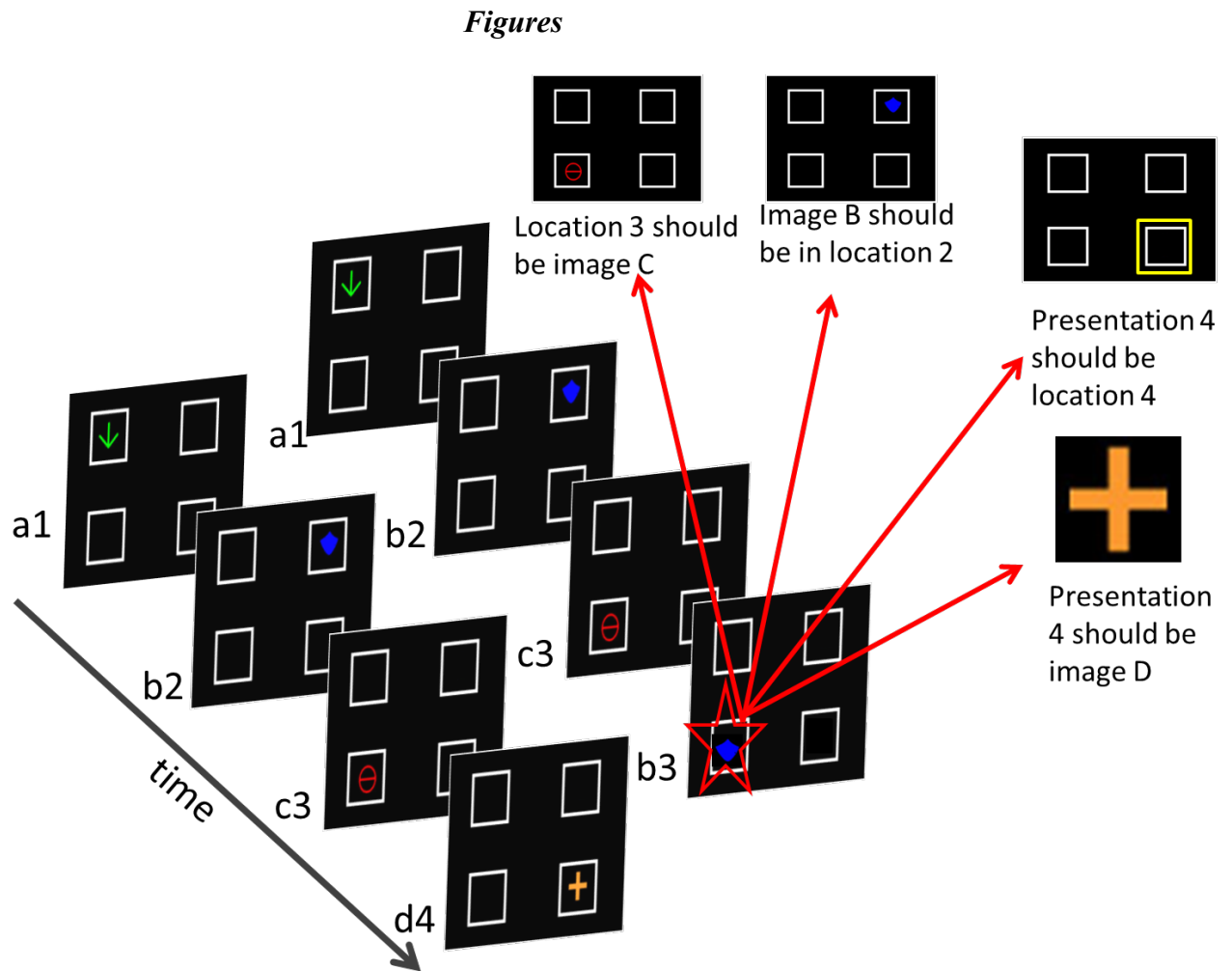
Figure 5-1 lustration of possible types of interference.

The four types of interference which could be occurring on All probe trials for subjects in the Both Consistent training condition.
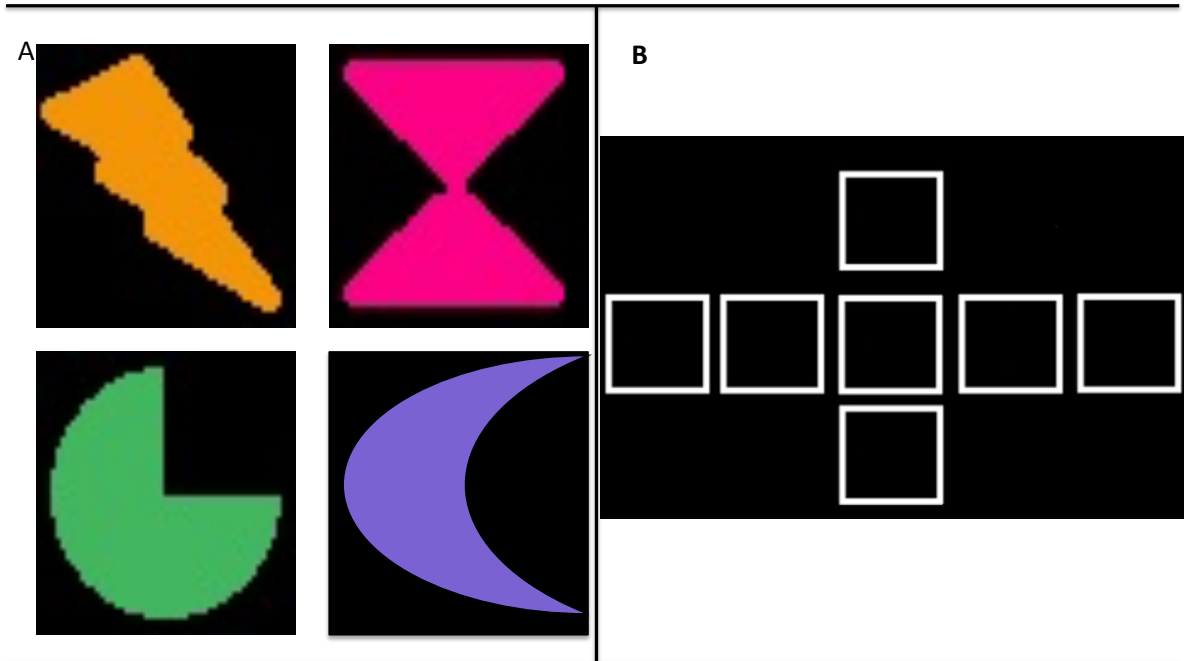
Figure 5-2 Novel objects and locations used in Experiment 4 probes

A. Four unique objects were added for novel object and novel both probes. B. Locations which are constant with those used in the replication of experiment 1 and Experiment 2 were used during training while the three novel locations, far left, center, and far right, were novel locations used only for probe trials.
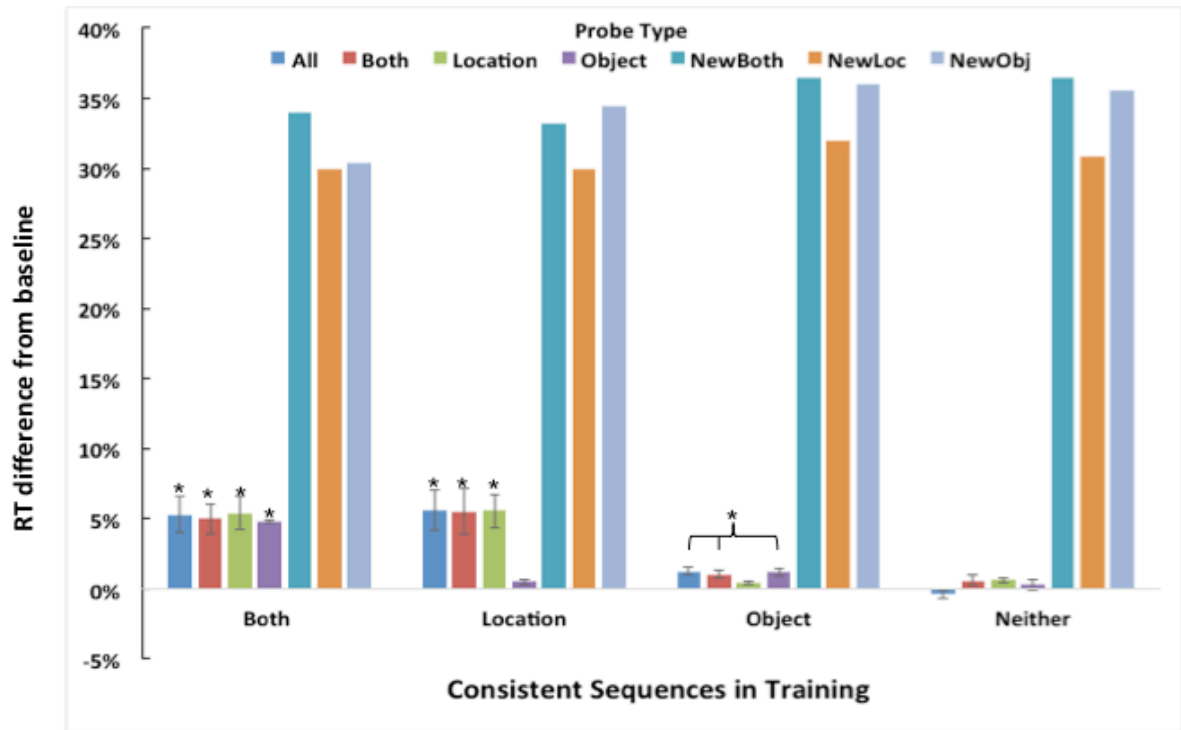
Figure 5-3 Response time costs to probe trials

Response time costs to probe trials as a percentage of baseline time. New objects and locations greatly increased response time costs independent of training condition. Error bars show the Standard Error of the Mean (SEM).

6. EXPERIMENT 5

Comparing Human and Pigeon Performances

Introduction

As birds and humans have had at least 300 million years of separate evolution there are many reasons why they may learn or respond differently given the same training. While their visual systems and navigation systems have extensive homologies, the differences in processes offer important insights into ontogeny as well as the evolutionary pressures, which both phyla have experienced in the past. As phylogeny often mirrors ontology such insights may be particularly useful in informing how implicit learning effects infant development.

While human spatial encoding has a full map in the hippocampus with place cells, head direction cells, and other cells which it may utilize, no such equivalent cells have been identified in the avian hippocampal structure. The information utilized in setting place fields in humans is particularly relevant as it may explain what information is necessary and sufficient for the encoding of a specific location. In many primates this information is strongly driven by visual inputs. Even in rodents, visual landmarks are utilized unless they

are at extreme conflict with alternative cues. This makes the importance of what details about visual landmarks in navigation are very important for our understanding of cognitive maps. If place fields may be set from visual cues, then the knowledge of other locations within the context is accessible and may be utilized. However, if the information is insufficient to provide a clear place field, performance decreases and the knowledge of objects and their locations within the context is not available to control behavior.

Not only do birds and mammals differ in their hippocampal structure and possibly the methods used to encode locations, but their processing of visual information differs as well. Given the differences in processing of visual information between humans and pigeons, the use and learning of object based sequences may differ in many important ways. To fully examine the extent to which humans and birds learn and utilize object and location sequences, Experiment 1 was altered and presented to human participants.

Summary

With hundreds of millions of years of separate evolution it is not terribly unexpected that the avian and mammalian brain have diverged. Though many homologous areas have been identified, much of our understanding of visual and spatial processing in mammals requires some alteration to be applied to avian brains. In particular spatial processing in both phyla can achieve similar ends while utilizing similar but different processing streams. To examine the impact these differences have on the detection and utilization of sequential visual and spatial patterns, human subjects were presented with the same task as pigeons were in Experiments 1.1 and 1.2.

Experiment 5: Human performance on Object-Location sequence tasks

Rationale:

This study focuses on determining whether evidence of object-location binding seen in our avian studies can also be identified in humans. In our initial work, we have found evidence that object identity and location in a repeating sequence are encoded during instrumental learning involving those objects. Specifically, when a sequence of four objects is presented repeatedly, object features that occur in a predictable sequence are encoded. Such incidental encoding may allow the participant to anticipate the next location in a sequence even if such knowledge is not necessary. This ability to anticipate may allow the participant to prepare their next response and be able to increase the speed with which they can earn rewards. However, such learning may lead to a decrease in performance when such associations are violated, increasing their responding time. Incidental encoding can also inform the participant of information which may not be relevant to perform the task, such as which object will appear.

Subjects:

The participants were ~100 undergraduate students at the University of California Los Angeles.

Apparatus:

The apparatuses used were the same as those used in Experiment 1.2 with the exception of the running box and grain hopper being removed and the computer monitor with touch screen attached was placed in a quiet room. After the first third of the participants were run, images were changed to those of bugs (Figure 6-1)

Methods:

Behavioral Training:

The behavioral training was similar to that of the last phase of training in Experiment 1.2. Participants were instructed to tap an image when it appeared on the screen as quickly as possible. Reinforcement was provided by informing the subjects of their last response time at the same rate as in Experiment 1.1 and 1.2. Training lasted for the first 50 trials of a session.

Behavioral Testing:

Behavior test sessions were identical to those used in Experiments 1.1 and 1.2 and lasted for 150 trials.

Results

Results were calculated each subject's average response time cost as a percentage of baseline for every probe. A mixed ANOVA was calculated on the percentage difference in the response time on probe trials from baseline. A significant main effect of training group was found $F(3,3) = 11.40$, $p < 0.05$. A significant main effect of probe type was found $F(3,3) = 13.02$, $p < 0.05$. Additionally there was a significant interaction between group and probe type $F(3,12) = 5.92$, $p < 0.05$. No significant difference was found between the Both and All probes in subjects trained in the both consistent condition. However in both the Both consistent training there was significant difference in changes to response time between the object probes ($M = -0.001$, $SD = .00405$) and all other probe types ($M = 0.0117$, $SD = .00471$) , ($t(32) = 8.4297$, $p < 0.05$). No other groups differed from 0. See figure 6-2.

A follow up study was run in which participants were asked if they noticed a pattern in the order of locations, images, or both and to describe it. For the Both consistent

condition 4/4 subjects reported noticing both the order of objects and locations, ¾ described the pattern as the objects appearing at a place in order suggesting that they were aware of the object and location pairing. In the Location consistent training 3/3 subjects reported noticing the sequence of locations, and 1/3 believed there may have been a pattern to the objects. For the object consistent condition ¾ subjects reported noticing the order of objects and interestingly all three subjects also believed that there was some more complex pattern to the order of locations. 2/3 subjects run in the neither consistent condition reported noticing an order for location though they could not describe it and 1/3 reported believing that there was an order to the objects.

Discussion

Human participants responded very similarly to pigeons in many aspects of this task. Just as pigeons in Experiment 1 had an increase in response time for probe trials which broke location sequences after location consistent training, humans had an increase in response time when the location sequences present in training were disrupted if location was predictable in training. And neither humanb participants nor avian subjects suffered response time costs with violations to Object Consistent training. However there were many differences between humans and birds in performance.

When in the Both Consistent condition the order of objects did not have strong control over behavior. Despite humans reporting that they detected the object consistency in surveys, their serial response time did not alter with violations of the pattern. Also, participants who were trained on the Both Consistent condition did not demonstrate binding of object and their locations. Once again, this did not affect behavior even though almost all subjects reported being aware of the object and location associations. Human visual cues

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may have different abilities to control response time tasks given that they did notice such patterns.

These differences in behavior may stem from several different causes. First was the difference in the procedure as it was presented to them. While birds learned the task through trial and error, human participants were given instructions to respond as quickly as possible. This may have altered their behavior, as they knew exactly what the task was. While pigeons may have been unsure if there would be a reward when anything changed from training, the human participants knew that all that was asked of them was to touch objects as soon as they appeared on the screen. Additionally human participants only received one training session in comparison to the hundreds of days of training experienced by the pigeons.

Human participants were also viewing the display from a much greater distance. Most humans positioned themselves at least a foot and a half from the touch screen, allowing them to have a clear view of the whole screen at once, and only needing to move a hand while maintaining eye contact with the goal object. Pigeons stayed close to the screen, a mere few inches away at all times, and moved their head and body to scan or respond to different locations. This difference might change the scale at which visual processes operated. Also, though pigeons moved their whole bodies to perform the task, humans moved only their hand.
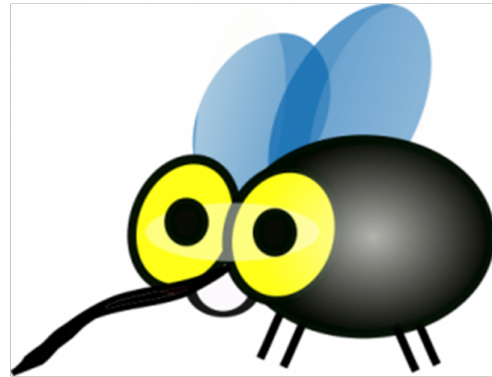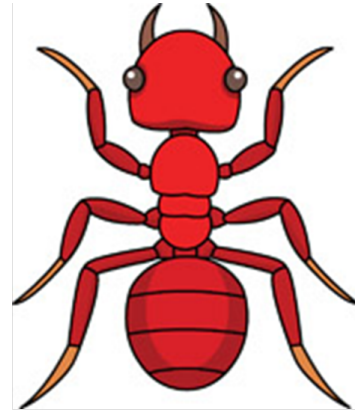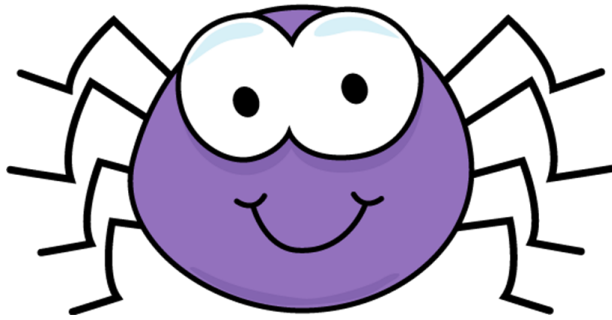
Figure 6-1 Objects used for human participants

The four objects used for human participants. Humans were instructed to smash the bugs as soon as they appeared on the screen. Locations were the same as the replication of Experiment 1.
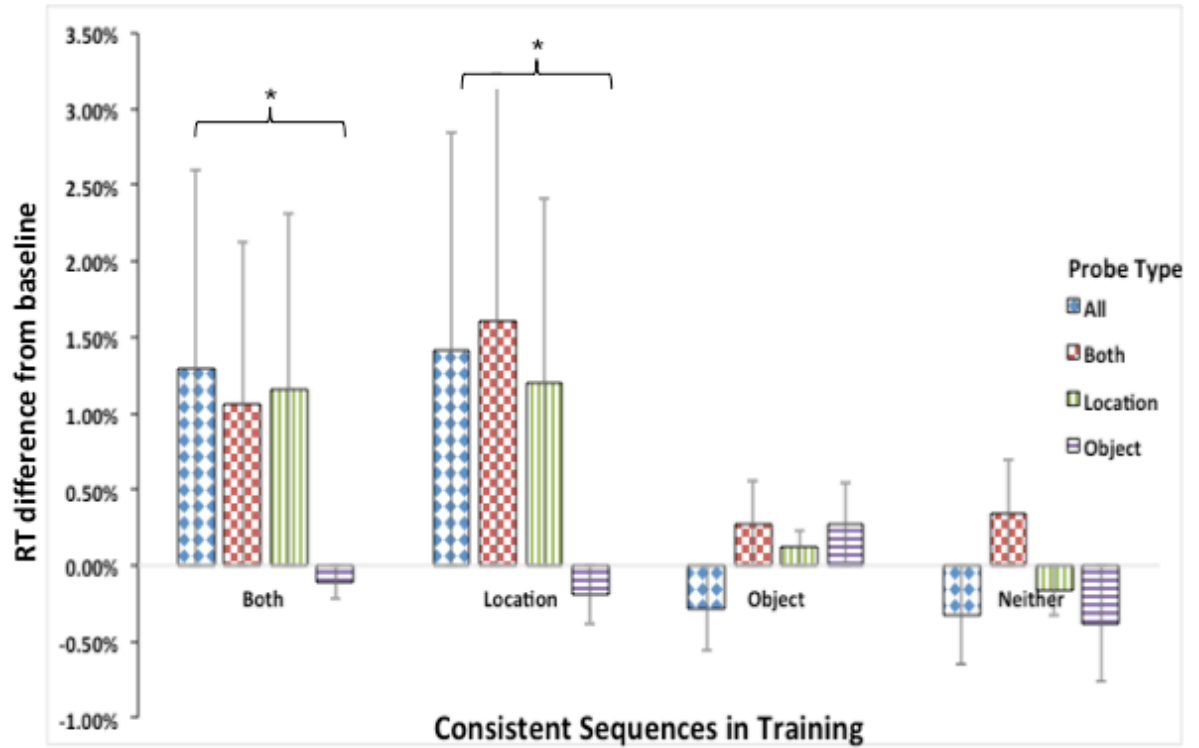
Figure 6-2 Human subject results.

Results from human subjects as percent change from baseline. Training was similar to Experiment 1. Error bars show the Standard Error of the Mean (SEM).

7. GENERAL DISCUSSION

This work found several novel and interesting results. First was the finding that the incidental learning of object and location order was possible with object sequence encoding in pigeons, a result, which should allow for further research on object and location pattern learning in animal models. As phylogeny reflects ontology this research can be used to help understand pattern learning in early development. As most past research had explicitly stated what was to be learned it only offered limited insight into how humans may encode such patterns. The task used here had no incorrect options, and only one location was available at a time. As such, no knowledge of the sequences was ever required for accurate performance. However pigeons encoded the sequences of objects as well as locations, indicating that this model may inform implicit and incidental learning.

The five different training conditions used allowed for the results of each training condition to be placed in context with other similar exposures. This allows the results to be better understood. For instance, the training conditions which lead to the object identity being encoded may have a direct interaction with how object-location information is utilized in responding. In manipulations in which the Object Consistent group responded differently to breaks in the sequences occurred no object or location binding was detected. As changes in the salience of features is known to alter what aspects of a task are learned, this is of little surprise. As interaction with an object increased, the importance of that object's identity

may have increased as well. However this led to less time spent moving or scanning the whole screen, perhaps decreasing the salience of the locations used.

Binding

This work found some of the first evidence for object-location binding in birds. Subjects in three different studies displayed a greater response time cost to probe trials which broke object-location binding after training in a Both Consistent condition. However, simple experience with object-location pairings was insufficient to create this effect. Several reasons for this were presented and further work should attempt to explore what aspect of the Both Consistent training allowed this effect to be seen. It is entirely possible that the subjects in the Binding Consistent group did in fact learn the object-location pairings but approached the task differently and did not display a response time cost.

The effects of the sequential aspects of training could be looked at through several different studies. One important aspect of the training to identify is whether the object and location must have attention allocated to them before the object appeared in order for binding to occur, or if it is simply the dependable structure of the trials. To address this question, half of the presentations could occur at a dependable time and location while others alter. For example presentations 1 and 3 could be fixed while presentations 2 and 4 alternate their position within the sequence across trials. This would allow for the location on the retina to change between trails, but attention to be preemptively allocated. If retinal location consistency is required for object-location binding, further work should be done to investigate how such locations' consistency effects visual processing in the avian system. Pigeons may process information differently depending on which fovea received the information (Ortega, Stoppa, Güntürkün, & Troje, 2008). However these studies were

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looking at visual concept learning and have had many alternative explanations, as well as conflicting results (Cook Lab, unpublished).

The details of what causes object-location binding to occur in pigeons may be useful in understanding why so many procedures fail to find it in avian models. One possible explanation is that in many procedures the same objects are re-used and the location identity is only dependable within a trial. This would lead to the bird learning that objects can move or that many objects may appear in a given location over sufficient time. One way to investigate what aspects of this disrupts object-location binding, as well as answer the question of what is binding to what would be fairly simple. Two training conditions could be maintained; one in which there are four locations and eight objects, each object only appears at one location but each location has two objects, either of which may which utilize the space. The second training condition would have eight locations and four objects, with each object having two locations but each location only having one object. If binding occurs in one of these training conditions but not the other, researchers could determine if locations become bound to objects or if objects become bound to locations.

Object sequence learning

Both avian and human subjects did not have an increase in response time when the order of objects was disrupted under normal training. However, with increased exposure time to the object on each presentation through a VR3 schedule of advancement, avian subjects did display evidence for having encoded the order of objects. Additionally, when both the order of objects and the order of locations were consistent, avian subjects had an increase in response time to disruptions of the objects' sequence. However this was primarily attributed to breaking the object-location binding. As object identity is less useful

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in optimizing the response movement to the goal, it is not surprising that this task may have had difficulty detecting any object sequential encoding. However, the importance of the object identity in the Both Consistent training condition suggests that pigeons are capable of using such information in their responses. That object identity is a less salient part of these procedures is particularly interesting. The object's presentation is what cues the possible availability of a food reward. It seems odd that these clear cues did not have a stronger association with the reward. It could be that the objects were all treated as equally likely to be rewarded and through the randomization of the location order, the birds generalized between one and the next.

Comparisons with humans

The differences between our human subject study and those with pigeons allow us to examine several interesting possibilities. The most obvious is the effect of verbal instructions and encoding of the task. While we did not specifically test if pigeons had explicit knowledge of the pattern, humans were able to report the rules of the training sequences they experienced. However, when asked what they were doing, they reported that they were only touching the locations as quickly as they could after the object was presented. Pigeons may have similar explicit knowledge of the sequences. Though the birds displayed response time increases to the changes in the object order only when object-location binding was disrupted and not when it was maintained, this could reflect a different understanding of the 'instructions' rather than different learning.

Limitations

There are a few key limitations in the interpretation of this work. First, all experiments except those done on humans and Experiment 3 with the Binding Consistent

training, used the same subjects. After the VR3 advancement training object and location binding never recovered. It is difficult to tell how much the past training affected the response in the subsequent studies. Also, Experiment 4, which attempted to examine the causes of interference produced on probe trials, was unsuccessful. This information may be key for identifying what aspects of the sequential learning are necessary for object and location binding to occur as well as to identify if the delays in responding on other conditions are due to prospective or retrospective interference.

We never tested whether pigeons were aware of the patterns presented to them. These tasks were presumed to be primarily implicit tasks as they are with many humans. However, due to both the smaller and more consistent sequence set, it is possible that birds memorized the sequences in training. Though there was no cause to learn the pattern, it would greatly change interpretation of results. A follow-up study could offer birds a new type of probe trial in which multiple objects were presented at many locations. This would allow birds to select the stimulus, which they most associated with food at this point in the sequence. The results from these experiments would be offering significant finding in the implicit and incidental learning literature.

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