

UNRAVELING THE COGNITIVE MAP: A ROLE FOR
FEATURE-POSITIVE DISCRIMINATION IN SPATIAL SEARCH

by

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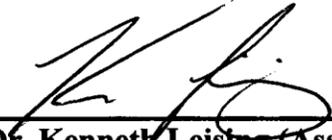
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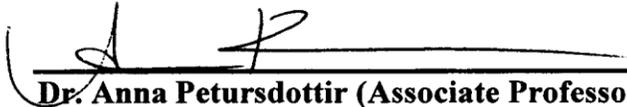
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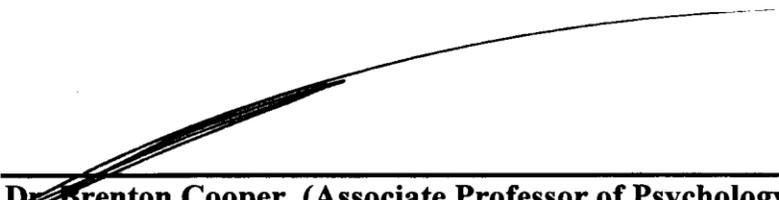
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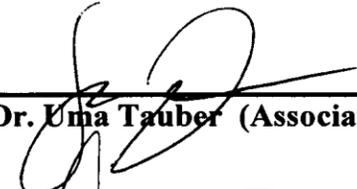
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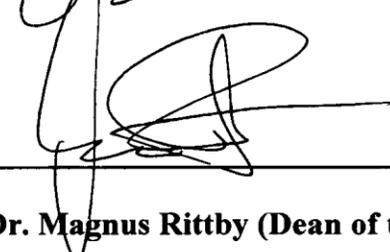
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Sincerely,
Chad

TABLE OF CONTENTS

Acknowledgments.....	ii
List of Figures/Appendices.....	v
Background.....	1
Associative Spatial Learning in Animals.....	10
Associative Spatial Learning in Humans.....	15
Feature Positive (FP) Discrimination.....	16
FP Discrimination in Animals.....	18
FP Discrimination in Humans.....	21
FP Discrimination during Spatial-Search tasks with Landmarks.....	23
Summary/Hypothesis.....	30
General Measures.....	30
Series 1: FP Discrimination of Landmark Properties during Spatial Search.....	29
Experiment 1	31
Intro.....	33
Method.....	31
Results.....	37
Discussion.....	41
Experiment 2	41
Intro.....	41
Method.....	42
Results.....	44
Discussion.....	46
Series 2: FP Discrimination of two types of Landmark Properties in a Small Scale Task.....	47
Experiment 3	49

Intro.....	49
Method.....	50
Results.....	52
Discussion.....	54
Experiment 4	55
Intro.....	55
Method.....	56
Results.....	60
Discussion.....	62
Series 3: FP Discrimination of two types of Landmark Properties in the Open Field	63
Experiment 5	64
Intro.....	64
Method.....	65
Results.....	68
Discussion.....	71
Experiment 6	71
Intro.....	71
Method.....	73
Results.....	75
Discussion.....	78
General Discussion.....	79
Appendices.....	86
References	91
Curriculum Vita.....	
Abstract.....	

LIST OF FIGURES

Figure 1: Associative Testing of Spatial Search.....	12
Figure 2: Apparatus 2D Touch Screen (Animals), 2D Monitor (Humans).....	25
Figure 3: Leising et al. Ruprecht et al. Procedure.....	26
Figure 4: Experiment 1 and Experiment 2 Procedure.....	35
Figure 5: Experiment 1 and 2 Results: Magnitude.....	37
Figure 6: Experiment 1 and 2 Results: Spatial Accuracy.....	39
Figure 7: General Procedure (Experiments 3-6).....	48
Figure 8: Acquisition Data- Experiment 3.....	52
Figure 9: Test Data- Experiment 3.....	54
Figure 10: Apparatus and Stimuli (Experiment 4)	55
Figure 11: Acquisition Data- Experiment 4.....	60
Figure 12: Test Data- Experiment 4.....	61
Figure 13: Apparatus and Stimuli (Experiment 5)	65
Figure 14: Acquisition Data- Experiment 5.....	68
Figure 15: Test Data- Experiment 5.....	69
Figure 16: Apparatus and Stimuli (Experiment 6)	71
Figure 17: Acquisition Data- Experiment 6.....	75
Figure 18: Test Data- Experiment 6.....	76

LIST OF APPENDICES

Appendix 1: Scripts for Human Search Tasks (2D and 3D).....	86
Appendix 2: Participant Debriefing Form and Questions.....	90

Background

More than two thousand years ago, Aristotle pondered the concept of an association. For instance, an animal may learn that food is *associated* with a certain sound or light, and expect food in the presence of such cues. Aristotle also contended that objects bound closely together in space tend to be associated together. If we encode some form of spatial information when we learn an association, a parsimonious account of spatial learning (i.e., using spatial associations to guide our search to a reinforcing target) might be that representations of space are built piece-by-piece from simple associations. In the last decade, there has been both empirical (e.g., Sawa, Leising, & Blaisdell, 2005; Leising, Garlick, & Blaisdell, 2011; Leising, Sawa, & Blaisdell, 2012), and mechanistic (Savastano & Miller, 1998; Balsam, Michael, & Yang, 2002; Miller & Shettleworth, 2007; 2008) support for the idea that spatial relations between events are encoded during spatial search in an automatic fashion.

We know considerably less about the nature of spatial relations encoded during conditional discrimination than we do about simple associations. During a serial feature-positive (FP) discrimination (a form of conditional discrimination), one stimulus, X, signaled the contingency between another stimulus (A) and a reinforced response (see Swartzentruber, 1995, for a review). In this example, A served as a discriminative stimulus that controlled whether or not your responses are reinforced, but in this case, A *required* X to signal whether one's responses will be reinforced. Landmarks are discriminative stimuli that control not only *if* (typically measured as the magnitude of responding), but also *where* responses occur. Landmarks inherently convey two sources of information: the direction (east), and distance (5 miles) of a target. If the discriminative stimulus, A, were to function as a landmark, it follows that the distance and directional information provided by a landmark might also fall under conditional

control. For instance, the direction you turn at an intersection (i.e., the LM) may be conditional upon whether you are approaching downtown from the north or the south.

To examine such a possibility, we could present participant's two trials in which X and Y (two diffuse backgrounds) precede a landmark, A, such that on each trial, A's spatial relation to a reinforced response is altered (i.e., $\leftarrow XA, YA \rightarrow$). After the training, we can ask two questions as to how the training was learned: (1) is the conditional cue or the landmark exerting control over the behavior (e.g., turn left vs. turn right)? In this example, X and Y would be perfect predictors of the landmark-response spatial relation, thus the landmark should be largely ignored minus a role for anchoring the response. (2) Do X and Y facilitate (e.g., turn on or off) responding to the landmark-response relationship or is the response controlled by the configuration of X and A? The answer to question 2 can be captured through the use of a transfer test (Bonardi, 1996), in which X and Y are paired with another landmark, like B for example (e.g., XB, YB). B's history was much like A's, however, B never required X or Y to facilitate responding to it (e.g., Bonardi, 1996). Strong responding to a test trial of XB indicates the conditional cue facilitated responding to the landmark-response relation, whereas, if responding drops considerably (i.e., fails to transfer), it would suggest that a solitary configuration (XA) was learned during training and it did not generalize to XB.

The following dissertation juxtaposed two cognitive mechanisms believed to play a part in spatial search behavior. The first mechanism is *spatial learning*, once thought to require a dedicated learning module separate from basic learning processes. Indeed, the systematic study of spatial variables within learning procedures has improved greatly improved our understanding of information processing (Cheng, 2009; Chamizo, 2002; Jiang, Olson, & Chun, 2000; Leising & Blaisdell, 2009; O'Keefe and Nadel, 1978; Olton, 1979; Tolman, 1948). After considerable

research, we know spatial information plays a critical role in learning (e.g., cue competition, causation, and navigation), memory (e.g., working memory subsystems, long-term memory encoding and retrieval), and embodied cognition. In the last decade, many basic learning effects (e.g., blocking, overshadowing, and conditioned inhibition) have been shown to operate during spatial learning (e.g., Leising, Garlick, & Blaisdell, 2011; Leising, Sawa, & Blaisdell, 2012; Rodrigo et al., 1997; Spetch, 1995; see Chamizo, 2002 for a review) and the notion of a separated spatial module has largely been abandoned (see Cheng, 2009). This has made room for models that posit a single general mechanism for learning spatial information (e.g., Miller & Shettleworth, 2007).

The second mechanism backing spatial search is the ability for organism's to form a representation of their environment with available cues (e.g., Knierim & Hamilton, 2011). This ability involves the mechanism of associative learning, and presumably, conditional discrimination (e.g., Molet et al., 2012). Unlike simpler instrumental cues (i.e., discriminative stimuli), conditional stimuli appear to control responding through a purely relational (or modulatory) association. Conditional stimuli are thought to facilitate responding in the presence of a discriminative stimulus, but do not require any direct connection to the desired outcome and do not directly elicit the target response. As a result, conditional stimuli exhibit unique properties, such as transferring to other discriminative stimuli (generalization) and resisting degradation of their relational nature to the target. These properties have led many to encourage "...the use of occasion setting (conditional) principles to augment associative theory in providing explanations of complex acquired behavior, particularly choice behavior" (Miller & Oberling, 1998, pg. 4).

This dissertation was concerned with the role of conditional discrimination in aiding

spatial search through the alteration or unlocking of spatial information relevant to nearby targets. In particular, this research investigated (1) under what conditions conditional discrimination develops between conditional stimuli and landmarks, (2) what types of spatial properties are best modulated by conditional stimuli, (3) what kind of information (general/spatial) is optimally encoded by organisms encountering a conditional stimulus, and (4) what conditions affect transfer of conditional information to other landmarks.

Associative Mechanism of Spatial Learning

It has long been the goal of experimental psychologists to propose an integrative model for spatial learning. All mobile vertebrates make daily navigational decisions within their unique environment (e.g., flat desert, dense rainforest, or ocean floor), whether it is approaching a food patch or evading danger. Behaviorists have long sought to parsimoniously model spatial behavior that spans a diverse array of species and environments, such as seeking a model that describes an organisms' ability to predict biologically significant events following pairings of initially neutral signals with those events (i.e., associative learning). It appears associative learning is a remarkably general phenomenon that has been found in a diversity of species, from humans to honeybees (e.g., Bitterman, 1996). The utility and flexibility of associative learning has led some researchers to examine the extent to which associative mechanisms are involved in spatial search, or specifically, spatial learning.

In principle, organisms learn their responses are followed by reinforcing outcomes (i.e., operant or instrumental conditioning), but also that crucial events close together in time or space, are associated together (i.e., associative conditioning). According to an associative theory (e.g., learning to associate a bell with food), individual cues that share a relationship with a reinforcing stimulus (i.e., the target stimulus) can be trained to by themselves to elicit an appropriate

response in respect to that discriminative stimulus. This was famously illustrated in Pavlov's dogs: a neutral bell, a conditioned stimulus (CS) was repeatedly followed in time by the presentation of food, an unconditioned stimulus (US) which evoked a salivation response. Of importance, the neutral bell was found, on its own, to elicit a conditioned response (CR; salivation) from the dogs (Pavlov, 1927). The bell was interpreted to have gained control over the conditioned response, a phenomenon referred to as stimulus control. Cues in nature rarely occur in isolation. Some cues overshadow one another, based on their perceptual salience, or attention grabbing abilities (Pavlov, 1927), while other cues block each other, based on the nature of their training history (Kamin, 1969). It became important for behaviorists to illustrate that these same principles are relevant when an animal builds a spatial representation of its environment, utilizing available visual cues that should presumably *compete* for control over search behavior (see below).

O'Keefe and Nadel (1978) revealed research that supported the dominant belief that a more habitual type of spatial learning (taxon) seemed to be a distinct process from more complicated spatial searching or mapping. O'Keefe and Nadel (1978) also described a more flexible and goal directed form of spatial learning termed the locale system, which they believed housed a cognitive map. The taxon system described what learning theorists refer to as stimulus-response (S-R) learning. During S-R learning, a beacon (i.e., the stimulus very near to the target; S) paired closely in space to a biologically significant event (i.e., food or safety; the target) would elicit approach (the response; R), when the beacon was encountered in the future. The discovery of the target near a beacon would stamp in the S-R relationship, allowing for long habitual chains of spatial behavior to be strengthened (i.e., the daily commute to work becomes habitual after the behavioral chain is repeated). O'Keefe and Nadel recognized a role for

associative processes during taxon learning. For instance, devaluation or elimination of the target (i.e., extinction) caused a drop in spatially specific search behavior much like any other simple conditioned response. O'Keefe and Nadel (1978) were less willing to recognize a role for associative links in forming the cognitive map backing their locale system.

The locale system was originally described as being much more flexible, but also more complex, than the taxon system. The increase in flexibility came from constant updates as the animal navigated the environment from various directions and perspectives. As a pigeon searches an open-field for food, for example, O'Keefe and Nadel (1978) suggested that the pigeon formed a rich mental representation of the environment, or cognitive map, which was updated constantly with novel or changing conditions. Such a statement begs a testable alternative: perhaps distinct cues within the environment (e.g., a nearby landmark northwest of the food patch; a distal landmark southeast of the food patch) competitively contribute as independent sources we use to weigh and form a cognitive map, rather than being seamlessly integrated. We might test either alternative by altering the information value of a single cue, and observing changes in search accuracy in presence of each stimulus. If cues (landmarks) integrate across individual phases, regardless of whether other stimuli are separately modified, a general cognitive map would be supported. Conversely, if cues compete while building a cohesive map, modification of single stimuli might create perturbations to the spatial control of other elements, presumably because each stimulus makes its own finite contribution to the discriminative control of spatial search. O'Keefe and Nadel's (1978) distinction of two systems spurred decades of research. Some of the tenets of their original hypothesis have survived rigorous evaluation; some of them have not.

The most recent incarnation of a two-system theory of spatial cognition was postulated by Neil Burgess (2006; 2008). Burgess argued that learning about landmarks and beacons is supported by egocentric representations (i.e., representations from the perspective of the searcher; taxon learning) while learning about environmental properties (e.g., boundaries) is supported by allocentric representations (i.e., representations from the perspective of the total environment irrespective of the searcher's orientation). Burgess explained that "allocentric spatial coding" is the encoding of the Euclidian spatial relations of distance and direction among objects in external space. For example, the relationship between the various pieces of furniture in your living room can be independent of any single perspective. In contrast, egocentric spatial coding is the encoding of the spatial relationship between the subject and external stimuli such as landmarks, which indicate the distance and direction of a target: for example, the spatial relationship between furniture in your living room as perceived from the kitchen.

Decades later, we have a modestly updated understanding of what O'Keefe and Nadel (1978) termed the locale system. The major departure Burgess made from O'Keefe and Nadel was that the allocentric representation suggested by Burgess was limited to environmental boundaries whereas O'Keefe and Nadel (1978) proposed that all features in the environment would be encoded into an allocentric cognitive map. Burgess additionally suggested the necessary translation of egocentric into allocentric and allocentric into egocentric. This interaction provided an opportunity for competition of visual features both at the time an allocentric relation is translated into behavior, as well as when lower level features of landmark representations are translated into allocentric maps. Investigation of such cue competition has been mostly conducted using standard associative tests such as blocking and overshadowing (see Leising & Blaisdell, 2009, for a review). Such investigations would be difficult to interpret

without an integrated model that describes a mechanism by which cues compete for control of search behavior.

Such an integrated model of allocentric learning was recently proposed by Miller and Shettleworth (2007). The model centered on two sources of information, a) the “features” of the environment (e.g., boundaries, corners, geometry) and b) discrete cues embedded within the environment (e.g., beacons, landmarks). The model proposed that like simple cues participating in classical conditioning, spatial cues in the environment compete for associative value. The higher the associative value a cue has, the higher its ability to elicit an appropriate conditioned response from the animal. Miller and Shettleworth’s (2007) model was fit for spatial learning in that geometric aspects of the environment (e.g., corners of the testing arena) are allowed to participate in competition for associative value along with the discrete landmarks. One particularly unique aspect of the model was the concept of “feature-enhancement”. According to feature enhancement, geometric aspects of the environment (e.g., borders and corners are ever present during search tasks that measure the encoding of landmarks) will most efficiently gather associative strength, potentially diminishing competition between landmarks. “Feature-enhancement” begs that spatial search studies targeting landmarks occur in environmental arenas of different shapes, sizes, and complexity as each element is free to build its own spatial control irrespective of the participating landmarks.

Focusing purely on the spatial information conveyed by the landmark, Ruprecht, Quintana, Wolf, & Leising (2014b) posited that spatial accuracy during search tasks is a function of the available landmarks’ 1) Proximity, 2) Stability, and 3) Reliability, in relation to the target location. *Proximity* is a pure measure of distance between a landmark and a target (e.g., Cheng 1989; Ratliff & Newcombe, 2008). *Stability* is the variance of a landmark’s vectors (distance and

direction) to the target across trials (e.g., Biegler & Morris, 1993). Finally, *reliability* is the probability reward will occur in the presence of a landmark, irrespective of its distance or direction in relation to the target. Reliability, therefore, is inherently non-spatial, and reflects contingencies encountered during training.

Focusing on the first determinant of spatial accuracy, *proximity*, Knierim and Hamilton (2011) argued that literature has long agreed that animals and humans use distal cues (called extramaze cues) as the most critical source of information for the use of mental representations of space. Part of this belief stemmed from historical reasons as researchers of spatial search often attempted to diminish the value of local cues (i.e., intramaze cues) to ensure that subjects were not using simple sensory responses in reaction to the nearby cues (i.e., landmarks, beacons, the boundary of the room or maze, etc.) Knierim & Hamilton (2011) critically argued that distal (extramaze) cues have a predominant role in setting the spatial orientation via their profound impact on head direction cell system. This assertion is critical to predictions I made for Experiments 3 through 6 which altered the type of spatial information that the more proximal (landmark) and more distal (background) cue provided to the organism about the spatial location of the target. Hamilton's perspective would argue that the more distal cue should provide reorientation information to the organism (head left vs. head right; directional) whereas the proximal cue should define specific spatial locations (the target is one or two locations away from the LM).

Below I review evidence that supports the notion that associative mechanisms contribute to allocentric representations in a piecemeal fashion. Investigations of this nature are not only beneficial to understanding the foundations of spatial learning, but also evaluating what we already know about simple associations in more ecologically valid settings (i.e., spatial search

settings vs. simple yes/no discriminations) that require organisms to evaluate, move, and reevaluate their location. Many models of associative learning describe the acquisition of response strength as a function of training and perceptual salience (i.e., the attention grabbing qualities of stimuli; e.g., Rescorla & Wagner, 1972). Real-time models of conditioning now include the role of time in cue-competition effects but do not incorporate elements of space. For instance, one model (Schmajuk, 2010) can account for 93% of general conditioning phenomena as they occur across the backdrop of time, but fails to incorporate any parameters that account for how close (distance), or in what direction a cue is from a reinforcing target in space.

Spatial learning is not a truly distinct process; indeed, it is difficult to separate it from our simple ability to mentally associate objects with one another. The following section reviews evidence for an associative account of allocentric learning via studies on landmark learning, integration, and competition.

Associative Mechanism of Spatial Learning in Animals. Using small-scale search tasks, we can assess the role of associative mechanisms in spatial search behavior by modifying the properties of landmarks. Landmarks encode at minimum, a direction and distance from a reinforcing target. They share a consistent spatial relationship to the target, much like the relationship a traditional CS shares with a US in time (e.g., Stimulus A, a tone, always occurs 5 seconds before food; landmark A always occurs 5 feet to the left of food; see Leising & Blaisdell, 2009, for a review). Based on pioneering work by Cheng and Spetch, there is convincing evidence that organisms utilize and integrate landmarks according to a vector-sum model (e.g., Cheng & Spetch, 1998). There is now a wealth of investigations on landmark based spatial -search coming from a variety of species, including pigeons, humans, rodents, and insects (Cheng, 1994; Cheng & Spetch, 1995, 1998; Kamil & Cheng, 2001; Spetch, Cheng, &

MacDonald, 1996; Spetch, Cheng, MacDonald, Linkenhoker, Kelly, & Doekson, 1997; Spetch et al., 1992; Spetch & Mondloch, 1993). One avenue of research investigating the role of associative processes in spatial relations involves altering the information value of landmarks across multiple phases of training (see Leising & Blaisdell, 2009 for a review). Three such procedures, overshadowing, blocking, and sensory preconditioning are summarized below as each phenomenon illustrates examples of associative tests being applied to landmark learning tasks. These experiments set up the logic for the application of conditional discrimination tests to landmark learning search tasks.

Overshadowing during spatial search. Pavlov (1927) originally reported that more intense auditory stimuli overshadow less intense ones in controlling food-related responses. Thus, overshadowing captures the concept that perceptually *salient* cues should acquire more associative strength at a higher rate because of their ability to capture more attention from the organism. Recalling the vector-sum model, the concept of overshadowing readily applies to space. According to other research on spatial learning (Chamizo et al., 2006; Cheng, 1992; Spetch, 1995), proximal landmarks are very salient, whereas landmarks more distal are not as salient. It would not be surprising that proximal landmarks tend to overshadow behavioral control by more distal ones, however, the possibility had not, until recently, been fully examined during a spatial search task.

Leising, Garlick, and Blaisdell (2011) reported an overshadowing effect in the spatial domain using a search task with pigeons. Subjects were given a linear arrangement of eight visually defined circles on a touchscreen-equipped monitor, and were required to peck the circle that led to reward. The landmarks were patterned circles that filled one (Phase 1) or two (Phase 2) of the response location disks themselves (Figure 1a). Across trials, landmarks shifted

positions in the array but always shared a consistent spatial relationship with the target.

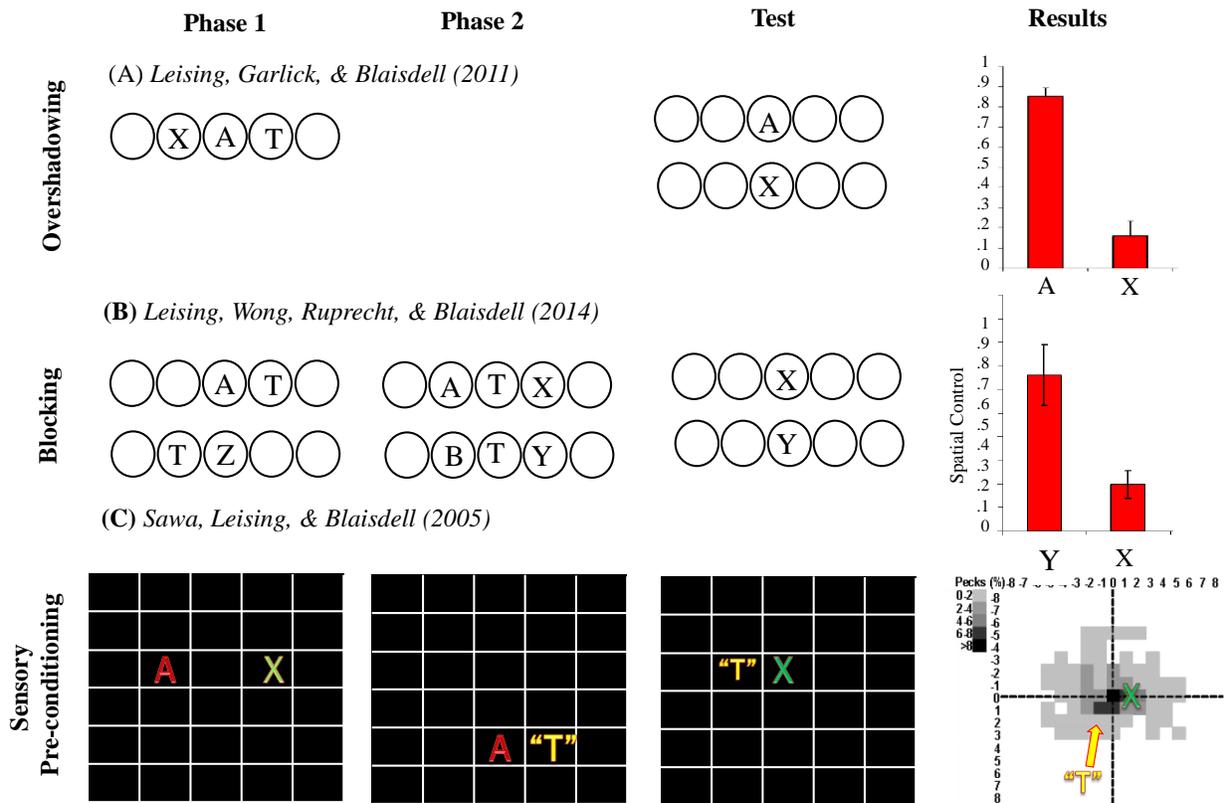


Figure 1 shows the procedure (left 3 columns) and results of Leising et al., 2011 (overshadowing in a spatial task; top row), Leising et al., 2014 (blocking in a search task; middle row), and Sawa et al., 2005 (sensory pre-conditioning during a search task; bottom row).

In Experiment 1, subjects received compound trials of AX with A closer to the target than X, and trials of LM Y, with Y bearing the same distance from the target as did X. At test, LM X exhibited poorer spatial control than did LM A and LM Y when tested alone (see Figure 1A). A second experiment using the same procedure demonstrated that this overshadowing effect could not be attributed to generalization decrement, a common alternative account of overshadowing effects (e.g., Pearce, 1987). Thus spatial overshadowing in this procedure likely reflected an elementary associative learning phenomenon and not an integrated locale system. O’Keefe and Nadel’s locale system would have represented both A and X in a cognitive map irrespective their distance from the target. Cue-competition between LMs based on salience is evidence for

associative learning; at test, performance with each LM would have been similar. Additional evidence was required to illustrate if competition between landmarks could be attributed to differences in training history.

Blocking during spatial search. The blocking effect illustrates that competition for associative strength is influenced by a cue's training history, as well as the training history of cues that we observe in compound with them (Kamin, 1969). In a typical blocking procedure, A is paired with a US in Phase 1, and then a compound of A and a second cue, X, is paired with the US in Phase 2. Responding to X on a subsequent test is diminished relative to responding to CS X in a control group that lacked the Phase 1 A-US pairings, or received random presentations of the US in relation to A (Kamin, 1969; Moore & Schmajuk, 2008). One explanation for this effect is that A gained substantial associative strength in Phase 1, rendering X in Phase 2 a redundant, less relevant cue. The observation of blocking in the spatial domain is essential to an associative account of spatial learning, as much of what we understand about cue competition centers around the training history of cues.

Leising, Wong, Ruprecht, & Blaisdell (2014) demonstrated blocking among single landmarks in pigeons with an analogous touchscreen procedure. In Phase 1, each trial consisted of one disc lit with a color designating LM A and subjects were reinforced for pecking at the module or disc (the target) one unit to the side of LM A or LM Z (Figure 1b). In Phase 2, LMs A and X (a different color) together signaled the location of the hidden target with LM A bearing the same spatial relationship with the target as in Phase 1, and LM X located at the symmetrically opposite side of the target from LM A. As a crucial control group, LMs Y and B also signaled the target at the same redundant spatial location. At test, LM X exhibited poorer spatial control than did LM B. Blocking of the magnitude of behavior can occur between

individual landmarks. The spatial control of responding, moreover, was sensitive to the training history of cues, causing considerable interference to the learning or expression of redundant landmarks (see Stahlman & Blaisdell, 2009, for a demonstration with rats in the open field). The spatial control of animals search behavior is sensitive to two forms of cue-competition when cues are paired with a hidden target location. Often, cues are encountered prior to attaining a reward or the discovery of a hidden target. In associative learning, a sensory preconditioning procedure has been used to evaluate the concept that associations may form between neutral cues in the absence of a US (e.g., we associate trees with birds without the tree having to provide us food, or the birds violently attacking us). Therefore, a final aspect of associative learning to be assessed in the spatial domain was whether cues close in space become associated together, irrespective of whether or not a reinforcing food target was currently present.

Sensory Preconditioning during spatial search. Evidence for sensory preconditioning is vital to the concept of an association, first posited by Aristotle that cues co-occurring in time are associated together. During sensory preconditioning, two cues (e.g., A and B) are paired, initially with no food, followed, by a second phase where only B receives pairings with food. After training, the important effect is an observation of elevated responding to A, which indicates that A and B were associated prior to any food delivery. Sensory preconditioning is best interpreted from an S-S learning perspective, the two stimuli were linked together in time, therefore, when B is paired with a reinforcing outcome in Phase 2, A is able to elicit some responding at test, based on the fact that A and B were encoded within the brain (S-S) during Phase 1.

Sawa, Leising, and Blaisdell (2005) sought to capture the phenomenon of spatial sensory preconditioning, utilizing a similar touchscreen search task (Figure 1c). In Phase 1, pigeons

received compound presentations of LM A and LM X on some trials and of LM B and LM Y on other trials. LMs A and B served as first-order landmarks (i.e., LM1) while LMs X and Y served as second-order landmarks (i.e., LM2). Each element of the compound maintained a stable within-compound spatial relationship but the screen location of the compounds varied across trials (see Figure 1C). In Phase 2, pigeons learned to find the hidden target in the presence of LM A and LM B. The hidden target always bore the same spatial relationship to LM A, but not LM B. At test, pigeons received non-reinforced tests of LM X. Because the X-A and A-Target spatial relationships (i.e., the target is *to the right* of A) were stable during training, integration of these maps should have lead pigeons to search to the immediate left of LM X at test. Consistent with the predictions of spatial integration, the frequency of searches during tests of LM X were clustered around the response location to the left of LM X, indicating that pigeons had encoded the X-A and A-Target spatial maps and integrated them to allow computation of an X-Target map. Capturing sensory preconditioning in a spatial task prompts continued investigation into the extent that conditioning phenomena operate during landmark-based search tasks in animals.

While the demonstration of these effects in the spatial domain is by no means comprehensive, the findings summarized above point to a clear role for associative processes in the formation of allocentric representations, particularly during small-scale search tasks. It is important to also examine the generalizability of this evidence to our own species.

Associative Mechanisms of Spatial Learning in Humans

The role of associative mechanisms in spatial learning with humans, in comparison to animals, is far less clear. The discussion of human spatial learning, like animals, is large in scope, therefore, it is best to constrain the review to the investigation of what processes help

build allocentric representations (i.e. cognitive maps) of one's short-scale environment.

Interestingly, there are reports both in favor and against integration of cognitive maps in humans.

In favor of cognitive maps, Molet, Jozefowicz, and Miller (2010) showed in a 2D search task that humans could integrate or superimpose two separate spatial relationships by linking a common element (i.e., spatial integration) during sensory preconditioning, much like Sawa et al. (2005) illustrated in pigeons (see above). In addition, Molet, Bugallo, and Gambet (2011) were able to illustrate this same integration in a 3D environment, using a 4 x 4 array of treasure chests enclosed inside a homogenous square arena. In both the 2D and 3D tasks, participants chose the position associated with a superimposed spatial map, moreover, requiring the participants to employ a single-choice method helped eliminate the possibility of generalization across phases (see Sawa et al., 2005). Molet et al.'s (2011) demonstration of spatial integration in 3D search is particularly striking, as the evidence amassed against spatial integration in humans has been obtained primarily via 3D search tasks.

Feature Positive Discrimination

Though conditional stimuli do not resemble conventional classical or instrumental associations, they have been found to exhibit many basic learning effects. When procedures investigating the acquisition of conditional discrimination incorporate this structure, conditional stimuli are found to be subject to basic learning effects (e.g., Shanks, 2010). Despite the importance of spatial information in generating an appropriate response, there has been little research investigating whether spatial information can be controlled by a conditional stimulus and the extent to which spatial control by a conditional stimulus will transfer to other targets.

Serial Feature-positive Discrimination. A popular treatment for investigating conditional discriminations is the FP (Feature-positive) discrimination. During FP

discrimination, one stimulus, the *feature* (i.e., conditional stimulus), hierarchically modulates the information value of a lower-order stimulus. In an operant FP discrimination (e.g., Honey & Watt, 1998; Baeyens et al., 2001), the organism learns that a feature signals when responses are reinforced in the presence of a discriminative stimulus, and that an absent feature means no responses are reinforced in the presence of that same discriminative stimulus. At a minimum, this training features two trial types: XA+ and A- (i.e., in the presence of XA+, organisms learn their responses are followed by a reinforcer; in the presence of A-, responses yield no reinforcer). Successful acquisition of a FP discrimination is evidenced by an elevation of responding only on trials of A that are preceded by X in comparison to A alone trials. The FP discrimination was first introduced with pigeons using a match-to-sample task (Cummings & Berryman, 1961), in humans (Sidman, 1971) and then using an operant lever-pressing task with rats (Holland, 1983). More recently, it has been utilized with human participants in a video game preparation (Baeyens et al., 2001; see below).

During serial FP discriminations, it is widely believed that X serves to modulate information about A, independent of X's own relationship to the reinforcer (e.g., Schmajuk & Holland, 1998; Bonardi & Jennings, 2009). The independence of X to the basic A→US contingency, for instance, can be tested by extinguishing X after FP discrimination training (e.g., Rescorla, 1986). If post-extinction responding to XA remains high, it is generally taken as evidence of X's unique modulatory relationship to A and the reinforcer (Holland, 1983; Holland, 1996). An alternative, configural-based explanation (Pearce & Hall, 1980; Pearce, 1987; 1994), describes learning of XA as an entirely distinct compound from X or A alone; thus, extinction of X in isolation would deal little damage the original compound's excitability as X is now discriminated as an entirely separate signal from XA. Thus far, it has been difficult to parse the

hierarchical and configural accounts for solving conditional discriminations apart (e.g., Bonardi, 2012). During FP discriminations, however, it is interesting to note that, “many of the conditions which support hierarchical [conditional] learning are contradictory to the conditions that support configural learning” (Miller & Oberling, 1998, p. 7).

Recall presenting a participant with two trials: XA+ and YB+. A second measure of X’s conditional properties can be implemented by pairing the conditional cue X with a second stimulus, B, which was previously trained with a different conditional cue, Y. This transfer test measures the transfer of control from a trained compound to a novel compound (e.g., Bonardi, 1996; Exp. 2). The general finding is that during transfer tests, conditional cues behave differently from simple excitatory cues, in that their transfer potentials are limited and selective. Should XB elicit just as much activity as XA? It depends; activity during a transfer trial, XB, has been found to depend on 1) the discriminability of the two trial types, and 2) the training history of X and B. Concerning the former, Bonardi (1997) found that B was susceptible to modulation by X, to the extent that the organism could discriminate XB from the original XA trial, thus, the more animals discriminated XB from XA in training, the stronger responding transferred to XB. Concerning the latter, B’s ability to be set by X, was determined by its history as an ambiguous target (Swartzentruber, 1995; but see Schmajuk & Holland., 1998). In sum, these transfer tests (validated by previous research) can be used to test whether many of the same determinants of general FP discrimination (i.e., discriminability of the two comparison conditional stimuli; training history of both the comparison conditional cues and lower-level stimuli) exerted similar control on the spatial distribution of responding.

FP discriminations in animals. The study of FP discriminations has enjoyed a long history within the animal literature (see Swartzentruber, 1995 for a review). Holland (1995), for

example, utilized an FP procedure and both of the aforementioned transfer tests to examine the properties of a conditional cue in an *operant* (response-required) FP discrimination. During training, rats received training with two pairs ($X \rightarrow A+/A-/Y \rightarrow B+/B-$), as well as exposure to a third stimulus (C+) trained without a conditional cue. Holland (Experiment 1) tested whether a conditional cue (X) would transfer to a stimulus (B) trained in a separate compound relationship (YB), transfer to a stimulus (C) with no previous pairings with a conditional cue, and whether control by the conditional cue would survive extinction treatment (X-). Transfer tests showed good transfer of X to B, weak transfer to C, and no disruption of control by X following extinction. Close inspection of these data indicate that transfer of control by the conditional cue X to B was incomplete. This finding is consistent with much of the literature on FP discriminations and suggests the conditional cue acts to facilitate the flow of activation between the specific stimulus and outcome with which it was trained. Given a conditional cue controls *if* a subject will respond in the presence of the target (*yes* or *no*), we know less about how a conditional stimulus controls *when* and *where* a subject responds. The *when* of responding during FP discriminations, however, has received some attention in the animal literature and is worth discussing as time discrimination serves as an analogue to spatial discrimination.

FP Discrimination and Temporal Processes with Animals. Studies targeting timing during FP discrimination have found that the effectiveness of X in facilitating responding to A is determined both by its contingency and its temporal contiguity with A (Bonardi & Jennings, 2007; Holland, 1986, 1998; Holland et al., 1997; Miller & Oberling, 1998; Nakajima, 2009). Holland, Hamlin, and Parsons (1997) were the first to parametrically vary a temporal factor during FP training. Rats trained with a 5-s or 25-s $X \rightarrow A$ interval were then tested with $X \rightarrow A$ intervals ranging from 0 to 55 s. Transfer performance was maximal at the trained interval and

worsened with greater discrepancy between training and testing interval in an approximately scalar manner (between the 5-s and 25-s groups). More relevant to the current experiments, temporal control by A has been shown to come under the control of a conditional cue. Bonardi and Jennings (2007) trained rats to expect food 6-s after A when preceded by X and 30 s after A when preceded by Y. Transfer tests, in which the gap between the conditional stimulus and discriminative stimulus was extended from 5 to 29 s, demonstrated that timing was controlled by the conditional cue. In sum, temporal relationships encountered during training can influence responding in FP procedures.

FP Discrimination and Spatial Processes with Animals. Much less research has investigated whether a conditional cue can control *where* a subject responds. Research on spatial processing during FP tasks is less often framed as “conditional cue control” and is often investigated via the experimental *context* (e.g., the room, an experimental chamber) modifying the information value of a lower-order stimulus. For instance, Eacott, Easton, and Zinkivskay (2005) reported a task which resembles an FP paradigm, except for the exclusion of any nominal outcome. Rats were exposed to two items (A and B) in different positions within an E-maze in Context X (e.g., dark, solid surface). Previous training had established an expectation that the objects would switch positions when a second trial was conducted in a different context (Y). The start location was the center arm and the items were positioned such that they could not be seen from the long alley connecting all of the arms at the end of the start arm. In between the first and second trial, the rats were exposed to one of the items in their home cage (i.e., habituated). Upon return to the second context (Y), the rats’ innate preference led them to choose the arm with the non-habituated item. The context, therefore, modulated the response decision (left or right) that lead to the non-habituated item.

In addition to reports of contextual control, it has been readily demonstrated that animals can alter their responses in a spatially specific way during conditional discrimination (e.g., in rats: Bussey et al., 1996; in chimpanzees: Martinez & Matsuzawa, 2003). However, it bears to mention that often such alterations between two responses (respond left vs. respond right) aren't inherently *spatial* in nature. For instance, Bueno and Scaduto (2008) trained operant FP discriminations to rats that were given the choice of pressing a left or right bar. The location of the correct lever on any given trial was therefore conditional on the combination (e.g., X-A-Right or Y-B-Left). After 100 training sessions, the rats were presented transfer tests (X-B and Y-A). Transfer of responding was less than complete and response generalization, measured by a higher alternation between each lever at test compared to training was reported. Bueno and Scaduto (2008), however, were unable to isolate whether general interference (induced by the specificity property of FP discrimination, see Bonardi, 1996 for details) or conflicting spatial information drove the generalization of responding between the levers at test (see Ruprecht et al., 2014b, for a possible dissociation of these two forms of interference in humans).

FP discrimination in Humans. FP discrimination studies have less of a history within the human learning literature. Participants often complete video game or computer tasks modeled after animal preparations. Bayens et al. (2001), for instance, trained college students that X (a computer image) modulated whether A (an enemy's laser-shield) was malfunctioning during a Martian attack game. On trials in which X preceded A by several seconds (e.g., $X \rightarrow A+$), participants learned to emit more blaster shots at the invading pack of Martians than on trials when A was presented alone (e.g., A-). Baeyens et al. found that FP discrimination was stronger when X preceded A in time (serial, $X \rightarrow A+$) than when X and A appeared simultaneously, a finding commensurate with results from the animal literature (Holland, 1996). Second, extinction

of X did not disrupt responding to the sequential $X \rightarrow A$ compound, confirming that the extinction test was a viable method for testing FP discrimination by X in humans as well. Finally, extinction of X had no effect on responding to the simultaneous XA compound, a finding inconsistent with the animal literature (Pearce, 1997). The third finding indicated that humans, more so than animals, employed a relational (conditional) approach to learning discriminations even when stimuli were paired simultaneously.

FP Discrimination and Spatial Processes in Humans. There has been at least one experiment, to my knowledge, that examined an analogue to FP discriminations via contextual control of spatial responding. The entire context served as the conditional cue, modifying the spatial relation of the landmarks that occurred within in. Molet et al. (2012) trained human participants in a 3D virtual environment to locate treasure within an area of response locations. In the first phase, participants learned the spatial relationship between two stimuli (A and B), which differed across two contexts (X and Y). Although the stimuli shifted position across trials within contexts, the spatial relationships remained constant in each context. In Phase 2, participants learned the relationship between A (with B absent) and a hidden treasure located in one of the response locations. At test, participants were given trials with B alone in either context X or Y. This clever test evaluated whether the context would selectively retrieve the original spatial relationship between A and B, which would guide the participants to respond at different locations depending on the context in which B was presented. Participants predominately searched at the location relative to B in each context that was consistent with the A-B spatial relationship learned in that context (see Molet et al., 2008 for a similar demonstration in the temporal domain). Both similarities and difference have been found between FP discriminations with contexts or punctate cues serving as conditional stimuli (Hall &

Mondragon, 1998; Yoon, Graham, & Kim, 2011). The use of contexts combined with the absence of other commonly used tests of conditional control (e.g., transfer tests) indicated the need for more research.

FP Discrimination during Spatial-Search tasks with Landmarks

Colleagues and I have investigated FP discriminations during spatial search tasks in experiments with both pigeons (Leising, Hall, Wolf, & Ruprecht, 2015) and humans (Ruprecht et al., 2014b). Much like the touchscreen experiments detailed earlier (e.g., Sawa et al., 2005; Leising et al., 2008; 2011), pigeons pecked a touchscreen array for grain (top left of Figure 2), whereas humans responded on a very similar array during a computer game to uncover hidden treasure (top right of Figure 2). As the bottom of Figure 2 illustrates, pigeons and humans were presented with a colored background display (i.e., conditional cue X) followed a few seconds later by a patterned visual stimulus (i.e., LM A) positioned within one of eight linearly arranged response discs. The landmark signaled which of the remaining response locations was designated as a hidden target, but only on trials in which the target was preceded by the conditional background (Figure 3). Once a number of FP spatial discriminations had been trained, subjects and participants were submitted to various transfer tests that assessed which individual component of the discrimination (background vs. landmark) determined (a) the general *magnitude* of responding, and (b) where the target was expected along the array (*spatial accuracy*).

Experiment 1 (Leising et al., 2015 and Ruprecht et al., 2014b) demonstrated a spatial-search task in which spatial control of responding was directly controlled by a landmark, and generally modulated by a conditional stimulus (see top of Figure 3). For pigeons, the transfer tests indicated that the conditional cue enhanced responding to a landmark above that of

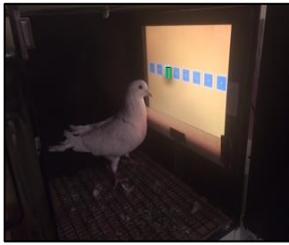
responding to the landmark alone, but to a lesser degree than the trained FP spatial discrimination. This is consistent with much of the literature on conditional control (see Schmajuk & Holland, 1998 for a review). The same pattern of results was also found when evaluating the spatial accuracy of responding. Furthermore, analysis of the spatial distribution indicated that the percentage of pecks at the target during novel-landmark and background-only tests were at chance levels.

Responding on Transfer trials (in which a previously trained background and landmark were placed into a novel configuration) was below that of the trained FP spatial pairs, indicating that the magnitude is not simply the summation of direct connections between the background-landmark and landmark-target associations. Rather, as predicted, magnitude was largely controlled by the conditional cue facilitating responding to a specific landmark-target association. Though aspects of the design discouraged configural learning, the deficit on transfer trials may have reflected learning of a background-landmark configuration and subsequent generalization decrement during the novel background-landmark pairing (see general discussion for more details). The landmark itself appeared to generate no responding via a direct landmark-target association, as evidenced by little-to-no responding on landmark-alone trials. Secondly, evaluation of the spatial distribution of responding on the trained FP Spatial and novel background-landmark test trials indicated that, as predicted, the landmark primarily controlled spatial search.

The design of Experiment 1 of Leising et al. (2015) was separately implemented (with some mechanical changes) to investigate human spatial search. Ruprecht et al. (2014b) reported the same disruption in magnitude and spatial control by a conditional cue when a novel landmark was introduced. One large obvious difference between species was illustrated by the magnitude

of responding to novel conditional cues and novel landmarks.

Apparatus



Pigeon Touchscreen



Human Touchscreen

General Procedure

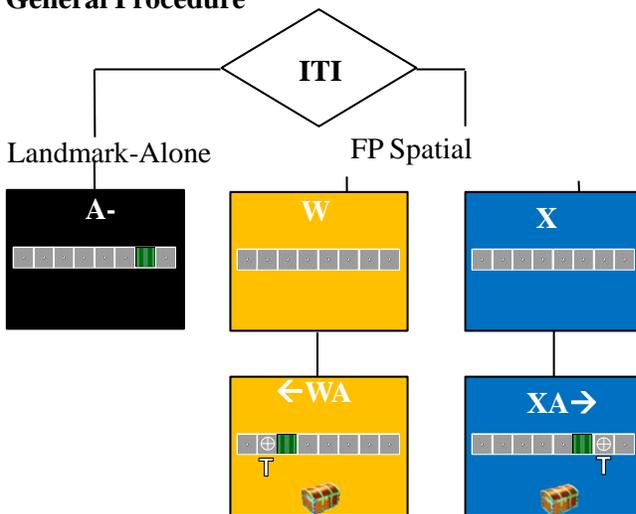


Figure 2 shows the touchscreen apparatus for pigeons (top left) and humans (top right). The bottom shows the general procedure. The landmark A, for example, shared a consistent spatial relationship (left vs. right) to the target location when preceded by the conditional cue W or X respectively. This apparatus and procedure was used in Leising et al. (2015) and Ruprecht et al. (2014b). The pigeon touchscreen (pictured left) was used for Experiment 1; the human touchscreen for Experiment 2 and Experiment 3

Both species showed a disruption in magnitude between transfer and the trained background-landmark pair but only humans showed similar spatial control during both test trials. In other words, although humans were less confident (fewer overall responses to the target) during transfer tests, the responses they did emit indicated their knowledge about the landmark-target association encountered during training. This may have reflected human's greater propensity for relational learning, or simply that pigeons are more likely to be disrupted by small changes in stimulus conditions. In sum, the initial tests demonstrated that better spatial and temporal proximity to a hidden target in a spatial-search task resulted in 1) a primary role for the target in

controlling spatial search, and 2) learning of specific landmark-target associations.

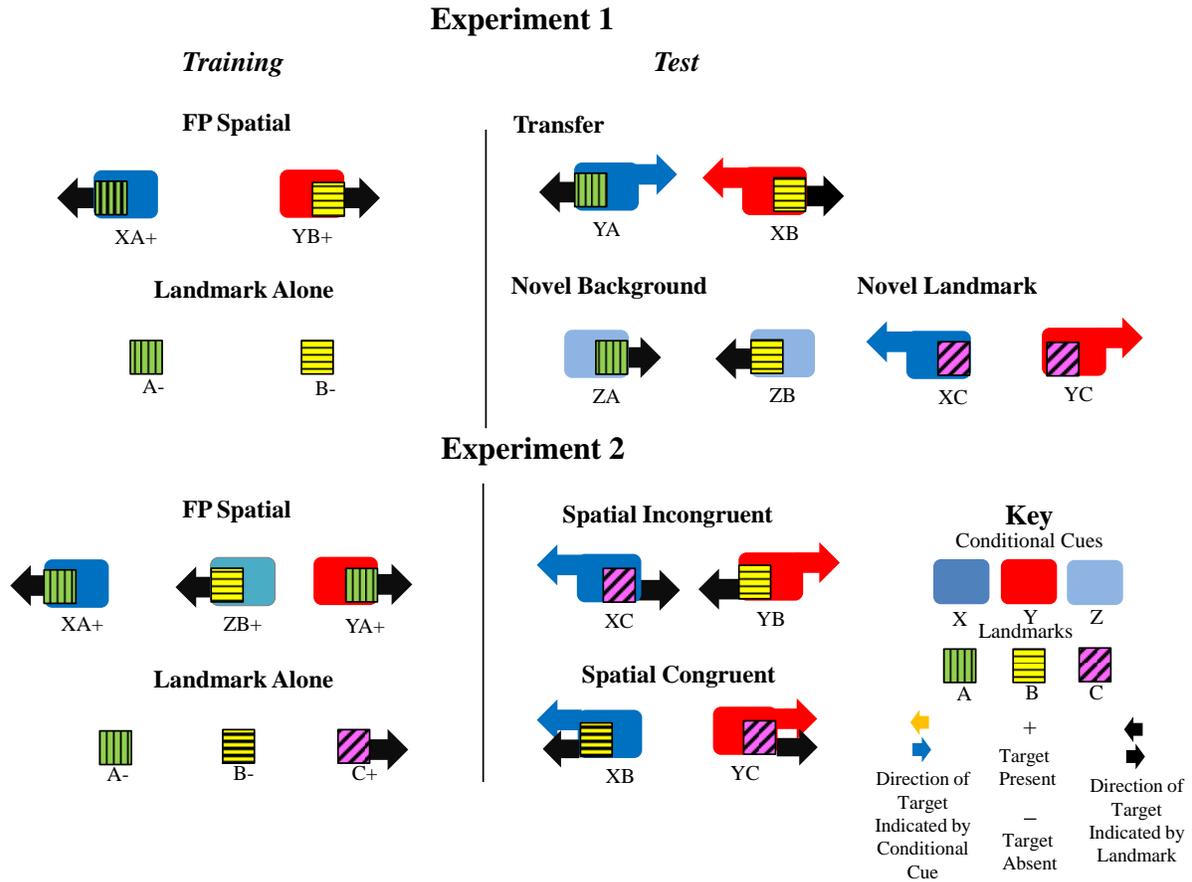


Figure 3 shows the procedure of Leising et al. (with pigeons, 2015) and Ruprecht et al. (with humans, 2014b); Experiment 1 top row, and Experiment 2 (bottom row). The left column describes the training trials, black arrows indicated the direction indicated by the target (landmark). The right column illustrates the test trials. Colored arrows indicate the direction, in relation to the landmark, previously prompted by the diffuse, colored background from training (i.e., the conditional cue).

It was the first experiment to demonstrate that animals and humans were capable of learning the conditional task with a high degree of accuracy, as the proportion of responses at the target during non-reinforced tests of the FP spatial trials averaged 79% for pigeons, and 85 % for humans.

In Experiment 2, Leising et al. (2015) and Ruprecht et al. (2014b) trained the same landmark with two different conditional cues such that the spatial relationship of the landmark to the hidden target was ambiguous without exposure to the preceding conditional cue (see bottom of Figure 3 for procedure). For example, on XA trials the target was located to the left of A,

whereas, on YA trials the target was located to the right of A. This type of training should encourage spatial control by X and Y in the presence of A. Additionally, we trained another background-landmark pair (ZB), as well as a simple discriminative stimulus (landmark C) to signal the direction of the target in the absence of a conditional background. Therefore Experiment 2 pitted the effects of target training history and spatial congruence between conditional backgrounds and landmarks together.

In the congruent tests for pigeons, the magnitude of responding differed between the trained background-landmark pairs (XA, YA, and ZB) and the novel combinations of XB and YC, which did not differ from one another. The disruption in magnitude occurred despite congruent spatial information regarding the location of the target by both the conditional cue and the landmark during XB and YC trials. Therefore, this disruption could only be indicative of landmark-target specificity or generalization decrement and not spatial interference. The magnitude of responding was similar during incongruent and congruent transfer trials. These results suggested the overall magnitude of responding is sensitive to changes in the stimulus conditions, but not spatial interference, on each trial. Spatial accuracy, however, did not differ between test trials of the trained background-landmark pairs and congruent transfer tests (XB and YC). This result suggested spatial control is less sensitive to changes in the stimulus conditions.

For pigeons, any difference in spatial control between congruent and novel-incongruent transfer trials could not be attributed to conflicting spatial information. There was no observable difference between YB (incongruent) and XB (congruent), but a large difference between performance on XC (incongruent) and YC (congruent). Lastly, spatial control by the landmark during incongruent trials with YB, but not XC, was comparable to that of the trained

background-landmark pairs. Spatial interference reduced spatial control only when a conditional cue was paired with a landmark (C) that did not participate previously in a FP Spatial relationship.

Again, it was permissible to compare these animal results with those reported by Ruprecht et al. (2014b) with humans. Both pigeons and humans in both experiments responded less on incongruent trials, but with no disruption in spatial accuracy. The results of Ruprecht et al. (2014b), however, differed with respect to the influence of training history on transfer during novel-incongruent trials. Spatial interference *did not* disrupt spatial control during a transfer test of a conditional cue with a landmark that lacked previous background-landmark training. In other words, the training history of the landmarks in our FP discrimination procedure made a difference for pigeons, but not for humans.

Though the results were inconsistent with traditional configural theory (Pearce, 1987, 1994), they were largely consistent with modern configural theories (see Pearce & Mackintosh, 2010 for a review). In standard configural learning, the distinct configuration produced on XA trials would elicit little responding on trials in which the conditional cue is paired with a new landmark. However, newer conceptions of configural learning (e.g., Honey and Watt, 1998; Kutlu & Schmajuk, 2012; Vogel, Brandon, & Wagner, 2003) include a role for both elements and configurations through connections to a hidden unit. This approach allows multiple stimuli (e.g., backgrounds and landmarks) to be connected to the same hidden unit. For example, in the search tasks X, A, Y and B would all be connected to the same hidden unit (e.g., P) by virtue of their functional equivalence (target to the right). At present, hierarchical and neo-configural theories make so many of the same predictions that there is little room for empirical evidence to distinguish between them (e.g., Bonardi et al., 2012). The inclusion of spatial or temporal

information in FP discriminations may prove fruitful for researchers pursuing the distinction. For example, the magnitude, but not spatial control of responding was disrupted during some novel-congruent trials with B. It's not clear how neo-configural theories would account for these data.

In sum, the procedure implemented by Leising et al. (2015), and Ruprecht et al. (2014b), investigated a new dimension of conditional control during FP discriminations: spatial control. Of most interest, the procedure allowed isolation of both the magnitude and spatial control by the conditional background and the landmarks. By investigating stimulus control using two measures (magnitude and spatial accuracy), their findings indicated that a conditional stimulus is capable of controlling both the magnitude and location of the response, whereas, the landmark controls only the location of the response. Despite the importance of conditional discrimination to understanding response decisions, there remains a significant amount of disagreement regarding the basic mechanisms for solving these discriminations. Embedding serial FP discriminations within a spatial task has great potential for teasing apart existing accounts of conditional discrimination.

Summary

I have thus far identified several similarities between conditional discrimination in the spatial domain (assessed via small-scale search tasks) and conventional conditional discrimination, including partial transfer to novel targets depending on training history (i.e., spatial congruence; transfer tests). Additionally, I have discussed similarities between conditional discrimination in both the temporal and spatial domain. Taken together, these results suggest that spatial control of responding is similar to that of temporal control, and furthermore, that in some scenarios, the conditional cue provides information beyond simple facilitation of the landmark-target association. My research was needed to identify what kind of spatial information

we can encode from a conditional cue, given the parameters of the search task. To this end, the following series of experiments drove at these lingering questions by investigating a search scenario in which spatial control falling under conditional control should have been optimal (Experiments 1 and 2), as well as explore whether it is more ideal that a conditional cue provide distance or direction information during the acquisition of landmark learning (Experiments 3, 4, 5, and 6).

General Measures

Across all 2D and 3D studies (Experiments 1-6), we had three dependent variables of interest, the 1) magnitude, 2) spatial accuracy and 3) latency of responding. *Magnitude* refers to how much responding occurred on a given trial type/ test, irrespective of location, summed within a given trial and then averaged across all trials of that same type. *Spatial accuracy* referred to the proportion of a response (% of total) at a location in space. Since we expected all participants and subjects to differ in their overall amount of responding, spatial accuracy was calculated as a proportion of responses ($\frac{\text{AMOUNT OF RESPONSES AT INDIVIDUAL LOCATION}}{\text{TOTAL \# OF RESPONSES}}$).

Given the training in Series 1, responses were only made 1 location to either side of a landmark allowing us to calculate a difference score as follows:

$$\text{Difference Score} = (\text{Proportion at Target} - \text{Proportions at Other Locations (e.g., Opposite)})$$

Given the training in Series 2 and Series 3, responses were only expected to be made 1 or 2 locations to either side of a landmark allowing us to calculate a difference score as follows:

$$\text{Difference Score} = (\text{Proportion at Target} - \text{Average Proportion at 3 alternative Locations})$$

Difference scores came out to a range of [-1] and [+1]. [+1] indicated absolute preference for the target at test; [-1] indicated absolute preference for alternative locations; [0] indicated no

preference/ chance responding. *Latency* was measured in seconds (s), beginning with the start of a trial and ending with the first selection of the target response location.

Series 1- Conditional Discrimination of Landmark Properties during Spatial Search

Previous research has identified two training parameters critical to observing conditional control of responding to the target, as opposed to *direct* control by the conditional stimulus *irrespective* of the target (e.g., Bonardi & Jennings, 2007; Holland, 1986, 1998; Holland et al., 1997; Miller & Oberling, 1998; Nakajima, 2009). The first parameter is that the onset of the conditional stimulus should precede that of the target. The second parameter is that the conditional stimulus should enhance the salience of the target. The effects of establishing a conditional stimulus include improved transfer of control by the conditional cue.

These properties have encouraged researchers to investigate the nature of conditional stimuli (i.e., under what conditions do they develop, what kinds of stimuli can they modulate, what kind of information is stored with a conditional stimulus, and what conditions affect transfer of modulation to other stimuli), however, these investigations have yet to fully investigate the spatial relations encoded within each relationship. There is good evidence that a conditional stimulus can store spatial information regarding a target-outcome association, particularly in animals. We understand relatively little, however, about the conditions under which the strongest spatial control will develop. Series 1 (Experiments 1 and 2) aimed to render landmarks entirely ambiguous. It was the goal of this series to create a situation in which landmarks were on their own entirely ambiguous and required modulation by the conditional cues to provide any sort of reliable spatial information.

Experiment 1

In Experiment 1, laboratory pigeons were trained on the following FP spatial trials \leftarrow WA, XA \rightarrow , \leftarrow YB, ZB \rightarrow , including the two landmark-alone trials, A- and B-. On FP spatial trials, if a pigeon pecked one response location to the right or left of the landmark, A, they would be reinforced with a presentation of grain. The reinforced direction (right or left) depended on the preceding conditional background, W or X. Recall however, that despite their proximity to the target, landmarks were low in stability *and* reliability. We hypothesized that due to the each landmark's instability, on transfer tests, (e.g., WB, YA) the conditional cue should control spatial accuracy rather than the landmark. In sum, Experiment 1 was the first experimental demonstration, to our knowledge, of a conditional cue disambiguating an ambiguous landmark's spatial information in animals.

To summarize Experiment 1 (and 2) within a spatial framework, we wanted to test if a conditional background, high in reliability (trials with conditional cues had a high contingency with reward), and high in stability (across trials, the direction of the target, anchored to the landmark was highly stable depending on the conditional background presented), could control responding to a landmark that was low in reliability (the landmarks themselves had a low contingency with reward), but also low in stability (the landmarks maintained an inconsistent distance and direction to the target location). We hypothesized that animals could utilize non-spatial, stable conditional cues to alter the spatial relation of unstable landmarks. This ability, to our knowledge, had never been thoroughly demonstrated or tested in an experimental setting. A behavioral manifestation of this prediction would be strong responding aimed in the direction indicated by the conditional cue during transfer tests, whereas, poor transfer (i.e., a reduction in the magnitude or spatial accuracy of responding) would be evidenced by inaccurate responding

to the opposite side of the landmark, indicating perhaps that conditional relationships play a limited role in modulating the spatial information organisms encode about landmarks.

Method

Subjects. Twelve white Carneaux pigeons (*Columba livia*; Double T Farm, Iowa) served as subjects. Pigeons were maintained at 85-90% of their free-feeding weights. They were individually housed in a colony with a 12-hr light-dark cycle and had free access to water and grit. Experimental procedures occurred during the light portion of the cycle. Subjects had previously participated in several studies, but both the orientation and nature of the task were novel (pigeons will not have the experience of pecking an array). All research was conducted in accordance with an approved TCU IACUC protocol.

Apparatus. Training and testing was conducted in a flat-black Plexiglas chamber with stimuli presented by computer on a color LCD monitor (L1750, HP, Palo Alto, CA). Pecks to the monitor were detected by an infrared touch screen (EZ-170-WAVE, ezscreen, Houston, TX) mounted on the front panel. A food hopper (Coulbourn Instruments, Allentown, PA) was located in the center of the front panel, its access hole flush with the floor, and capable of delivering mixed grain when activated. Across the experimental phases, reinforcement occurred as follows; responses to the hidden target resulted in a 3-second(s) access to mixed grain followed by a 15-s inter-trial interval (ITI) before the next trial begins.

Stimuli. Visual stimuli during the task fell into three categories; response locations, conditional stimuli, and landmarks. Response locations were a series of 8 squares that were 2 cm². The conditional stimuli were presented as colored backgrounds that surrounded the response locations and filled the remainder of the display. The background colors used were solid red, blue, cyan, and orange. In the absence of an active conditional cue, the background appeared black. During FP spatial training, 1 of 6 possible response locations (i.e., locations 2-6)

served as a landmark. If a response location is selected to be a landmark, it will be replaced with an image of a 4.8 cm (l/w) green (thin vertical white stripes), yellow (thick horizontal stripes), or pink (thick diagonal strips) box. Assignment of color to landmarks and conditional backgrounds was fully counterbalanced across participants. On any given trial, one location among response locations 2 – 7 served as a target, whereas, one of locations 3 - 6 will serve as the target. If a response location was selected to be a landmark, the black square at that location will be replaced with an image of a colored and patterned visual stimulus. The spatial relationship between a landmark and the hidden target was consistent across trials (e.g., to the left of A), but the location of the hidden target along the array will vary. All pecks to the target (which appeared as a normal empty response location) resulted in the presentation of treasure. All experimental events were controlled and recorded with a desktop computer and orchestrated via Microsoft Visual Basic 6.0 software.

Procedure. 12 white Carneaux pigeons were shaped via a mixed Pavlovian-instrumental procedure to peck a white square displayed in the center of the monitor. After pecking was reliable, eight visual squares were arranged in row in the center of the monitor. On each trial, one of the eight squares will be selected as the target and filled white to full brightness while the remaining squares are filled to 35% brightness. Within and across sessions the brightness of the target location was reduced to 50% brightness and responses at the target were reinforced on a continuous reinforcement (CRF), Random-ratio (RR) 2, and then RR4 schedule (c.f. Leising, Sawa, and Blaisdell, 2012).

FP Spatial training. FP training consisted of four types of trials (left side of Figure 4), WA+, XA+, YB+, and ZB+. A square serving as a landmark (e.g., A) was replaced with one of the three colored patterns described above. On XA and ZA trials, the color of the entire display

(X) changed for a fixed-time 40-s interval. The onset of A was delayed according to a variable-time 10-s schedule (ranging from 5 to 15 s in increments of 5 s) but always co-terminated with X. Thus, A was presented for a mean duration of 30 s.

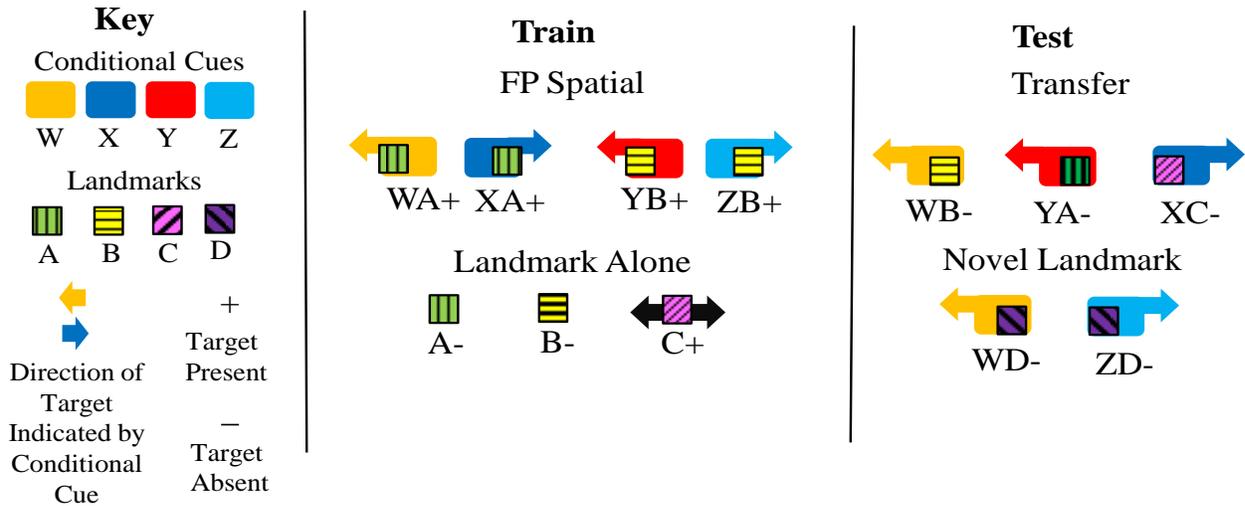


Figure 4 summarizes the Procedure for Experiment 1 and Experiment 2. The left column describes the training trials, black arrows indicated the direction indicated by the target (landmark). The right column illustrates the test trials. Colored arrows indicate the direction, in relation to the landmark, previously prompted by the diffuse, colored background from training (i.e., the conditional cue).

The target was always one location to the left or right of A, depending on the conditional cue, and pecks during A were reinforced until offset. YB and ZB trials are conducted in a similar manner, with the target being one location to the right or left of B, again, depending on the conditional cue for that particular trial type. Finally, C served as an ambiguous excitatory target, in that 50 % of the C trials featured the target to the right of C and the other 50% featured the target to the left of C. As is required to promote FP discrimination, all pigeons also received individual, non-reinforced trials of landmarks A and B as well.

The placement of a target within the response squares varied from one trial to the next. Target locations were selected randomly without replacement from locations 3-6. There was an unstable relationship between the location of a landmark and the conditional background, background and the hidden target, and between the background and the landmark, but the spatial

relationship between the landmark and the target remained stable across all training trials. At the start of training, the location of the target will be marked with a white square at 50% brightness, while the remaining locations will be filled to 35% brightness. Within and across sessions the brightness of the target location will be reduced to 35% brightness and responses at the target were reinforced on a CRF, RR2, and then RR4 schedule. Sessions initially consisted of 48 trials with 12 trials of each type. Once subjects reached the RR4 schedule of reinforcement, the number of trials per session increased to 64 with an equal number of the eight trial types (8 presentations per trial type).

After the brightness of the target was reduced to 35%, it was indistinguishable from the remaining response locations, thus the pigeons were then required to search for the hidden target based solely on its spatial relationship to the landmark. After all 12 pigeons completed two sessions in which the target was unmarked, responses were reinforced on an RR4, the correct response needed to be made on 80% of FP spatial trials, and the discrimination ratio (pecks at the correct location divided by all responses) needed to be greater than or equal to 75%; the pigeons will then be individually advanced to test.

Testing. The right side of Figure 4 displays the test trials of Experiment 1. The order of test trials each day was counterbalanced across all subjects in each testing condition. Over two sessions (with one normal day of training in the middle), the trained pigeons received one non-reinforced test trial of A, B, C, WA, XA, YB, ZB, YA, XC, and WB per session for six sessions, shuffled throughout the session. Test order was counterbalanced across subjects and across days. A test session consisted of (a) an equal number of reinforced (XA and YB) and non-reinforced trials (A and B) as in training, and (b) a block of six consecutive non-reinforced test trials. On FP spatial test trials, the landmark always appeared 10 s after the conditional cue. Landmark-

alone trials were always 30-s in duration. The magnitude and spatial accuracy of responding, in relation to the landmark was measured during all test trials..

Results

FP Spatial Training. Of the 12 original subjects placed in this experiment, 2 pigeons failed to ever reach the training criterion of 75% or more. Therefore, the following data comes from 10 birds. The number of sessions (days) it took for the pigeons was 111($SD = 14$).

Response Magnitude. Prior to collapsing, the magnitude of responding was calculated by summing all pecks detected within the 8 response locations for each trial type, and averaging across the ten pigeons. All mean comparisons were obtained via t -tests, when appropriate, effect size was reported via Cohen's d (e.g., Rosenthal & Rosnow, 1991).

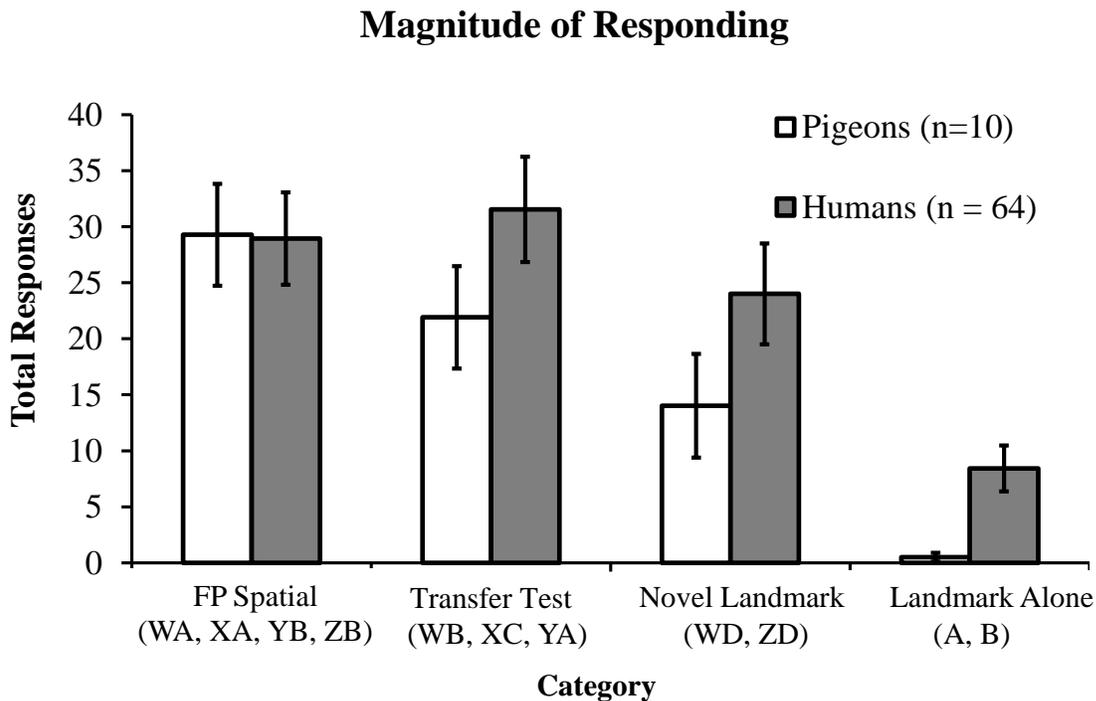


Figure 5 summarizes the Magnitude Data for Experiments 1 and 2. The y-axis shows the total amount of responses during each test category, irrespective of which location was pressed. Data from Experiment 1 is indicated by the white bars. Data from Experiment 2 is indicated by the gray bars. Error bars represent the standard error of the mean.

Categories. When comparing response magnitude, each separate test was collapsed into four functional categories, FP-spatial (WA, XA, YB, and ZB), transfer (WB, YA, and XC), novel-landmark (WD and ZD), and landmark-alone (A and B). Magnitude did not differ between any single test trial within the same category, all $t(9)s < 1.46$, $ps > .17$, $ds < .97$, with the largest within category difference being between transfer trials XC and YA.

Between Category Analysis. Figure 5 displays the mean number of responses for each category. A repeated measures analysis of variance (ANOVA) with category (FP spatial, transfer, novel-landmark, and landmark-alone) as the repeated measure conducted on the magnitude of pecking revealed a significant main effect of category, $F(3, 27) = 17.4$, $p < .001$, $\eta^2 = .65$. Post-hoc analysis (Tukey's Highly Significant Difference HSD) compared each category to one another. As illustrated in Figure 5, pigeons pecked more during the FP spatial trials ($M = 29.2$, $SD = 14.3$) than during the Novel-landmark ($M = 14.1$, $SD = 14.6$; $p < .001$) and Landmark-alone ($M = .5$, $SD = .39$; $p < .001$) categories, but pecked the same amount as the transfer category ($M = 21.9$, $SD = 14.4$; $p = .31$), indicating a complete transfer of conditional control on magnitude (the amount of pecks) during transfer tests but *not* the novel-landmark tests. Pecking during the transfer trials themselves did not differ from the novel landmark trials ($p = .25$).

Spatial Accuracy. Across all trial types, less than 2% the pigeon's pecks occurred at any other location than those immediately to the left or right of the landmark. The proportion of pecks to each location was therefore calculated and then subtracted from the amount of pecks to the location on the opposite side of the landmark (i.e., proportion of taps to target - proportion of taps to the opposite location) creating a *difference score* (see General Behavioral Measures).

Categories.

Spatial Accuracy

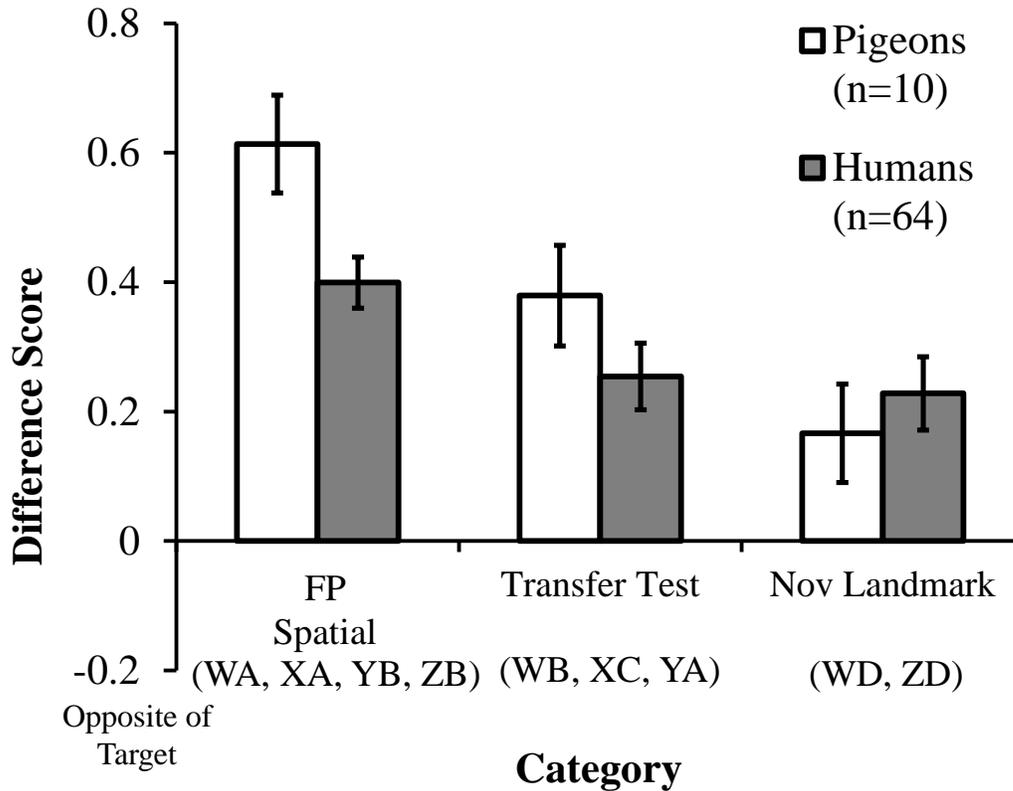


Figure 6 summarizes the spatial accuracy data for Experiments 1 and 2. The y-axis shows the difference scores during each test category, which were calculated by subtracting the proportion of responses to the opposite side of the LM from the proportion of responses to the target. Data from Experiment 1 is indicated by the white bars. Data from Experiment 2 is indicated by the gray bars. Error bars represent the standard error of the mean.

The difference scores (ranging from +1 for high target preference and -1 for high opposite preference) served as the dependent variable for spatial accuracy and were collapsed into the same four categories as the magnitude scores were. Like the magnitude data, no groups within the same category differed, all $t(9)s < .63$, all $ps > .54$, $ds < .42$, with the largest discrepancy in difference scores within a single category occurring between the two transfer trials XC and YA. Choosing to peck one side or the other of the landmark at random would result in a difference

score of 0. Thus, we first conducted three single sample t-tests to compare the mean difference scores within each category to zero. The t-tests revealed that the pigeons were far more likely to peck the target than by chance during the FP spatial, $t(9) = 8.31, p < .001$, and Transfer trials, $t(9) = 4.86, p < .001$, however, accuracy during the Novel-landmark trials *did not* reliably differ from chance, $t(9) = 2.18, p = .05$.

Between Category Analysis. Figure 6 illustrates the spatial accuracy of pigeons in Experiment 1. We compared the difference scores between the same four categories as the magnitude measure. Because there was a near zero amount of pecking during the Landmark-alone trials (A,B), and because there is no clear “target” location on these test, we dropped this category from the spatial accuracy analysis. A repeated measures ANOVA (Category: FP Spatial, Transfer, Novel-landmark) conducted on the difference scores revealed a main effect of category, $F(2, 18) = 17.5, p < .001, \eta^2 = .66$. Tukey’s HSD within the main effect of category revealed that pigeons were much more accurate during the FP Spatial trials ($M = .61, SD = .23$) than both the transfer ($M = .37, SD = .24; p = .01$), and the novel-landmark ($M = .16, SD = .24; p = .002$). Moreover, pigeons were more accurate during transfer trials, than novel-landmark trials ($p = .03$).

Discussion

Experiment 1 showed definitively in animals that a conditional cue could modulate the spatial information of a landmark. Pigeons showed the highest degree of confidence (magnitude) during FP spatial trials, and pecked considerably less during both novel-landmark and landmark-alone trials. Of greatest interest, pigeons pecked a comparable amount during transfer trials, giving us some strong evidence for transfer of modulation from the original FP spatial trials to novel trials (see General Discussion). While we previously reported that pigeons failed to

transfer robust responding to novel situations (i.e., transfer trials), given the ambiguity of landmarks A and B in Experiment 1, some vigor in responding was transferred. The spatial accuracy data did not, in contrast, support complete transfer of spatial control. Pigeons were far more accurate during FP spatial trials from training than during novel situations (i.e., transfer and novel-landmark trials), but still pecked well above chance.

Previous research has demonstrated in a similar task that animals (e.g., pigeons) and humans differ in their ability to transfer modulatory information to new situations (e.g., Ruprecht et al., 2014b; Shanks, 2010). Experiment 2 presented a very similar paradigm to human participants with mild mechanical changes to assess whether spatial information encoded about the conditional cues would be transferrable for humans.

Experiment 2

In Experiment 2, we implemented the same task with some mechanical changes to study human search behavior. We hypothesized that humans could also utilize non-spatial, stable conditional cues to alter the spatial relation of unstable landmarks. A behavioral manifestation of this prediction would be strong responding aimed in the direction indicated by the conditional cue during transfer tests.

Method

Participants. A total of 82 undergraduate psychology students (41 females, 41 males, aged 18-26) at Texas Christian University (TCU) participated as a partial fulfillment of course requirements.. All students had no previous experience with either preparation, and were uninformed as to the purpose of the experiment. Participants were trained and tested individually; the experiment's max duration was set at 60 min but students could finish early. All experiments were conducted in dedicated human cognition testing rooms. All research was

conducted in accordance with TCU's Human Participant Ethics Committee and an approved IRB protocol.

Apparatus. A Hewlett Packard Touchsmart computer was used to display stimuli. Participants touched the screen to emit responses. The location of the mouse on the computer was represented by a crosshair stimulus. Responses to the hidden target location resulted in 2-s access to the image of hidden treasure followed by a 5-s ITI before the next trial begins. In order to increase the response cost of incorrect responses, participants were given an ammunition bar that shrinks with every response. The length of the bar was designed to match the shots needed for an average participant, but simply refilled if the ammunition was exhausted.

Procedure. 82 TCU undergraduates (41 female and 41 male) were seated in a chair .5 meters from the touchscreen monitor. The top left of Figure 2 shows the experimental apparatus. Participants were instructed to sit comfortably in the chair and observe the screen with their elbows comfortably rested on the table. The participants will maintain this basic position throughout the experiment.

Pretraining. Prior to pre-training, the participants were read the following script by an experimenter:

“From time to time this row of boxes will appear. When the boxes are available, it also means one of them is hiding a hidden treasure. Your task is to find the box which reveals the hidden treasure. Take this opportunity to explore the screen and locate the hidden treasure. Keep in mind that on some trials you will only have to press the box once to reveal the treasure, but other trials may require several presses to the correct box to reveal the treasure.”

Participants were then allowed to explore and press the 8 response locations. A press to 1 of the 8 response locations revealed a treasure chest in the lower portion of the screen. The participants then needed to successfully locate two more hidden treasures, this time by pressing 2-4 times into the same box, before being advanced to training.

FP Spatial Training. Prior to training, participants were read the following instructions:

“During the warm up, the background of the screen was black, but on future scenarios you’ll notice different colored walls, or perhaps, different filled patterns on the boxes themselves (experimenter points to the boxes). This is very important! During the next task there will also be scenarios when finding a treasure is NOT possible. First, explore all the boxes by pressing them, to identify when and if there is hidden treasure during a given scenario, and when there is not. You’ll know when a new scenario begins when the screen goes blank and things change again. The duration of the experiment will be dependent on how well you do. At some point a label will come up that tells you to come get the experimenter.”

Like the pigeons in Experiment 1, four types of training trials were presented to the participants in Experiment 2. Training in Experiment 2 differed from Experiment 1 in the following ways: Upon selecting the target on FP spatial trials (WA+, XA+, YB+, ZB+), and C+ (CR+, CL+) trials, a treasure chest graphic appeared in the center of the monitor, 2 cm (bottom border) from the bottom. When the treasure appeared, the cursor disappeared and presses were not be recorded. The treasure presentations lasted 2 seconds. No fading of the target’s location occurred for the humans, as they were verbally instructed to hunt for a hidden target.

Criterion. To advance to testing, all participants needed to complete 3 blocks of 8 discrimination trials with 75% accuracy or higher (measured as a discrimination ration of XA to A or YB to B). Moreover, each subsequent block featured a higher response requirement: Block 1 featured a continuous reinforcement schedule (CRF) with every tap to the target being rewarded with treasure; Block 2 featured a random ratio 2 (RR-2) schedule with every tap to the target having a 50% chance of being rewarded; Block 3 featured a RR-4 schedule, with every tap to the target having a 25% chance of being rewarded. After the participants completed these three blocks (participants repeated any failed block over again, up to 4 total times), they received an on-screen message alerting them to get the experimenter before being advanced to test. If a

participant failed to advance to the next block up to 4 times, the program exited and the experimenter thanked the participant for their participation and were asked to leave the room.

Test

After participants reached the stop screen, they were read the following instructions:

“On scenarios after this signal, you should still do your best to find the box that previously hid the treasure, but no treasure will be shown (though we are still keeping track). This is because we don’t want you to know whether you chose correctly or not, we just want to know which target you think is hiding the treasure. Though we are not giving you feedback, your accuracy is still being recorded and we will let you know how you did very soon. Now, find as much treasure as possible!”

Participants then received two blocks of 8 non-reinforced trials, the first block: A, B, C, WA, XA, YB, ZB, XC, and YA; the second block: A, B, C, WA, YB, XA, ZB, XC, and YA. Following the testing session, participants were asked a number of questions that ascertained which cue (the background or landmark) was guiding their responses during the test trials, particularly during the transfer trials.

Results

FP Spatial Training. Of the 82 original subjects placed in this experiment, 18 participants failed to reach the training criterion of 75% accuracy on FP Spatial trials (WA, XA, YB, and ZB). Therefore, the following data came from 64 participants (32 Males and 32 Females). The average number of FP spatial trials it took these 64 participants to reach test criterion varied given each participant passed each block on ($M = 69.8$, $SD = 11.9$).

Response Magnitude. The magnitude of responding was calculated by summing all pecks detected within the 8 response locations for each trial type, and averaging across the ten pigeons.

Categories. When comparing response magnitude, each separate test was collapsed into four functional categories, FP-spatial (WA, XA, YB, and ZB), transfer (WB and YA), novel-

landmark (WD and ZD), and landmark absent (A and B). Mean comparisons were obtained via *t*-tests, when appropriate, effect size was reported via Cohen's *d* (e.g., Rosenthal & Rosnow, 1991). Prior to collapsing, magnitude did not differ between any tests within the same category, all *t*s < 1.28, *p*s > .19 *t*s < *d*s < .32.

Between Category Analysis. Figure 5 displays the mean number of responses for each test. A mixed design ANOVA with category (FP-spatial, transfer, novel-landmark, and landmark-alone) as the repeated measure and gender (Male, Female) as the between subjects factor conducted on magnitude revealed a significant main effect of category, $F(5, 95) = 15.9, p < .001, \eta^2 = .21$. The main effect of gender and the interaction were *n.s* (*p*s > .33). Tukey's HSD compared each category to one another within the main effect of category. As illustrated in Figure 5, participants responded more during the FP-spatial ($M = 28.9, SD = 32.9$), transfer ($M = 31.5, SD = 37.5$), and novel-landmark ($M = 24.1, SD = 36.1$) trials than to the landmark-alone trials ($M = 8.42, SD = 16.9; p < .001$), but did not differ from one another (*p*s > .7).

Spatial Accuracy

Categories. Across all trial types, less than 1% the participant's responses occurred at any other location than those immediately to the left or right of the landmark. The proportion of presses to each location was therefore calculated and converted into difference scores and collapsed as in Experiment 1. Again, the difference scores within the same category did not differ prior to collapsing, all *t*s < 1.67, all *p*s > .15, *d*s < .42. Recall that chance responding would result in a difference score of zero. We conducted three single sample *t*-tests to compare the mean difference scores within each category to zero. The *t*-tests revealed that the participants were far more likely to tap the target than by chance in during the FP spatial, $t(63) = 10.09, p < .001$, Transfer, $t(63) = 4.93, p < .001$, and Novel-landmark trials, $t(63) = 4.02, p < .001$.

Between Category Analysis. Figure 6 illustrates the search accuracy (difference scores) of humans during Experiment 2. A mixed design ANOVA conducted on the difference scores with Category (FP Spatial, Transfer, and Novel-Landmark) as the repeated measure, and gender (male, female) as the between-subjects measure, revealed a main effect of category, $F(3, 57) = 4.92, p < .008, \eta^2 = .07$ on difference scores. The main effect of gender and the interaction were *n.s.* ($ps > .97$). Post-Hoc analysis within the main effect of category revealed that FP Spatial trials ($M = .39, SD = .31$) elicited more accurate responding than transfer ($M = .25, SD = .41; p = .03$) and Novel-landmark ($M = .22, SD = 14.6; p = .01$), which did not differ from one another ($p = .89$).

Discussion

While the pigeons made successful FP spatial discriminations across a large amount of days ($M = 111$; see Experiment 1), 64 of 82 undergraduates were able to achieve 75% discrimination ratios within a single session. When tested, humans differed from pigeons in that the transfer of magnitude was complete for not only transfer trials (like the birds), but also for the novel-landmark trial types. Much like the pigeons, however, the participants responded less accurate during both transfer and novel-landmark trials. This finding was not originally expected however, we should point out while both pigeons and humans were *less accurate* during transfer trials, compared to the original FP spatial trials; both species were far more accurate on transfer trials than chance alone (a difference score of 0). Both pigeons and humans successfully and definitively applied conditional spatial information to novel situations at test (see General Discussion). Experiment 1 and 2 validated that it is possible to train distal cues to modify spatial information of more proximal landmarks.

Series 2- FP discrimination of two types of LM Properties in Small-scale Spatial Search

In the previous two experiments, only the spatial direction of the target (left vs. right) in relation to the landmark was manipulated. One aim of Series 2 was to manipulate the second dimension of information a landmark can provide about a target's location: *distance*. As mentioned earlier, we can understand in a rudimentary sense that proximal landmarks tend to accurately guide responses, whereas, distal landmarks, far from the target, seem to promote guide a more general form of search, such as directing one's general heading. Additionally, research has shown that pigeons and humans will average the spatial and temporal information provided by cues to estimate the location of reward with respect to a moving target (Cheng, Spetch, & Miceli, 1996). In Experiments 3 and 4, the distance and direction of the target relative to the landmark were indicated separately the by conditional cue and landmark, respectively.

Ruprecht et al. (2014b) and Leising et al. (2015) reported little evidence for the conditional cue to encode any individual directional information on its own when the pigeons and humans could easily defer to the redundant landmark for this information (e.g., transfer test $\leftarrow XA \rightarrow$; pigeons and humans responded in the direction of landmark A). Experiments 1 and 2 showed that pigeons and humans could definitively encode spatial information solely from a conditional cue as long as the landmarks themselves were rendered ambiguous (recall that A and B were poor spatial predictors of the target on their own and required FP spatial trials to gain relevance; e.g., $\leftarrow WA; XA \rightarrow$). Since Experiments 1-2 were conducted under different training circumstances as Leising et al. (2015) and Ruprecht et al. (2014b), Experiments 3 and 4 aimed to detect whether the conditional cues in our small scale task were more optimal at modulating the direction (left vs. right) of the target, or modulating the distance (near vs. far) of the target, in relation to the landmark.

College undergraduates were assigned to two groups. Both groups received training with the following trial types: XA, YA, XB, and YB. In Group 1, the conditional backgrounds indicated the direction of the target (left or right) in relation to the landmark, whereas the landmark itself determined the distance of the target (one or two locations away from the landmark). In Group 2, the conditional backgrounds indicated the distance of the target (one or two locations away from the landmark), whereas the landmark itself determined the direction of the target (left or right of the landmark).

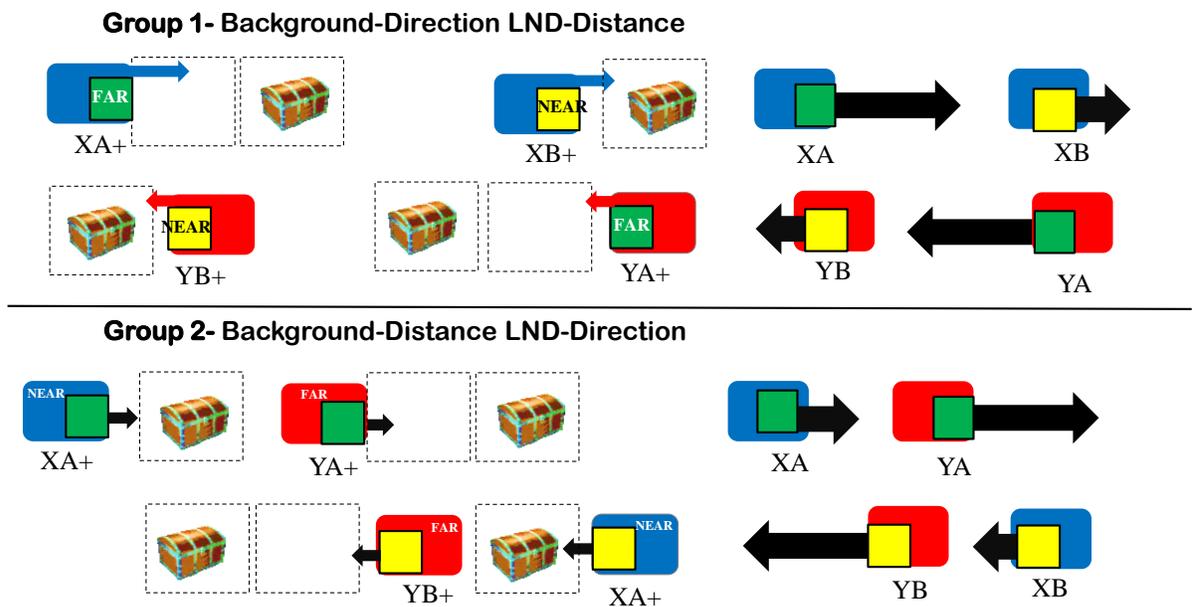


Figure 7 shows the general procedure of Experiments 3-6. To indicate direction, the dotted lines are hypothetical response locations, the goal is either far (2 response locations) or near (1 response location) from the target. If the conditional cue indicated distance, NEAR or FAR are marked on the colored conditional cue, likewise, the targets are marked if they indicated distance. Colored arrows indicate the direction, as signaled by the conditional cue (Group 1), whereas, black arrows indicate the direction if the LM signaled it (Group 2).

This study was studied across two very comparable tasks: a small scale 2D task (Experiment 3) and a small scale 3D task (Experiment 4) in order to gauge whether each landmark property would become more salient in three dimensions.

Experiment 3

Experiment 3 tested undergraduate's use of conditional cues and landmarks that conveyed varying spatial information (distance or direction, respectively). We utilized the same touchscreen apparatus from Experiment 2. It was hypothesized that Group 1 (Conditional-Direction; Landmark-Distance) would acquire the FP spatial discrimination faster than Group B (Conditional-Distance; Landmark-Direction). This behavioral prediction would manifest in Group 1 reaching the target much faster during FP spatial training (lower latencies; a faster learning curve) than Group 2, and also that Group 1 would make much less overall errors than Group 2. Transfer tests similar to Experiments 1 and 2 were conducted following ample FP Spatial training. It was hypothesized that when tested at identical periods in acquisition; Group 1 would respond at a higher magnitude and be more spatially accurate than Group 2.

Method

Participants. A total of 12 undergraduate psychology students (6 females, 6 males, aged 18-23) at Texas Christian University (TCU) participated as a partial fulfillment of course requirements. A total of 12 undergraduate students (6 females, 6 males, aged 18-20) at Kanazawa University participated in exchange for 1,000 yen (approximately 10 U.S. dollars at the time of this print) to spend at the University co-op and bookstore. All students had no previous experience with either preparation, and were uninformed as to the purpose of the experiment. Participants were trained and tested individually. The experiment's max duration was set at 60 min but students could finish early. All experiments were conducted in dedicated human cognition testing rooms. All research was conducted in accordance with TCU's Human Participant Ethics Committee and an approved IRB protocol and in parallel, an approved Kanazawa IRB protocol. Both protocols were successfully submitted and approved by an

international advisory committee operated by the National Science Foundation and the Japanese Society for the Promotion of Science.

Apparatus. The same two-dimensional, touch-based computer game from Experiment 2 was used in Experiment 3. For American students, the touchscreen task was run on a Hewlett Packard Touchscreen computer, for Japanese, it was run on a Sony Touchscreen computer with equal dimensions.

Stimuli. Stimuli were presented as described in Experiment 2, and featured the same blue, red, cyan, and orange backgrounds, as well as the patterned green, yellow, pink, and purple landmarks. Participants still received treasure and had an ammo bar as in Experiment 2.

Procedure. Participants underwent pre-training, FP spatial training, and testing as in Experiment 2 with the following major exceptions: 1) All participants in Experiment 3, regardless of performance, were advanced to testing after completing 72 trials (48 FP spatial trials, 24 landmark alone trials, see below). 2) Across all of training, participants were reinforced on an FR-1 schedule of reinforcement, meaning every response to the target resulted in the release of treasure (i.e., was reinforced). 3) In the script, participants were told the following sentence, “*On all training trials, try to release the treasure as fast as you can without sacrificing any accuracy.*” Also in the script, one sentence that described the response requirements (e.g., “sometimes you must hit the box more than once to reveal the treasure”) was deleted (see Appendix 1).

FP spatial training. Training consisted of four types of trials (see Figure 6), XA+, YA+, XB+, and YB+. A square serving as a landmark (A or B) was replaced with one of the two color-line patterns described above as in Experiment 2. On all FP spatial trials, the color of the entire display (X) will change for a fixed-time 40-s interval. The onset of A or B will be delayed

according to a variable-time 10-s schedule (ranging from 5 to 15 s in increments of 5 s) but always co-terminate with X or Y. Thus, A will be presented for a mean duration of 30 s.

The target always occurred to the right or left side of the landmark along the array. In group 1, this direction depended on the background: reinforcement could occur only in positions to the right of A, or to the left of B. In group 2, this direction depended on the landmark: reinforcement being to the right or left of either landmark depending on whether the landmark was A or B. The physical appearance of backgrounds X or Y and landmarks A or B was counterbalanced across participants.

The target was always placed either one (near; 1 response location away) or two (far; 2 response locations away) response locations away from the landmark. In group 1, the distance of the target depended on the landmark being presented, for instance, the target was always far away (two spaces) from landmark A, and near (one space) to landmark B. In group 2, the distance of the target in relation to A or B was conditional on the presentation of X (near) or Y (far). To encourage completion of the FP spatial discrimination, all participants received non-reinforced trials of A and B as well, which did not clearly indicate any particular distance or direction. No treasure was presented on A and B trials. The average time it took to complete a trial (latency) and the amount of errors (accuracy) were recorded during acquisition of FP spatial training to detect differences in performance between the two groups. Unlike Experiment 2, there was no criterion for reaching testing. Participants were given 64 FP training trials (including 48 FP spatial trials) and then all advanced to testing.

Testing. Participants were tested on two shuffled blocks of XA, YA, XB, YB. At test, the average proportion of responses at the target for the trials of interest (XA, XB, YA, and YB) was subtracted from the average proportion of the 3 other candidate locations around the LND,

generating a difference score (see General Behavioral Measures for formula). Difference scores close to 1 indicate strong spatial control. Difference scores close to zero indicate weak spatial control. Difference scores less than zero indicate a total preference for other non-target response locations.

Results

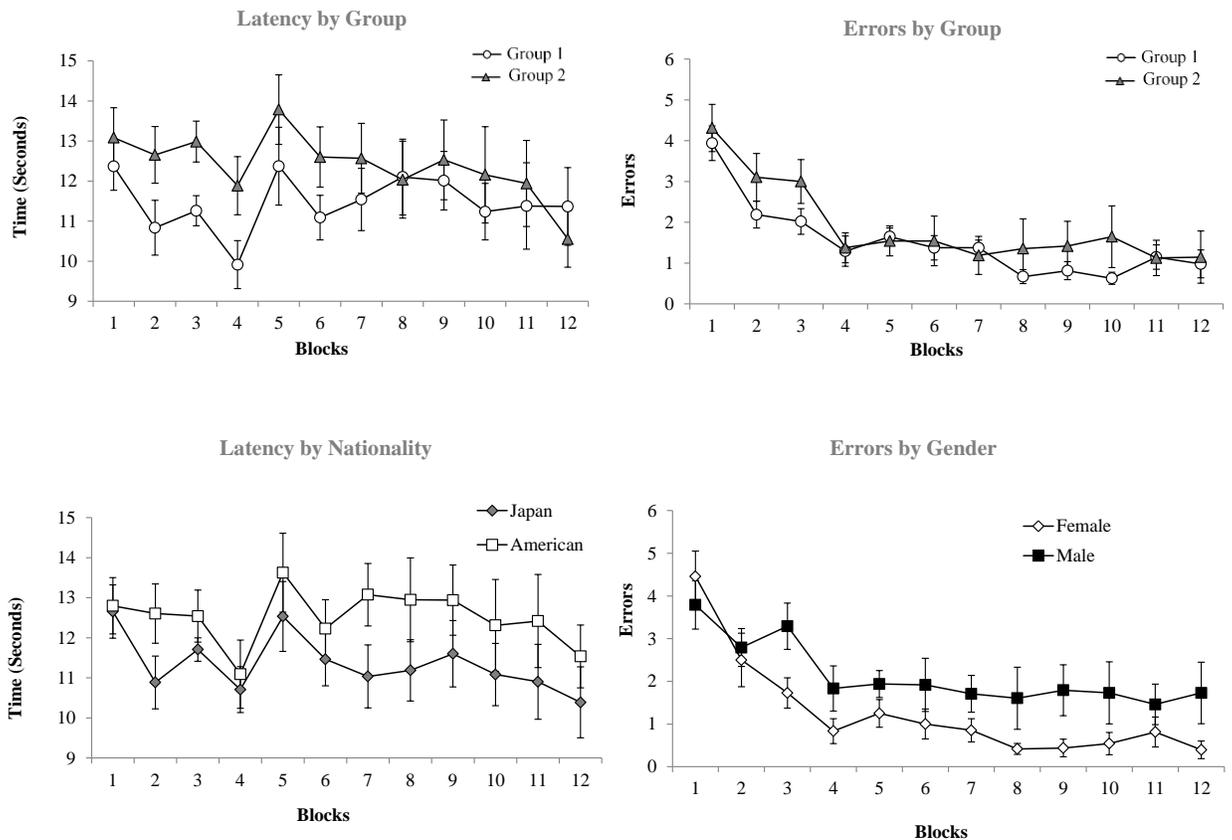


Figure 8 shows the latency and error data from Experiment 3. The x axis shows blocks of training. Each block represents 4 FP spatial trials averaged. The left column illustrates latency to respond across the 12 blocks. The right column illustrates the number of errors that occurred across the 8 blocks. Error bars represent standard error of the mean. The top row compares Group 1 ($n = 12$) to Group 2 ($n = 12$). The bottom left of Figure 8 compares the latency of American participants ($n = 12$) to Japanese participants ($n = 12$). The bottom right of Figure 8 compares the number of errors made by males ($n = 12$) and females ($n = 12$). Error bars represent standard error of the mean.

FP Spatial Training. All 24 original participants placed in this experiment reached the training criterion of 75% accuracy on FP Spatial trials (WA, XA, YB, and ZB).

Latency Analysis. The left side of Figure 8 displays latency data. To assess whether Group 1 or Group 2 completed the FP Spatial training trials, a 2 x 2 x 2 x 12 mixed design ANOVA with Nationality (American vs. Japanese), Gender (Male vs. Female), and Group (1 vs. 2) as the between subjects variables, and block (1-12) as the repeated measure was conducted on latency (s). The ANOVA revealed a significant main effect of Nationality, $F(1, 11) = 4.08, p = .05, \eta^2 = .19$, all other main effects of group, gender, as well as all other interactions were *n.s.*, all $F_s < 2.67, p_s > .12, \eta^2 < .14$. Interestingly, the largest *n.s.* effect was the main effect of group (see Figure 11). Tukey's HSD conducted within main effect of Nationality revealed that U.S. undergraduates took slightly longer ($M = 12.13$ s) to reach the target than Japanese undergraduates ($M = 11.1$ s).

Error Analysis. The right side of Figure 8 shows the average amount of errors rats made on FP spatial trials. A 2 x 2 x 2 x 12 mixed design ANOVA with Nationality (American vs. Japanese), Gender (Male vs. Female), and Group (1 vs. 2) as the between subjects variable, and block (1-12) as the repeated measure was conducted on the number of errors. The ANOVA revealed a significant main effect of block, $F(1, 11) = 11.61, p < .001, \eta^2 = .42$, and a significant main effect of gender, $F(1, 11) = 4.35, p < .001, \eta^2 = .53$. All other main effects (including group) and interactions were *n.s.*, $F_s < 1.17, p_s > .30, \eta^2 < .06$. Tukey's HSD conducted within the main effect of gender confirmed that males made more errors ($M = 2.13$) than females ($M = 1.26$), $p < .05$.

Test Analysis. Figure 9 shows the main test data from Experiment 3. A 2 (Nationality: American vs. Japanese) x 2 (Group: 1 vs. 2) x 2 (Gender: Female vs. Male) main effects ANOVA was conducted on the difference scores for FP Spatial tests (XA, XB, YA, YB

averaged). The ANOVA revealed *n.s.* main effects for group and gender, $F_s(1, 20) < .8, ps > .38, \eta^2 < .03$.

Discussion.

Experiment 3 successfully demonstrated that college undergraduates could use conditional background to definitively modulate the *distance* or *direction* of reinforcement while the landmark itself modulated the second dimension of information. Experiment 3 did not confirm our hypothesis that the distal background would be better at modulating direction (Knierim & Hamilton, 2011) based on the latency and error acquisition data, nor the test data. One possible reason for this null finding may have been the fact that the simple nature of the touch task created a floor effect. Recall that 100% of participants completed the FP spatial trials accurately (75% correct or more).

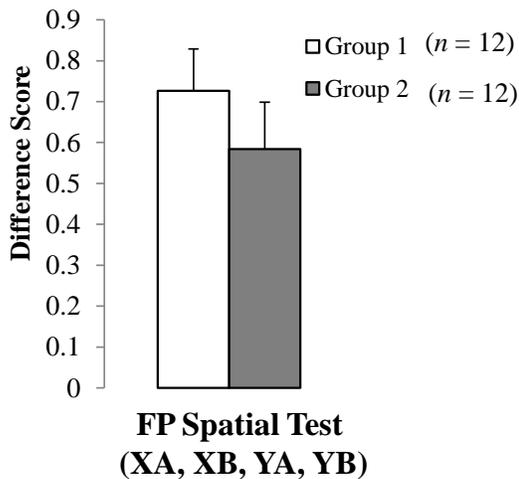


Figure 9 shows the difference scores from Experiment 3 averaged across the 4 FP spatial trials, XA, XB, YA, and YB. The y-axis represents the difference score which was calculated by subtracting the average proportion of responses to other four respective locations from the proportion of responses that occurred at the target. Error bars represent standard error of the mean.

This may have made it difficult to detect differences in performance due to manipulating the

information of either cue. A second possibility is that in a two-dimensional environment, it is difficult to argue that the background is truly distal. The apparent lack of depth between the background and the target location may have promoted no important functional value between the background and the nearby landmark. This led us to assess spatial search in a small scale search task (Experiment 4) but also a much larger open-field task (Experiment 6) in order to increase ecological validity.

Experiment 4

Experiment 4 tested undergraduate’s use of conditional cues and landmarks that conveyed varying spatial information (distance or direction, respectively). We utilized a small scale three-dimensional task that involved orientating to a room, assessing the conditional background and landmarks present, and then navigating to the target location (see Figure 10).

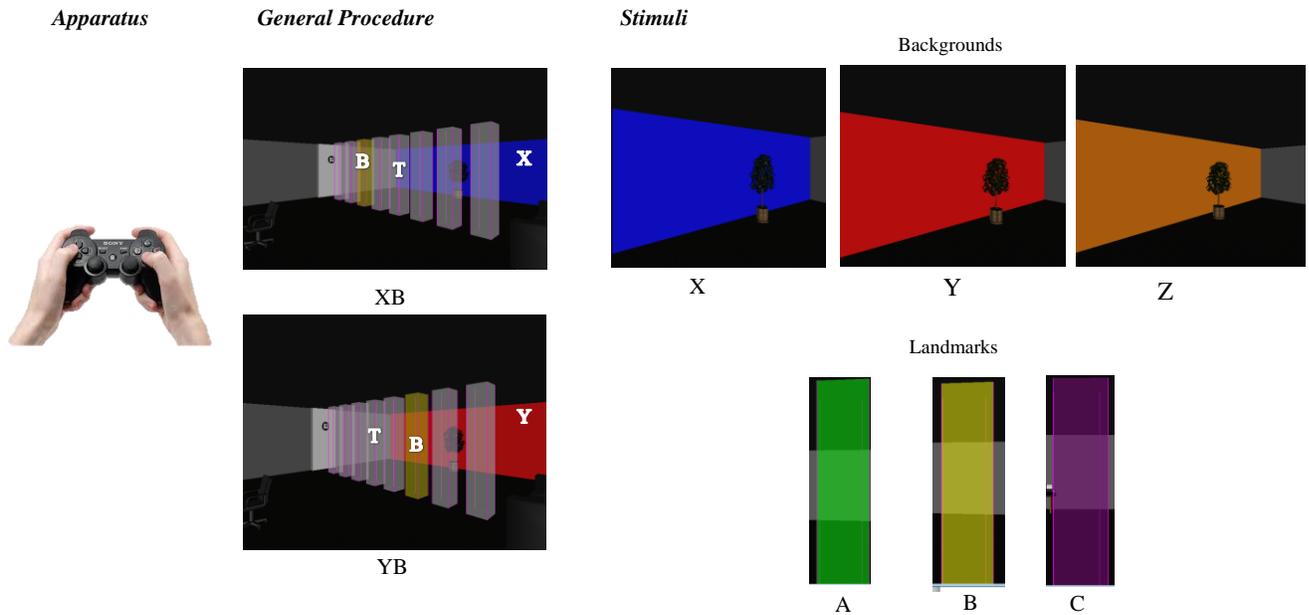


Figure 10 displays the apparatus (PlayStation 3 © controller) that participants used to navigate their avatar around the arena. The general procedure (center) and stimuli (right) used in Experiment 6 occurred in a small virtual room. Conditional backgrounds filled up the back wall located behind the array of 8 response location (i.e., portals). One portal was selected to be a landmark (A,B, or C) and filled with a green, yellow, or pink color.

It was hypothesized that Group 1 (Conditional-Direction; Landmark-Distance) would acquire the FP spatial discrimination faster than Group B (Conditional-Distance; Landmark-Direction). This

behavioral prediction would manifest in Group 1 reaching the target much faster during FP spatial training (lower latencies; a faster learning curve) than Group 2, and also that Group 1 would make much less overall errors than Group 2. Transfer tests similar to Experiments 1 and 2 were conducted following ample FP Spatial training. It was hypothesized that when tested at identical periods in acquisition; Group 1 would respond at a higher magnitude and be more spatially accurate than Group 2.

Method

Participants. A total of 12 undergraduate psychology students (6 females, 6 males, aged 18-24) at Texas Christian University (TCU) participated as a partial fulfillment of course requirements. A total of 12 undergraduate psychology students (8 females, 4 males) at Kanazawa University participated in exchange for 1,000 yen (approximately 10 U.S. dollars at the time of this print) to spend at the University co-op and bookstore . All students had no previous experience with either preparation, and were uninformed as to the purpose of the experiment. Participants were trained and tested individually; the experiment's max duration was set at 60 min but students could finish early. All experiments were conducted in dedicated human cognition testing rooms. All research was conducted in accordance with TCU's Human Participant Ethics Committee and an approved IRB protocol and in parallel, an approved Kanazawa IRB protocol. Both protocols were successfully submitted and approved by an international advisory committee operated by the National Science Foundation and the Japanese Society for the Promotion of Science.

Apparatus. Participants completed Experiment 4 on a hard-top computer within the Vizard © computer software. A PlayStation 3 © remote controlled all experimental movement

and responses. Participant's moved their on-screen avatar with the left analog stick, rotated the camera with the right analog stick, and made response selections by hitting the x button (see Figure 10). The experiment took place from the "first-person" viewpoint of the participant.

Stimuli. Visual. Experiment 4 featured a virtual room with square dimensions. Inside the room were 4 distinct objects, imported from Google Sketch-up © warehouse to serve as landmarks aiding in orientation. On the north wall (see Figure 10), was a plant, on the east wall was a large bay window, on the south wall was a desktop computer, and on the west wall was a small clock. There were also 8 rectangular portals placed in a centralized array at equal distances from one another. The north wall changed colors if it was a FP spatial trial. The three colors were blue (e.g., X), red (e.g., Y), and orange (e.g., Z); counterbalanced across participants. One portal served as a landmark on each trial, and it changed to a 50% transparent shade of yellow (e.g., A), green (e.g., B) or purple (e.g., C). Each portal had a very thin rectangular outline that appeared red, however, when the participant stepped into the portal, the thin frame turned light green. This was meant to aid the participant in knowing whether or not they were standing inside a portal or not.

Auditory. When participants moved, they received auditory feedback in the form of steps. When a participant made a response selection anywhere outside of the target portal, they heard a Legend of Zelda © "error" sound clip. Finally, when the participant made the correct selection (i.e., pressed X while standing inside the target portal), they heard a Legend of Zelda © "treasure" sound clip.

Procedure. The procedure of Experiment 5 had three main phases: 1) Pre-training, FP Spatial Training, and Testing.

Pretraining. Participants were seated at a table and instructed on the proper usage of the game controller, including the directional and camera joysticks, and the response selection button. The participants began in a square testing room that featured a row of 8 portals, with 4 objects for orientation. No conditional cues or landmarks were present; all walls were a blank grey, and the portals a transparent grey color. The Participants were then read the following script (but see Appendix 1):

“Can you see the row of portals in the center of the field? When the portals are presented, it also means one of them is possibly the passage to a treasure room. Your task is navigate and select which portal transports you to the hidden treasure. Take this opportunity to explore the screen and locate the hidden treasure. If you make an incorrect response (i.e., the wrong portal), an error buzzer will sound. Try selecting these portals at random until you hear a treasure sound. When you return to the field look for the treasure again, it will be inside a new portal this time!”

Participants were allowed to search and find the hidden portal along the array of portals. Participants were required to search for 4 trials, and that they were confident that they understood how the controls, including navigation, camera rotation, and button selection worked.

FP Spatial Training. After completing pre-training; the participants were told the following instructions:

“During the warm up, the walls of the arena were always a static gray color, on future scenarios you’ll notice different colored walls, or perhaps, different patterned portals themselves. This is very important! During the next task there will also be scenarios when finding a treasure is NOT possible. First, explore all the portals by pressing A on the controller when you are standing inside of them, just like in pre-training, to identify when and if there is hidden treasure during a given scenario, and when there is not. You’ll know when a new scenario begins when the screen goes blank and you see room reappear. Try to navigate to the precise location of the treasure portal as efficiently as possible and minimize error. The duration of the experiment will be dependent on how well you do. At some point a label will come up that tells you to come get the experimenter.

Participants then received the 6 same training trials described in Experiment 3 depending on their group assignment. The participants had an unlimited time to choose the correct portal on all 36 FP spatial trials, however, the landmark alone trials (having no goal), timed out after 10 s. The ITI for training and testing was 3 s. Once participants completed 72 trials, they came upon a stop signal. The experimenter returned and read them the following instructions:

Test. “On raids after this signal, you should still do your best to find the portal that previously transported you to treasure, but no treasure will be shown (though we are still keeping track). This is because we don’t want you to know whether you chose correctly or not, we just want to know which target you think is hiding the treasure. You will only be allowed to choose one portal per scenario do reorient yourself, think carefully and choose a portal. Though we are not giving you feedback, you’re accuracy is still being recorded and we will let you know how you did very soon. Now, show us what you learned about plundering!”

Participants then received two shuffled blocks of the following 6 trials: XA, XB, YA, YB, A, B. For analysis, the time it took the participants to record a response (latency), and the proportion of their selections off all other portals subtracted from the target (i.e., the difference score; a measure of spatial accuracy, see Experiment 3) were collapsed into three meaningful categories: 1) FP-Spatial (XA, XB, YA, YB), 2) Novel-Background (ZA, ZB), and Novel-LM (XC, YC).

Results

FP Spatial Training. All 24 original participants placed in this experiment reached the training criterion of 75% accuracy on FP Spatial trials (WA, XA, YB, and ZB).

Latency Analysis. The left side of Figure 11 displays the latency data. To assess whether Group 1 or Group 2 completed the FP Spatial training trials, a 2 x 2x 2 x 9 mixed design ANOVA with Gender (Male vs. Female), Group (1 vs. 2), and Nationality (American vs. Japanese) as the between subjects variables, and Block (1-9) as the repeated measure was conducted on latency (s). The ANOVA revealed *n.s.* main effects of group, nationality, as well as all interactions, including two and three way interactions, all $F_s < 2.91$, $p_s > .12$, $\eta^2 = .26$. Interestingly, there was a significant main effect of gender (bottom row of Figure 11), $F(1,16) = 11.5$, $p < .001$, $\eta^2 = .41$, and a significant main effect of block, $F(8, 128) = 8.56$, $p < .001$, $\eta^2 = .34$. Tukey’s HSD conducted within the main effect of gender showed that females ($M = 14.8$ s, $SD=$) took much longer to arrive at the target than male participants($M = 7.26$ s, $SD=$), $p < .001$.

Error Analysis. The right side of Figure 11 shows the average amount of errors participants made on FP spatial trials. A 2 x 2 x 9 mixed design ANOVA with Gender (Male vs. Female), Group (1 vs. 2), and Nationality as the between subjects variables, and Block (1-9) as the repeated measure was conducted on errors. The ANOVA revealed a significant main effect of block, $F(8, 128) = 8.43, p < .001, \eta^2 = .34$, all other main effects (including gender) and all interactions were *n.s.*, $F_s < 3.02, p_s > .1, \eta^2 < .15$.

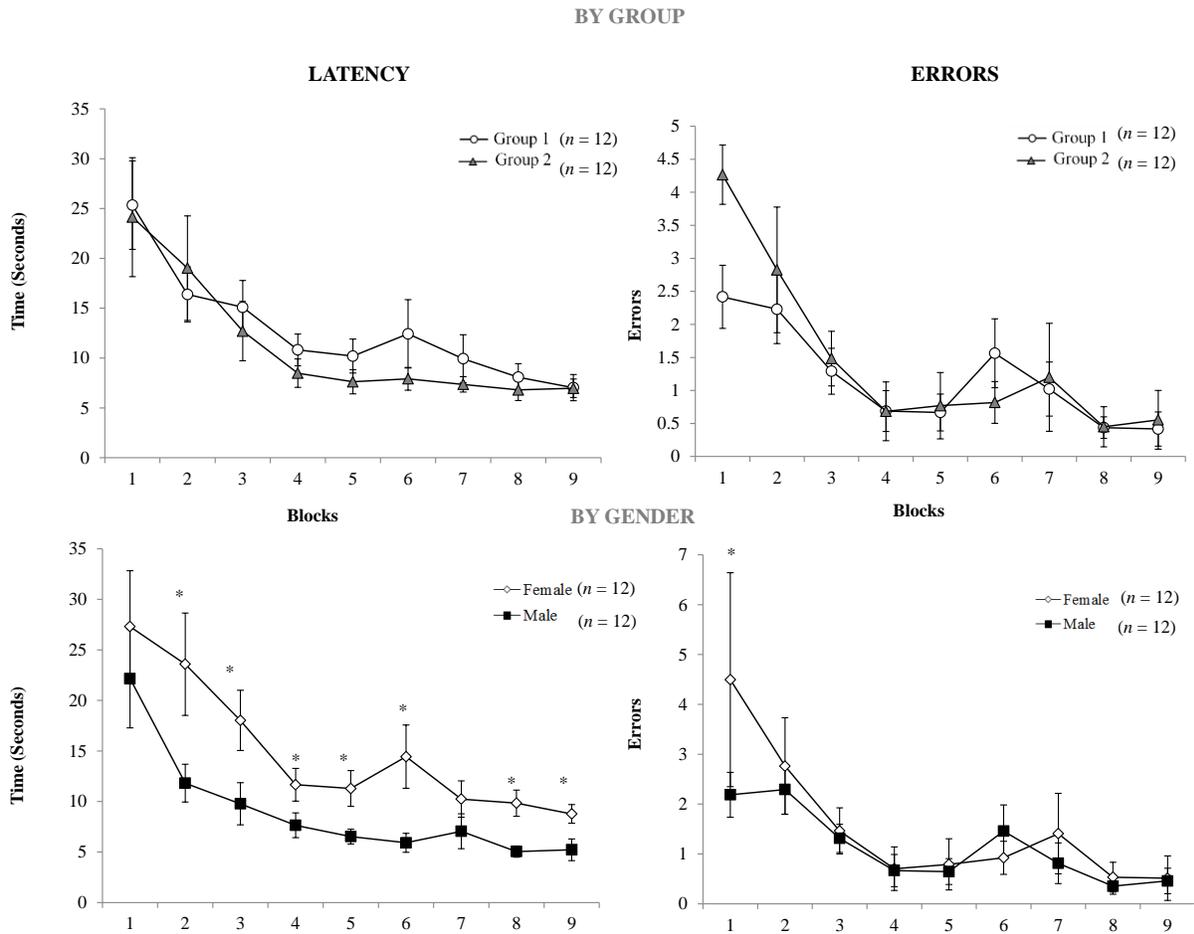


Figure 11 shows the latency and error data from Experiment 4. The x axis shows blocks of training. Each block represents 4 FP spatial trials averaged. The left column illustrates latency to respond across the 9 blocks. The right column illustrates the number of errors that occurred across the 9 blocks. Error bars represent standard error of the mean. The top row compares Group 1 ($n = 12$) to Group 2 ($n = 12$). The bottom row compares males to females. Error bars represent standard error of the mean.

Test Analysis. Figure 12 illustrates the test data from Experiment 4. A 2 (Group: 1 vs. 2) x 2 (Gender: Female vs. Male) x 3 (Category: FP spatial, Novel-Background, Novel-LM)

repeated measures ANOVA with category as the repeated measure was conducted on the average latency to respond as well as the difference scores (accuracy).

The ANOVA on latency revealed a significant main effect of category, $F(1, 16) = 4.83, p < .001, \eta^2 = .23$, and a main effect of nationality, $F(1, 16) = 12.1, p < .003, \eta^2 = .43$. Tukey's HSD conducted within the main effect of category revealed that participants took considerably less time to make a selection during Novel-Background ($M = 12.2$ s) and Novel-LM ($M = 12.6$ s) than during FP Spatial trials ($M = 15.3$ s).

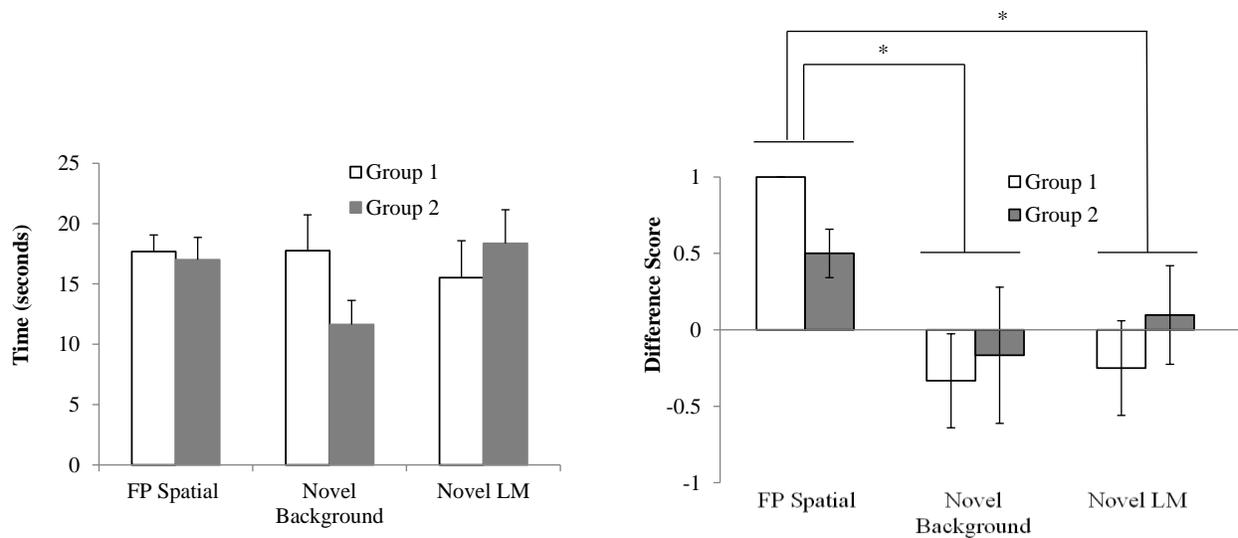


Figure 12 illustrates the test data from Experiment 4. On the left side, the y-axis depicts the time it took participants to make a selection in seconds. On the right side, the y-axis represents the difference score which was again calculated by subtracting the proportion of responses at all other response locations from the proportion of responses that occurred at the target. Error bars represent standard error of the mean. * = $p < .05$

Tukey's HSD conducted within the main effect of nationality revealed that Japanese participants took much longer to select a response portal ($M = 16.6$ s), than American participants ($M = 10.1$ s).

The ANOVA on the accuracy data (difference scores ranging from 1 to -1) revealed a significant main effect of trial type, $F(1, 16) = 37.8, p < .001, \eta^2 = .70$. Tukey's HSD conducted within the main effect of trial type revealed that participants were far more accurate during FP

spatial trials ($M = .71$), than during Novel-Background ($M = -.07$) and Novel-landmark trials ($M = -.43$), $p < .001$, which themselves did not differ, $p = .23$.

Discussion

Experiment 4 successfully demonstrated that college undergraduates could use a conditional background to definitively modulate the *distance* or *direction* of reinforcement while the landmark itself modulated the second dimension of information in a three dimensional search task. Experiment 3 did not confirm our hypothesis that the distal background would be better at modulating direction (Knierim & Hamilton, 2011) based on the latency and error acquisition data, nor the test data. Again, one reason for this null finding may have been the simplified, small test arena created a floor effect. Recall that 100% of participants completed the FP spatial trials accurately (75% correct or more). This may have made it difficult to detect differences in performance due to manipulating the information of either cue. A second possibility is that in the small room, it is difficult to argue that the background is truly distal to the array of portals, although unlike the two-dimensional setup of Experiment 3, there was perceived physical space between the background wall and the array. The negligible depth between the background and the target location may have promoted no important functional value between the background and the nearby landmark. I defend, however, that it was important to run an analogue of the previously validated touchscreen paradigm (Ruprecht et al., 2014b) that resembled it as much as functionally possible. Indeed, we observed a significant gender effect on latency, and a more negligible effect ($\eta^2 < .15$) on errors made. This difference was not apparent in the two dimensional paradigm. The desire to observe a group difference drove us to present the training in a much larger open-field task both with animals (Experiment 5) and humans using a virtual reality (VR) apparatus (Experiment 6) in order to increase ecological validity of the search task.

Series 3:

Experiments 3 and 4 demonstrated a limited role for gender and nationality in modulating whether the conditional stimulus best conveys distance or direction information about a landmark. One might argue that in the two-dimensional screen task, and the three-dimensional search small scale search task, the background is just far too close to the landmarks and array for information value (i.e., distance vs. direction) to make have made a marked effect on acquisition and test behavior. To investigate for a possible group difference, we investigated rats using landmarks in an open-field food search task (Experiment 5) and humans using large, distal conditional cues in an analogous 3D open-field while wearing the immersive Oculus Rift headset (Experiment 6).

Experiment 5

A large majority of past and current research on the experimental research of spatial search behavior is conducted on rats. The two major variants include the Morris Water Maze (e.g., Hamilton et al., 2009) and the dry-land search task (e.g., Ruprecht, Taylor, Wolf, & Leising, 2014a) in which rats uncover buried food. One motivation to use rats for this dissertation came from the Neuroscience community's ample understanding of head direction cells, grid cells, and place cells in rodent models of search behavior.

Distal cues provide critical information for reorienting the animal in terms of the apparatus and distal cues providing crucial "frames of reference". Local yet distal extramaze cues in a small scale open-field search task exert strong control over place cells (Barry et al., 2006; Bures et al., 1997; Gothard et al., 1995). Nearby intramaze cues, however, are thought to provide spatial input via a path integration computation embodied by grid cells of the medial entorhinal cortex (Hafting et al., 2005; McNaughton et al., 2006; O'Keefe & Burgess, 2005;

Knierim & Hamilton, 2011). Behavioral neuroscientists desire to parcel the neural structures involved in the use of any type of visual cue (distal or proximal), therefore Experiment 5 was conducted as a behavioral assay of the current search task.

Experiment 5 tested rat's search behavior in an open field when a conditional cue or landmark conveyed differing sources of spatial information (distance or direction). It was hypothesized that Group 1 (Conditional-Direction; LND-Distance) would acquire the FP spatial discrimination faster than Group B (Conditional-Distance; LND-Direction). This behavioral prediction would manifest in Group 1 rats arriving at the buried food pellet much faster during FP spatial training (lower latencies; a faster learning curve) than Group 2 rats, and also that Group 1 rats would make much less overall errors (i.e., visiting or digging non-target cups) than Group 2. Transfer tests similar to Experiment 3 and Experiment 4 were conducted following ample FP Spatial training. It was hypothesized that when tested at identical periods in acquisition; Group 1 would respond at a higher magnitude and be more spatially accurate than Group 2.

Method

Subjects. Sixteen experimentally naïve Long–Evans rats (*Rattus norvegicus*; 8 male and 8 female) obtained from the Institute for Animal Reproduction (Inaraki, JP) served as experimental subjects for Experiment 5. The adult rats were approximately 56 days old when they arrived to the laboratory, and began the experimental pre-training at approximately 66 days of age. The rats were single-housed within a vivarium in wire mesh cages with a substrate of wood shavings under the cages. Rats were maintained on a 12-h dark/12-h light cycle. All experimental manipulations were conducted during the light portion of the cycle (between 12p.m. and 4 p.m., Japanese Standard Time). A progressive food restriction schedule was

imposed over the week prior to the beginning of the experiment, until each female rat received 9 grams of food and each male rat received 13 grams of food each day, respectively. Rats were not allowed to drop below 90% of their free-feeding weights before and during the experiment. All rats were handled daily for 30 s during the week prior to the initiation of the study. All research was conducted in accordance with an approved TCU IACUC protocol. In parallel, this study was reviewed and approved by Kanazawa University Animal Experiment Committee, and carried out in accordance with the Guidelines for the Care and Use of Laboratory Animals of Kanazawa University, Japan (AP-143253). Both protocols were also co-submitted and approved by international advisory committees of the National Science Foundation and the Japanese Society for the Promotion of Science.

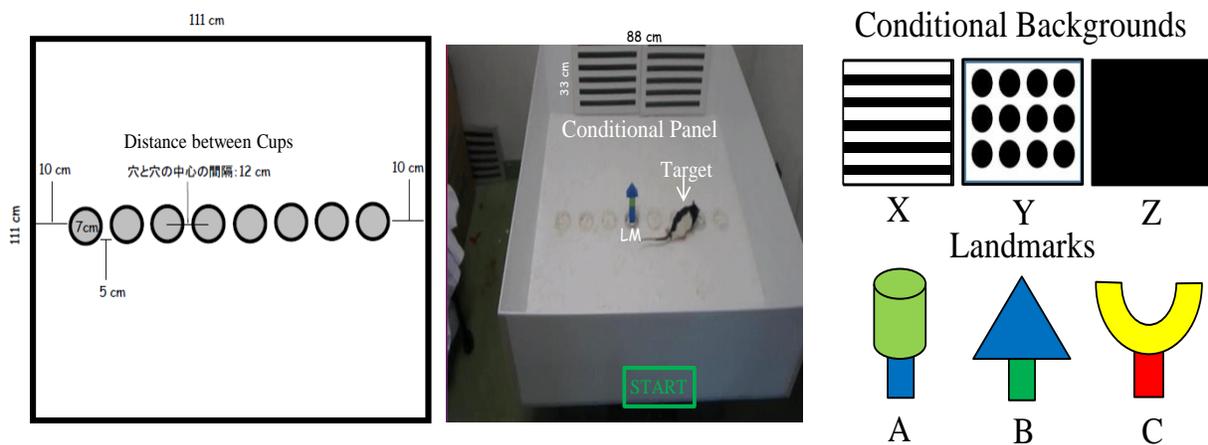


Figure 13 shows the apparatus (left) and stimuli (right) utilized in Experiment 5.

Apparatus. Experiment 5 was conducted on an open-field maze designed to allow rats to search for a buried piece of food under one of 8 cups. The maze (left side of Figure 13) was a square (131cm x131cm) piece of particle board that was 1.5cm thick. The board was painted flat white. Walls made of white polypropylene boards were 30 cm high, and surrounded all 4 sides of

the maze. Bore into the maze were 8 holes (6.75 cm in diameter), placed equally along an array 5cm from one another. The 8 hole array was centered 10 cm away from either side of the square maze and was placed perfectly centered along the side walls (i.e., the center axis of the array was 55.5 cm from either side). Cups filled with substrate and cereal (if selected to be a target location; see stimuli and procedure) as well as landmark statues were placed in the 8 holes.

Stimuli. For rats on the open-field, cues came in the form of background panels, landmarks, and response locations (cups; see middle of Figure 13). The background panels were plastic rectangular sheets measuring 88 cm long and 30 cm high. The panels were a spotted pattern (e.g., Stimulus X), striped pattern (Y), or solid black (Z) (see right side of Figure 13). The landmarks were small colored statues of different shapes that could fit into or take the place of a single response location (middle of Figure 13). The 8 response locations were cups (7 cm) wide, and arranged in a line X cm apart from rim to rim. The cups were filled with a white paper substrate that matched the white floor of the open-field. The target location for rats on FP spatial trials was baited with a small piece of chocolate cereal (Rakuten Global Market ©).

Procedure. Experiment 5 consisted of 3 general phases: 1) pre-training, 2) FP spatial training, and 3) testing.

Pre-training. Rats in Experiments 5 were habituated to the apparatus and then shaped to search within Tupperware © cups filled with wood shavings. Across 3 days, rats were initially trained to approach and dig progressively deeper and for smaller pieces of chocolate cereal (Rakuten Global Market ©). Since the plus maze required no digging (pellets were inserted into shallow holes at the end of the arm), rats in Experiment 4 did not undergo pre-training. Pre-training occurred inside a small plastic tub and no distal cues or landmarks were available to the rats.

Rats in Experiment 5 were then given two days to explore the open-field. All four walls of the maze remained blank white throughout pre-training (i.e., no panels were placed on the far wall). During open-field pre-training, all 8 response locations contained a portion of a cereal (buried progressively into the cups). Latency to find the buried cereal was measured and recorded. All 16 rats had to successfully visit all response locations and unearth a fully buried cereal pellet during pre-training before being advanced to FP spatial training. All but one of the 16 rats was able to complete pre-training in the six allotted days.

FP Spatial Training. Rats were trained in a similar experimental manner as humans, with mostly mechanical changes (see Figure 7 for the General Procedure). One major difference was that rats received only 6 trials a day of XA, YA, XB, and YB, A and B shuffled and counterbalanced across subjects. Each day, the latency (seconds to reach the target and uncover the hidden food) and accuracy (number of errors or incorrect holes searched until finding the target) were recorded.

Rats were brought to the Experimental room and held in a holding cage. An experimenter picked the rat out of the holding cage, and placed it at the start location (S; see Figure 13) facing away from the open-field. A separate experimenter began recording time as soon as the rat had turned away from the wall, and also manually recorded the number of errors for each trial. On FP spatial trials (XA, XB, YA, and YB) rats were allowed to explore a maximum of 3 minutes before being taken off of the table. Rats received 10 normal days of training, then, on day 13-16, they received probes of XA, XB, YA, YB, each replacing 1 regular training trial a day as to not induce extinction. All rats then trained an additional 5 days of training (Days- 19-21) before receiving probes of XA, XB, YA, YB, replacing one normal trial each from days 23-27. On test trials, the rat's behavior was video recorded.

Testing. As mentioned above, probes took the place of a single training trial for 6 days. On test trials, no cups were baited, and the cups were filled with a clean paper substrate. Rats were allowed to search for 60 s. A trained experimenter filmed the search behavior. Later, the video was analyzed. The amount of visits each rat made to each hole were coded and recorded.

Results

FP Spatial Training. One rat in Group 2 failed to complete FP spatial training whatsoever for 5 days and was removed from the study, making the final subject count 7 rats for group 1, and 8 rats for group 2.

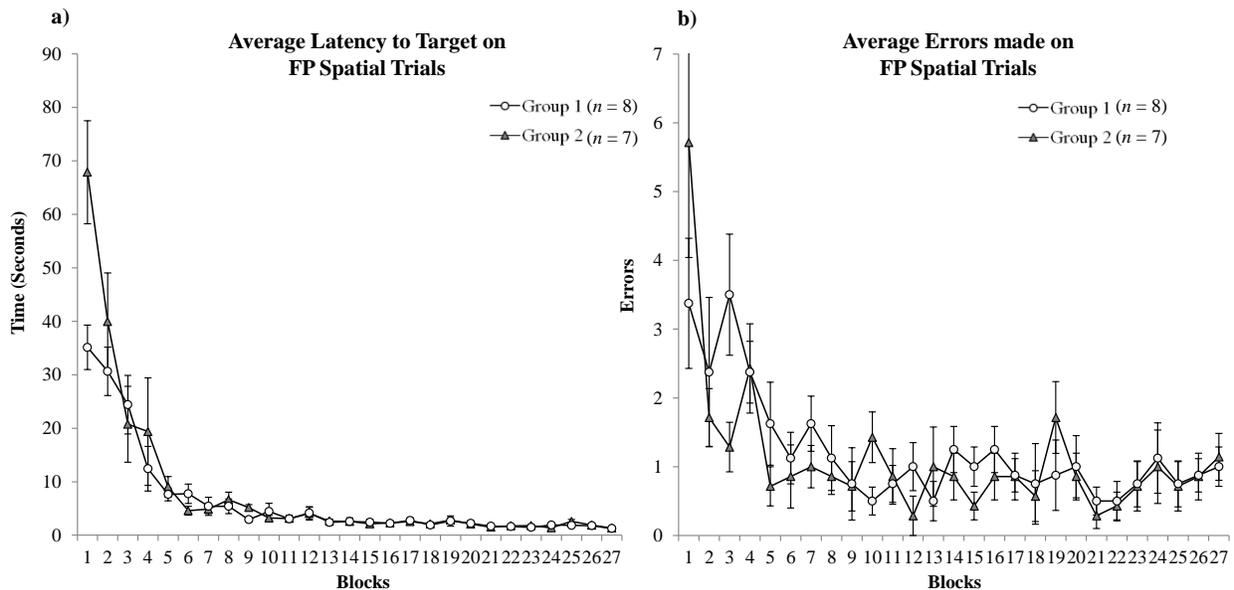


Figure 14 shows the latency and error data from Experiment 5. On the left, the y-axis represents the time in seconds it took rats to reach the target cup and uncover the buried food. On the right, the y-axis depicts the amount of wrong cups the rats visited before visiting the target cup. The x-axis represents 27 blocks or days. Each day featured 4 FP spatial trials (XA, XB, YA, YB) which were averaged for each block. Error bars represent standard error of the mean.

Latency Analysis. The left side of Figure 14 shows the average latency data collected from the rats on FP spatial trials, XA, YA, XB, and YB each day. To assess whether Group 1 or Group 2 completed the FP Spatial training trials, a 2 x 27 mixed design ANOVA with Sex (Male vs. Female) and Group (1 vs. 2) as the between subjects variable, and block (1-27) as the

repeated measure was conducted on latency (s). The ANOVA revealed a marginally non-significant main effect of group, $F(1, 13) = 3.15, p = .06, \eta^2 = .19$, as well as a significant main effect of block, $F(26, 286) = 37.07, p < .001, \eta^2 = .74$, as well as a significant interaction between group and block, $F(26, 286) = 3.26, p < .001, \eta^2 = .2$. The main effect of sex and all of its interactions, including the three way interaction of sex, group, and day were all *n.s.*, $F_s < 1.02, p_s > .44, \eta^2 = .08$, with the largest effect being the three-way interaction. Tukey's HSD conducted within the significant interaction of group x day showed on 7 of the 27 training days ($p_s < .01$), Group 1 reliably finished FP Spatial trials faster on average than Group 2, whereas only 1 day ($p < .001$), Group 1 finished faster. All other 19 days, the two groups did not differ in terms of latency.

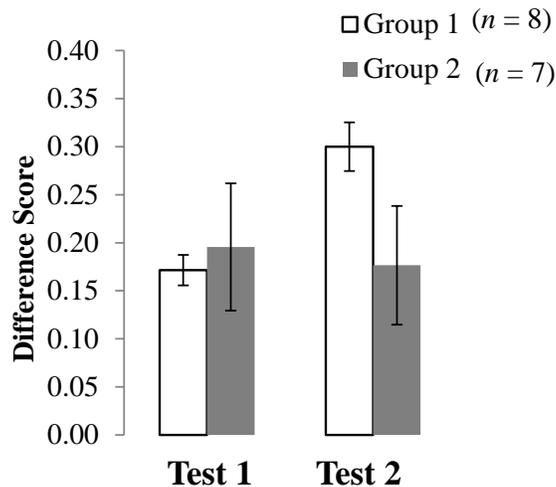


Figure 15 shows the difference scores from Experiment 5 averaged across the 4 FP spatial trials, XA, XB, YA, and YB on test 1 (halfway through acquisition) and test 2 (at the end of acquisition). The y-axis represents the difference score which was calculated by subtracting the average proportion of responses to other four respective locations from the proportion of responses that occurred at the target. Error bars represent standard error of the mean.

Error Analysis. The right side of Figure 11 shows the average amount of errors rats made on FP spatial trials XA, YA, XB, and YB each day. A 2 x 27 mixed design ANOVA with

Gender (Male vs. Female) and Group (1 vs. 2) as the between subjects variable, and day (1-27) as the repeated measure was conducted on errors. The ANOVA revealed a significant main effect of day, $F(26, 286) = 6.44, p < .001, \eta^2 = .36$, all other main effects (including gender) and all interactions were *n.s.*, $F_s < 1.3, p_s > .1, \eta^2 < .11$, with the largest *n.s.* effect being the interaction between group and day.

Test Analysis. Figure 15 shows the main test data from Experiment 3. A 2 (Group: 1 vs. 2) x 2 (Sex: Female vs. Male) main effects ANOVA was conducted on the difference scores for FP Spatial tests (XA, XB, YA, YB averaged). The ANOVA revealed *n.s.* main effects for group and gender, $F_s(1, 20) < .8, p_s > .38, \eta^2 < .03$.

Discussion

Rats were trained in two groups that a conditional panel signaled either the direction or distance of a hidden food pellet. Additionally, each group received the second source of information from individual landmarks, respectively. This was the first demonstration of rats successfully learning a FP spatial discrimination in the open field. Rats in Group 1 (Background-Direction; LND-Distance) took significantly less time and differed across time (i.e., blocks) from Group 2 providing some limited (main effect of group: $p = .06$) evidence for confirming our hypothesis that Group 1 would learn the FP Spatial discriminations quicker. A severe limitation to the study however concerns the null finding of group affecting the amount of errors. Latency is a performance based variable, therefore, it is very possible that animals in Group 1 were just faster at running than animals in Group 2. In light of the failure to observe a separate role for distance and direction during FP spatial discriminations, we sought to implement a larger-scale open field task for humans in a more immersive environment .

Experiment 6

Recall that I and Knierim et al. (2011) have proposed that distal cues provide critical information for reorienting us in space because the distal cues providing crucial “frames of reference”. Nearby intramaze cues, however, are thought to provide spatial information about the precise location of the target (distance) via a system within medial entorhinal cortex (Hafting et al., 2005; McNaughton et al., 2006; see General Discussion). In Experiment 6, we aimed to implement a larger, open-field search task that incorporated FP spatial discriminations. We trained undergraduates to navigate a realistic pizza environment (World-Viz ©). An array of Italian buildings was shaded blue, red, or orange to indicate what direction (Group 1) or how far (Group 2) the target portal was from the landmark portal (see Figure 16). A colored portal landmark told participants how far (Group 1) or what direction (Group 2) the reinforced target portal was.

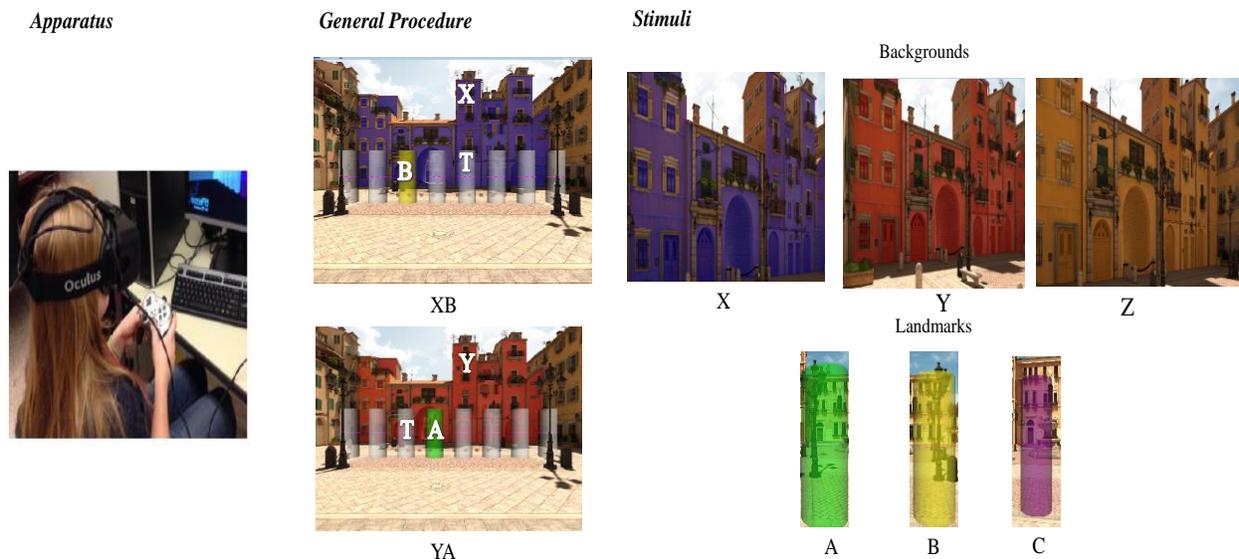


Figure 16 displays the apparatus (Oculus Rift) worn by the participants during the training, the general procedure for FP spatial discriminations, and stimuli used in Experiment 6 (far right). Conditional backgrounds filled up the piazza buildings located behind the array of 8 response location (i.e., portals). The color of the buildings determined the direction (Group 1) or distance (Group 2) of the target portal, whereas, the color of the LND portals determined the distance (Group 1) or direction (Group 2) respectively.

It was hypothesized that Group 1 (Conditional-Direction; LND-Distance) would acquire the FP spatial discrimination faster than Group 2 (Conditional-Distance; LND-Direction). This behavioral prediction would manifest in Group 1 reaching the target much faster during FP

spatial training (lower latencies; a faster learning curve) than Group 2, and also that Group 1 would make much less overall errors than Group 2. Transfer tests similar to Experiments 1 and 2 were conducted following ample FP Spatial training. It was hypothesized that when tested at identical periods in acquisition; Group 1 would respond at a higher magnitude and be more spatially accurate than Group 2.

Method

Participants. A total of 12 undergraduate psychology students (6 females, 6 males, aged 18-24) at Texas Christian University (TCU) participated as a partial fulfillment of course requirements. All students had no previous experience with either preparation, and were uninformed as to the purpose of the experiment. Participants were trained and tested individually; the experiment's max duration was set at 60 min but students could finish early. All experiments were conducted in dedicated human cognition testing rooms. All research was conducted in accordance with TCU's Human Participant Ethics Committee.

Apparatus. Participants completed Experiment 6 on a hard-top computer within the Vizard © computer software. A PlayStation 3 © remote controlled all experimental movement and responses. Participant's moved their on-screen avatar with the left analog stick and made response selections by hitting the x button (see Figure 10). The experiment took place from the "first-person" viewpoint of the participant. The participants also wore the Oculus Rift © headset to control the camera from the perspective of their own head.

Stimuli. Visual. Experiment 6 featured a large piazza with rectangular dimensions. On the north wall (see Figure 16), was an array of buildings. There were also 8 cylindrical portals placed in a centralized array at equal distances from one another. The north row of buildings changed colors if it was a FP spatial trial. The three colors were blue (e.g., X), red (e.g., Y), and

orange (e.g., Z); counterbalanced across participants. One portal served as a landmark on each trial, and it changed to a 50% transparent shade of yellow (e.g., A), green (e.g., B) or purple (e.g., C). Each portal had a very thin circular outline that appeared red; however, when the participant stepped into the portal, the thin frame turned light green. This was meant to aid the participant in knowing whether or not they were standing inside a portal or not. The participant had to tilt down the view with the Oculus to see the line, adding to the immersion.

Auditory. The participants received identical audio feedback as in Experiment 4 when they moved or made a correct/incorrect response.

Procedure. The procedure of Experiment 6 had three main phases: 1) Pre-training, FP Spatial Training, and Testing.

Pretraining. Participants were seated at a table and instructed on the proper usage of the game controller, including the directional and camera joysticks, and the response selection button. The participants began in the piazza with a row of 8 grey portals. No conditional cues or landmarks were present.

The Participants were then read the following script:

“Can you see the row of portals in the center of the piazza? When the portals are presented, it also means one of them is possibly the passage to a treasure room. Your task is to navigate and select which portal transports you to the hidden treasure. Take this opportunity to explore the screen and locate the hidden treasure. If you make an incorrect response (i.e., the wrong portal), an error buzzer will sound. Try selecting these portals at random until you hear a treasure sound. When you return to the field look for the treasure again, it will be inside a new portal this time! Also, use this time to get used to the Oculus Rift and notify us if you feel dizzy or uncomfortable”

Participants were allowed to search and find the hidden portal along the array of portals. Participants were required to search for 8 trials, and that they were confident that they understood how the controls, including navigation, camera rotation via the Oculus, and button selection worked.

FP Spatial Training. After completing pre-training; the participants were told the following instructions:

“During the warm up, the walls of the arena were always a static gray color, on future scenarios you’ll notice different colored walls, or perhaps, different patterned portals themselves. This is very important! During the next task there will also be scenarios when finding a treasure is NOT possible. First, explore all the portals by pressing X on the controller when you are standing inside of them, just like in pre-training, to identify when and if there is hidden treasure during a given scenario, and when there is not. You’ll know when a new scenario begins when the screen goes blank and you see yourself reappear in the piazza. Try to navigate to the precise location of the treasure portal as efficiently as possible and minimize error. The duration of the experiment will be dependent on how well you do. At some point a label will come up that tells you to come get the experimenter.

Participants then received the 6 same training trials described in Experiment 5 depending on their group assignment. The participants had an unlimited time to choose the correct portal on all 36 FP spatial trials, however, the landmark alone trials (having no goal), timed out after 10 s. The ITI for training and testing was 5 s. Once participants completed 72 trials, they came upon a stop signal. The experimenter returned and read them the following instructions:

***Test.** “On raids after this signal, you should still do your best to find the portal that previously transported you to treasure, but no treasure will be shown (though we are still keeping track). This is because we don’t want you to know whether you chose correctly or not, we just want to know which target you think is hiding the treasure. You will only be allowed to choose one portal per scenario do reorient yourself, think carefully and choose a portal. Though we are not giving you feedback, you’re accuracy is still being recorded and we will let you know how you did very soon. Now, show us what you learned about plundering!”*

Participants then received two shuffled blocks of the following 10 trials: XA, XB, YA, YB, A, B, ZA, ZB, XC, and YC. For analysis, the time it took the participants to record a response (latency), and the proportion of their selections off all other portals subtracted from the target (i.e., the difference score; a measure of spatial accuracy, see Experiment 3) were collapsed into three meaningful categories: 1) FP-Spatial (XA, XB, YA, YB), 2) Novel-Background (ZA, ZB), and Novel-LM (XC, YC).

Results.

FP Spatial Training. All 12 original participants placed in this experiment reached the training criterion of 75% accuracy on FP Spatial trials (WA, XA, YB, and ZB).

Latency Analysis. The top left of Figure 17 displays latency data for Experiment 6. To assess whether Group 1 or Group 2 completed the FP Spatial training trials, a 2 x 2 x 9 mixed design ANOVA with Gender (Male vs. Female), and Group (1 vs. 2) as the between subjects variables, and block (1-9) as the repeated measure was conducted on latency (s). The ANOVA revealed a significant main effect of block, $F(8, 64) = 11.5, p < .001, \eta^2 = .59$, and a significant two-way interaction of block by gender, $F(8, 64) = 3.02, p < .006, \eta^2 = .27$, all other main effects of group, gender, as well as all other interactions were *n.s.*, all $F_s < 3.97, p_s > .08, \eta^2 > .32$. Interestingly, the largest *n.s.* effect was the main effect of gender (illustrated in the bottom center of Figure 17). Tukey's HSD

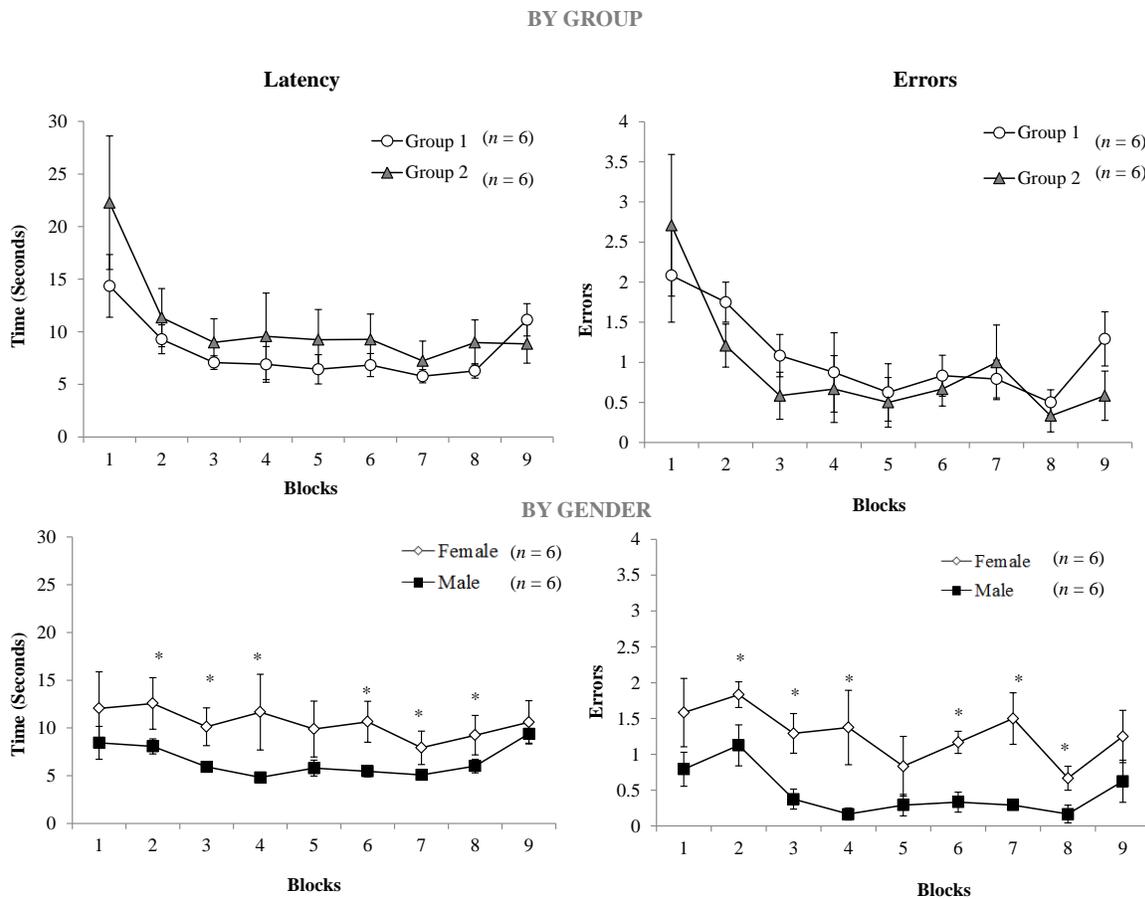


Figure 17 shows the latency and error data from Experiment 6. The x axis shows blocks of training. Each block represents 4 FP spatial trials averaged. The left column illustrates latency to respond across the 9 blocks. The right column illustrates the number of errors that occurred across the 9 blocks. Error bars represent standard error of the mean. The top row compares Group 1 ($n = 6$) to Group 2 ($n = 6$). The bottom row compares males to females. Error bars represent standard error of the mean.

conducted within the significant interaction of gender and block revealed that female participants took significantly longer to reach the target than males at Blocks 3 through 8, all $ps < .04$.

Error Analysis. The top right of Figure 17 shows the average amount of errors rats made on FP spatial trials. A 2 x 2 x 9 mixed design ANOVA with Gender (Male vs. Female), and Group (1 vs. 2) as the between subjects variable, and block (1-9) as the repeated measure was conducted on the number of errors. The ANOVA revealed a significant main effect of block, $F(1, 11) = 9.32, p < .001, \eta^2 = .53$, and a main effect of gender, $F(1, 11) = 13.24, p < .001, \eta^2 = .62$ (bottom row of Figure 17). All other main effects (including group) and their interactions were *n.s.*, $F_s < 1.83, ps > .08, \eta^2 < .32$, with the greatest *n.s.* difference being the main effect of group. Tukey's HSD revealed that males made less errors on FP spatial trials ($M = .51$) than females ($M = 1.49$), $p < .006$.

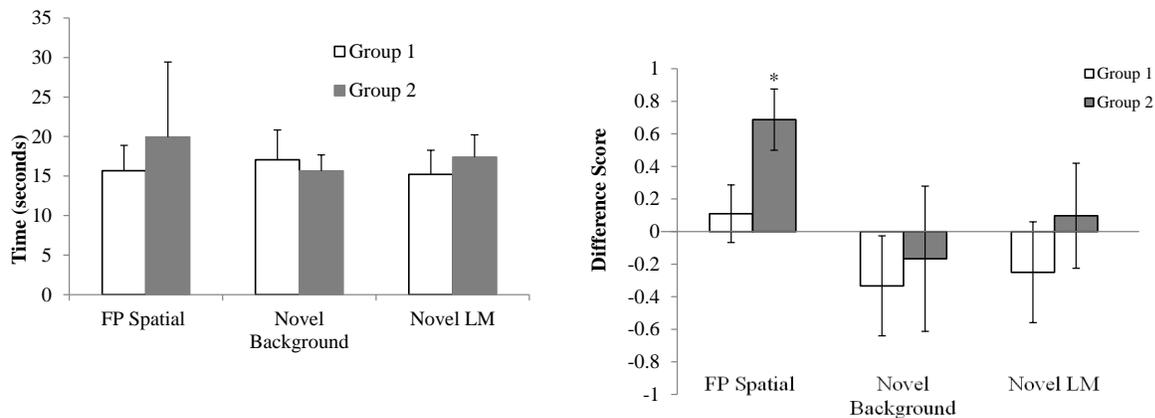


Figure 18 illustrates the test data from Experiment 6. On the left side, the y-axis depicts the time it took participants to make a selection in seconds. On the right side, the y-axis represents the difference score which was again calculated by subtracting the average proportion of responses at all other response locations from the proportion of responses that occurred at the target. Error bars represent standard error of the mean. * = $p < .05$

Test Analysis. Figure 18 illustrates the test data from Experiment 6. A 2 (Group: 1 vs. 2) x 2 (Gender: Female vs. Male) x 3 (Category: FP spatial, Novel-Background, Novel-LM) repeated measures ANOVA with category as the repeated measure was conducted on the average latency to respond as well as the difference scores (accuracy). The ANOVA on the latency data

revealed *n.s.* main effects for group, gender, and category, and all interactions, with the largest *n.s.* difference in latency accounted for by the two way interaction of group x gender, $F(1, 8) = 6.38, p = .06, \eta^2 < .61$. Tukey's HSD conducted within the main effect of nationality revealed that Japanese participants took much longer to select a response portal ($M = 16.6$ s), than American participants ($M = 10.1$ s).

The ANOVA on the accuracy (difference score ranging from -1 to 1) revealed a main effect of category, $F(2, 16) = 3.86, p = .04, \eta^2 = .32$. Tukey's HSD conducted within the main effect of trial type revealed that participants were far more accurate during FP spatial trials ($M = .48$), than during Novel-background ($M = -.41$) and Novel-landmark trials ($M = -.08$), $p = .03$, which themselves did not differ, $p = .23$.

Discussion.

Experiment 6 successfully implemented the FP spatial task into a more realistic environment for examining human open field behavior. FP spatial discriminations were successfully learned (i.e., 75% correct across the 36 FP Spatial trials) by all 12 participants while walking through the virtual piazza.

Experiment 6 yielded similar results to Experiment 4 in that 1) gender seemed to play a role in latency and in errors made (with males arriving at the target sooner and more accurately than females), and 2) at test, the only reliable result was that previously trained FP spatial trials elicited much more accurate responding. This is not surprising given that both Novel-background and Novel-LND trials leave one dimension of spatial information (distance or direction, respectively) out, rendering responding to random guesses on these tests (see Figure 18).

Experiment 6 importantly pitted a much more distal background (relative to the landmarks and the response location array); however, the relative ease with which participants

could approach the portals in the piazza may have again have yielded a ceiling effect. In future studies on FP spatial discriminations, it may be necessary to further spatially separate the conditional cue and landmark, in so much that neither cue can be seen at the same time, or the two cues are separately significantly in time. The immersive VR experience may provide the complexity and distraction necessary to break away from the possible floor effects of the current task, and shows promise for future three dimensional search task studies.

General Discussion

Six experiments explored a role for FP discriminations in guiding search behavior via conditional backgrounds modifying the spatial information of a landmark.

In Experiment 1, laboratory pigeons were trained on the following FP spatial trials \leftarrow WA, XA \rightarrow , \leftarrow YB, ZB \rightarrow , including the two landmark-alone trials, A- and B-. The reinforced direction (right or left) depended on the preceding conditional background, W or X. Recall however, that despite their proximity to the target, landmarks were low in stability *and* reliability. The hypothesis that due to the each landmark's instability, on transfer tests, (e.g., WB, YA) the conditional cue should control spatial accuracy was largely confirmed. Pigeons pecked a comparable amount during transfer trials, giving us some strong evidence for transfer of modulation from the original FP spatial trials to novel trials. Experiment 1 was the first experimental demonstration, to our knowledge, of a conditional cue completely modulating a landmark's spatial information in animals.

In Experiment 2, we implemented the same task with some mechanical changes to study human search behavior. The hypothesis that humans could also utilize conditional backgrounds to alter the spatial relation of ambiguous landmarks was largely confirmed. Both pigeons and

humans were *less accurate* during transfer trials, compared to the original FP spatial trials; both species were far more accurate on transfer trials than chance alone (a difference score of 0).

Experiment 3 tested Japanese and American undergraduate's use of conditional cues and landmarks that conveyed varying spatial information (distance or direction, respectively). The hypothesis that Group 1 (Conditional-Direction; Landmark-Distance) would acquire the FP spatial discrimination faster than Group 2 (Conditional-Distance; Landmark-Direction) was not supported. One possible reason for this null finding may have been the fact that the simple nature of the touch task created a floor effect making it difficult to detect differences in performance due to manipulating the information of either cue. In the two-dimensional environment, it was difficult to argue that the background was ever truly distal (i.e., a definitive "extramaze" cue; Knierim & Hamilton (2011)).

Experiment 4 tested undergraduate's use of conditional cues and landmarks that conveyed varying spatial information (distance or direction, respectively) in a small scale three-dimensional task that involved orientating to a room from a single start zone, assessing the conditional background and landmarks present, and then navigating to the target location (see Figure 10). Again, the hypothesis that Group 1 (Conditional-Direction; Landmark-Distance) would acquire the FP spatial discrimination faster than Group 2 (Conditional-Distance; Landmark-Direction) was largely disconfirmed. Tests did show that FP spatial discriminations were readily learned with a high degree of accuracy. It appeared males arrived to the target quicker than females, however, the time it takes to arrive to the target is a performance variable, making it difficult to claim that males were "better" than females at learning the task, particularly given the negligible difference in incorrect portals visited.

Experiment 5 tested rat's search behavior in an open field when a conditional cue or landmark conveyed differing sources of spatial information (distance or direction). The hypothesis that Group 1 (Conditional-Direction; LND-Distance) would acquire the FP spatial discrimination faster than Group 2 (Conditional-Distance; LND-Direction) was supported by the latency data: Rats in Group 1 (Background-Direction; LND-Distance) took significantly less time and differed across time (i.e., blocks) from Group 2 (main effect of group: $p = .06$). A severe limitation to Experiment 5 however concerned the null finding of group affecting the amount of errors across blocks. Latency, again, is a performance variable that often correlates with more learning, but does not guarantee any differences in learning. The possibility of learning differences only grows dimmer given the null finding of any error differences. It is still interesting that the rats in Group 1 approached much quicker to the target, albeit as inaccurately as the other group.

Experiment 6 trained undergraduates to navigate a realistic pizza environment (World-Viz ©). An array of Italian buildings was shaded blue, red, or orange to indicate what direction (Group 1) or how far (Group 2) the target portal was from the landmark portal (see Figure 16). A colored portal landmark told participants how far (Group 1) or what direction (Group 2) the reinforced target portal was. The hypothesis that Group 1 (Conditional-Direction; LND-Distance) would acquire the FP spatial discrimination faster than Group 2 (Conditional-Distance; LND-Direction) was largely unsupported. Experiment 6, like the three dimensional search task in Experiment 4 revealed that 1) gender seemed to play a role in latency (with males arriving at the target sooner than females), and 2) at test, the only reliable result was that previously trained FP spatial trials elicited much more accurate responding.

A central motivation for conducting this dissertation, and in particular, Experiments 3—6, was that the Neuroscience literature makes separate predictions on the relative contributions of brain regions when utilizing distal cues for adjusting one's heading (direction) and proximal cues for honing to a nearby target (distance). Distal cues provide critical information for reorienting the animal in terms of the apparatus and distal cues providing crucial "frames of reference". Local yet distal extramaze cues in a small scale open-field search task exert strong control over place cells (Barry et al., 2006; Bures et al., 1997; Gothard et al., 1995). Nearby intramaze cues, however, are thought to provide spatial input via a path integration computation embodied by grid cells of the medial entorhinal cortex (Hafting et al., 2005; McNaughton et al., 2006; O'Keefe & Burgess, 2005; Knierim & Hamilton, 2011). Behavioral neuroscientists hoping to parcel the neural structures involved in the use of any type of visual cue (distal or proximal), may utilize a study similar in nature to Experiments 3—6 in which the background alters one dimension of spatial information relative to the proximal landmark.

A major limitation to the work in general was the failure to identify consistent group differences in spatial learning. As mentioned above, the horizontal array may be simple enough to solve that a floor effect masked any noticeable differences in learning. One possible remedy may be to use more extensive grids that span not only the horizontal planes but also vertically, thereby creating larger coordinate maps. Moreover, in each study, the response locations were clearly marked as separate from the environment. Humans, in particular, may have used a cognitive strategy such as counting (e.g., 1 or 2; for distance) or language (e.g., left or right; for direction) to identify the correct target, thus masking any differences in pure spatial learning. Two possible prescriptions for such a strategy might involve masking the boundaries of the response locations so that participants cannot count or label the spots. This would presumably

increase the difficulty of the task demonstrably, allowing more room for group variations in responding to occur. A second prescription for the null group difference finding may be to actually target the presumed cognitive strategy head on. One might insert interference tasks between FP spatial trials that tax a participant's usage of counting or language. One might predict that counting interference tasks may have more of a marked decrement on making distance (1 vs. 2) discriminations whereas lexical distractions (e.g., word generation) might affect direction (left vs. right vs. up vs. down) discriminations.

The paradigms presented here offer some clinical advantage. From gerontology literature, we know that a great deal of spatial deficits seem to occur as organisms reach a more advanced age. Aged mammals (rats), for instance, show deficits in allocentric processing (e.g., landmark integration), while showing no clear deficit in egocentric processing (e.g., beacon learning; Begega et al., 2001). Such age-related impairments in spatial learning are likely to be related to the vulnerability of the hippocampus and surrounding limbic structures to neurodegenerative processes (Lister and Barnes, 2009; Stranahan and Mattson, 2010). More troubling, deficits in allocentric processing appear to occur due to the normal course of aging, notwithstanding any additional degenerative disorders, such as Alzheimer's disease or Dementia (Raz et al., 2005, Yankner et al., 2008). Complications in allocentric learning have been widely observed in older adults (Moffat and Resnick, 2002, Iaria et al., 2009, Harris and Wolbers, 2012, Wiener et al., 2012). At present, however, the precise neural deficits inducing these changes in navigational competency at advanced age are largely misunderstood. The risk to aged loved ones is clear. Degradation in allocentric processes (e.g., recognizing where in town one's car is traveling), while more procedural aspects of memory are preserved (e.g., knowing how to operate and drive a vehicle) poses a specific risk to public safety and the well-being of the elderly.

Wiener and colleagues (2013) conducted the first study to directly investigate the effects of cognitive aging on specific navigational strategies. The researchers concluded that “although we are not aware of any studies testing for a potential dissociation between the dorsolateral and dorsomedial striatum, we speculate that stimulus–motor response learning processes as required for the associative cue strategy might be similarly affected by aging as hippocampus-dependent place-based processes, whereas beacon-based navigation might be more resistant to age-related change.” (Weiner et al., 2013; p. 6). Therefore, the development of small-scale, as well as comparable large-scale search tasks that can dissociate navigational strategies (landmark use, conditional discrimination, transfer of conditional control) is paramount to later identification of the neural underpinnings underlying any one competency.

In sum, there was a large clinical incentive to a) research conditional discrimination during spatial search tasks with a normal population, and b) determine if any detected deficits are constrained to three dimensional search tasks, or to the two dimensional search task. Prior to tackling what elements of spatial processing are lost due to aging, however, behavioral studies on what spatial information is encoded during FP discriminations needed to be investigated across an array of paradigms. To date, the majority of navigational studies in aged adults have occurred in 3D virtual search tasks (e.g., Harris & Wolbers, 2012; Weiner et al., 2013). FP spatial discrimination undoubtedly provides a framework for several everyday spatial tasks such as navigating your car to work, or making your way through a crowded parking garage to locate your car.

Understanding the mechanism supporting conditional discriminations has been thought to be critical to unraveling some of the remaining questions regarding the structure of human memory (Miller & Oberling, 1998; Rescrola, 1992). Computational models of memory first

captured the sophisticated and flexible choice behavior enabled by conditional stimuli. One of the first connectionist models to address this structure of memory (Collins & Quillian, 1969, 1972), introduced links between nodes to represent causal and descriptive relations between concepts, as well as the attribute of property inheritance, whereby nodes (concepts) inherit properties hierarchically from the nodes above them. Subsequent models (Anderson et al., 2004) opted for the use of semantic networks, in which the weights of the links can be altered to better represent the actual relationships between concepts (or stimuli) in the environment. Recent parallel-distributed theories have added to the sophistication of these models (see McClelland & Rogers, 2003), but the sophistication, in most cases, is still built on modulation (excitatory) of propositions (binary associations with truth value). For example, in “How do we know that Socrates is Mortal?” Aristotle suggested that we reason from two propositions, in this case: “Socrates is a man; and all men are mortal” (McClelland & Rogers, 2003, pg. 310). Consequently, a better understanding of the attributes (causal, spatial, and temporal) represented in such hierarchical structures modulating binary associations will lead to more comprehensive and accurate modeling of human memory.

Finally, it should be noted that transfer tests (pitting cues with varying histories together for the first time) have some possible clinical and diagnostic potential. Activity during transfer tests that pit cues with varying information (e.g., previous training history, novelty, spatial incongruence) could be used to further categorize types of spatial memory decrement in aged or diseased populations (e.g., spatial interference, memory loss, attention loss). Previous studies have found a high correlation between scores of dementia and performance on conditional discrimination tasks, and have encouraged subsequent research with different conditional discrimination procedures to better understand deficits associated with dementia (Gallagher and

Keenan, 2009; McClelland & Rogers, 2003; Steingrimsdottir & Arntzen, 2011). The visuospatial conditional discrimination procedures proposed here add spatial cognition demands to standard discrimination tasks. Spatial cognition deficits, in particular, have also been correlated with dementia. One future direction stemming from this dissertation research is to investigate behavior during these tasks with diseased young and aged adults (e.g., older adults suffering from Alzheimers; children with Autisim Spectrum Disorder). By investigating pigeons, rats, and humans, it is clear that there appears to be role for FP discrimination during spatial search task. We still have more to learn about what aspects of spatial search with landmarks are uniquely human, as well as what aspects we shared with our brethren.

Appendix 1

2D Human Script

The following script was used for Experiment 2 and Experiment 3.

***Bold Text was Instructions for the Experimenter.** Regular text was read aloud to the participant.

[1]Seat the Participant then read the following

Positioning: Please sit in this chair as straight as possible with your body comfortably leaned back. Place your elbows to the side and let us know that you can aim at the screen without any discomfort.

[2]Pre-training:

Open the pretraining computer program and start the program, then read the following:

Behind one of these boxes is a hidden treasure and your task is to find the box which reveals the hidden treasure. Sometimes the treasure will be revealed after clicking the correct box once, however other times it will be revealed after multiple clicks to the correct box. Take this opportunity to explore the screen and locate the treasure.



2-3 Min

[3] Post Pre-training: Pause to let the participant complete two trials. Ask if there are any questions? Read the following:

Notice that the treasure box's location changed over time. In the actual experiment the treasure's location will be switched after each new scenario begins. You'll know when a new scenario begins when the screen goes blank, the boxes disappear, and the colors and patterns change.

When the experiment starts, you will want to explore all of the boxes, to identify when and if there is hidden treasure during a given scenario.

During the actual experiment, there will be features that differ during each scenario to help you remember which box the treasure might be behind. These features include the color of the background patterns on the boxes themselves. The treasure will never be behind the patterned box.

This is very important. During the next task there will be scenarios in which finding a treasure is NOT possible. After identifying these scenarios, the correct response is not to click.

When the boxes change, it is your job to identify if and where the treasure is, or if there is not one. Is everything clear, do you have any questions?

[4] Pre- Experiment

Open the Training computer program and start the Experiment up. Pause at the black screen and wait to hit "F10". Read the following:

Again, your task is to find as many hidden treasures as possible. Keep in mind there is only one location hiding the treasure, but you may continue to hit the treasure box and collect multiple treasures. Pay close attention and please do not press the screen at random. You will only have a limited time to determine whether there is a target or not, and if a target is present, to respond at the target location. If you have

found the hidden target, you will see the treasure just like in pre-training. Remember, sometimes you have to shoot the correct target many times to reveal the treasure.

Learning to distinguish scenarios reflects your performance. *This is a memory test*, so once you have figured out the pattern, you need to remember it, and shoot the correct box, or **if appropriate, not shoot at all!** You may finish anytime between 20 and 40 min, the duration is dependent on how well you do (i.e., learning when to fire at the targets and when to withhold firing). At some point a label or white box will come and the scenarios will stop. Let us know when this happens. Good luck finding the treasure!

Exit with the keyboard and mouse in hand and press F10!



30-40 Min

[5] Post Experiment; Test trial instructions : After the stop screen, read the following:

During these next scenarios continue to click the target where you remember the treasure being hidden, however this time the treasure icon will not be shown regardless of whether or not you are correct. This is because we don't want you to know whether you chose correctly or not, we just want to know which target you think is hiding the treasure. Though we are not giving you feedback, your accuracy is still being recorded.

Now, find as much treasure as possible!

Press the on-screen button to continue the test.



8-10 Min

[6] Post-Test: Press F-10 one more time to exit the program and close out the Visual Basic windows so that you are back to the desktop, tell the participant:

Great job, you are almost done, I am just going to ask you a few debriefing questions.

[7] Hand them a debriefing form, don't forget to include the participants last a name, as well as their counterbalancing assignment.

3D (small scale) Human Script

The following script was used for Experiment 4

[1]Seat the Participant then read the following

Positioning: Please sit in this chair as straight as possible with your body comfortably leaned back. Hold the controller with two hands in front of you or in your lap.

[2]Pre-training:

Explain the Playstation controller to the participant, identifying the functionality of the left analog (movement), right analog (camera spin), and selection button (the X button on the controller). Open the pre-training program (so they can see the room) then read the following:

Can you see the row of portals in the center of the field? When the portals are presented, it also means one of them is possibly the passage to a treasure room. Your task is navigate and select which portal transports you to the hidden treasure. Take this opportunity to explore the screen and locate the hidden treasure. If you make an incorrect response (i.e., the wrong portal), an error buzzer will sound. Try selecting these portals at random until you hear a treasure sound. When you return to the field look for the treasure again, it will be inside a new portal this time!”

[3] Post Pre-training: Pause to let the participant complete minimum 4 trials. If the participant struggles to move, help them with the activity. Ask if there are any questions? Then Read the following:

3-5 MIN

“During the warm up, the walls of the arena were always a static gray color, on future scenarios you’ll notice different colored walls, or perhaps, different patterned portals themselves. This is very important! During the next task there will also be scenarios when finding a treasure is NOT possible. First, explore all the portals by pressing A on the controller when you are standing inside of them, just like in pretraining, to identify when and if there is hidden treasure during a given scenario, and when there is not. You’ll know when a new scenario begins when the screen goes blank and you see room reappear. Try to navigate to the precise location of the treasure portal as efficiently as possible and minimize error. The duration of the experiment will be dependent on how well you do. At some point a label will come up that tells you to come get the experimenter.

This is very important. During the next task there will be trials in which finding a treasure is NOT possible. These trial will time out.

RESPOND AS QUICKLY AND ACCURATELY AS POSSIBLE TO FINISH ON TIME!!!

(“Is everything clear, do you have any questions?”)

[4] Pre- Experiment

Open the Training program and start the program. Pause at the black screen and wait to hit “F10”. Read the following:

Find as many hidden treasures as possible. Keep in mind there is only one portal hiding the treasure. Pay close attention and please do not button press at random. You will only have a limited time to determine whether there is a treasure or not, and if a treasure is present, to respond at the treasure location. If you have found the hidden treasure, you will hear the treasure sound just like in pre-training.

Learning to distinguish trials reflects your performance. **This is a memory test**, so once you have figured out the patterns, you need to remember it, and choose the correct portal, or **if appropriate, not choose/press the X button at all!** You many finish anytime between 20 and 30 min, the duration is dependent on how well you do (i.e., learning when to choose portals and when to withhold responses).

At some point you will hear an alarm noise (like an electronic clock, please put down the controller and find an experimenter at this time!!!!!!)

Good luck finding treasure!

Press Start on computer and exit the participant



20-30 Min

[5] Post Experiment; Test trial instruction: After the Alarm sound, read the following:

During these next trials, continue to select the portal where you think the treasure is hidden, however this time the treasure sound will not be shown regardless of whether or not you are correct. This isn't because we want you to have no idea whether you chose correctly or not, we just want to know which portal you think is hiding the treasure. You only have one choice at test so be as accurate as possible. Though we are not giving you feedback or treasure, your accuracy is still being recorded.

When you see a THANK YOU, come get me
Now, show us what you have learned!

Press the on-screen button to continue the test.



8-10 Min

[6] They will notify you that a Thank You sign has occurred. Press escape to exit the program, and make sure to save the data (click Yes)

Appendix 2

Debriefing Questions

The following debriefing questions were given to all TCU human participants. (Used for Human Experiments 2,3,4 and 6)

Did you notice that the colored background was switched for some trials? Especially the recent trials you completed when no feedback was given?

On the switched trials, how confident were you in your responses?

Would you say the background or the landmark (the patterned box) guided your responses most on the switched test trials? It is ok to say you don't really know or both?

If I tested you again with new colors and patterns, would you rely on colors or patterns more to guide your response?

Please Read the Following Debriefing Paragraph

Finding things in space, like our lost car keys for example, can be difficult. We believe higher-order processes might be at work, requiring us to integrate spatial information across time. In this task, you observed a series of colored backgrounds and then observed a filled pattern inside of one square. The first colored background always determined whether or not the second patterned square was paired with treasure, but also told you where (left vs right) the treasure was hidden. The characteristics of spatial memory are still being debated, and the purpose of this research is to gather more information on the nature of spatial memory by testing your ability to integrate information over time (e.g., few or many items, short or long display, simple or complex items). Thank you for your participation. Please do not discuss the specifics of this experiment with your friends or peers. We want all of our participants to start the task with no previous knowledge. If you have any questions, or would like additional information please contact Chad Ruprecht in the Department of Psychology. He can be reached by calling his office or by e-mail (c.ruprecht@tcu.edu). Thanks again!

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EDUCATION

Degrees

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| 2015 (tentative) | <i>Ph.D. Experimental Psychology</i> , Texas Christian University |
| 2012 | <i>M.S. Experimental Psychology</i> , Texas Christian University |
| 2010 | <i>B. S. (Magna cum Laude) Psychology</i> , Sam Houston State University |

SCHOLARSHIP

Peer-Reviewed Publications

- Ruprecht, C.M.,** Elliott, A., & Leising, K.J. (in prep). Feature-positive spatial discriminations in pigeons and humans. *Psychonomic Bulletin & Review (Target Journal)*
- Ruprecht, C.M.,** Leyva, J.A., MeeKeehan, M., & Leising, K.J. (in prep). Spatial responding as a function of task complexity and overtraining. *Behavioural Processes (Target Journal)*
- Leising, K.J., Hall, J.S., Wolf, J.E., & **Ruprecht, C.M.** (2015). Feature-positive discriminations during a spatial-search task with pigeons. *Journal of Experimental Psychology: Animal Learning & Cognition*
- Leising, K.J., Wong, J., **Ruprecht, C.M.,** & Blaisdell, A.P. (2014). Blocking between landmarks on the touchscreen and in ARENA with pigeons. *Learning & Behavior*. 42(4): 357-64
- Ruprecht, C.M.,** Wolf, J.E., Quintana, N.I. & Leising, K.J. (2014). Feature-positive discriminations during a spatial-search task with humans. *Learning & Behavior*. 42(3) 215-230.
- Ruprecht, C.M.,** Izurieta, H.S., Wolf, J.E., & Leising, K.J. (2014). Overexpectation in the context of reward timing. *Learning & Motivation*. 47, 1-11.
- Leising, K.J., **Ruprecht, C.M.,** & Stahlman, W.D. (2014). Modulation of variation by response-reward spatial proximity. *International Journal of Comparative Psychology*, 27(2). 326-337
- Wolf, J.E., Urbano, C.M., **Ruprecht, C.M.,** & Leising, K.J. (2014). Need to train your rat? There's an app for that! *Behavior Research Methods*. 46(1)206-14.
- Ruprecht, C.M.,** Taylor, C.D., Wolf, J.E., & Leising, K.J. (2014). Task complexity modifies the search strategy of rats. *Behavioural Brain Research*. 258(1) 208-217.
- Leising, K. J., Wolf, J. E., & **Ruprecht, C. M.** (2013). Visual discrimination learning with an iPad-equipped apparatus. *Behavioral Processes*, 93, 140-47.

GRANTS AND FELLOWSHIPS

- 2015 [\$3,468] **Using iPads to improve student learning and research** in the course Experimental Psychology.
<http://www.research.tcu.edu/default.asp?id=page&pid=sp213&parent=199>
- 2014 [\$50] **Outstanding Presentation by a Young Scientist.** 74th Annual Meeting of the Japanese Animal Society. Inuyama, Aichi, Japan.
- 2014[\$11,500] **Eastern Asia/ Pacific Summer Fellowship** (*National Science Foundation & Japanese Society for the Promotion of Science*). Investigating conditional spatial discriminations in 3D environments. In collaboration with Dr. Tohru Taniuchi at Kanazawa University, Japan.
- 2013 [\$2500] **Summer Institute for Spatial Cognition.** (*Spatial Intelligence Learning Center*) Funded to attend an institute in Santa Barbara, California for 2 weeks. Director: Dr. Nora Newcombe,
- 2010 [\$90,000] **Teaching Fellowship** (*Texas Christian University*)
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TEACHING EXPERIENCE

Full Instructor

- Spring 2015 Social Psychology, *Columbia College*
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ABSTRACT

UNRAVELING THE COGNITIVE MAP:

A ROLE FOR FEATURE-POSITIVE DISCRIMINATION IN SPATIAL SEARCH

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The ability to use cues to navigate through the environment is a trait shared by all mobile organisms. This dissertation focused on spatial search behavior in two mammalian species (rats and humans) and an avian species (pigeons) to explore similarities and differences in learning and memory. A major aim of the project was to explore the role of conditioning (feature-positive discrimination) in building allocentric representations of space. The experiments were implemented on either a two-dimensional touchscreen monitor (humans and pigeons), three-dimensional open field task (humans and rats), or a VR equipped (Oculus Rift) video game (humans). We hypothesized that a conditional background could un-gate spatial information about a landmark, allowing the organism to integrate the cues, and search accurately. The results indicated that trained conditional cues could readily transfer their spatial information to novel pairings with familiar landmarks at test. This ease of transfer indicates that feature-positive discriminations do play an important role in modifying our search decisions in the presence of landmarks. Making species comparisons during search tasks will further elucidate the true psychological mechanism backing our extraordinary ability to navigate through space. The search tasks developed in this dissertation hold potential to guide future diagnostic measurements that can detect decrements in spatial cognition, and distinguish individual differences in strategy.