9-12-2014

Spatial Discrimination in the Virtual Morris Water Task: The Influence of View Similarity

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SPATIAL DISCRIMINATION IN THE VIRTUAL MORRIS WATER TASK: THE INFLUENCE OF VIEW SIMILARITY

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THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Master of Science
Psychology

The University of New Mexico
Albuquerque, New Mexico

July, 2014

SPATIAL DISCRIMINATION IN THE VIRTUAL MORRIS WATER TASK: THE INFLUENCE OF VIEW SIMILARITY

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ABSTRACT

Previous research in the Morris Water Task (MWT) and Virtual Morris Water Task (VMWT) examined how distal cues, or cues placed outside the pool, enabled an organism to orient themselves to navigate towards the hidden platform (Kolb & Whishaw, 2009). Recently Cheng and colleagues (2008) have created a model that predicts navigational performance based upon the similarity of views of the distal cues encountered within an environment. This model has successfully predicted performance for rats and simulated agents within a rectangular environment. The present study evaluates the view based similarity model with human subjects in the context of the VMWT. Three different distal cue configurations were tested that varied in value of pixel difference. In Experiment 1 subjects were required to navigate to a hidden platform in the VMWT and their behavioral performance corresponded to the pixel difference predictions of the model. In Experiment 2 subjects were reinforced for a correct choice between two visible

platforms. Finally, in Experiment 3, the pixel comparison model was implemented to determine if it could predict the preference for directional responding to the relative location in previous virtual poolshift experiments (Hamilton et al., 2009). The predictions of the model correspond with behavioral performance in VMWT hidden platform paradigms (Experiment 1), but it made inaccurate predictions for explicit discrimination tasks (Experiment 2) and VMWT hidden platform tasks once the pool was moved within the room (Experiment 3).

CHAPTER 1 BACKGROUND

Historical Context of Morris Water Task and Virtual Morris Water Task

The process of moving from one place to another is so automatic that it seems trivial. Virtually all organisms are able to move and return to a place that has been previously associated with reward. Mammals, birds, fish, insects, even robotic agents are able to encode a spatial memory and subsequently navigate to the previous goal location. The ability for an organism to learn spatial navigation is a vital component for the organism's survival. The question then remains: what cues does an organism attend to when navigating around its environment? How does an organism discriminate between patterns of cues that look similar? These questions have been extensively studied through a variety of techniques in a wide assortment of organisms.

Early work in the study of navigation examined the behavior of rats in plus mazes (+) and T mazes (for an extensive review see Knierim & Hamilton, 2011). Debate originally centered on what type of responding the animals were displaying (Fig. 1). Were the rats navigating through these mazes based on a motor memory sequence of turns described as “response learning” (Spence, 1936), or were they moving towards a beacon, or “place learning” (Tolman, 1948)? The answer is that animals are able to utilize different types of learning strategies depending on what information is provided (Restle 1957).

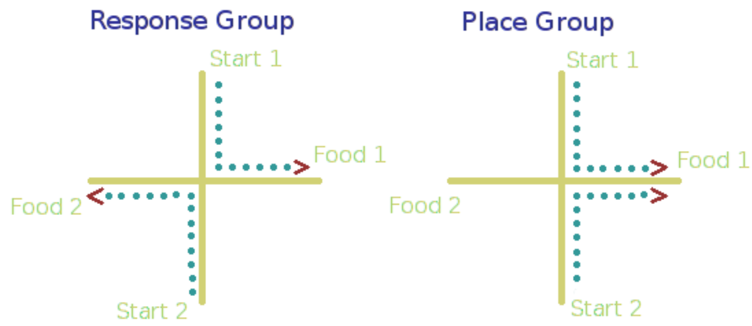


Figure 1: Response vs Place Learning

Contrasting styles of navigation learning. The response group is reinforced to make a left turn from each start position. The place group is reinforced to move towards a location within the room from each start position. Either strategy is easily learned depending on the information available to sample within an environment.

This behavioral 'choice' is not due to an innate psychological preference but instead due to the visual information provided to the animal during training. For example, animals are more likely to utilize place learning in mazes that are brightly lit whereas dimly lit mazes produce easier response learning (Restle, 1957). Instead of accommodating the observable behavior into an existing theory of learning, it is vital to focus on objectively categorizing the behavior within the environmental context that elicits it (Skinner, 1950).

While the T and + mazes illustrated that learning navigational strategies depended on the place and response information available to the subject, these mazes were confounded in their claim of testing spatial memory. The walls of the maze ultimately constricted behavior into binary or quaternary decisions—up or down, left or right.

Navigation in the open world is more freeform and allows for many more movement directions. To alleviate these concerns of path choice, and to create a paradigm with greater construct validity in its claim of testing spatial memory, the Morris Water Task was created.

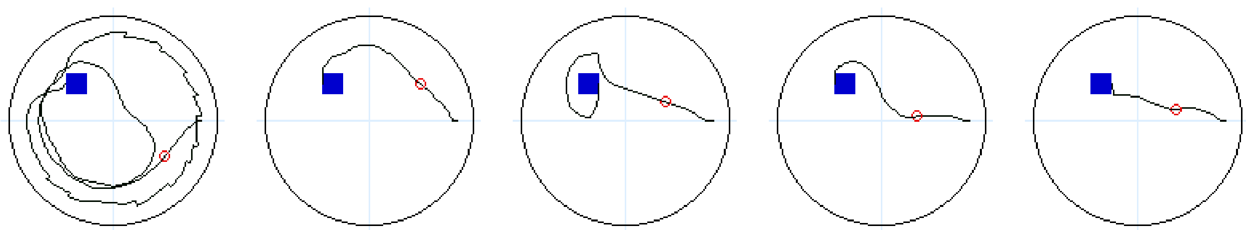
The Morris Water Task (MWT), as explained by Richard Morris (Morris, 1984) is a behavioral test that assesses the spatial memory of an organism. The task consists of a circular pool filled with opaque water. Hidden in the pool is a submerged square platform that the subject must learn to swim to in order to complete the trial.

Placing an animal in a pool of temperate water is mildly aversive and the animal is highly motivated to move towards solid land. Over the course of training, the animal is placed in the pool at various release points. By varying the starting point around the pool, the subject is required to navigate directly to the platform using different swim routes. This navigational learning is how spatial memory is operationalized in this behavioral task. Learning is evident when the animals take direct trajectories to the platform from multiple release points. The free form responding of the Morris Water Task (relative to the T and + mazes) allows for a variety of dependent measures within the task. Traditionally, latency to reach the platform and path length traveled to the platform are used to gauge how the subject learns the task (Hamilton et al., 2009). Additionally, by plotting the trajectory of the subject's swim path, more qualitative analysis can be performed to examine the subject's behavior as a function of time within a trial.

Table 1

Subject #15's Acquisition of Direct Trajectory Over Experimental Blocks

Block 1	Block 2	Block 3	Block 4	Block 5



Note: One subject's development of a straight trajectory over 5 blocks from the East release point. Each block consists of 4 trials from each start point (north, south, east, west). Initially subjects perform a thigmotaxis response, illustrated by circling of the pool. The trajectory becomes more direct with successful spatial acquisition of the platform.

This study used the Virtual Morris Water Task (VMWT), a computer simulation of the MWT. The subject navigated through a virtual pool environment, just as the rats swim in the MWT. While the computer simulation does not provide an identical experience of swimming in a pool, the two tasks are still comparable in measures of spatial learning (Foreman, 2000). Behaviorally, the MWT and the VMWT also share many similarities in dependent outcomes. Initial trials are marked by random search strategies and thigmotaxis. Once learning is acquired, both participants in the MWT and the VMWT learn to take more direct trajectories to the goal location (Fig 2).

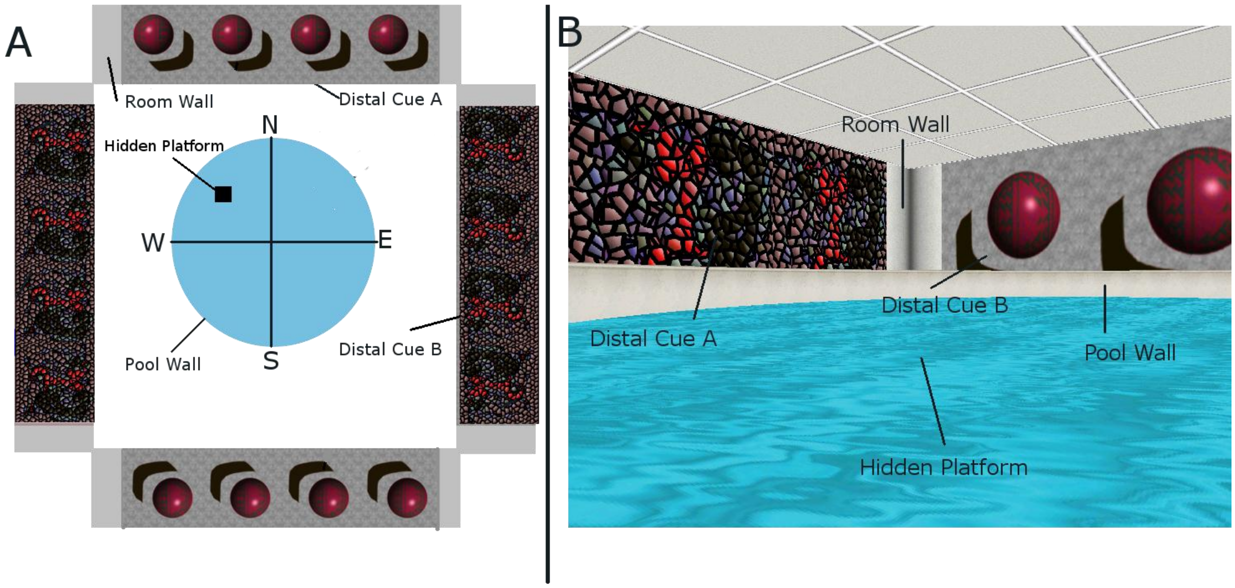


Figure 2: Overhead and First Person View of VMWT

Panel A depicts a bird's eye view of the VMWT environment. Each environment contains a hidden platform in the same location and various configurations of the same cue set. Panel B illustrates a first person view of the VMWT environment as the subject would see.

Manipulations of distal cues in the VMWT result in similar behavioral modulation as in the MWT. A rotation of the distal cues produces a rotation of the navigational trajectory (Yoganarasimha & Knierim, 2005). The subject must experience a variety of views during training to be able to navigate to the platform. Restricting access to parts of the pool via plexiglass in the MWT (Sutherland, 1987) or with a virtual barrier in the VMWT (Hamilton, Driscoll & Sutherland, 2002) impairs the acquisition of direct trajectory to the platform from novel release points. The VMWT also activates hippocampal regions in humans just as the MWT does in rats (Astur & Constable, 2000;

O'Keefe & Nadal, 1978). The similarity to the MWT combined with the ease of use of testing on a computer make the VMWT an ideal candidate for testing spatial memory deficits in clinical populations (Hamilton, 2003). Taken together, these results illustrate that manipulation of the visual information provided to the subject in both the MWT and VMWT results in modulation of the subject's navigational trajectory.

Analysis of Environmental Cues by Pixel-Based Comparison

It is clear that within a VMWT environment there is a requirement of a minimum number of cues necessary to provide for learning a direct trajectory to a hidden platform (Prados, 1998). There must be enough distal cues present to allow for spatial learning. However, embedded within these cues, it remains to be determined what information signal is sufficient to be able to disambiguate the platform location within an environmental context. The disambiguation of the platform location is essentially a task of spatial pattern separation. Spatial pattern separation is the mechanism of orthogonalizing inputs to distinct outputs (McNaughton & Morris, 1987). As the inputs become more similar, then the task of separating between inputs becomes computationally more difficult (Fig 3). The ability to quickly and accurately discriminate between similar inputs is impaired in various psychological disorders, most notably in schizophrenia. (Sahay, Wilson & Hen, 2011). Pattern separation also declines in cognitively normal adults as they age (Holden et al., 2012). A real world example of spatial pattern separation involves driving to work and parking your car in a parking garage each day as opposed to parking on different streets (Aimone, Deng & Gage, 2011). It is more difficult to recall the location you parked in the parking garage as the garage floors are visually similar and over time memories of previous parking days interfere with the current day. Thus, objectively categorizing spatial pattern separation along a continuum of difficulty, as we attempted to do in our series of experiments, might enable us to develop new cognitive assays to identify memory degradation in patient populations.

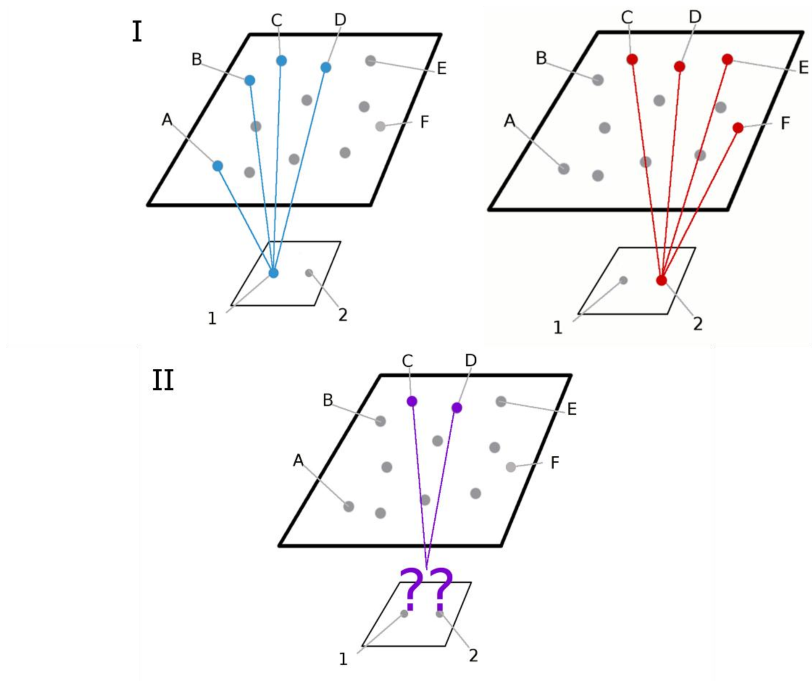


Figure 3: Pattern Separation

An abstract representation of pattern separation. In panel 1, sufficient inputs (ABCD vs EFCD) are trained to distinct outputs (1 & 2). This orthogonalization is successful given enough unique input. However in Panel II, when ambiguous, or overlapping inputs are provided pattern separation fails.

The purpose of our research study is to evaluate a pixel comparison model as a candidate metric in examining how human subjects are able to perform spatial pattern separation in the VMWT. While adding and removing visual cues of the environment will affect navigation, it remains difficult to objectively quantify this change as a continuum of difficulty in the process of spatial pattern separation. One possible solution is to compare the pixel content of images. If we consider all the possible views a subject can experience in the VMWT as a number of images composed of pixels, then we can calculate the degree to which the images, or views, differ from the goal location. For example, if a room has different pictures on each wall then the view from the goal location will be distinct from all other views. If the view from the goal location is much different than the view from the opposite quadrant of the pool then we would predict that learning to navigate to the goal location would be relatively easy since the image inputs are distinct. However if the room is bare with just white walls then every view will be mostly similar. There would be little disambiguating information (quantified by difference in pixels) and we would predict learning direct trajectories to the platform would be impaired. There is compelling evidence that insects use this basic image/view comparison function (Wystrach, 2011). We acknowledge that human visual perception is much more complex. We are not suggesting that rats and humans employ this pixel based comparison in their navigation, but we will use Cheng's et al.'s (2008) methodology as a way to compare how behavioral performance is modulated as a function of the pixel difference within two locations of a virtual environment.

Systematic Confusion of Diametrical Opposite Corners

Cheng's (1986) previous experimental results suggest that organisms systematically mistake diametrically opposite corners of a rectangular environment due to the visual similarity and the geometric relationship of each corner. This effect was demonstrated by reinforcing navigation to one corner, and then subsequently rotating the environment and removing distinct stimuli featured in two corners (Fig 4). Rats were able to disambiguate between pairs of adjacent corners, but performed at chance level when attempting to disambiguate diametrically opposite corners (Cheng, 1986). This systematic effect has been demonstrated in a variety of organisms ranging from ants (Wystrach, Beugnon, & Cheng, 2011) to young children (Spelke & Wang, 2003).

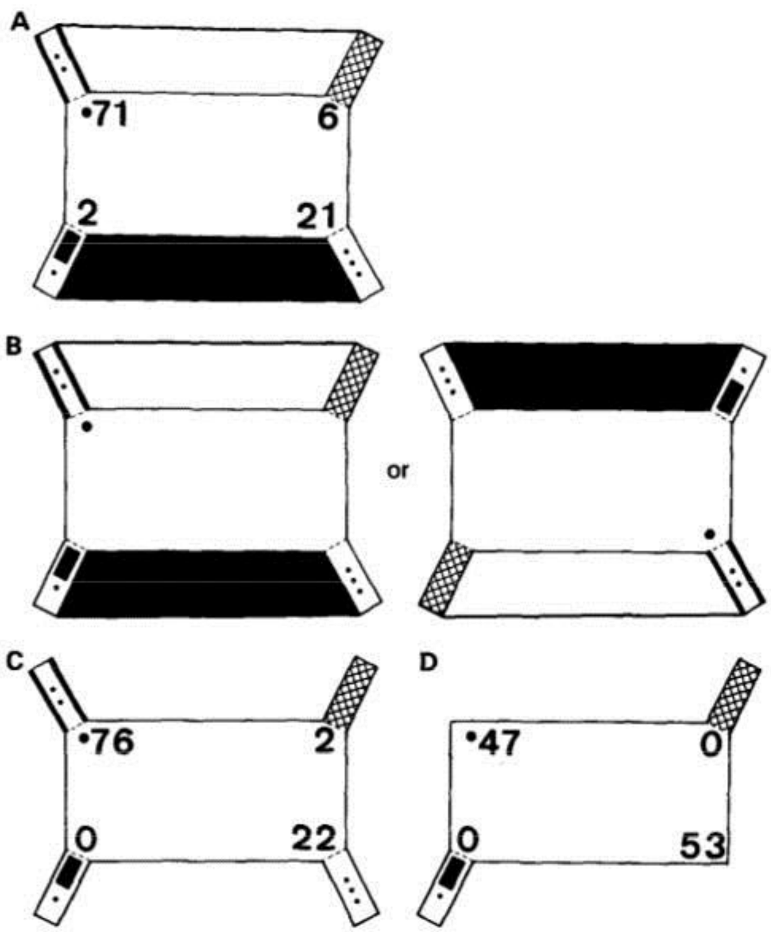


Figure 4 – Systematic Rotational Error

Reprinted from Cheng (1986). Rats were initially trained to navigate to a corner in an environment with 3 black walls, one white wall and feature strips in each corner (Panel A). A rotational transfer test in which the environment is rotated 180° from trial to trial

(Panel B). Results of the transfer test in which no feature stripes were removed (Panel C) or diagonally opposite corner feature stripes were removed (Panel B). Numbers indicate percentage of visits.

Recent efforts have been made to quantify the visual similarity between two locations within an environment through numerical analysis. This approach involves calculating the global pixel difference of locations within an environment by use of panoramic images (Stürzl, Cheung, Cheng, & Zeil, 2008). The mean squared pixel difference between the panoramic images within the environment is then calculated as an approximation of the visual content of the environment. The pixel comparison of the panoramic views taken within an environment can then be used to evaluate predictions of navigation for various species of subjects. This basic pixel comparison has successfully predicted behavioral performance in rats and simulated agents' behavior.

If the global pixel comparison results in low values (implying that the virtual environment contains similar views between the platform location and the diametrically opposite pool position) and human navigation performance is negatively influenced by view similarity, then this result suggests that humans might be utilizing a view based comparison approach that can be modeled by the difference in mean squared pixels of an environment. If visual similarity computed in this way is sufficient to account for the navigational performance in these environments, then we would expect to observe behavior vary as a function of similarity (which could be considered related to pattern separation). Therefore we would predict that humans will be able to learn direct trajectories to the hidden platform as a function of the degree of visual similarity contained within an environment.

The series of experiments for this study involved examining a pixel based comparison approach as a continuous metric of spatial pattern separation within the VMWT. The first experiment examined how subjects were able to learn to take direct trajectories towards a hidden platform as a function of the environmental cue configuration. This was an implicit measure of spatial pattern separation as it requires both successful pattern separation of cues and also spatial memory of which trajectory to take to navigate to the hidden platform. The second experiment required the subjects to choose correctly between two visible platforms as function of environmental cue configuration; this was an explicit discrimination task between cues, as the spatial memory component to move towards a visible platform was not as challenging as a single hidden platform. Finally the third experiment compared the predictions made by the pixel comparison approach to behavioral performance of a previous dataset of humans in the VMWT. Humans in the VMWT (Hamilton et al., 2009) demonstrated a preference for directional responding once the pool was translated within a room. Subjects were trained on a hidden platform VMWT task and after the location of the platform was acquired the pool was virtually repositioned such that the absolute spatial location of the pool was centered in the opposite quadrant of the pool. Instead of navigation to the previously trained absolute location, the subjects navigated in the direction of the platform location relative to the pool (Fig. 5). The repositioning of the pool created a conflict between the reference frame of the pool (corresponding to the relative location of the platform) and the reference frame of the room (corresponding to the absolute location of the platform). These behavioral results suggest that the distal cues of the room impart directional information while the apparatus cues of the pool convey distance information.

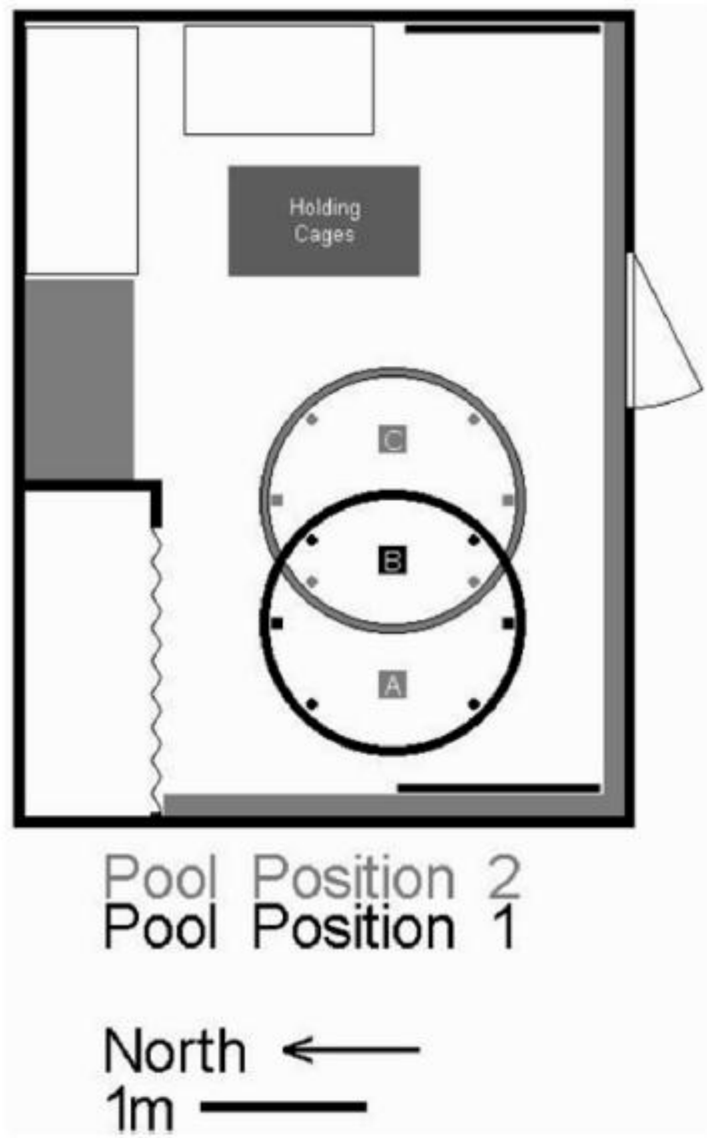


Figure 5: Absolute vs Relative Location. Reprinted from Hamilton et al, (2008). The previous behavioral results of the study concluded that subjects trained to navigate to platform location B in pool position 1 will navigate to the relative location C once the pool is repositioned north. If this behavior is based upon view similarity then the panoramic image of pool position 2 platform C should have a similar pixel value to position B in the original pool position. However if these views are not similar then we

must assume that there are additional mechanisms that provide for a preference of directional responding.

Cheng et al. (2008) has speculated that instead of reference frames imparting direction and distance information, this preference for directional responding could perhaps be explained by a view based comparison. The view of the target position relative to the pool could look visually similar to the view of the trained reference platform. Likewise, the view of the target position relative to the room would look visually dissimilar from the trained platform position. This would explain the preference for the directional responding: it is a navigational movement towards matching the current view of the repositioned pool to the remembered view of the trained reference platform. Experiment 3 calculated the pixel difference between views of the platform in pool position 1 and the view from the relative location in pool position 2 to determine if the global pixel comparison could possibly account for the preference of directional responding once the pool was translated.

Our study is novel in that it is an assessment of spatial pattern separation removed from the confound of proximity. Traditionally, the spatial pattern separation assay utilized a delayed match to sample paradigm in which a cue was presented, a brief intermission followed, and then two cues were subsequently displayed. The subject was then required to pick the first viewed stimulus. The shorter the distance between the two trial cues the greater the difficulty in discriminating between them. Our experiment removed this confound of distance and required a subject to make a spatial comparison based upon view content (Fig 6). Two distant locations could have extremely similar views; therefore the subject was required to not rely on distance as a means to discriminate between cues but rather to sample the view of the distal cue configuration that provides the most unique information.

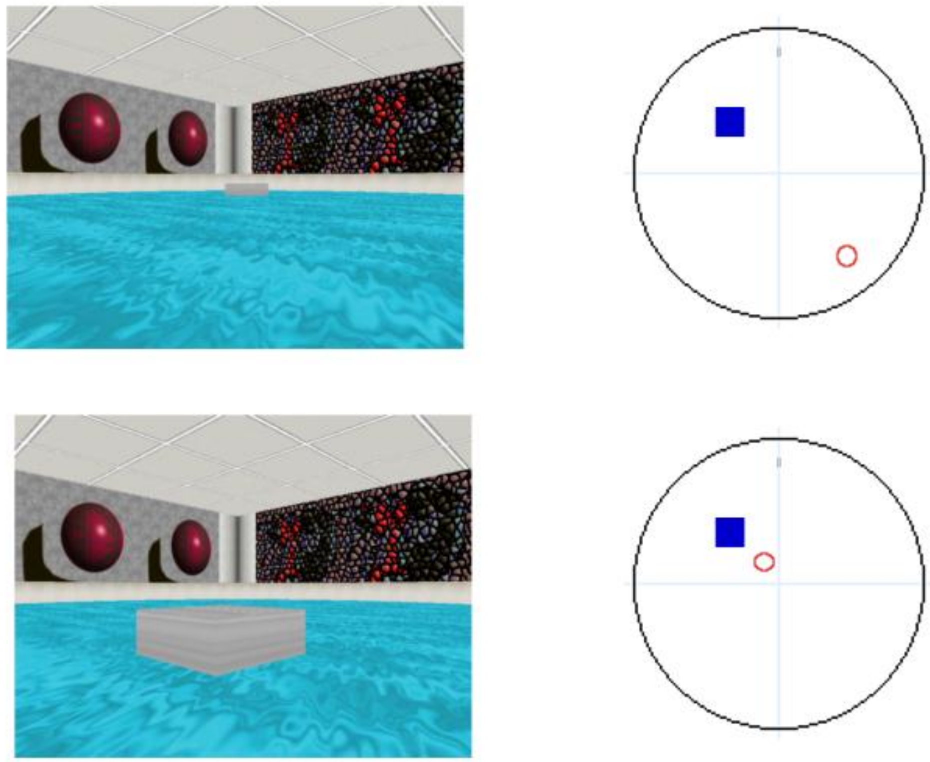


Figure 6 – Spatial Pattern Separation Based Upon View Difference

Whereas previous spatial pattern assays required a discrimination based on two dimensional cues varied by distance, the experiments performed here in the VMWT remove the confound of distance. Since distant locations of the pool could look visually similar, distance is an ambiguous metric for discrimination. Subjects instead must rely on a comparison of view content within a three-dimensional environment. The left column illustrates a first person view of the VMWT from different locations in the pool (right column).

CHAPTER 2 GENERAL METHODS AND MATERIALS

The first two experiments described utilized the same recruitment protocol, VMWT behavioral testing, and environmental cue configurations.

Virtual Morris Water Task Apparatus

The pool surface of the VMWT was an opaque blue pattern 75 arbitrary virtual units in diameter. The pool wall was a grey texture spanning 15 virtual units above the pool texture. The participant's field of view was 45°. Hidden from the participant's view was an escape platform comprising 4.1 virtual units (1.75% of the area of the pool). The hidden platform was 24.75 units diagonal from the center of the pool in the northwest position. The cues and starting position were constrained so that a participant could not take a straight trajectory toward a cue to reach the hidden escape platform.

Laptop navigation required keyboard input with the UP arrow key moving the participant 0.75 virtual units of pool surface and the RIGHT and LEFT arrow keys turning the participant's perspective 10° (Fig 7). The participant was unable to move backwards. Traversal of a virtual distance equal to the diameter of the pool took a minimum of approximately 4 s to complete while a full rotation in the absence of forward movement took approximately 2.5 s. Auditory feedback also accompanied the task. The volume level was 50% max volume for all participants. While moving, the participant heard the sound of moving water. Upon reaching the escape platform an affirmative bell rang and confirmation was displayed on the screen. If the trial exceeded 60 s then a discordant noise sounded and the platform was made visible requiring the participant to navigate to it.

Figure 7: Laptop used for stimulus presentation

The VMWT was executed on a Dell Studio 1558 laptop computer with an ATI Mobility Radeon HD 5470 graphics card, Intel Core TMi3-350 Processor (2.27 gHz) running Windows 7 OS. The laptop monitor was 20' and displayed at maximum brightness.

Trial Procedure

The experiment consisted of an initial training segment in a neutral environment which contained distal cues including a door, a shelf, a window, and a poster. The training environment was identical for all participants. The initial training segment allowed participants to become accustomed to the demands of the task and also served as a basis for exclusion. If a participant was unable to learn to take direct trajectories to the hidden platform during these training trials, their data was rejected for analysis (although they still completed the experiment and received course credit). The exclusion criteria was applied by examining the qualitative trajectory of the swim path during the final training block. The exclusion criteria screened out participants that were unmotivated or unable to learn the task even in a neutral setting. Since the exclusion criterion was based upon the same training segment for all participants, each participant had an equal chance to be excluded independent of their performance in the experimental condition.

The initial training segment was followed by the experimental condition. The training segment lasted four trials, and the experimental condition lasted 5 blocks. Each block was composed of 4 trials and in each trial the participant was released from a cardinal release point (N, S, E, W). The order of these release points were randomly selected for each block. After the final experimental block, there was a probe trial in which the platform was removed and the subject was required to navigate around the pool for 60 seconds. Upon completion of the experiment the subject filled out a questionnaire assessing their previous videogame experience and their confidence of the location of the hidden platform.

Experimental Conditions

All the virtual environments used in the series of experiments were composed of a circular pool situated in a square room with four walls. The experimental conditions differed in the distal cue configuration that decorated the walls. As shown in Figure 8, a selection of cues were tiled in three various configurations: (1) A **Symmetrical** configuration with opposite walls mirroring each other, (2) An **Adjacent** configuration with identical walls connected at opposite corners, (3) A **Feature Strip** configuration which was the same as the symmetrical configuration except with a single feature strip on one wall.

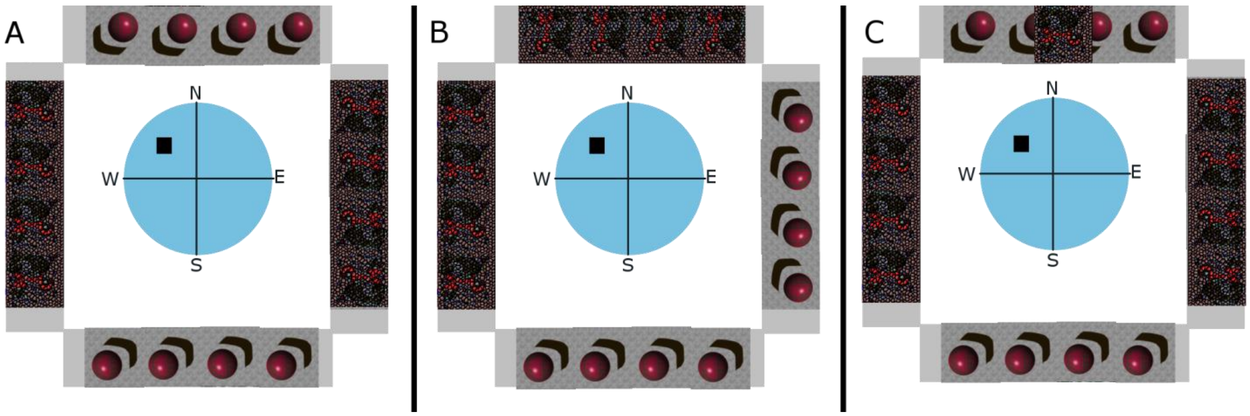


Figure 8 : Environmental Configurations

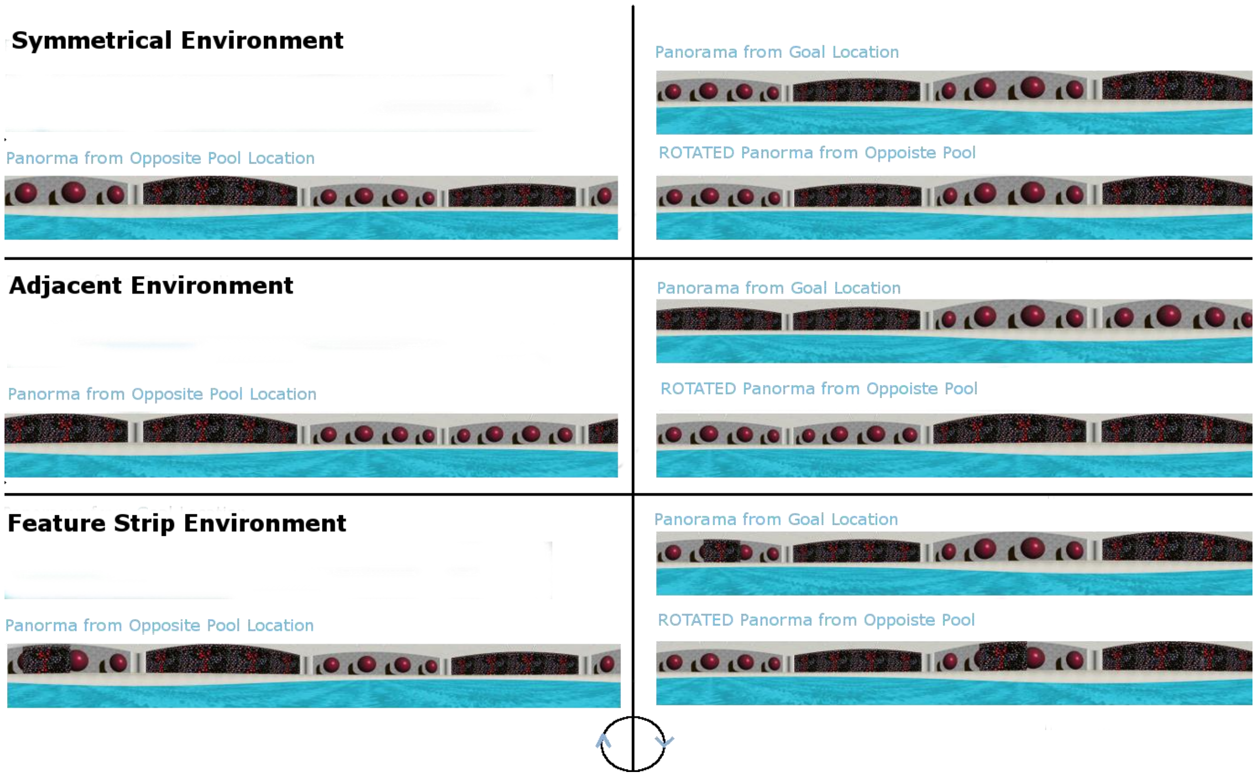
Possible configurations of cue sets in VMWT. Panel A: Symmetrical configuration where opposite walls mirror providing little unique information. Panel B: Adjacent configuration in which two walls join together at distinct corners. Panel C: Feature Strip configuration which is the same mirroring of the symmetrical configuration except with the presence of one demarcating cue placed on the north wall.

Each condition differed in terms of the information provided by the distal cues as quantified through the mean squared pixel difference. For each configuration two different sets of cues were used for a total of six environments. Each participant experienced only one cue set. Subjects' performance was averaged over environment within configuration type which resulted in three experimental conditions.

Global Pixel Comparison

For each virtual environment panoramic pictures were obtained by combining 360 screenshots of the rotated first person view. Panoramic pictures were taken at two different locations. The reference panoramic picture was obtained at the platform location (at pool level) in the NW quadrant of the pool. The second comparator panoramic picture was taken in the location diametrically opposite of the platform in the SE pool quadrant.

The mean squared pixel difference was calculated by processing the reference and comparator panoramic pictures using a pixel comparison algorithm. This process first rotates the comparator panoramic picture for each possible orientation of the reference panoramic picture.



$$\mathrm{MSDP}(\mathbf{I}^{\mathrm{A}},\mathbf{I}^{\mathrm{B}}) = \frac{1}{N}\sum_{i=1}^{N}(I_i^{\mathrm{A}}-I_i^{\mathrm{B}})^2$$

Figure 9: Pixel Comparison

A pixel comparison of panoramic pictures was taken to identify the visual similarity of locations within each virtual environment. Panel A: Panorama of the goal location is compared to a rotated panorama from the diametrically opposite pool position (Panel B).

Once the rotated comparator panorama is aligned, the squared difference along columns for three color channels is summated into a matrix of mean squared pixel difference MSDP values. The ratio of the minimum value divided by the maximum value indicates the pixel similarity of two views within the environment.

Once the best possible orientation--the one that minimizes image difference--is achieved, the algorithm performs an elemental wise subtraction for each pixel location between the reference and comparator panorama image. The difference is squared to produce only positive values. Then, the squared pixel differences are summated across color channels to produce a 5760 x 600 matrix corresponding to the absolute difference values between pixel elements Finally, a ratio of the minimum and maximum value of the summated matrix is calculated to obtain the mean squared pixel difference value of the environment. These values are depicted in Table 2.

Table 2

Pixel Comparison Values Between Platform View and Comparator View

Cue Configuration	Minimum Mean Squared Pixel Difference	Maximum Mean Squared Pixel Difference	Ratio	Ranking Relative to Cue Set
Symmetrical	9575931139	60755194595	0.157615019	Least Different
Adjacent	38612734942	57816638294	0.66784815	Most Different
Feature Strip	15512605164	66469654318	0.232902329	Intermediate

Recruitment Protocol

Undergraduate students at the University of New Mexico volunteered to participate in the study for course credit. Only individuals between the ages of 18-35, with normal/corrected vision and no history of neurological disorders were allowed to enroll in the study. No personal or mental inventories were collected. Participants were randomly assigned to each experimental group. All participants provided informed consent and were fully debriefed in accordance with the guidelines of human research at the University of New Mexico.

CHAPTER 3 EXPERIMENT 1: HIDDEN PLATFORM NAVIGATION (IMPLICIT DISCRIMINATION)

The first experiment was a hidden platform paradigm in which the subject was required to use the distal cue configuration to learn to navigate to the location of the submerged platform. Each subject first completed a short training segment in a neutral environment. Subjects were excluded from the study if they failed to learn the location of the hidden platform. Exclusion numbers are listed in Table 3. The subsequent experimental condition then differed in terms of the cue configuration. The purpose of this first experiment was to determine if the dependent measures of latency and path length would be modulated as a function of the independent measure of pixel content value represented by the cue configuration.

Table 3

Number of Subjects Excluded Based Upon Training Performance

Environment	N	Gender Ratio	Subjects Excluded
Symmetrical	15	6 M / 9 F	4
Adjacent	18	8 M / 10	3
Feature Strip	19	8 M / 10 F	2
Total	51	22 M / 29 F	9

Pre-Trial Latency in Neutral Environment

Before analysis of the experimental condition, statistical analysis was performed on the training segment to confirm that groups did not differ on performance in the same neutral environment (Fig 10). A repeated measures ANOVA was performed on the latency data of the training blocks with the training trials as a within subjects factor and the environment configuration as the between subjects factor. There was no significant main effect on latency by environmental configuration in the training environment ($F(2,45) = .168$, $p = .846$).

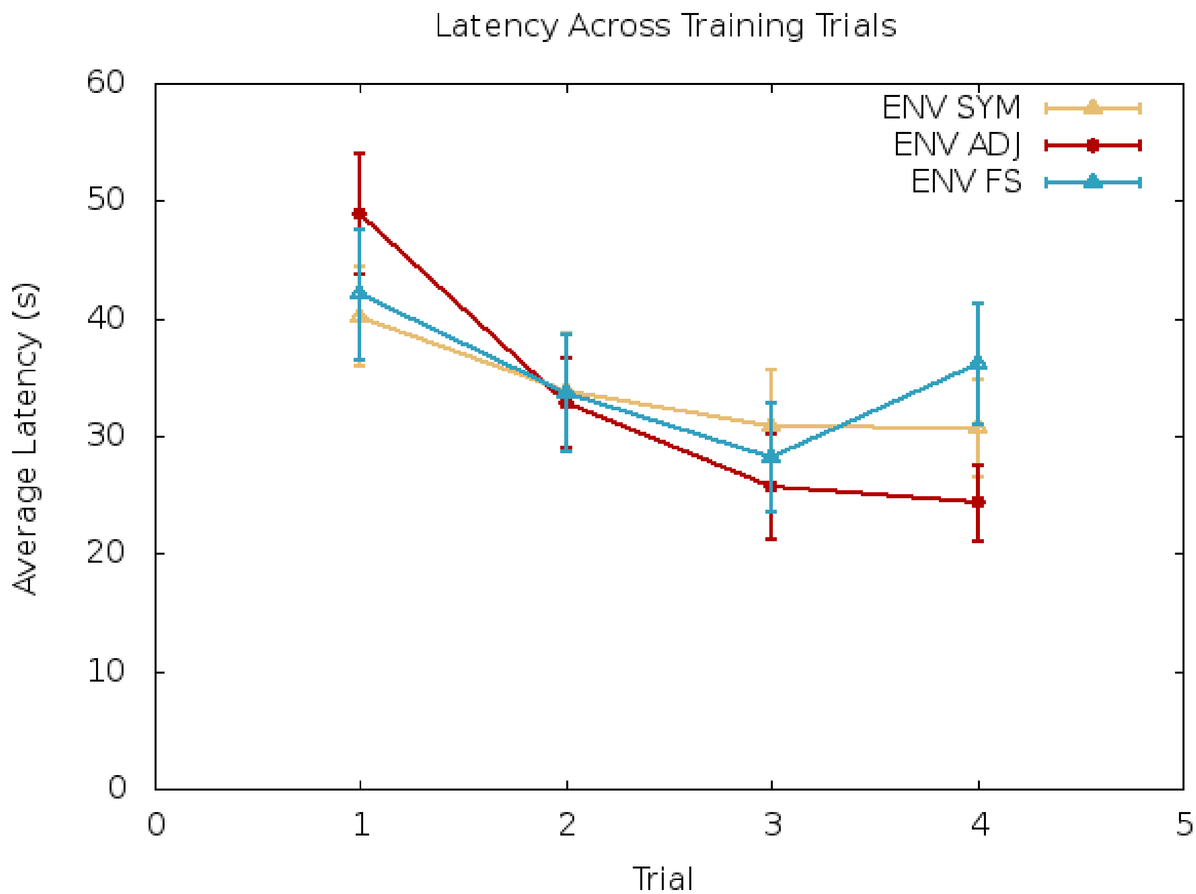


Figure.10. Virtual Morris Water Task—Training Performance in a Neutral Environment. *Latency in seconds (Mean ± SEM) to locate the platform over 4 trials of hidden platform training. ENV SYM refers to the Symmetrical configuration, ENV ADJ refers to the Adjacent configuration, and ENV FS refers to the Feature Strip configuration.*

An additional repeated measures ANOVA was performed on the path length data to confirm that subjects did not individually differ on their ability to learn direct trajectories to the platform in a neutral training environment (Fig 11). There was no significant main effect for path length in a neutral training environment (F(2,45)= .0.68, *p* = .934).

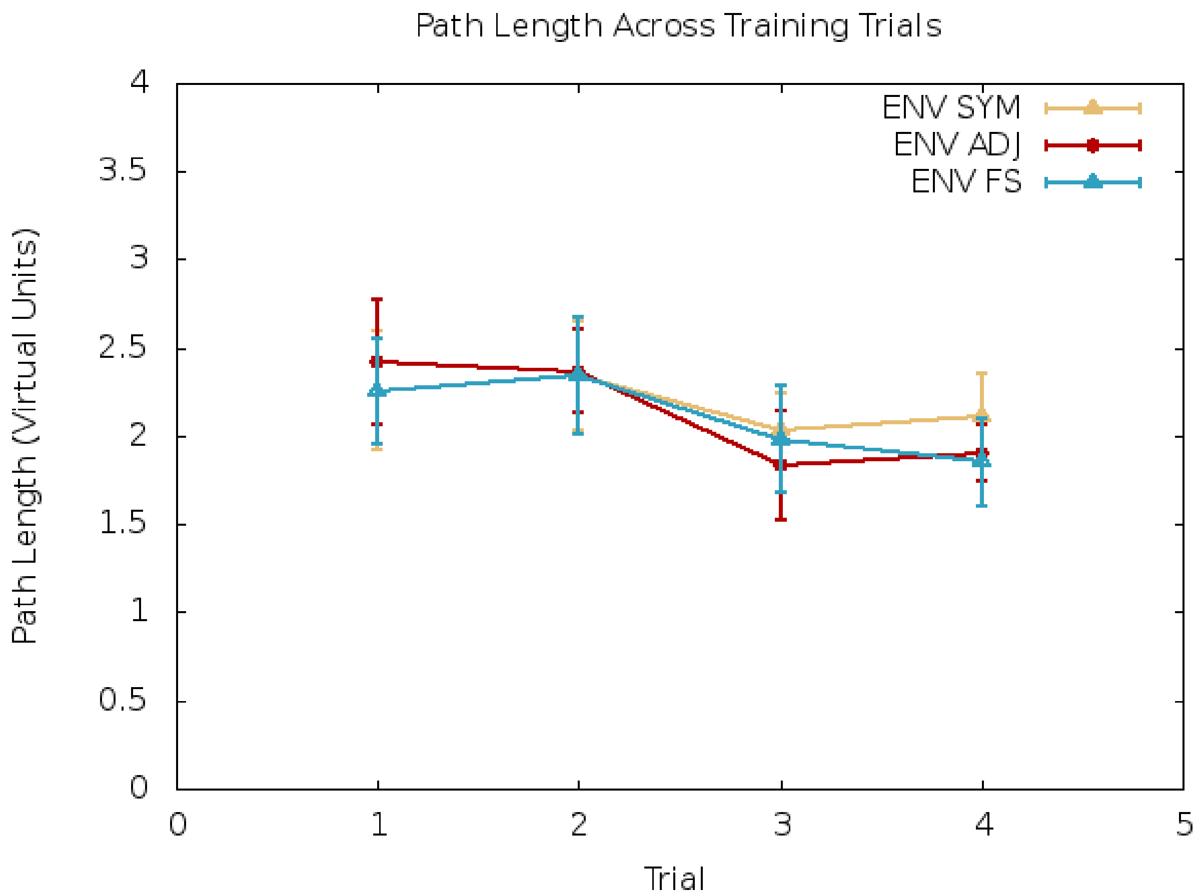


Fig.11. Virtual Morris Water Task—Training Performance in a Neutral Environment. *Path length in virtual units (Mean ± SEM) to locate the platform over 4 trials of hidden platform training.*

Configuration Trial Results

Qualitative Results

A research assistant blind to the experimental condition judged the path trajectory of each subject. Based on an assessment from Block 1 to Block 5 the rater marked the Adjacent configuration as being the most successful in learning to take direct paths (17 out of 18), the Feature Strip configuration as having intermediate performance (10 out of 19) and the Symmetrical configuration as having poor learning performance relative to other configurations (2 out of 15). An example of three subjects' performance is illustrated in Figure 12

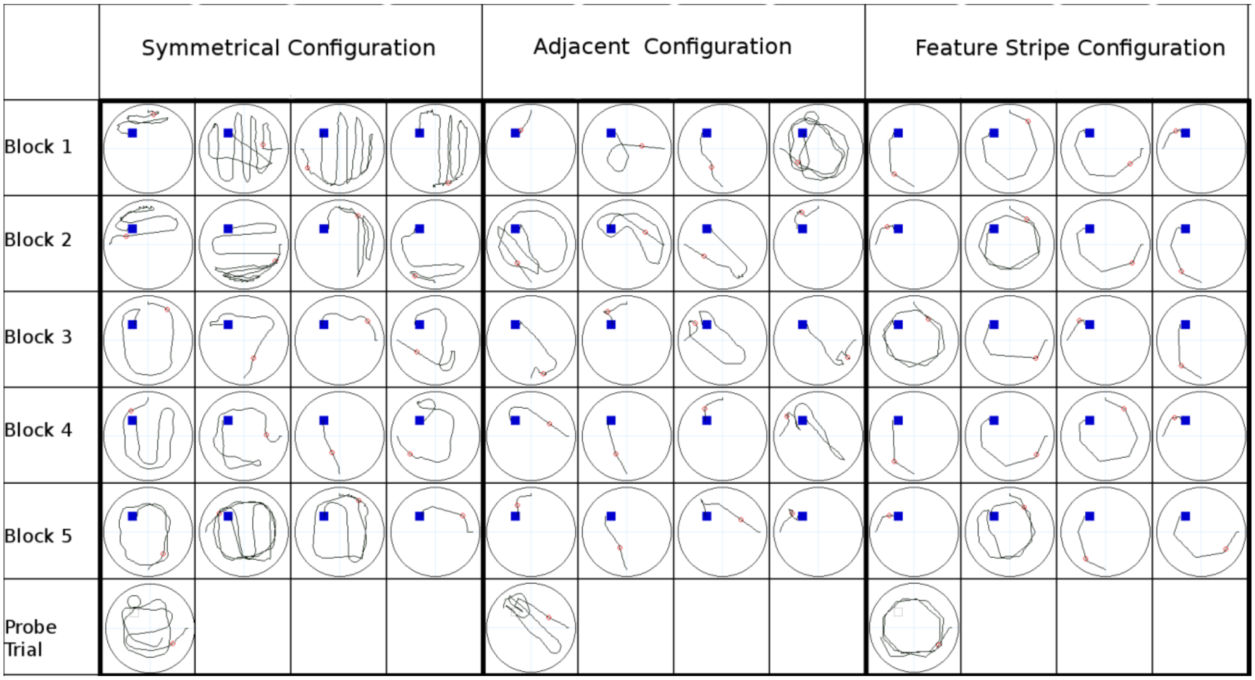


Figure 12: Example Path Trajectories

Experimental trials representative of each condition. There were 5 trial blocks and each block consisted of 4 trials starting at each cardinal release point (N, S, E, W). The experiment concluded with a probe trial in which the hidden platform was removed and the subject was required to navigate around the pool for 60 seconds. In these three particular examples, only the subject in the adjacent condition learned to take a direct trajectory over the course of the experimental trials.

Quantitative Results

A repeated measures ANOVA was performed to determine if latency was significantly different as a function of the environmental configuration (Fig 13). The five blocks of the experimental trial was the within subjects factor. The environmental configuration and sex of the subject were entered into the model as between subjects factors. There was significant main effect of environmental configuration ($F(2,45)=32.147$, $p=.0001$ and partial eta squared = .588). There was also a significant interaction of block and environmental configuration, implying that learning differed in a linear order throughout the blocks of the experiment ($F(2,45) = 4.208$, p =021).

A follow-up least significant difference (LSD) test to examine the significant main effect revealed that latency to reach the platform within each environment configuration was significantly different. The Symmetrical configuration was significantly different than the Adjacent condition (Mean Difference = 18.185, $p = .0001$) and significantly different than the Feature Strip condition (Mean Difference = 9.63, $p = .0001$). Latency performance was significantly different in the Adjacent configuration than the Feature Strip (mean difference = 8.549, $p = .0001$.) There was no significant main effect for sex on latency ($F(1,45)=1.078$, $p = .305$).

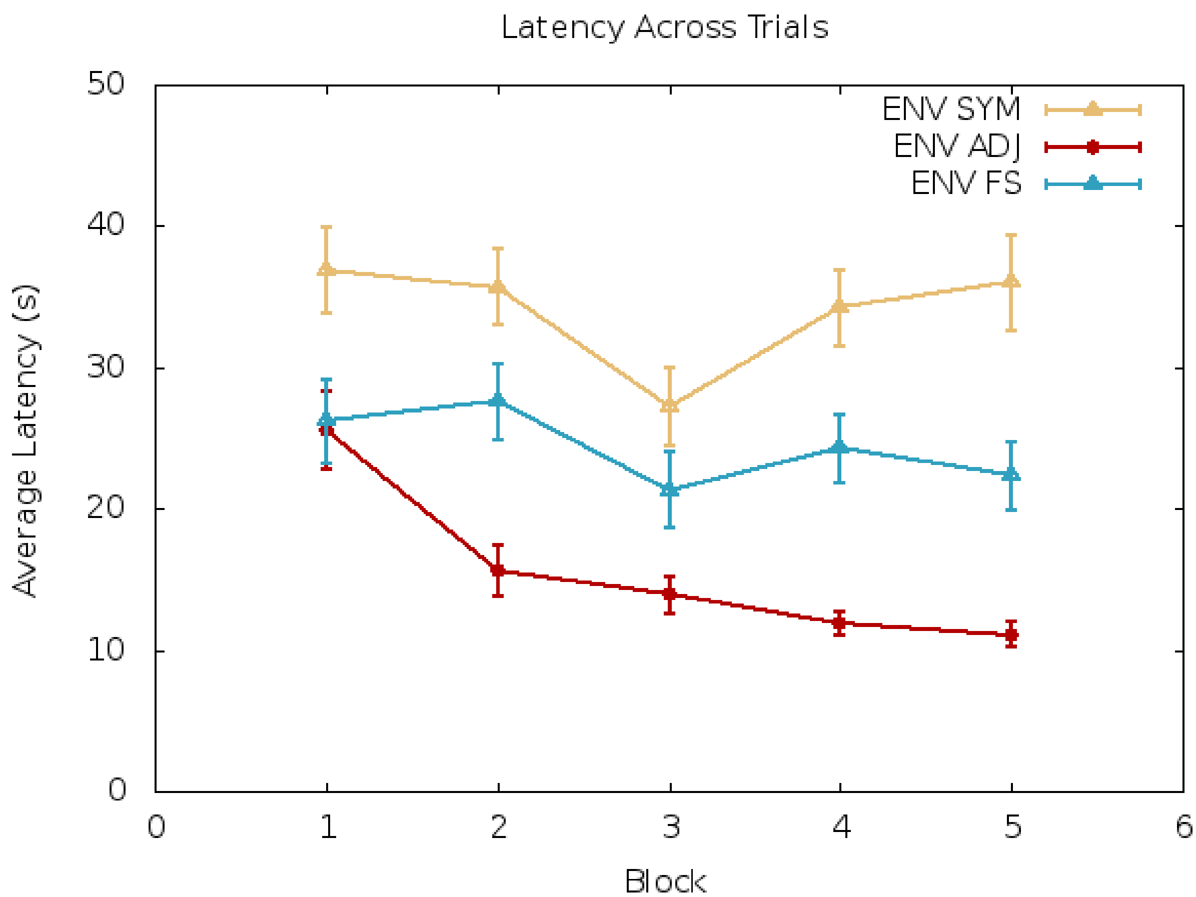


Fig.13. Virtual Morris Water Task—Trial Performance in Different Environmental Configurations.

Latency in seconds (Mean ± SEM) to locate the hidden platform over 5 blocks (consisting of 4 trials from different release points). Each configuration was significantly different, and there was a significant interaction between environmental configuration and linear contrast across the five levels of blocks.

A repeated measures ANOVA was performed to determine if path length was significantly different as a function of the environmental configuration (Fig 14). The five blocks of the experimental trial was the within subjects factor. The environmental configuration and sex of the subject were entered into the model as between subjects factors. There was significant main effect of path length as a function of environmental configuration ($F(2,45)=44.83$, $p = .0001$ and partial eta squared = .666). There was also a significant interaction of block and environmental configuration, implying that learning differed in a linear order throughout the blocks of the experiment ($F(2,45) = 3.368$, $p = 0.43$).

A follow-up LSD test to examine the significant main effect revealed that block path length within each environment configuration was significantly different. The symmetrical configuration was significantly different than the Adjacent condition (mean difference = 2.38, $p = .0001$) and different than the Feature Strip condition (mean difference = 1.26, $p = .0001$). Latency performance was significantly different in the Adjacent configuration than the Feature Strip (mean difference = 1.12, $p = .0001$). There was no significant main effect for sex on latency ($F(1,45)=.268$, $p = .607$).

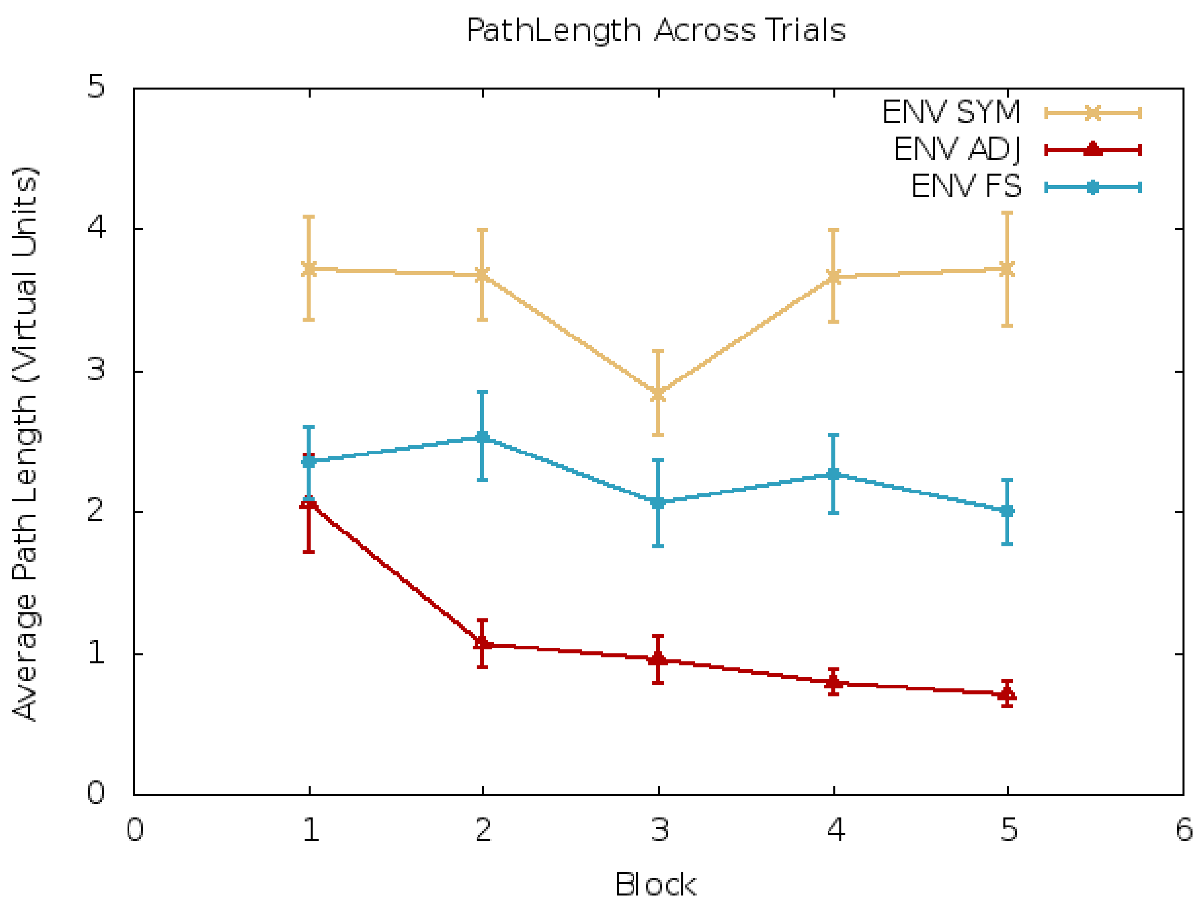


Fig.14. Virtual Morris Water Task—Path Length in Different Environmental Configurations.

Path length in virtual units (Mean ± SEM) to navigate to the hidden platform over 5 blocks (consisting of 4 trials from different release points). Each configuration was significantly different, and there was a significant interaction between environmental configuration and linear contrast across the five levels of blocks

A one way ANOVA was performed to determine if the time spent in the platform quadrant during a single probe trial differed as a function of the environmental configuration (Fig 15). There was a significant main effect of time spent in correct quadrant and environmental configuration ($F(2,50) = 25.95$, $p = .0001$). A follow-up

LSD comparison indicated that time spent in the correct NW quadrant was significantly different for the Adjacent configuration compared to the Symmetrical configuration (Mean Difference= 26.1, p = .001), and significantly different than the Feature Strip configuration (Mean Difference = 28.0, p =.001).

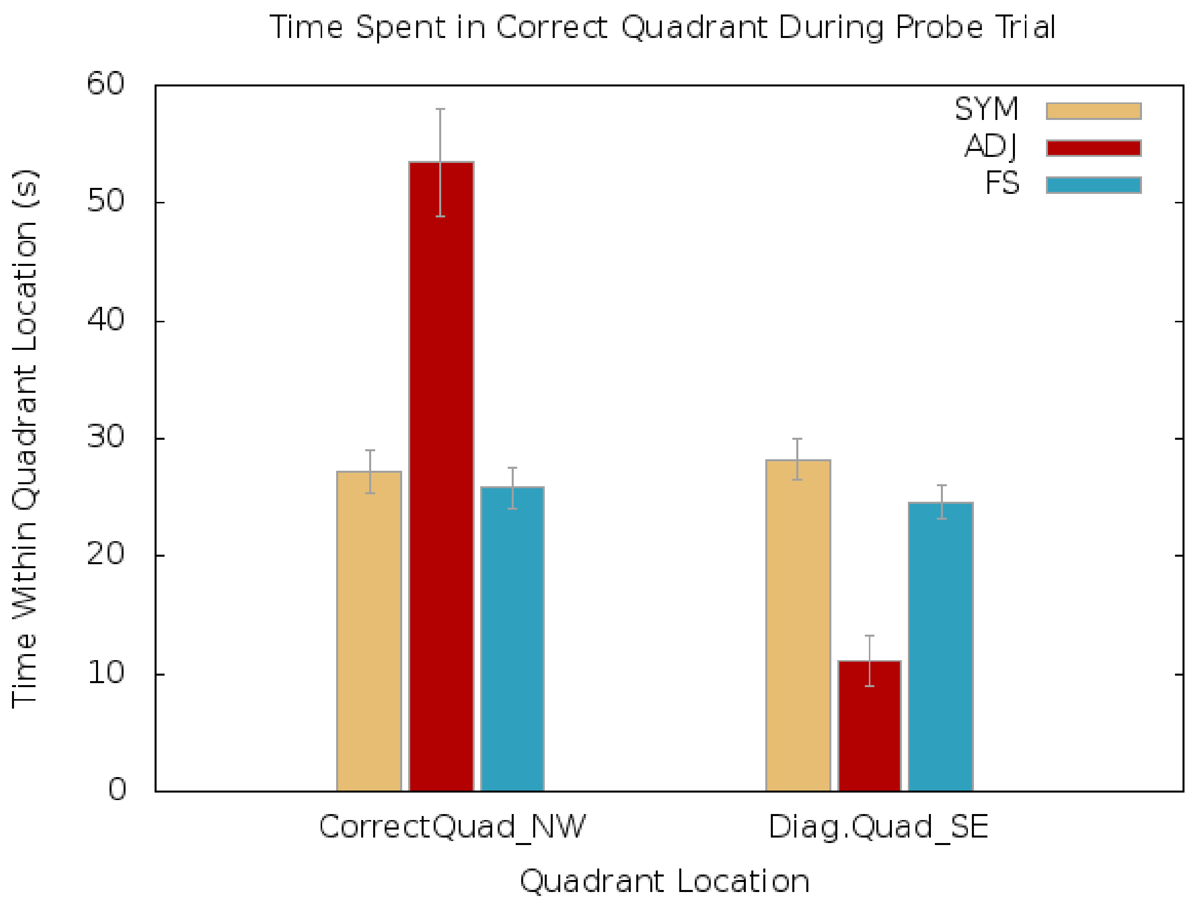


Fig.15. Virtual Morris Water Task—Time Spent in the Platform Quadrant

During a 60 second probe trial the platform was removed. Time in seconds (Mean ± SEM) that was spent in the correct quadrant (NW) as opposed to the diametrically opposite quadrant (SE) is shown. There was a significant main effect for the probe trial and the Adjacent configuration

Discussion

The significant effect of latency and path length imply that navigational performance was modulated as a function of the visual content of the environment. The follow up multiple comparison test confirmed that environments rated as low in pixel difference (thus more visually similar) led to significantly longer latencies than environments rated high in pixel difference. Additionally, navigational performance was significantly different in environments containing a Feature Strip as opposed to Symmetrical environments that did not contain a feature strip. The pixel difference introduced by the feature strip was negligible in terms of a global pixel comparison, yet the behavioral performance in the feature strip configuration was intermediate for the hidden platform training. It is important to note that the performance in the probe trial for the Feature Strip was at chance level similar to the Symmetrical configuration. Thus it is clear that successful spatial pattern separation occurred within the Adjacent configuration but it is less clear if the addition of the feature strip was sufficient for adequate learning performance.

CHAPTER 4 EXPERIMENT 2: DUAL VISIBLE PLATFORMS (EXPLICIT DISCRIMINATION)

The results of Experiment 1 indicated that there was a significant main effect for latency to reach the hidden platform and environmental configuration, but there still was variable performance across all conditions. Subjects in the Feature Strip configuration had intermediate performance compared to the Symmetrical and Adjacent configuration. It is unclear whether this hierarchical behavioral performance across conditions was due to an inability to discriminate between locations within an environment (due to the similarity of pixel content within the environments) or due to difficulty in learning more direct trajectories within the behavioral paradigm of the hidden platform VMWT. To examine more explicit cue discrimination, Experiment 2 directly addressed this issue by utilizing a two cued visible platform paradigm. Within the pool there were two visible platforms. The NW platform was the reinforced platform. Navigation to the reinforced platform ended the trial with positive confirmation and allocated points to the participant. Conversely, navigation to the SE platform, the incorrect platform, produced a discordant sound and a deduction of points. There was no reward for obtaining the points once the experiment ended. The same VMWT environments and pixel comparison as Experiment 1 were used, the only difference being the two cued platforms replaced the hidden platform task of Experiment 1.

Methods

21 Undergraduate student participants (16 Female, 5 male) were randomly assigned to three experimental conditions. Three participants were excluded from the experiment due to inadequate training performance and were not included in experimental analysis.

Results

A repeated measures ANOVA was performed to determine if the correct platform choice was significantly different as a function of the environmental configuration (Fig 16). A correct response to the platform was scored as a 1. A response to the incorrect platform was scored as -1. Performance was summated over four trials within a block. Chance performance within a block would equate to 0. The six blocks of the experimental trial was the within subjects factor. The environmental configuration and sex of the subject were entered into the model as between subjects factors. As depicted in Figure 15, there was significant main effect of environmental configuration and correct platform choice ($F(2,15)=4.21$, p =.035 and partial eta squared = .360). There was no significant linear trend of learning over the course of the six experimental blocks.

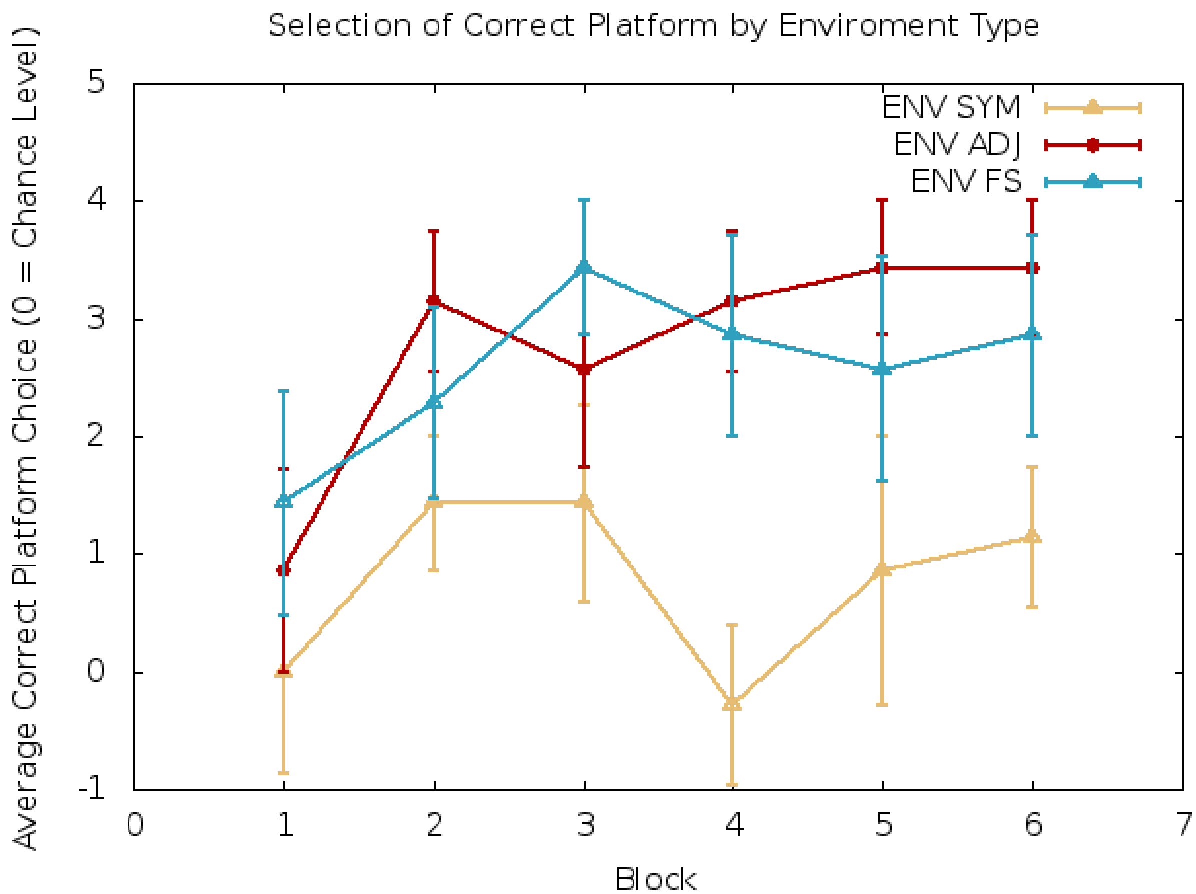


Figure 16: Visible Two Platform Correct Platform Selection

In the same environmental configurations as Experiment 1, subjects were required to choose between two visible platforms. Navigation to the correct NW platform was scored 1, and incorrect choice (SE platform) was scored -1. Each block consisted to 4 trials with a summated score within a block ranging from all wrong (-4) to chance (0) to all correct (4).The Adjacent configuration had significantly different performance than the Symmetrical configuration.

A follow-up LSD test to examine the significant main effect revealed that correct platform choice was significantly different only between the Symmetrical and Adjacent configuration (mean difference = 2.18, p= .011). The Feature Strip configuration experienced variable performance to be not significantly different than either condition, although as Figure 16 illustrates, performance in the Feature Strip configuration was more similar to performance in the Adjacent configuration as opposed to the Symmetrical configuration.

There was also a main effect of sex and environmental configuration ($F(1,15)=7.676$, $p = .014$. Partial Eta Squared .339). However this effect might not be interpretable due to the mismatch of groups (F = 15, M = 6) reflective of the demographics of the gender difference among psychology undergraduates. Previously, Driscoll et al., (2005) reported significant sex differences in the VMWT although it is unclear if these sex differences still occur in dual visible platform discrimination tasks.

Discussion

The explicit discrimination between the dual visible platforms in Experiment 2 required the subject to use the distal cue configuration to disambiguate between two options. Performance in this task, as depicted in Figure 16, suggest that subjects in the Symmetrical configuration performed this choice at chance level. Subjects in the Adjacent configuration were successfully able to discriminate between the two platforms, just as subjects were able to learn a direct trajectory in Experiment 1. Subjects in the Feature Strip configuration were also able to successfully discriminate between two explicit cues demonstrating improved performance compared to the implicit discrimination required in Experiment 1.

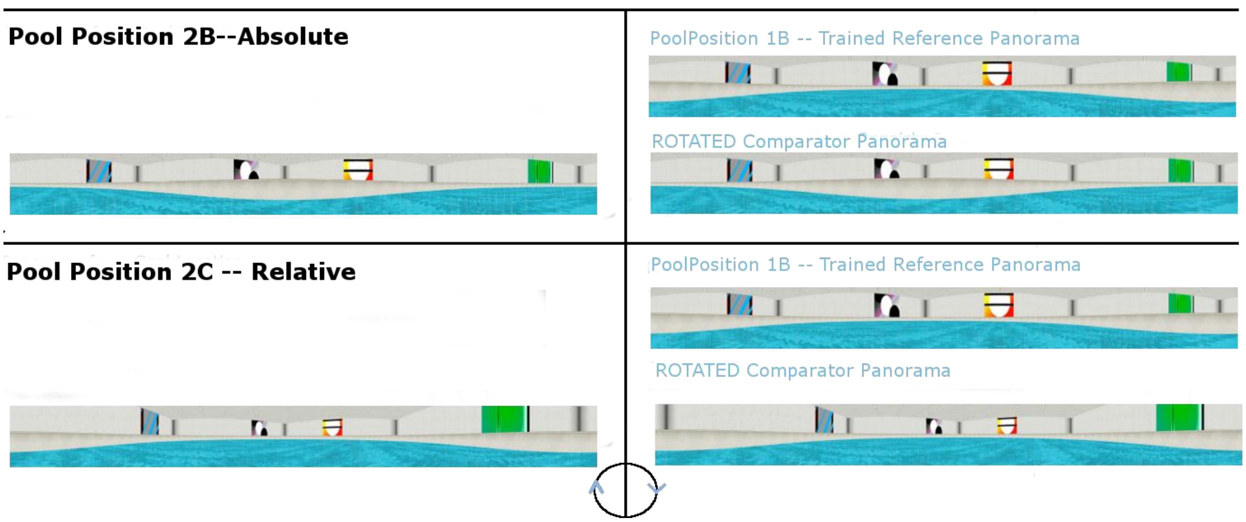
CHAPTER 5 EXPERIMENT 3: PIXEL BASED COMPARISON OF POOLSHIFT PHENOMENON

Experiment 3 was an investigation to see if the global pixel comparison approach could possibly account for the preference of directional responding encountered in the

VMWT after pool reposition. If the pixel content of the panoramic view from the relative location of the pool is similar to the panoramic view of the trained platform location then that could possibly explain the preference of directional responding. However, if the pixel content of the views were dissimilar, then that would suggest that some other mechanism is establishing the preference for directional responding.

Materials and Methods

This experiment acquired panoramic images from two locations in a previous poolshift VMWT study (Hamilton et al., 2009). No additional behavioral data were



collected. To determine how these locations differed as a function of the global pixel comparison, the same pixel comparison approach was used as in Experiments 1 and 2. The rotations of the panoramic images are depicted in Figure 17.

Figure 17: Rotation of Panoramic Views from Pool Position 1 and Pool Position 2

The reference panoramic image was captured at pool position 1, platform B. The comparator panoramic Absolute Location was captured at pool position 2, platform B and the Relative Location image was captured at pool position 2, platform C.

Results

Table 4

Pixel Comparison Values Between Relative and Absolute Locations

Reference Location (Trained Platform)	Comparator Location	Minimum Mean Squared Pixel Difference	Maximum Mean Squared Pixel Difference	Ratio (Min / Max)
PoolPostion_1_B	Pool_2_B (Absolute)	1.78E+010	4.21E+010	0.4224
PoolPostion_1_B	Pool_2_C (Relative)	2.39E+010	4.42E+010	0.5394

Note. Lower values imply that the translated Comparator Location were more visually similar to the view of the trained Platform location in the original pool position, 1_B.

As shown in Table 4, the comparison of the minimum pixel content for the original pool platform B and the repositioned pool location C was $2.39e^{10}$. This value is somewhat higher than a comparison between views of the absolute location, platform B in pool position 1 vs. pool position 2 ($1.78e^{10}$). Since the global pixel comparison is lower for the absolute location, yet subjects still navigated to the relative location C, then we must conclude that the preference for directional responding cannot wholly be depicted by a pixel comparison in the VMWT.

Discussion

In this final experiment, the global pixel comparison predicted that the panorama of the

Absolute location in the second pool position resembled the panorama of the trained Reference platform location in the first pool position. However past behavioral results indicate that both humans (Hamilton et al., 2009) and rats (Hamilton et al., 2009) demonstrate a preference for responding towards the Relative location after the pool is translated within a room. These results would suggest that directional responding of humans in the VMWT towards the Relative location cannot be predicted by our implementation of the global pixel comparison.

CHAPTER 6 GENERAL DISCUSSION

These series of experiments examined the use of a pixel comparison model as a candidate metric to objectively assess spatial pattern separation in the VMWT. The conclusion of these experiments is that a global pixel comparison approach is not sufficient to account for the behavioral outcomes of humans in the VMWT. In environments that varied in terms of the similarity of views between the platform location and a comparator location through the configuration of distal cues, behavioral performance was only predicted in environments that were totally ambiguous or non-ambiguous. The addition of a small noticeable cue or the translation of cue elements resulted in pixel predictions that did not reflect the navigational behaviors exhibited.

Acquisition of a direct trajectory in the hidden platform is reliant on a minimum number of distal cues to establish a vector for movement. Sampling of the distal cues is necessary for orientation during the initial segment of the trial. Since the apparatus cue, the pool wall, is symmetrical it provides only information about distance since all parts of its geometry are visually identical. Therefore navigation to the hidden platform requires enough unique information embedded in the distal cues to allow for spatial pattern separation.

By manipulating the arrangement of these distal cues we were able to impair learning a direct trajectory to the hidden platform. Previous studies have also demonstrated that manipulations of distal cues, such as rotation, deletion, or translation result in subsequent shifts in search strategies during a probe trial (Knierim & Hamilton 2011). In this study we attempted to quantify how much information was provided by different configurations of the same cue set through the use of a global pixel comparison between the view of the platform location and the diametrically opposite pool location. However the hypothesis that behavioral performance would follow the predictions generated by the comparison of pixel difference within an environment was not accurate for all virtual environments.

A possible reason for the divergence between human performance and the predictions made by our implementation of the global pixel comparison could be indicative of the importance given to cues sampled. Humans predominately direct their gaze at distal cues of the wall and apparatus cues of the pool wall, but they do not foveate on the pool texture itself (Hamilton et al, 2009). For humans and rats the pool provides little visual information; the view of the pool water is an input channel that is not actively monitored (Pashler, 1994). This is in contrast to the global pixel comparison which is objective, or blind to all cues, and assigns equal importance to all pixels inputted. Luminance changes from the waves in the water of the MWT, or texture aliasing in the VMWT might contribute to noise that produces error in a strictly pixel based comparison. The effect of the pixel comparison model attributing more weight to the local apparatus cues rather than the distal wall cues is clearly demonstrated in Figure 9. The rotation of the panoramic image in the opposite quadrant was perfectly aligned in the Symmetrical configuration. However, in the Adjacent and Feature Strip configuration the pixel comparison model was unable to line up the distal cues of the reference view and the rotated comparator location. Presumably the pixels of the pool and the pool wall contributed too much noise for the pixel comparison to orient the reference and comparator panoramic views based upon the distal cues. Therefore a more direct comparison between human behavior and pixel comparison prediction may require biasing the pixel comparison to attribute more importance to viewing areas of the environment that are known to be sampled by organisms. Within the MWT and the VMWT, the viewing areas sampled by humans and rats are divided into apparatus cues (anything that can be "touched") and distal cues (Knierim & Hamilton, 2011).

Perhaps the global based pixel comparison approach could be optimized by segmenting the comparison between these apparatus and distal reference frames. Instead of a global pixel comparison spanning the entire image, a more precise model could be made by performing the comparison exclusively within the apparatus or distal frame of reference. For example, in Experiment 3 (Figure 17) the global pixel comparison model correctly rotates the Absolute panorama to align the distal cues with the reference panorama while mismatching the level of the water against the pool wall. However, the Relative panorama, predicted as being more visually dissimilar from the reference location than the Absolute location, is rotated seemingly in accordance with the water of the pool wall instead of the distal cues. It would seem that these global matchings were made by weighting one frame of reference over the other. Therefore a comparison of two panoramic images *between* reference frames which are then summated together—as opposed to equally weighting all pixels in the panoramic image—might yield a more optimized approach to view based matching. This hypothesis could be tested by simulating Hamilton et al.'s (2009) approach to reducing visual saliency of cues. By reducing the visual saliency of the apparatus cue through filling the water level up all the way as to obscure the pool wall, subjects demonstrated a preference of place responding. Through rerunning the global pixel comparison with all pixels of the apparatus cue eliminated, we could determine how well the panoramas are rotated by exclusively comparing the distal frame of reference

In terms of performance, the divergence between prediction of the pixel comparison and human behavior was primarily evident with the addition of the Feature Strip. The Symmetrical configuration was rated as very low in unique pixel content whereas the Adjacent configuration was rated as being relatively high in unique pixel content. Behavioral discrimination--both implicit (finding a hidden platform) and explicit (choosing between visible options) were consistent with the predictions made by the pixel comparison algorithm for these ambiguous and non-ambiguous environmental configurations. The Feature Strip configuration meanwhile, was ranked slightly higher in pixel difference than the Symmetrical configuration but had variable behavioral performance compared to the other configurations.

The variable behavior exhibited in the Feature Strip configuration throughout Experiment 1 and Experiment 2 might reflect different task-related requirements for spatial pattern separation. In Experiment 1, subjects in the Feature Strip configuration performed intermediately in latency and path length compared to other configurations. However, during a probe trial, behavioral performance in the Feature Strip was comparable to performance in the Symmetrical configuration. In an explicit discrimination, behavioral performance in the Feature Strip configuration trended towards significant difference from the Symmetrical configuration. Thus it is clear, from the significant difference in latency and path length that the additional pixel difference provided by the feature strip allowed for improved spatial pattern separation relative to the Symmetrical configuration. When the demands of the task became much easier, as in the case of the two visible platforms, performance in the Feature Strip configuration trended towards performance in the Adjacent configuration. Yet during the probe trial, when the task required confidence and perseveration in the platform location, performance in the Feature Strip configuration was at chance level similar to the Symmetrical Configuration. Thus, the difficulty of spatial pattern separation within an environment of distal cues may vary depending on the demands of the task with implicit discriminations involving navigational perseveration being more difficult than explicit choice discrimination.

Limitation and Future Directions

A limitation of this study is that it only captures two views of an environment, the platform view and a comparator view in the opposite pool quadrant. While the contrast between these two views does capture much of the pixel information embedded within the environmental configuration, a more accurate depiction could be made if more locations were sampled. For example, Sturzl and colleagues (2008) used a robotic gantry arm to capture panoramic pictures from equally spaced distances within a rectangular environment. Creating a precise map of an environment by sampling a grid of panoramic views corresponding to each point within an environment allows for more precise modeling of navigational trajectories. These image mappings could be used as inputs for simulated models to determine which components of the environment attract movement trajectories.

An important consideration in comparing the results of the MWT and VMWT across species is the issue of motivation to successfully perform the task. The motivational drive to complete the task might not be equivalent across species or even across individuals. According to the Yerkes-Dodson law (1908), performance is optimal only at a certain level of arousal. Rats' performance in the MWT reflects this inverted U shaped curve with navigational performance being optimal in a specific range of water temperature (Morris, 1984). It is unclear if the requirements of the VMWT provide adequate arousal to successfully perform the task at an optimum level. Additionally, since this is a study involving college-aged adults, there could exist an interaction between the sex of the experimenter and the sex of the subjects resulting in variance that is unaccounted for by a simple investigation of sex differences between subjects. Further parametric tests involving different levels of monetary compensation, and recording of the experimenter's sex will be required to assess these methodological issues.

The dependent measures of the navigational trajectory in the VMWT in this study could also be enhanced by collection of physiological data such as visual eye tracking and EEG imaging. Examining the saccades of the fovea during a trial could enable researchers to relate the sequence of distal cue sampling to changes in movement trajectory (Hamilton et al, 2009). Event-related neural components associated with pattern separation could possibly be monitored to identify when successful discrimination is made during the subject's initial sampling of the distal cues (Luck, Mangun, & Hillyard, 1994).

Finally, while a laptop is sufficient for our purposes of testing, it is important to realize that navigation with a keyboard might be a confound when considering the neural correlates of spatial navigation (Taube, Valerio, & Yoder, 2012). Exciting advances in immersive virtual reality (Figure 18) could enable more complete assessments of navigation. Creation of an artificial world that updates as a function of head movement would be a much more ecological approach to visual perception (Gibson 1979). These techniques could possibly enable a more "life-like" cue sampling as the subject moves their head instead of using an input device such as a mouse or keyboard.

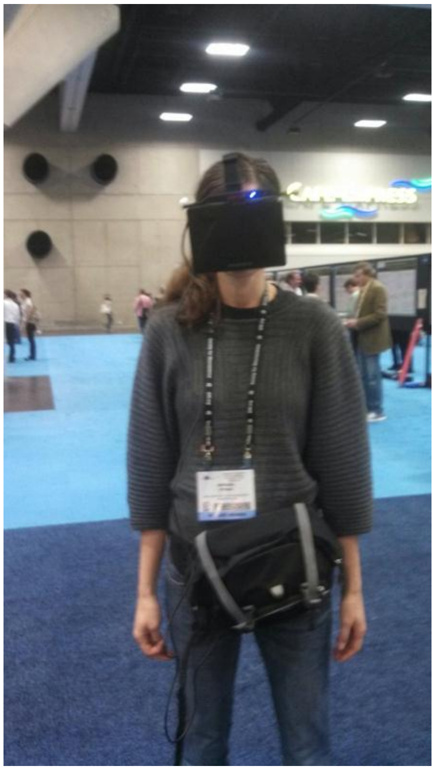


Figure 18: Headmounted Virtual Reality Unit

Reprinted with permission. UNM graduate student Sephira Ryman demonstrates the Oculus Rift, a head mounted virtual reality unit. A dual retinal display changes depending on head movement. A fanny pack sensor also updates the display based upon locomotion. This immersive experience could provide more ecological validity in testing spatial navigation than using a traditional laptop or screen projector.

Conclusion

The global pixel comparison approach implemented here was not sufficient in predicting behavioral outcomes. The comparison model had difficulties in predicting performance in environments in which a Feature Strip was included. The pixel comparison also failed to describe the preference for directional responding observed when the pool was translated. Thus we must conclude that a global pixel comparison cannot predict the behavior of humans in certain virtual environments. The pixel model comparison however was able to predict performance in cue configurations that were Symmetrical and Adjacent, indicating that there is a possibility that the information provided by distal cue arrangements can be numerically quantified.

The experiments previously described were novel in that they offered a new way to examine spatial pattern separation based upon views encountered in a 3d environment. A view based comparison approach could be a useful means in examining how organisms are able to discriminate between spatial memories. Finally, the development of a continuous metric of spatial pattern separation could be a useful tool in diagnosing psychopathologies and age-related cognitive decline. The reliability and portability of the VMWT interface lends itself well to testing humans in a clinical setting. If additionally we could establish an objective metric of difficulty in the VMWT through distal cue pixel-based comparisons, then we could examine how performance is impaired as an individual ages.

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