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Research report

Human place learning in a virtual Morris water task: some important constraints on the flexibility of place navigation

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Abstract

We investigated human place learning in a computerized version of the Morris water task (VMWT) under comparable conditions to those employed by Sutherland et al. (Sutherland et al. Psychobiology, 1987;15:48–57) with rats. Participants viewed a computer-generated environment and were trained to locate a hidden goal in one half of a circular pool (region 1). The opportunity to navigate in and view cues from region 2 was systematically varied during training. Participants were then started from region 2 to assess transfer. Accurate transfer performance was dependent upon prior experience viewing distal cues from region 2 while on a trajectory to the goal, a finding we interpret as inconsistent with the automatic formation and modification of a cognitive map (O'Keefe J, Nadel L. The Hippocampus as a cognitive map. Oxford, UK: Clarendon Press, 1978). Additionally, the transfer data reported here closely match the data obtained by Sutherland et al. with rats suggesting some generality in the principles involved in place learning.

Keywords: Place learning; Virtual Morris water task; Navigation; Hippocampus

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1. Introduction

Place learning and navigation have been of interest to experimental psychologists for many years [10,28,37] and have been intensely studied over the past three decades by researchers concerned with the biological bases of learning and memory. Much of the contemporary research on place learning has measured the behavior of rats and mice in the Morris water task (MWT; [18,19]). In the MWT animals are trained to locate a hidden escape platform submerged in a circular pool of opaque water. Normal animals learn to navigate to the hidden platform in the absence of local cues, indicating that distal, extramaze features are sufficient to support place learning. Animals that have mastered the task take more or less direct paths from any of several starting points around the perimeter of the pool and if the platform is removed they persist in searching in the region of the pool where the platform had been. Further, once the platform location has been learned any subset of cues can be removed from the environment without disrupting performance provided that at least two cues remain [27] (but see Ref. [29]).

The MWT has been useful for testing psychological theories of place learning and evaluating the effects of a variety of biological factors including lesions [21,33], pharmacological manipulations [24,36], genetic background [39], aging [4], and prenatal environment [8]. For example, it is now well established that MWT learning is impaired following damage to the hippocampus [21,33] and initial acquisition is dependent upon hippocampal synaptic plasticity [20,22]. In addition to hippocampus, processes related to place learning have been linked to numerous other brain regions, however, the particular computational roles played by the components of this distributed place

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learning system are still matters of debate. Of course, a more complete understanding of the bases of place learning requires a thorough understanding of the biological mechanisms, but will also rely in large part upon an adequate description of the underlying psychological processes. The latter can be substantially facilitated by theory- and data-driven research programmes using model spatial learning paradigms such as the MWT.

Recently, researchers have begun to study human place learning in a computerized (virtual) version of the MWT (VMWT) which offers a far greater degree of control over the environment than is typically possible in real space [3,9]. In the VMWT, participants view a computer-generated environment from a first-person perspective and navigate using a keyboard or joystick. Although there are obvious differences between real-world and virtual navigation, such as the lack of salient proprioceptive and vestibular signals in the latter, the available data suggest that humans learn to locate the platform based upon a constellation of distal cues in a manner similar to rats. For example, humans learn to take straight trajectories to the platform in the presence of conspicuous distal cues and show behavioral changes in relation to environmental manipulations involving distal cues similar to those described with rats [9,11,12]. It also appears that virtual place learning requires and engages a similar neural substrate including hippocampus and related structures [2,15]. These similarities suggest that tasks like the VMWT may provide a useful methodology for investigating basic spatial learning principles.

Historically there have been two alternative theoretical perspectives regarding the principles involved in place learning. Cognitive mapping theory was originally described by Tolman [37] and more recent formulations have been extremely influential in guiding research on spatial learning and navigation [23,25]. According to O'Keefe and Nadel [23] a spatial mapping system localized in the hippocampus constructs and routinely updates a unitary topographical representation of the environment (a cognitive map) in which the available cues are represented. Such a representation could support a variety of flexible behaviors such as calculating novel trajectories to known spatial locations from any point represented in the map. Thus, the spatial learning principles described by O'Keefe and Nadel can be contrasted with the principles thought to be involved with classical and instrumental conditioning. For example, cognitive maps are proposed to automatically incorporate the available stimuli in an all-or-none manner and independently of reinforcement [23].

An alternative explanation has its basis in associative learning theory and proposes that organisms learn spatial locations via changes in stimulus approach and avoidance tendencies [28]. Under this type of account, place learning is explained in terms of incremental changes in associative strength among stimuli (e.g. distal cues) and responses (e.g. approach behaviors) and it is assumed that place learning follows similar rules of acquisition to those operating in classical and instrumental conditioning [5,14]. Associative explanations of novel, or flexible, spatial behaviors are typically limited to those based upon stimulus generalization and do not involve appeals to representations such as a cognitive map, although spatial behaviors may come under the control of potentially complex stimulus relationships or configurations [30,35].

In considering the types of behavior that would support the existence of spatial cognitive maps, Tolman [37] proposed that favorable evidence would be demonstrated whenever an organism's behavior is independent of the specific responses emitted to locate a region in space. Morris [18] reported findings that fit nicely with Tolman's prediction and have been considered a classic demonstration of cognitive mapping in the rat. He repeatedly released rats from a single, fixed release point in the MWT and coined the term 'instantaneous transfer' to describe the animals' near perfect performance when started from a novel location. Subsequently, Jacobs et al. [11] reported a similar result in human virtual place learning. One interpretation of the instantaneous transfer phenomenon is that subjects form a cognitive map during initial training from which novel trajectories to the goal could be computed without requisite, additional learning processes. In both cases cited above, however, the degree to which individual subjects had experience navigating in the novel region of the environment is unclear. It is probable that the subjects in these experiments did not navigate directly to the platform at the beginning of training, rather, they may have navigated in each section of the environment and, therefore, gained experience viewing cues and navigating to the goal from the various regions of the pool [31]. It follows that transfer performance may be good to the degree that the subject had experience navigating in or around the region containing the novel starting location.

Sutherland et al. [31] tested this hypothesis in the MWT by systematically varying the opportunity to view and/or navigate in the half of the environment containing the novel start location (see Ref. [31], Fig. 1). Seven independent groups of rats were trained to locate a hidden platform located in one half of the pool (region 1). Physical and visual access to the other half of the pool (region 2) were restricted by a clear Plexiglas barrier and a black curtain respectively. Two groups (A and B) were permitted physical and visual access to the entire pool, but were started in different regions. All of the remaining groups were released from region 1. Two groups (C and G) were not permitted to navigate in region 2, however, only Group C had visual access to the features in region 2. Another group (F) could navigate in either region, but could not view both regions simultaneously. Two additional groups (D and E) were treated similarly to groups A and F, but were allowed to navigate in region 2 at the end of each training trial block without access to region 1. The inclusion of these 'forced swim' conditions allowed Sutherland et al. [31] to test for independent effects of navigation in region 2 and navigating through region 2 on a path to the platform. In a subsequent transfer phase all viewing and navigation restrictions were removed and all groups were released from region 2. Only groups that could view the available cues while navigating through region 2 on a path to the goal showed good transfer. Forced swim in region 2 did not significantly improve performance, suggesting that experience viewing distal cues from and navigating in this

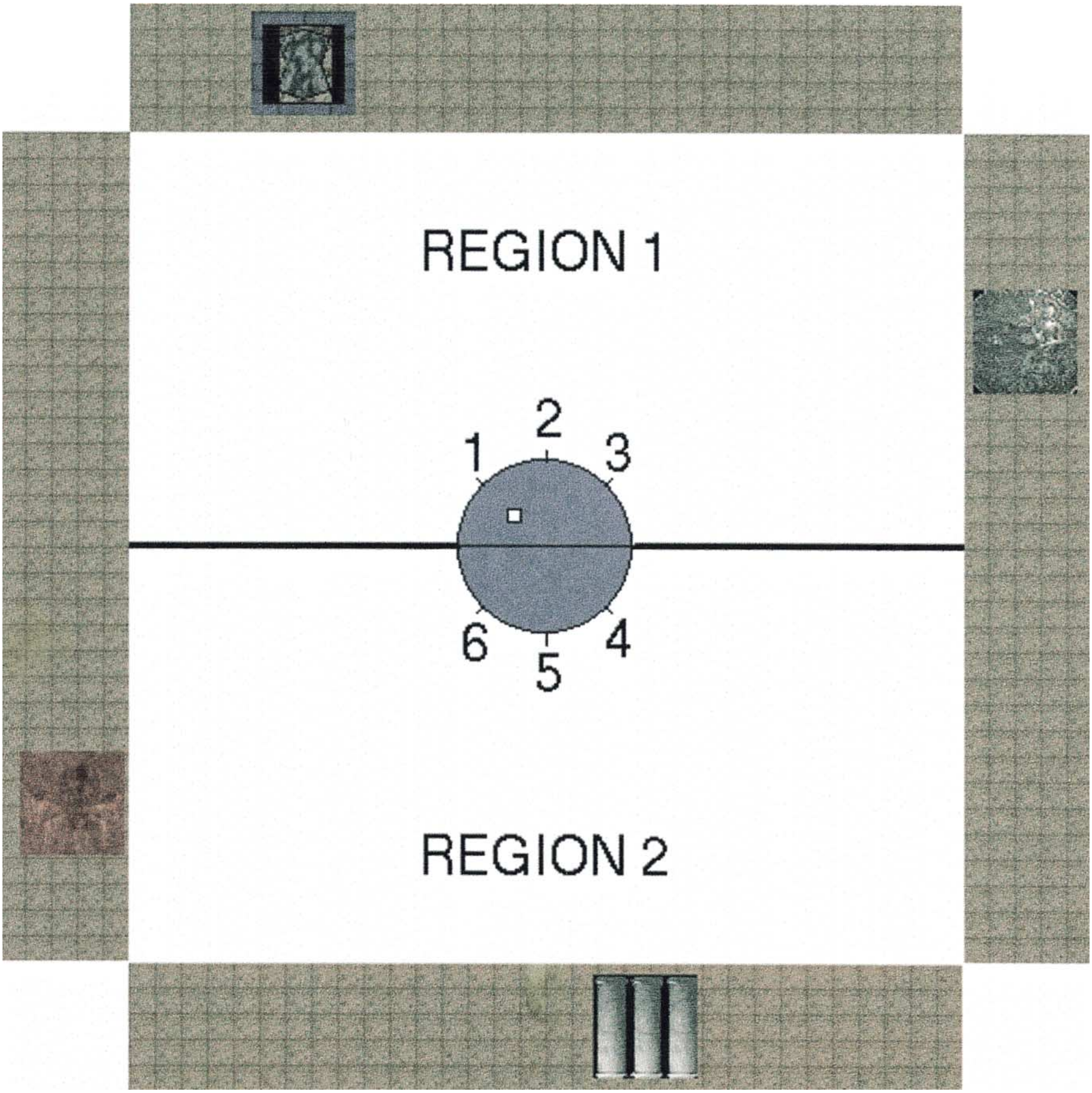

Fig. 1. Layout of the virtual environment. Distal walls and cues are laid flat. The circular pool was centered in the room. The platform (white square) was located in region 1 and centered in one quadrant of the pool. The starting locations are numbered (1–6) around the perimeter of the pool. The black line shows where the opaque partition was placed for groups E, F, and G and where the invisible barrier was placed for groups C, D, E, and G.

region were not sufficient to support subsequent navigation to the platform. These data indicate that the rats did not form spatial representations of the type that would support instantaneous transfer, but, rather, learned to locate the platform within a familiar range of views and trajectories to the goal experienced during training.

Whether instantaneous transfer occurs in human spatial learning remains an open question. To address this issue we investigated VMWT learning under a set of experimental conditions identical to those employed by Sutherland et al. [31]. If participants construct and automatically update a topographical map of the virtual environment on the basis of a restricted set of views and trajectories to the goal experienced during training, then they should be capable of generating accurate trajectories to the goal from a novel starting location. Such an outcome would provide strong support for the principles described in O'Keefe and Nadel's cognitive mapping theory. On the other hand, if generating an appropriate, novel trajectory to the goal depends upon the types of experience just described, then support for the type of spatial mapping described by O'Keefe and Nadel would be lacking. Rather, this alternative would be consistent with an associative account in which spatial behaviors such as approach tendencies are acquired incrementally as the result of experience viewing distal cues while navigating to the goal. Because we chose manipulations identical to those employed in a published report using rats, the obtained data will allow a direct comparison of rat and human performance in these conceptually similar tasks. If rats and humans respond similarly, a strong argument can be made for the generality of the present findings as well as for the use of virtual navigation tasks to inform the general principles involved in place learning.

2. Materials and method

2.1. Participants

One hundred and seventy-five (56 male and 119 female) University of New Mexico undergraduate students participated as part of a course requirement. The participants ranged in age from 18 to 41 years old ($M = 20.07$, S.D. = 3.49). Individuals with impaired vision, a history of neurological disorders, or with prior experience in VMWT experiments were not permitted to participate. Eight males and 17 females were randomly assigned to each of the seven experimental conditions. All participants gave informed consent in accordance with the guidelines for human research at The University of New Mexico and were fully debriefed upon completion of the experimental session.

2.2. Materials

The virtual environment consisted of a circular pool located in the center of a room with a square floorplan. Fig. 1 depicts the layout of the environment and Fig. 2 shows a representative view of the environment from a participant's perspective. Two equally-sized regions were created by dividing the environment in half (see Fig. 1). An opaque, blue pattern was used to create the surface of the pool, which was surrounded by a circular wall that extended approximately 10% of the pool diameter above the pool surface. The distal room walls were visually identical and were located approximately twice the pool diameter from the center of the room. There were four distal cues which were the only visual features of the environment that disambiguated spatial locations. The cues were placed flush with distal walls and all cues were placed off-center vertically by a fixed amount determined prior to experimentation. A single cue was located on each distal wall and there were two cues in each region of the environment. The location of cues was also constrained such that participants could not take a straight trajectory toward a cue from any starting location and find the platform. The square platform was approximately 1.75% of the pool area and when visible extended approximately half of the pool wall height above the pool surface.

Auditory feedback consisted of a bell which sounded when the platform was located, an aversive, discordant tone which sounded if the trial duration exceeded 60 s, and the sound of moving water which accompanied forward movement through the pool. An IBM-compatible computer controlled the presentation of the environment, auditory feedback, and data collection. Visual aspects of the experiment were displayed on a 17 in. color monitor and auditory feedback was delivered via headphones. Navigation was controlled using the keyboard arrow keys. The UP arrow key was used to control forward movement while the LEFT and RIGHT arrow keys controlled rotation. Backward navigation was not possible. 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.

A post-experiment questionnaire assessed the participant's age, experience playing video games, any strategies the participant may have employed, a subjective rating of task difficulty, and whether the participant believed the platform and starting location to be fixed or variable. Game playing experience was assessed by asking participants: How often do you play video games? (0: Never, 1: Rarely, 2: Occasionally, 3: Often). Task difficulty was rated on a 10 point scale (1 = Easy, 10 = Very difficult).

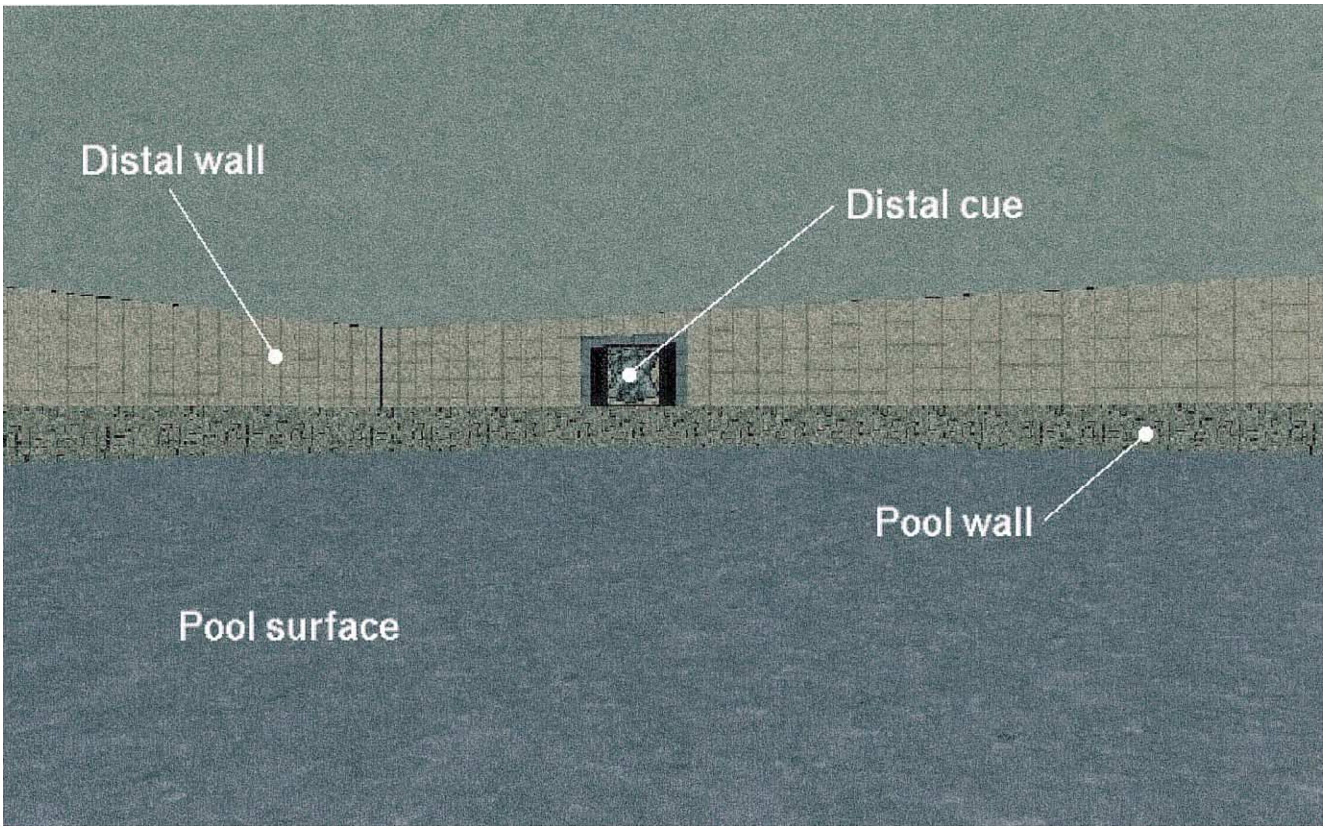

Fig. 2. A representative view of the virtual environment from the center of the circular pool. The pool surface, pool wall, distal wall, and a single distal cue are labeled.

2.3. Design and procedure

As discussed in the Introduction, the design and procedure of the present experiment were similar to those employed by Sutherland et al. [31] in their Experiment 1. The present experiment was conducted in two phases: A training phase and a transfer phase. During both phases the platform location was fixed in region 1 (see Figs. 1 and 3). The training phase consisted of six trial blocks during which each participant completed 18 hidden-platform trials (three trials per block). Starting locations were randomized without replacement such that participants were started from all three start locations in the start region during each block of training. There were seven independent conditions in which navigation and/or viewing restrictions were placed on region 2 of the virtual environment (see Fig. 3 and Table 1). Groups A and B could navigate in and view distal cues from both regions of the environment. Group A was started in region 1 whereas Group B was started in region 2. All other groups were started in region 1. Group C could view regions 1 and 2, but could not navigate in region 2. Group D was treated identically to Group C with one exception. At the end of each training trial block each Group D participant navigated in region 2 for an amount of time yoked to the amount of time spent in this region by a participant from Group A during the preceding trial block. Group D could not navigate in region 1 during this ‘forced swim’ period. At the end of the forced swim period normal training continued. Group E could neither view nor navigate in region 2, but received forced swim in region 2 at the end of each training trial block yoked to the amount of time spent in region 2 during the preceding trial block by a participant from Group F. During the forced swim period Group E could neither navigate in nor view the cues in region 1. Group F was trained with an opaque partition separating regions 1 and 2. The partition did not prevent navigation into region 2, but restricted the participant’s view depending upon the region in which they were located (i.e. only region 1 was visible when in region 1; only region 2 was visible when in region 2). Group G could neither navigate in region 2 nor view the distal cues in region 2. A transfer phase followed in which there were no navigation or view restrictions and each group was treated identically. The transfer phase consisted of 3 hidden-platform trials with starting locations limited to region 2 (locations 4–6). On the first transfer trial participants were started from location 5, with the subsequent starting locations selected randomly without replacement from locations 4 and 6.

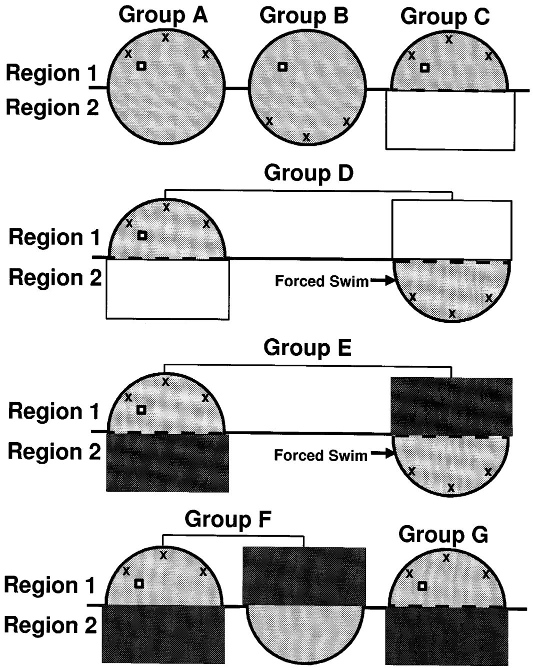

Fig. 3. Navigation and viewing restrictions during training (blocks 1–6) for each experimental group. Participants could navigate in and view the areas in light gray. Starting locations are marked by a small 'x'. The small, black open rectangle marks the platform location. The dashed line bisecting the pool indicates the presence of the invisible barrier which restricted navigation from the light gray region of the pool. The dark gray rectangles indicate the region of the environment that was not visible. The large, open rectangles indicate regions that could be viewed, but where access was blocked by the invisible barrier.

All participants were tested individually. Participants were instructed that they would begin each trial facing the perimeter wall of the virtual pool and that their goal was to escape from the water by finding the submerged escape platform as quickly as possible. No information regarding useful strategies, the location of the platform, the variability and number of starting locations, or any other design features of the experiment were made known to participants. As soon as the platform was located forward movement ceased, auditory feedback was provided, and a verbal message appeared on the display stating that the platform had been found. A limit of 60 s was allotted to locate the platform, after which the platform became visible, a discordant tone was sounded, and a verbal message appeared stating that the platform was now visible. Regardless of whether the platform was located when it was visible or hidden, the participant remained on the platform for 10 s, after which the screen faded and a new trial began. For each trial, the participant's position in x,y coordinates was recorded every 100 ms. Latency and path length to locate the platform were determined from this record. For analysis purposes, path length was expressed as the ratio of pixels traveled to the diameter of the pool. Upon completion of the VMWT, participants completed the post-experiment questionnaire. The experiment took approximately 30 min to complete.

Table 1
Regional starting, navigation, viewing, and forced-swim conditions during training for each group

Group	Start region	Navigation	View	Forced swim in Region 2
A	1	1 and 2	1 and 2	–
B	2	1 and 2	1 and 2	–
C	1	1	1 and 2	–
D	1	1	1 and 2	Yoked to Group A
E	1	1	1 or 2	Yoked to Group F
F	1	1 and 2	1 or 2	–
G	1	1	1	–

3. Results

All reported effects are significant at $P \leq 0.05$ unless otherwise stated.

3.1. Questionnaire

The number of participants correctly reporting that the platform location was fixed did not significantly vary with respect to group membership [χ^2 (6, $N=128$) $= 1.06$, $P = 0.98$]. Additionally, the number of participants correctly reporting that start locations varied did not significantly vary with respect to group membership [χ^2 (6, $N = 137$) $= 2.131$, $P = 0.91$]. On average, the VMWT was rated as relatively easy ($M = 3.35$, S.D. $= 1.99$) and a one-way analysis of variance (ANOVA) on difficulty rating did not reveal significant group differences [$F(6, 168) = 1.33$, $P = 0.25$]. A one-way ANOVA on video game-playing experience also failed to yield significant group differences [$F(6, 168) < 1$].

Self-report of strategies employed to find the platform were coded as either a *place* strategy or a *random* strategy. Place strategies were defined as any case where the participant reported using distal cues to disambiguate the platform location (e.g. 'I used pictures on the wall as landmarks in relation to the platform'). Strategies coded as random included cases where a circuitous strategy was reported (e.g. 'I just swam around in circles and tried to cover the whole pool'), cases where participants reported using distal cues in a manner inconsistent with a place strategy (e.g. 'I went along moving toward a picture until I hit the pool wall then I would turn and move toward another picture

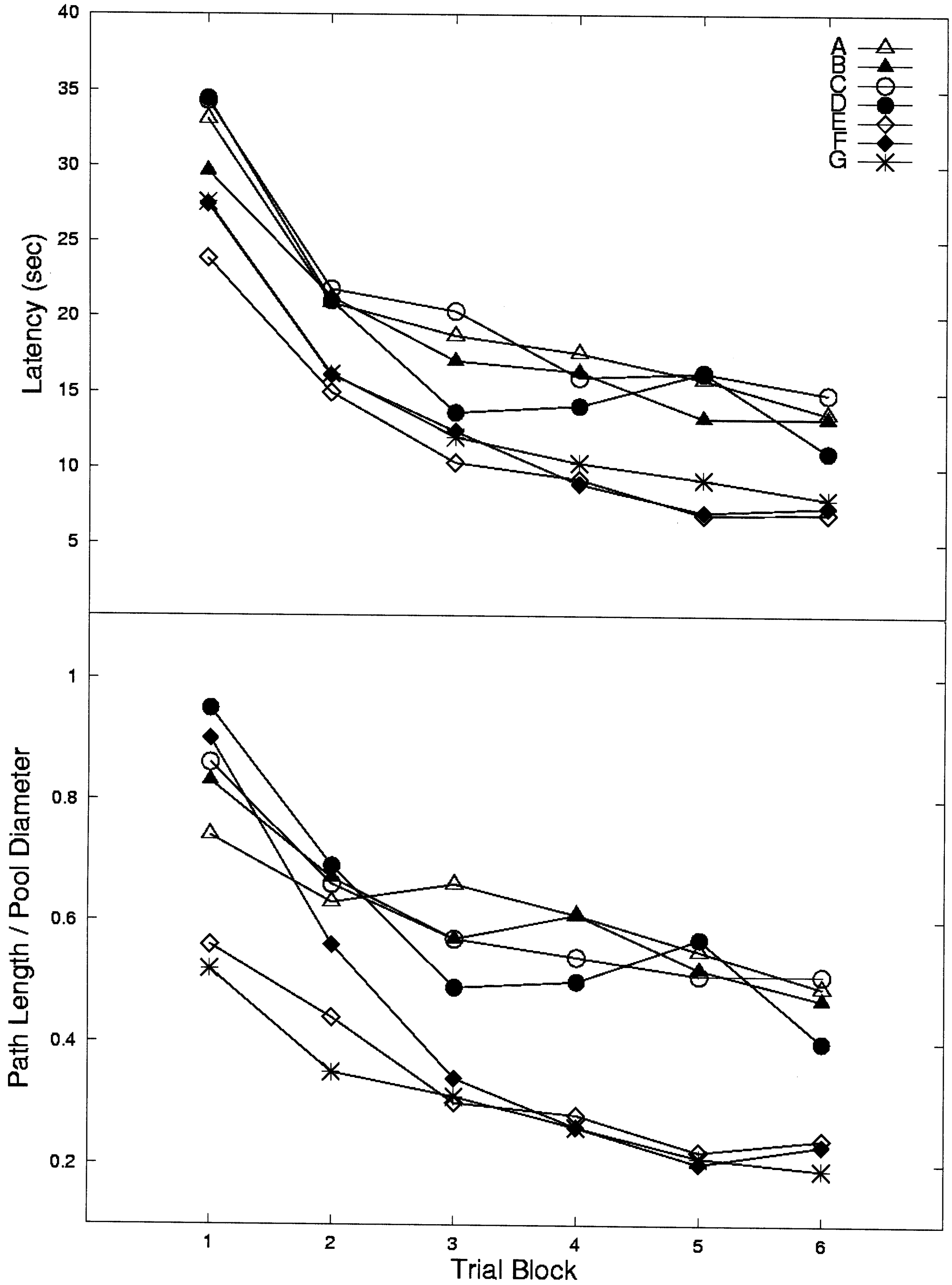

Fig. 4. Mean latency (TOP) and path length (BOTTOM) to locate the goal during the six training blocks for each of the seven experimental groups. Path length is expressed as the ratio of the total path length to the diameter of the pool.

and so on until I found that platform'), or any otherwise random strategy which was not classified as a place strategy. A total of 124 participants were classified as using a place strategy and the number of participants adopting a place strategy did not significantly vary with respect group membership [χ^2 (6, $N = 124) = 2.45$, $P = 0.87$].

3.2. Training

Each participant's mean latency and path length to locate the platform were calculated for each training trial block (see Fig. 4). The resulting means were then subjected to separate multivariate analyses of variance (MANOVA), with Group as a between-subjects factor (with seven levels) and Trial block as a within-subjects factor (with six levels). The Group × Trial block interaction failed to reach statistical significance for latency [Wilks' $\Lambda = 0.91$, approximate $F(30, 658) < 1$] and path length [Wilks' $\Lambda = 0.85$, approximate $F(30, 658) < 1$]. There was a significant decrease in latency to locate the platform as a function of Trial block [Wilks' $\Lambda = 0.41$, approximate $F(5, 164) = 45.43$]. There was also a significant Group main effect for latency to locate the platform [$F(6, 168) = 5.30$]. A contrast comparing groups trained with an opaque partition (Groups E–G) and those without (Groups A–D) revealed that the latter groups took significantly longer to locate the platform during training. This contrast accounted for 94.8% of the between-group variance in latency among a set of orthogonal contrasts. With respect to path length, there was a significant decrease as a function of Trial block [Wilks' $\Lambda = 0.57$, approximate $F(5, 164) = 24.97$]. There was also a significant Group main effect for path length to locate the platform [$F(6, 168) = 6.10$]. A contrast comparing groups trained with an opaque partition and those without revealed that the latter groups traveled significantly further to locate the platform. This contrast accounted for 95.4% of the between-group variance in path length among a set of orthogonal contrasts.

3.3. Transfer

Each participant's mean latency and path length to locate the platform were calculated for the transfer block and difference scores were computed by subtracting each participant's transfer mean from the corresponding means during the final block of training (see Fig. 5). The obtained values were subjected to a one-way ANOVA with Group as a single between-subjects factor (with seven levels). There was a significant Group main effect for difference latency [$F(6, 168) = 8.08$] and difference scores for path length [$F(6, 168) = 7.02$]. Fig. 6 shows representative training and transfer swim paths for each of the seven experimental groups. To better understand the group differences underlying the Group main effects we computed Fisher's LSD with $P = 0.05$ which yielded critical differences of 6.39 s for latency and 0.23 for path length. With respect to difference latency, Groups A and B were not significantly different from one another, but the five remaining groups took significantly longer than Group B to locate the platform. Identical outcomes were obtained for path length difference scores. Groups A and B were not significantly different from one another, but the five remaining groups traveled significantly further to locate the platform than did Group B. Contrasts designed to test the effectiveness of forced swim training revealed that forced swim did not have a significant effect with the invisible barrier (Group C vs. Group D) or an opaque partition (Group E vs. Group F). Additional post-hoc contrasts revealed that groups trained with an opaque partition had significantly higher difference latencies [$F(1, 171) = 34.48$, $P < 0.00001$] and path length difference scores [$F(1, 171) = 29.48$, $P < 0.00001$] than groups trained with no partition or the invisible barrier. Collectively, the results of the transfer analyses are similar to those reported by Sutherland et al. [31]. Their Groups C–G performed significantly worse than Groups A and B, which were the only two groups to show good transfer. Further, their groups trained with an opaque partition showed poorer transfer than the remaining groups, and forced swim did not improve transfer performance in their Groups D and E. One exception is the nonsignificant trend towards poorer transfer performance in Group A obtained in the present study which may be attributable to the relatively low percentage of time Group A spent navigating in region 1 during training (less than 26% during each of the training blocks). Thus, in effect the training experiences of Group A were comparable to those of Groups C and D.

In order to further compare and quantify the relationship between the present transfer results and those obtained by Sutherland et al. [31] we computed difference latencies as described above for each group of rats in their Experiment 1 (see Fig. 7). The seven groups from each study were then rank ordered according to the mean difference latency from lowest to highest and Spearman's rho was computed. The result was a perfect correspondence in group rank order between the two studies [$r_S = 1.0$]. There was also a significant correlation between rat and human difference latencies [$r = 0.967$, $F(1, 5) = 72.91$]. Comparison of the mean difference latencies shown in Figs. 5 and 7 for the respective studies shows the similarity of human and rat transfer behavior with respect to the environmental manipulations. Nonetheless, this particular finding should be evaluated with caution given the small sample size. We do, however, wish to remind the reader that the present study involved a set of manipulations designed to be comparable to those employed by Sutherland et al. [31] and that the probability of observing any particular permutation of the seven groups means in either study is quite small [$P = 1.98 \times 10^{-4}$].

4. Discussion

A major aim of the present study was to assess the conditions under which humans behave flexibly in a computerized (virtual) VMWT. To do so we tested whether participants demonstrate instantaneous transfer, that is, the ability to accurately navigate to a previously learned goal location from a novel starting location [18]. Participants were trained to locate a hidden goal in one half of a virtual environment and we systematically varied the opportunity to view distal cues from and navigate through the other half of the environment. The results indicate that humans do not always demonstrate instantaneous transfer in the virtual domain. Groups that were not permitted to navigate through the restricted half of the environment on a path to the goal during training performed significantly worse when started from this region than groups trained with no restrictions. Relatively poor transfer performance was obtained regardless of whether the entire environment was visible and forcing participants to navigate in the region containing the novel starting location did not improve transfer performance.

Significant group differences in training performance present a potential complication to the interpretation of the transfer findings. Groups trained with an opaque partition (Groups E–G) designed to restrict visual experience showed superior place navigation at the end of training compared to the groups trained without a partition (Groups A–D). One possible explanation of this finding is that the visible partition effectively constrained navigation to the half of the pool containing the platform, thus, Groups E–G may have focused their search in the appropriate area more than the remaining groups. If so, the group differences in training just described do not seriously complicate interpretation of the transfer results, because the groups that showed superior place navigation during training showed the poorest transfer. A more serious complication, precluding interpretation, would result if group differences in training were commensurate with or unrelated to any group differences observed in transfer. While the training and transfer performance observed in Groups E–G suggest an effect of the experimental manipulations, the poor transfer performance of these groups may also be attributable to the fact that they spent less time in the environment during training than Groups A–D. Such an interpretation is less favorable because the groups trained with navigation restrictions but no viewing restrictions (Groups C and D) demonstrated poor transfer, yet during training these groups learned the location of the platform at similar rates and asymptotic levels as groups trained with no such restrictions (Groups A and B). Importantly, this particular finding also indicates that evidence against instantaneous transfer was obtained when the potential complication noted above was not present.

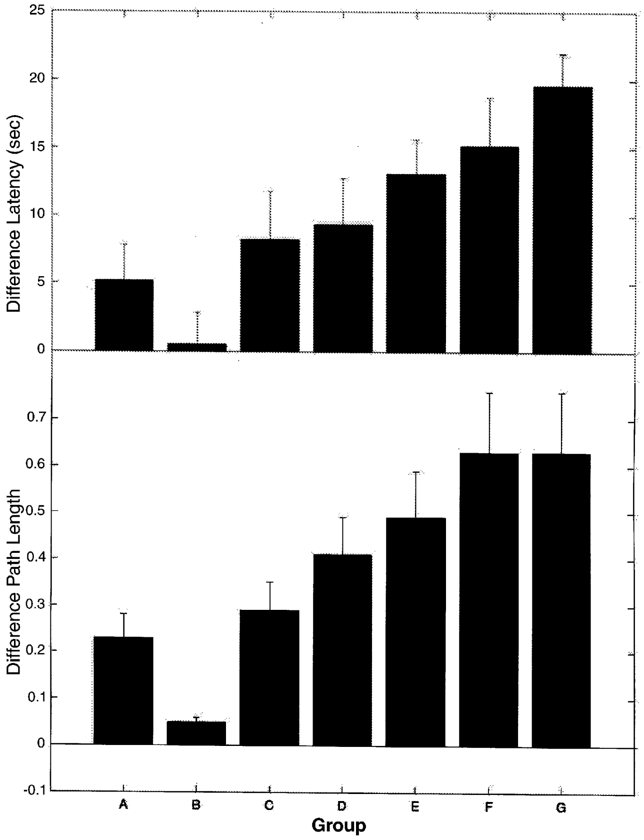

Fig. 5. Mean difference scores (+1 S.E.M.) for latency (TOP) and path length (BOTTOM) to locate the goal for each of the seven experimental groups. Difference scores were computed for each participant by subtracting the means obtained during the final training block from the corresponding means obtained during the transfer block.

An additional methodological issue of some importance involves the method by which navigation restrictions were controlled in the present study and the report published by Sutherland et al. [31]. Matthews and Best [17] suggested that the removal of the clear Plexiglass barrier by Sutherland et al. created a discrepancy between the training and transfer environments that could account for the poor transfer behavior observed in some groups. Training in the VMWT made it possible to restrict navigation to a particular region of the environment without introducing a visible barrier which, when removed, would lead to a detectable change in the environment. We found that training with an invisible barrier (Groups C and D) resulted in poor transfer behavior in humans. Because the virtual barrier provided no visual, olfactory, tactile, or other stimulus it cannot be the case that a generalization decrement of the type suggested by Matthews and Best accounts for the poor transfer behavior observed here. If one accepts the generality of the present findings then some support can be concluded for the interpretation offered by Sutherland et al. That is, that the lack of experience viewing the available distal cues while navigating through the region containing the novel starting location on a path to the goal caused the poor transfer behavior in their Groups C and D.

To address the generality of the present findings we quantified the relationship between human and rat [31] transfer performance and observed a near perfect correspondence between the responses of rats and humans to

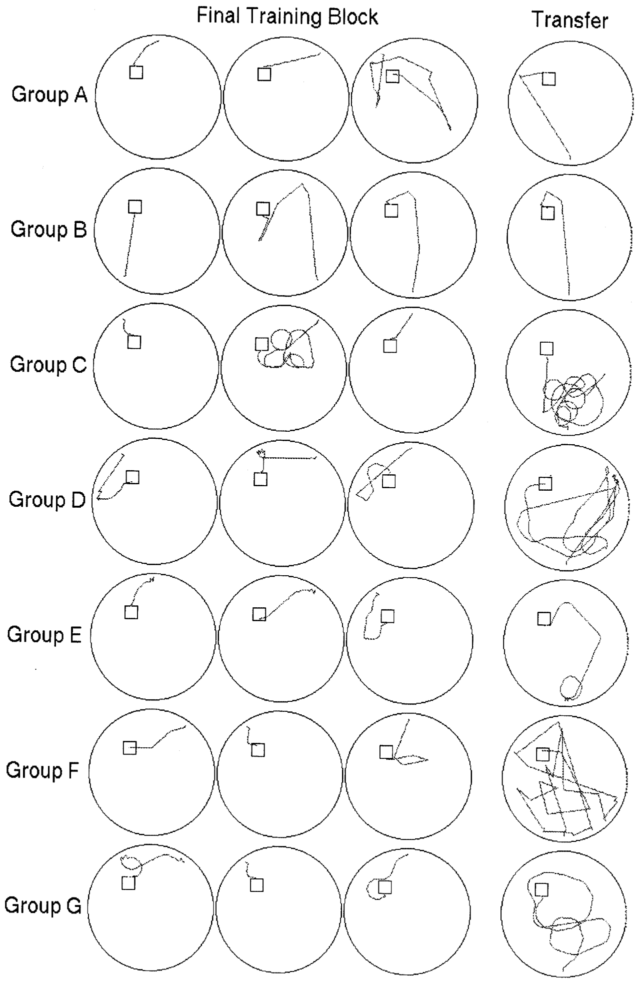

Fig. 6. Representative swim paths during the final training block (block 6) and the first trial of the transfer block (block 7). The paths were selected from individuals with median path length means during the final block of training.

comparable manipulations involving distal cues. It could be argued that basic differences in virtual and real-world navigation, such as the lack of olfactory and movement-related cues in virtual navigation, preclude a meaningful comparison. The similarities in the behavioral tasks and experimental manipulations provide reasonable justification for this comparison. Specifically, the MWT and VMWT depend upon visual stimuli [32] and the studies under comparison employed manipulations that were primarily visual in nature. Further, other forms of information relevant to real-world place learning, such as salient movement-related cues, are neither necessary nor sufficient to support place navigation in either task [9,16]. Although discrepancies between the kinds of stimuli available in real and virtual navigation are a potential source of task-related differences in behavior, these should not overshadow the fact that differences in rodent and human spatial learning could result from the operation of markedly different psychological processes or strategies (e.g. spatial vs. verbal, respectively). If so we would have expected to observe a quite different pattern of results in rats and humans. Nonetheless, the possibility that the behavioral similarities noted here resulted either from the operation of different psychological processes or discrepancies between relevant stimuli cannot be ruled out. However, that similarities between the human and rat behavioral data were observed in spite of the task-related discrepancies noted above represents an important contribution of the present report and at least suggests some basic similarity in the principles underlying visual learning of spatial locations.

There are other notable consistencies between the present results and findings from studies of spatial learning and navigation using nonhuman animals. For example, Whishaw [38] found that rats placed on the platform in the MWT were better at navigating to the platform location than animals tested under a number of control conditions (see also Refs. [13,34]; but see Ref. [7]), but the benefit of this type of experience was substantially less than the benefit afforded by prior experience navigating to the platform. Prados et al. [26] directly compared the benefit of actively navigating in the MWT with being passively placed on the goal and found that active navigation produced significantly better place navigation in a subsequent test phase. Similarly, Brown and Drew [6] found that preexposure to the visual features surrounding a radial arm maze while navigating failed to facilitate later spatial performance and Alyan [1] found that mice were proficient in homing from a novel location only when they had prior experience navigating through the region separating them from home. Collectively, these studies have yielded evidence against instantaneous transfer in spatial learning and the consistency between these findings

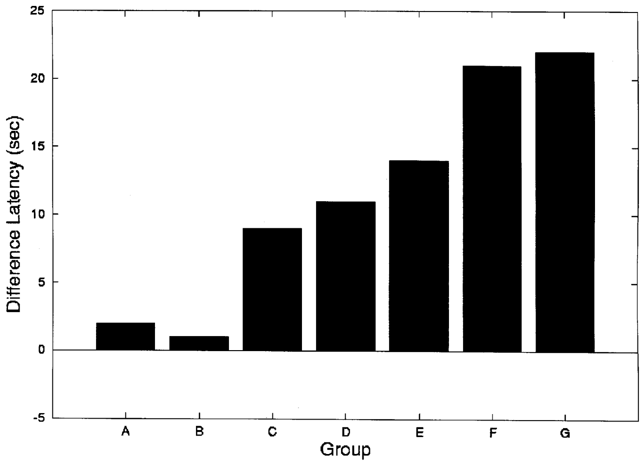

Fig. 7. Mean difference latencies for each group of rats tested by Sutherland et al. (see Ref. [31], Experiment 1). Difference latencies were computed by subtracting the mean latency to locate the platform during the final training block from the mean latency during the transfer block.

and the present results supports the notion that rodent and human spatial learning involve similar principles. The precise nature of these principles, however, remains a matter of debate.

According to O'Keefe and Nadel [23] animals construct and routinely update a cognitive map in which the topographical relationships among the available stimuli are maintained. Some authors have suggested that these cognitive mapping principles also operate in virtual space [11,12,15], citing evidence such as the control of place navigation by distal cues and intact place navigation following the removal of a subset of distal cues. Although important, these data offer only weak support for cognitive mapping theory. We hypothesized that if participants formed cognitive maps of virtual space then instantaneous transfer should have been demonstrated, thus, the present findings refute the notion that cognitive maps can be formed on the basis of limited experience viewing cues while navigating through the environment. These findings are consistent with an associative account in which accurate place navigation depends upon the establishment of associations between views of distal stimuli and the execution of specific trajectories to the goal. The range of possible explanations, however, need not be limited to this type of associative account. For example, the present data can be explained by Poucet's theory of spatial map formation in which animals must navigate through and experience multiple views of an environment in order to gradually construct a cognitive map [25], thus, our findings and those of Sutherland et al. may reflect the imperfect formation of a cognitive map as a result of the restrictions imposed during training. Future studies employing computerized and real-world spatial tasks will be needed to further clarify the types of representations and learning principles involved in human place learning. Because these principles appear to have generality, such studies will be useful in identifying the basic principles involved in place learning as well as informing theories of spatial learning and navigation.

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