Journal of Experimental Psychology:
Animal Behavior Processes
2007, Vol. 33, No. 3, 225–243

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0097-7403/07/$12.00 DOI: 10.1037/0097-7403.33.3.225

Beacon Training in a Water Maze Can Facilitate and Compete With Subsequent Room Cue Learning in Rats

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In Stage 1 of 4 experiments in which rats completed a water-maze blocking procedure, experimental groups were trained to use a predictive beacon (hanging above, connected to, or displaced from the platform) to find a submerged escape platform in the presence of predictive or irrelevant background cues and in the presence or absence of irrelevant landmarks. In Stage 2, a fixed beacon, landmarks, and background cues all predicted the platform location. A Room Test (landmarks and background cues only) showed that Stage 1 training with a fixed hanging beacon or the moving displaced beacon facilitated Stage 2 learning of predictive room cues for experimental relative to control subjects. In contrast, Stage 1 training with a moving pole beacon interfered with Stage 2 learning about predictive room cues relative to controls, whereas training with a fixed pole or moving hanging beacon had no effect. We conclude that multiple spatial learning processes influence locating an escape platform in the water maze.

Keywords: spatial learning, water maze, locale learning, facilitation, cue competition

Spatial learning plays a complex and central role in the daily lives of many animals. They learn to locate resources of food, water, shelter, and conspecifics and learn to avoid locations of danger (Collett, 2002). Increasingly, specific mechanisms of spatial learning have been studied in the laboratory (see Cheng & Newcombe, 2005; Collett, 2002; Gallistel, 1990; Save, Poucet, & Thinus-Blanc, 1998; Shettleworth, 1998). Much of this research has focused on O'Keefe and Nadel's (1978) categorization of spatial learning into locale learning (mapping) versus taxon learning (associative stimulus and response learning).

Locale learning refers to learning the location of a goal relative to a multicue, allocentric framework (an integration of available stimuli, which in a water maze include beacons, landmarks, sounds, odors, and environmental geometry). Important evidence that locale learning has occurred is the ability of a subject to approach a goal directly from any position in the environment (O'Keefe & Nadel, 1978). In contrast, taxon learning refers to learning the location of a goal on the basis of simple associative mechanisms of orientation and/or guidance. In orientation learning, the goal is located by learning a sequence of turns (a route from one location to another), whereas in guidance learning, the goal is located by approaching predictive cues, such as proximate beacons or landmarks. Neurophysiological evidence for the distinction between locale and taxon learning shows that the former depends on a functioning hippocampus (e.g., Morris, 1981; Morris, Garrud, Rawlins, & O'Keefe, 1982; O'Keefe & Nadel, 1978; Packard & McGaugh, 1996).

The present research attempted to bring together two trends that have influenced the study of spatial learning since O'Keefe and Nadel's (1978) analysis. The first trend has emphasized that concurrent mechanisms determine spatial learning. For example, Packard and McGaugh (1996) carefully examined Tolman, Ritchie, and Kalish's (1946) conclusion that rats learned the location of a reward in a T maze on the basis of place (locale) learning rather than response (taxon) learning. By applying lidocaine to the brain through cannulae implanted in the caudate (related to taxon learning) and the hippocampus (related to mapping), Packard and McGaugh revealed that both place and response learning occur, overlapping in time. The relative dominance of each learning type depends on the amount of prior training and which brain location is active.

Considerable additional research has confirmed that multiple learning mechanisms contribute to spatial learning and that their relative importance depends on the species, experience, and cue types available (Cheng & Newcomb, 2005; Save et al., 1998; Shettleworth, 1998). For example, food-storing birds and rats use flexible hierarchies of spatial learning, the expression of which changes with circumstances and previous experience (e.g., Brodbeck, 1994; Kamil & Jones, 2000; Roche & Timberlake, 1998; Shettleworth & Sutton, 2005). Observations of free-ranging rats also support the operation of multiple spatial mechanisms in establishing and using trails connecting burrows and feeding areas (Calhoun, 1962; Leonard & McNaughton, 1990). More recently, investigators have provided data showing that rats in spatial-learning tasks are controlled by combinations of the mechanisms related to beacons, landmarks, environmental geometry, and dead reckoning (e.g., Esber, McGregor, Good, Hayward, & Pearce,

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This research was supported in part by National Science Foundation Grant IBN 17175 to William Timberlake, by a research equipment grant from Indiana University to William Timberlake and Preston Garraghty, and by Howard Hughes Medical Institute research funds to Susan A. Sinning. We thank Allison Kukuch, Susan Moller, Emma Fortenberry, and Samantha Morgan for assistance and Peter Killeen and John Kruschke for advice.

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2005; Hayward, Good, & Pearce, 2004; Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001; Shettleworth & Sutton, 2005).

The second, seemingly opposing, trend in spatial-learning research has focused on showing that behaviors occurring in a spatial mapping task, such as the Morris water maze, can be attributed to Pavlovian conditioning mechanisms without the need to invoke locale learning (e.g., Sutherland, Chew, Baker, & Linggard, 1987; Whishaw, 1991; see reviews by Chamizo, 2003, and Mackintosh, 2002). The basic task in a water maze is to learn to locate a submerged escape platform in a large circular pool. A two-stage associative-blocking procedure is frequently used to demonstrate the involvement of Pavlovian conditioning in learning the location of the platform. In Stage 1, animals are trained to find a submerged platform located directly below a visible beacon suspended above the surface of the water. Before each trial, the beacon and platform together are typically randomly moved to another quadrant of the pool, thus making background cues (distinguishable but typically immovable visual and auditory aspects of the surrounding environment) irrelevant in predicting the platform location (Roberts & Pearce, 1999). In Stage 2, landmarks (large, discrete, movable cues in the environment surrounding the pool) are added to the background cues and the beacon as reliable predictors of the platform location. In a following Room Test, the beacon and platform are removed, and rats are tested with room cues alone (landmarks and background cues).

In most reported experiments, Stage 1 training with a beacon and platform typically interferes with Stage 2 learning of the location of the platform relative to the landmarks and background cues, as revealed by the poorer performance of the experimental rats, relative to controls, in finding the platform in the Room Test (with the beacon and platform removed, and only the landmarks and background cues present). Such interference with Stage 2 learning by Stage 1 training is typically explained by a model of cue competition based on limited associative strength supported by the reward (e.g., Kamin, 1969; Mackintosh, 1975; Rescorla & Wagner, 1972; see also Gallistel, 2003; Pearce & Hall, 1980). Blocking of subsequent learning is assumed to occur because Stage 1 training with a predictive beacon exhausts the rewarding capabilities of the escape platform, leaving little associative strength available for learning about the predictive landmarks and background cues present in Stage 2. Further evidence for associative explanations of spatial learning in the water maze includes additional competition phenomena, such as the following: latent inhibition (Prados, 1999), overshadowing (Redhead, Roberts, Good, & Pearce, 1997), and blocking of learning the location of a fourth landmark added following initial training with three landmarks (Rodrigo, Chamizo, McLaren, & Mackintosh, 1997).

There seems to be little doubt that associative-blocking effects can occur in the water maze; however, given the considerable evidence that multiple overlapping mechanisms contribute to other examples of spatial learning, it seems prudent to determine whether multiple mechanisms may also be at work in the water-maze blocking procedure (e.g., Graham, Good, McGregor, & Pearce, 2006; Hayward, McGregor, Good, & Pearce, 2003; Pearce, Graham, Good, Jones, & McGregor, 2006). After all, demonstrations of simple associative effects in the water maze do not theoretically or logically eliminate contributions of locale-learning (mapping) mechanisms. Similarly, demonstrations of locale-learning effects do not eliminate a contribution of associative learning mechanisms. Thus, the purpose of the present research was to distinguish circumstances under which learning the location of a hidden escape platform with respect to a beacon in Stage 1 of a typical water-maze blocking procedure produced associative competition versus integration (locale learning) with the predictive cues added in Stage 2.

We used variations of beacon types and procedures in Stage 1 of a water-maze blocking procedure to test the possible occurrence of two forms of cue integration and three forms of cue competition involving Stage 1 and Stage 2 learning:

1. Facilitation (cue integration)—increased learning of redundant predictive room cues (landmarks and background cues) in Stage 2 for experimental relative to control subjects as a function of fixed extramaze background cues (Experiment 1) and intramaze geometry (Experiment 4) present in both Stages 1 and 2.

2. Blocking—decreased learning of redundant landmarks in Stage 2 for experimental relative to control subjects as a result of Stage 1 moving beacon training (Experiments 1 and 3; see Roberts & Pearce, 1999).

3. Learned irrelevance—decreased learning of redundant predictive room cues in Stage 2 for experimental relative to control subjects following Stage 1 training with landmarks present and irrelevant (a moving beacon predicts the platform with landmarks present in Experiment 2; e.g., Redhead et al., 1997; Roberts & Pearce, 1999).

4. Overshadowing—decreased learning of redundant predictive room cues in Stage 2 in a control group because of simultaneous presentation with the predictive beacon (Experiment 2; e.g., Redhead et al., 1997).

A rat's ability to find the platform in a Room Test (only background cues and landmarks) is usually measured primarily by proportion of time spent in the predicted platform quadrant and is measured secondarily by the latency to cross the (empty) platform location. To separate initial and persistent search of a predicted platform quadrant, we report data separately for the first and second 30 s of a Room Test. We also examine possible learning of the general location of a platform by measuring the proportion of time spent searching the middle half of the pool (as opposed to the outside half of the pool, where animals often circle in close proximity to the wall when they haven't yet learned the platform location or have given up searching for it; McGauran, Harvey, Cunningham, Craig, & Commins, 2004). Finally, in a further effort to clarify the control of spatial learning in the water-maze blocking procedure, we followed the Room Test with another training day and a Preference Test—a single trial that separated the quadrant locations predicted by the beacon, landmarks, and background cues—to determine the relative accuracy and persistence of search for each type of predictive cue. We again distinguished the first and second 30 s of the trial and the proportion of time spent in the center half versus the outside half of the pool.

General Method

Subjects

The subjects for each experiment were 16 to 27 naive male Sprague–Dawley rats (*Rattus norvegicus*), with 8 or 9 rats in each group. Rats were 4–6 months old and were bred at the Indiana University Department of Psychology animal colony. The rats were housed individually and maintained under a 12:12 hr light–dark cycle. All subjects had continuous access to food and water. Experiments were conducted 6 days per week during a time within the middle 4 hr of the 12-hr light period.

Apparatus

Experiments were conducted in a fiberglass tank (152 cm in diameter and 60 cm in height), filled to a depth of 41 cm with water at room temperature (22° C). Black tempera paint mixed in the water helped prevent subjects from seeing the hidden platform from above and facilitated visual contrast for tracking the rat with Noldus Ethovision 3.1 software (Noldus Information Technology, Wagenin, the Netherlands) and a camera installed in the ceiling directly above the pool center.

The pool was located in a 2.72 × 2.46 m space formed by floor-to-ceiling black vinyl curtains hung from a ceiling track with rounded corners running close to the walls of the physical room. The top edge of the curtains was 23.5 cm from the ceiling. The pool rested on a sturdy wood and cement block platform at a height of 52 cm above the floor. The pool was positioned in the room so that its center was 1.28 m from the west curtain, 1.32 m from the north curtain, 1.16 m from the east curtain, and 1.36 m from the south curtain. The light fixtures and vents on the ceiling were symmetric with respect to the walls of the room so that visually one could not tell any quarter or half of the room from another by looking at the ceiling. One of the four flexible clamp lights illuminated each curtain wall from below.

A clear Plexiglas escape platform (10 cm in diameter and 1.5 cm below the surface of the water when raised), with circular ridges to facilitate climbing out of the pool, was typically located at one of four locations an equal distance from the center of the pool and 40 cm from the side of the pool. For tracking purposes, the four quadrants of the pool were labeled *north, west, east,* and *south* as a function of the bearing of the wall they were closest to. A door was located at the west corner of the north wall. The vinyl curtains were sealed and unsealed with Velcro tabs to allow the experimenter to enter and exit the room. Metal S hooks were used to hang landmarks 3.2 cm from the top of the curtains. The four landmarks included the following: a bright reflective yellow poster (58.4 cm × 88.9 cm, width × height) on the north side, a cowhide print black-and-white splotched sheet (226.1 cm × 109.2 cm) on the east side, a wide (48.3 cm × 68.6 cm) or tall (83.8 cm × 55.9 cm) poster on the south side, and a patterned oriental rug (118 cm × 158 cm) on the west side.

The first three experiments used a metal beacon shaped like a stubby, thick slice of pie, that is, a polyhedral solid with three rectangular sides and a top and bottom of parallel isosceles triangles. The two sides of the top and bottom triangles measured 13 cm, and the base was 10 cm, as was the thickness of the "slice." A black rod 1 cm in diameter was inserted into and welded perpendicularly to one of the isosceles triangle faces. When the beacon was suspended in place, the apex of the slice pointed toward the center of the pool, and the bottom of the slice was 23 cm above the water. Alternating black and white stripes on the beacon were produced by equally spaced strips of 1.9-cm wide black electrical tape applied at a 60° angle to the horizontal.

In Experiments 1 and 2, the beacon was hung over the submerged platform by clamping the attached 1-cm diameter rod to a horizontal rod of the same material bent at 90° near the edge of the pool and attached to a wooden support (painted to match the pool wall) that slipped over the pool's edge. The black 1-cm diameter horizontal rod was difficult to see, because it was 50 cm above the water surface and was viewed from most pool angles against black curtains. In Experiment 3, the same beacon was inverted and connected by its attached rod to the submerged platform so that finding the rod meant finding the platform. Experiment 4 used a slightly larger beacon (approximately 1 cm larger on each dimension) with similar shape, stripes, and orientation. It was displaced between the platform and the nearest point of the pool wall, with the beacon point 20 cm away from the platform and the bottom of the beacon only 14 cm above the water surface. It was suspended 24 cm above the water from a visible, obvious 10.2 cm wide × 24 cm long × 0.24 cm thick strip of aluminum, screwed to a wooden brace slipped over the edge of the pool.

Procedure

Stage 1 training. The experimental group received three training trials per day, and on each trial subjects were released into the pool facing the wall at one of four points, randomly drawn without replacement from northwest, northeast, southwest and southeast. Thus, three of the four possible release points were used on a given day, and these three points varied among sessions and in their order within a session. On each trial, the rat was allowed 60 s to find a submerged platform located in the same quadrant as the beacon. If the rat did not locate the platform within 60 s, the experimenter guided the rat to the submerged platform with her hand placed in the water with fingers curled slightly in front of the rat. If this failed, she placed the rat on the platform. Once on the platform, the rat was allowed to remain on the platform for 30 s. Following both Trial 1 and Trial 2, the rat spent 30 s in its compartment of a covered carrier located on the floor of the running room and was then introduced at a new starting location into the pool. Following Trial 3, the rat was towel dried and placed under a heat lamp outside the running room and was then returned to its home cage.

During Stage 1, only the experimental group or groups received training for 8–12 days with the predictive beacon. During Stage 2, the experimental groups from Stage 1 and the control groups introduced in Stage 2 were trained (as called for) with beacon, landmarks, and background cues predicting the location of the platform for three trials per day for 6–12 days. The number of trials in Stage 1 was typically determined by how long it took for the groups to reach asymptotic performance for a block, whereas the number of trials in Stage 2 was determined by how long it took for the control group to reach the level of performance of the experimental groups. To maintain a fixed relation among the landmark, beacon, and platform during Stage 2, we left the beacon and platform in the same quadrant for a particular rat, but the location of that quadrant was counterbalanced across rats.

During Stage 2, the four landmarks (consisting of posters and pieces of cloth with large and contrasting patterns) were hung equally spaced against the surrounding black curtains. The platform and beacon were fixed with respect to the room cues (landmarks and background cues) for each group and trial. Acquisition in both Stages 1 and 2 was tested with analyses of variance (ANOVAs) of groups by 2-day blocks (collapsing across trials). When significant main effects occurred in latencies, groups and 2-day blocks were compared with Tukey's tests (significance at $p < .05$).

Room Test. The Room Test trial took place immediately following the final three training trials. The rat always started from its unused release point for that day and was allowed to swim for 60 s. We recorded latency to cross the platform location, number of crosses, and the proportion of time spent in each quadrant. We also recorded time spent in the inner and outer half of the pool. Two-variable ANOVAs examined groups and trial half (first vs. second 30 s) effects for each measure. When group effects or interactions were present, specific comparisons were made with Newman–Keul's tests (significance set at $p < .05$).

Preference Test. After 1 day of retraining following the Room Test (plus one additional trial on the next day), we tested the rat's choice accuracy and preference for platform quadrants predicted by the beacon, the landmarks, and the background cues. Predicted quadrant locations for the platform were separated by moving the beacon one quadrant clockwise and moving the landmarks counterclockwise with respect to the quadrant predicted by the background cues (which could not be shifted). The rats were released facing the wall in the center of the remaining quadrant and were allowed to swim for 60 s while we recorded latency to cross each predicted platform location, proportion of time spent in each of the three quadrants, and time spent in the inner and outer half of the pool. Because the data for the Preference Test were so similar for each experiment (at least in part because of the marked attractiveness of the hanging beacon), we provide only a general summary of these data, focusing on the time spent in the quadrants predicted by the background cues versus the landmarks.

Experiment 1: Hanging Beacon With Fixed Versus Random Background Cues

Roberts and Pearce (1999) reported in their Experiment 1 that when rats were trained in Stage 1 to find a submerged escape platform predicted by a randomly moving pole beacon in the presence of stationary background cues (no landmarks present), this significantly blocked learning the location of the platform relative to the fixed landmarks (and background cues) in Stage 2. A 60-s Room Test with only landmarks and background cues present showed that a control group, which received the same Stage 2 training as the beacon group, spent around 40% of their time in the platform quadrant. In contrast, the Stage 1 moving beacon group spent approximately 25% (chance) of the test trial in the platform quadrant, thus indicating competition for this group in learning the landmarks and background cues in Stage 2.

The purpose of our Experiment 1 was to examine the generality of the beacon blocking effects of Roberts and Pearce (1999). We used a hanging beacon (rather than either the connected pole beacon or visible low cap beacon used by Roberts & Pearce, 1999) to mark the platform location. We also examined the effects of presenting the beacon and escape platform in Stage 1 as fixed or moving with respect to the background cues. During Stage 2 training for all groups, the background cues and four stationary landmarks were made predictive by locating the beacon and platform in the same quadrant for each trial.

Because the background cues were fixed for the fixed-beacon group in both Stage 1 and Stage 2 training, we anticipated they would provide a stable environmental framework that could facilitate relating the landmarks to the location of the beacon in Stage 2. Thus, we predicted that the fixed-beacon group would show facilitation relative to the control group in finding the location of the platform in the Room Test (with only landmarks and background cues present). In contrast, because the moving-beacon group in Stage 1 experienced no relation between the background cues and the beacon and platform locations, these rats should not show facilitation in the Room Test relative to the control group because there was no potential for improved Stage 2 learning through Stage 1 training of background cues. If anything, the moving beacon group might experience interference with relating the room cues to the platform location because of the learned irrelevance of the background cues in Stage 1.

The Preference Test, which unlinked the Stage 2 relation of the beacon, landmarks, and background cues so that each cue predicted different platform locations, may tell us the extent to which the groups learned the relation of the platform to the landmarks and to the background cues. Finally, the center-half test should reveal the extent to which any beacon training in Stage 1 (fixed or moving with respect to background cues) increased searching the center half of the pool in the Room and Preference Tests for experimental subjects relative to control subjects.

Method

Subjects were 27 naive male Sprague–Dawley rats (*Rattus norvegicus*) divided into three groups of 9 rats: the fixed-beacon group, the moving-beacon group, and the control group. During training for Stages 1 and 2 (three trials per day), a hanging beacon was always present 23 cm above the water and directly over the submerged platform. In the 10 days of Stage 1 training, the positions of the beacon and platform with respect to the background cues were always the same for the fixed-beacon group but were random with respect to the background cues for the moving-beacon group. During the 6 days of Stage 2 training, the positions of the beacon and platform were fixed, and landmarks were added, making the beacon, landmarks, and background cues all predictive of the platform location. The Room Test was administered on a fourth trial added to the 6th training day of Stage 2. Following a Stage 2 retraining day and one additional trial, we gave the Preference Test, simultaneously providing access to the different platform locations predicted by the beacon, landmarks, and background cues. See the General Method section for other details.

Results

Acquisition. Figure 1 shows average latency to the platform over five 2-day blocks in Stage 1 for the fixed-beacon and moving-beacon groups, followed by Stage 2 latencies over three 2-day blocks for the same beacon groups plus the control group. In Stage 2, landmarks were added to the beacon and background cues. The

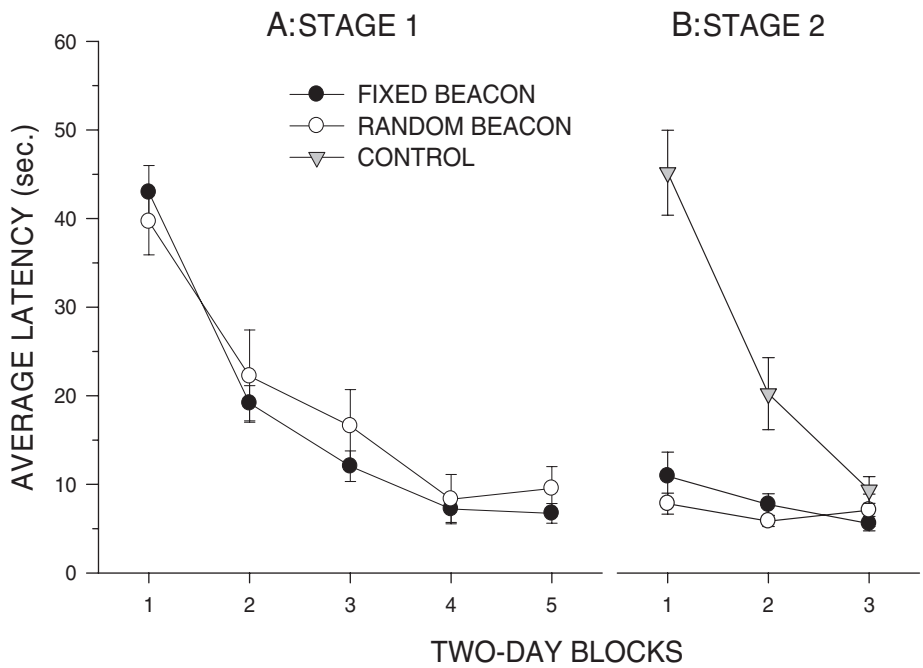

Figure 1. A: Latency (in seconds) averaged over three daily trials and 2-day blocks for the fixed-hanging-beacon group and the moving-hanging-beacon group to find the submerged platform during Stage 1 training. B: Latency (in seconds) averaged over three daily trials and 2-day blocks for the fixed-hanging-beacon group, the moving-hanging-beacon group, and the control group to find the submerged platform during Stage 2 training.

average latencies of both beacon groups over day blocks in Stage 1 were compared in an ANOVA that showed no group difference but showed an overall main effect for days, $F(4, 64) = 79.2$. Tukey's tests showed no significant difference of day blocks for each group after Block 3.

A two-variable ANOVA of average latencies during the Stage 2 condition with stationary predictive beacons and landmarks for both beacon groups and the control group showed an effect of groups, $F(2, 24) = 26.6$, blocks, $F(2, 48) = 42.7$, and a Groups × Blocks interaction, $F(4, 48) = 26.0$. Further analyses for each group showed no change over blocks for the moving-beacon and fixed-beacon groups, but Tukey's tests showed significant differences between the control group and the two beacon groups in Day Blocks 1 and 2 but not in Block 3, the final block of Stage 2.

Room Test. Figure 2A shows the proportion of time spent for each group in the platform quadrant predicted by the landmarks alone in the absence of the beacon. The dashed line at .25 represents the chance level for proportion of time spent in each quadrant, assuming they are equally accessible. A Groups (fixed beacon, moving beacon, control) × Test Half (first 30 s, second 30 s) ANOVA showed a groups effect, $F(2, 24) = 3.72$. Newman–Keul's tests confirmed that this main effect was due to the fixed-beacon group spending a greater proportion of time in the predicted platform quadrant (.46) than the moving-beacon group (.36) or the control group (.34); the last two did not differ. The ANOVA also showed a significant overall decrease in proportion of time spent in the predicted platform quadrant from the first half of the test trial (.42) to the second (.36), $F(1, 24) = 7.47$, with no interactions.

Figure 2B shows the average latency of each group to cross the platform location predicted by the room cues in the Room Test. An ANOVA showed a main effect of groups, $F(2, 24) = 3.92$, with Newman–Keul's tests showing that the fixed-beacon and moving-beacon groups (which did not differ) crossed the platform location significantly faster than the control group. The average frequency with which each group crossed the location of the platform during the trial paralleled the results for latency, $F(2, 24) = 5.90$, again with Newman–Keul's tests showing that both the fixed- and moving-beacon groups (which did not differ) crossed the predicted platform location more often than the control group.

Table 1 (Experiment 1) reveals a groups effect in center-half search in the Room Test, $F(2, 24) = 5.85$. Newman–Keul's tests showed that both the fixed-beacon group (.74) and moving-beacon group (.77) spent a greater proportion of time in the center half of the pool than did the control group (.59). Further, all groups contributed to a significant decrease in center-half search during the Room Test, $F(1, 24) = 9.58$, from the first 30 s (.74) to the second 30 s (.66).

Preference Test. Finally, the mean proportion of time spent in the different platform quadrants predicted in the Preference Test (data not shown) revealed no effects of group but revealed a marked effect of quadrant, $F(2, 48) = 17.1$; Newman–Keul's tests showed that proportion of time spent in both the beacon quadrant (.34) and the landmark quadrant (.25) significantly exceeded that in the background cue quadrant (.16). The greater time spent in the beacon quadrant was expected because of the attractiveness of the beacon hanging above the water. However, the greater time spent in the quadrant predicted by the land-

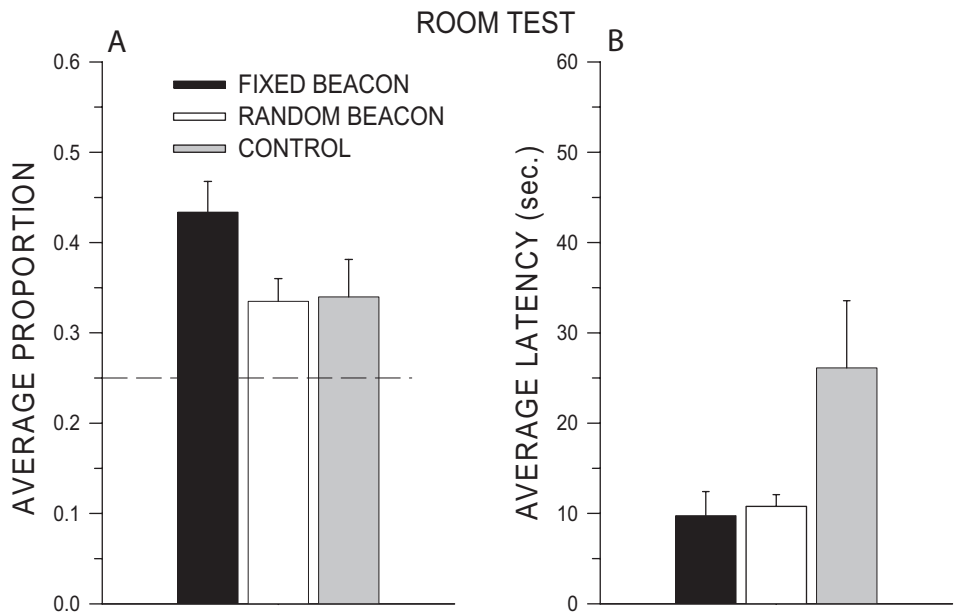

Figure 2. A: Average proportion of time (out of 60 s) spent by the fixed-hanging-beacon group, the moving-hanging-beacon group, and the control group in the quadrant predicted by the landmarks to contain the safety platform. The dashed line represents the chance proportion of time spent in each quadrant. B: Average latency (in seconds) for the fixed-beacon group, the moving-beacon group, and the control group to cross the platform location in the quadrant predicted by the landmark.

marks versus the background cues indicates that the landmarks controlled search for their platform quadrant better than the background cues did and presumably also did so in the just prior Room Test. Finally, as might be expected, the latencies to cross these different platform locations in the Preference Test showed a pattern inverse to that shown by the time spent measure, with the shortest latency to the platform location predicted by the beacon.

Table 1
Proportion of Time Spent Searching the Center (vs. the Outside) Half of the Water Maze for All Groups in Both the Room Test and the Preference Test of Experiments (Exps.) 1–4

	Room Test				Preference Test			
	First 30 s		Second 30 s		First 30 s		Second 30 s	
Experiment and group	Time	*SEM*	Time	*SEM*	Time	*SEM*	Time	*SEM*
Exp. 1: Hanging beacon								
Fixed	.76	±.05	.73	±.05	.85	±.04	.66	±.03
Moving	.85	±.02	.70	±.04	.61	±.06	.48	±.08
Control	.62	±.05	.57	±.06	.58	±.06	.47	±.07
M	.74		.66		.68		.54	
Exp. 2: Hanging beacon								
Learned irrelevance	.82	±.03	.75	±.02	.73	±.04	.55	±.08
Overshadow	.71	±.05	.59	±.06	.49	±.10	.52	±.05
Control	.71	±.06	.57	±.06	.48	±.09	.53	±.08
M	.75		.64		.57		.54	
Exp. 3: Pole beacon								
Fixed	.75	±.03	.60	±.10	.64	±.07	.49	±.07
Moving	.55	±.03	.67	±.04	.73	±.03	.55	±.05
Control	.62	±.08	.56	±.07	.71	±.06	.57	±.06
M	.64		.61		.70		.54	
Exp. 4: Displaced beacon								
Moving	.87	±.03	.75	±.04	.78	±.04	.73	±.05
Control	.67	±.04	.64	±.06	.76	±.05	.65	±.07
M	.77		.69		.77		.69	

In contrast to the absence of a groups effect on the proportion of time spent searching the predicted quadrants in the Preference Test, there was a strong groups effect on the proportion of time spent searching the center half of the pool, $F(2, 24) = 7.08$ (Table 1, Experiment 1). Newman–Keul's tests revealed that the fixed-beacon group (.75) showed significantly more center search than the moving-beacon (.55) and the control (.52) groups, which did not differ. Thus, in contrast to center search in the Room Test being facilitated by Stage 1 training with beacons fixed or random with respect to background cues, center search in the Preference Test was facilitated only by fixed-beacon training. This difference most likely reflected a persistence effect in the fixed-beacon group because the Preference Test was always preceded by the Room Test; however, it also might reflect the differences in test circumstances.

Discussion

Our data clearly showed, relative to the control group, a facilitatory locale-learning effect for the fixed-beacon group and no blocking effect for either the fixed- or the moving-beacon groups. The Room Test showed two types of result. In terms of proportion of time spent searching the platform quadrant, the fixed-beacon group exceeded both the control and the moving-beacon groups, which did not differ. This outcome supported our expectation that the fixed background cues present in Stage 1 produced a stable environmental framework that facilitated learning the location of the platform relative to the landmarks added in Stage 2. However, in terms of the latency to cross the platform location and number of crosses, both the moving- and fixed-beacon groups showed shorter latencies and more crosses than the control group, as well as a greater proportion of time searching the center half of the pool during the Room Test. Together, these results suggest that any beacon training in Stage 1 facilitates a relatively focused center search strategy relative to that shown by the control group, but results also suggest that increased persistence in search of the platform quadrant in the Room Test requires learning the location of the platform relative to a stable environmental framework (the fixed-beacon group).

Finally, because the background cues were always constant for the fixed-beacon group, it might be argued that this group's greater platform quadrant search in the Room Test was due to better control of search by the background cues alone, rather than to a facilitated learning in Stage 2 of the relation of the platform location to the landmarks. However, the Preference Test casts doubt on this explanation because when the background and landmark quadrants predicted different platform locations, the fixed-beacon group showed significantly more time in the platform quadrant predicted by the landmark cues. Further, training with or against the background cues in Stage 1 (fixed vs. moving groups) made no difference in terms of latency to cross the platform in the Room Test, again not what would be expected if stable background cues directly facilitated Room Test results. Thus, taken together, our data best support the hypothesis that a stable framework of background cues mediates rather than directly facilitates learning the location of the platform in Stage 2 learning. We revisit this issue in Experiments 2 and 4.

A second issue is why, in the Room Test, the moving-beacon group was comparable with the fixed-beacon group in latency and frequency of crossing the platform location and the extent of center search, but was significantly lower in proportion of time spent in the platform quadrant. The simplest explanation is that any Stage 1 beacon training increased the tendency of rats to search the center half of the pool, as opposed to the outer half, thereby increasing the likelihood of crossing the platform location without facilitating learning its specific location relative to the room cues. We return to this question in Experiments 3 and 4. A final issue is why the moving-beacon group, a group trained with background cues irrelevant in Stage 1, did not indicate any cue-competition effects relative to the control group in the Room Test. Experiments 2 and 3 focus on this question.

Experiment 2: Hanging Beacon With Irrelevant Room Cues and an Overshadow Control

The facilitation effect of Stage 1 training in Experiment 1 for the fixed-beacon group and the absence of a cue-competition effect in the moving-beacon group contrasts with the Experiment 1 results of Roberts and Pearce (1999), as well as with the pilot study results they reported in the introduction of their Experiment 3. It may be important that their pilot study trained against all room cues (both landmarks and background cues), making them irrelevant in predicting the platform location at the beginning of Stage 2. In contrast, our moving-beacon group, which did not show cue competition, was trained against only background cues. The first aim of the present experiment was to determine if making all room cues (both landmarks and background cues) irrelevant in Stage 1 would produce cue competition in Stage 2 in learning that room cues predict the platform location for a moving-beacon group.

A second possible explanation for the absence of cue-competition effects in Experiment 1 is that simultaneously presenting the landmarks and the salient beacon to the control group in Stage 2 might have produced overshadowing of the landmarks by the beacon. This result would be expected to decrease performance of the control group in the Room Test, thus increasing the size of the facilitation effect in the fixed-beacon group and making it harder to show a blocking effect in the moving-beacon group. It is worth noting that some doubt is cast on this explanation because the proportion of time spent in the platform quadrant in the Room Test for our control group did not appear different from that of the control groups reported in Roberts and Pearce (1999); nevertheless, given the potential for differences related to experimental circumstances and procedures, the possibility of an overshadowing effect in our control group seemed worth evaluating.

Thus, a second aim of the present experiment was to add an overshadow-control group, which received landmarks and background cues in Stage 2 training but received no beacon. If overshadowing by the beacon decreased Stage 2 learning by the control group of the location of the platform relative to the room cues in Stage 2, we would expect the performance of the overshadow-control group to exceed that of the regular (compound) control group during Stage 2 training and the Room Test.

Method

The subjects were 25 rats, divided randomly into a learned-irrelevance group (8 rats), a control group (8 rats), and an overshadow-control group (9 rats). Stage 1 training for the learned-

irrelevance group consisted of 10 daily sessions (three trials each day). On each trial, a hanging beacon was placed directly above the submerged platform, and on each trial the beacon and platform were randomly moved together with respect to the background cues and landmarks. During Stage 2, the positions of the beacon and platform were fixed with respect to all room cues (landmarks and background cues) for all groups, with the exception that the overshadow-control group received no beacon. The Room Test was administered on a fourth trial added on the 8th day of Stage 2. Following a Stage 2 retraining day and an additional trial, we gave the Preference Test, pitting against each other the platform locations predicted by the beacon, landmarks, and background cues. See the General Method section for other details.

Results

Acquisition. Figure 3A shows Stage 1 latency to reach the platform averaged over three daily trials by five 2-day blocks for the learned-irrelevance block; Figure 3B shows the same measure in Stage 2 averaged over daily trials by four 2-day blocks for the learned-irrelevance group, the control group, and the overshadow-control group. A repeated measures ANOVA over Stage 1 showed a significant improvement in latency to reach the platform across 2-day blocks, $F(4, 28) = 64.1$. A Tukey's test showed that the third block did not differ significantly from subsequent days, indicating rapid acquisition.

A two-way ANOVA over Stage 2 showed a main effect of groups, $F(2, 22) = 15.4$; 2-day blocks, $F(3, 66) = 55.9$; and a Groups × Blocks interaction, $F(6, 66) = 9.63$. These effects reflected a marked and similar improvement over blocks in the average latency of the control and overshadow-control groups, combined with the expected smaller improvement by the learned-irrelevance group. The groups differed slightly but significantly on the last Stage 2 block, $F(2, 22) = 5.40$. A Tukey's test showed that the learned-irrelevance and control groups reached the platform on average slightly faster than the overshadow-control group.

Room Test. Figure 4A shows essentially equal proportions of time spent in the quadrant predicted by the room cues (landmarks and background cues) for the learned-irrelevance group, the overshadow group, and the control group. The dashed line at .25 shows the chance level of being in the room cue quadrant, given four equally accessible quadrants. An ANOVA, testing proportion of time spent in the predicted platform quadrant for the variables of groups and test half, showed no effect for either, $Fs(2, 22) < 1$. In contrast, an ANOVA on proportion of time spent in the center half of the pool for groups and test half showed significant effects for groups, $F(2, 22) = 3.63$, and for test half, $F(1, 22) = 15.4$ (see Table 1, Experiment 2). All groups showed a marked preference for searching the center half of the pool, and a Newman–Keul's test showed that over the full test trial the learned-irrelevance group (.78) showed a significantly greater proportion of time spent in the center than the overshadow group (.65), which did not differ from the overshadow-control group (.64; averages of data in Table 1, Experiment 2). In the case of test half, the proportion of time spent searching the center of the pool during the first half of the Room Test trial (.75) was greater than for the second half of the trial (.64) over all groups (no interactions).

Figure 4B shows the average latency to cross the platform location predicted by the room cues. Although the learned-

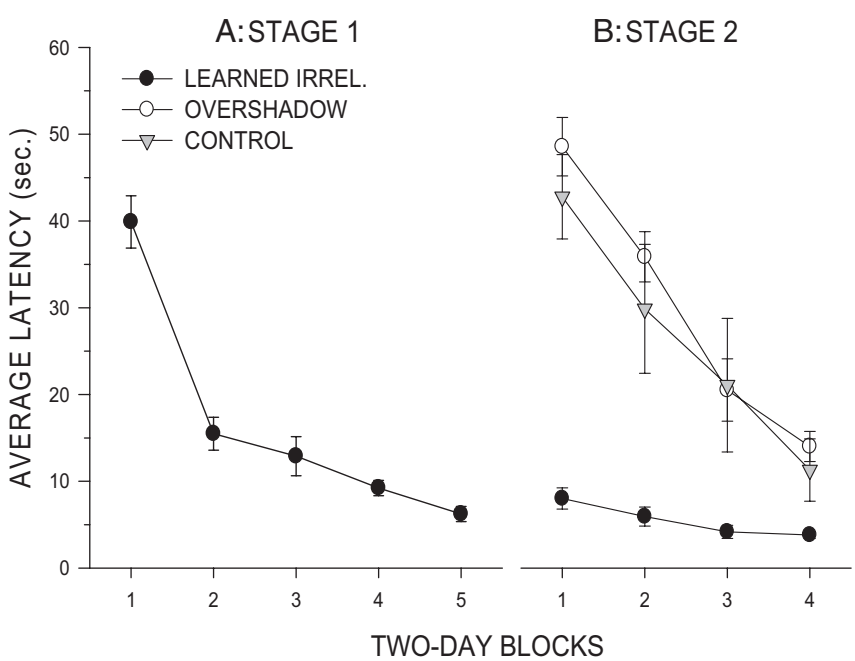

Figure 3. A: Latency (in seconds) averaged over three daily trials and 2-day blocks for the learned-irrelevance (irrel.) group to find the submerged platform during Stage 1 training. B: Latency (in seconds) averaged over three daily trials and 2-day blocks for the learned-irrelevance group, the control group, and the overshadow-control group to find the submerged platform during Stage 2 training.

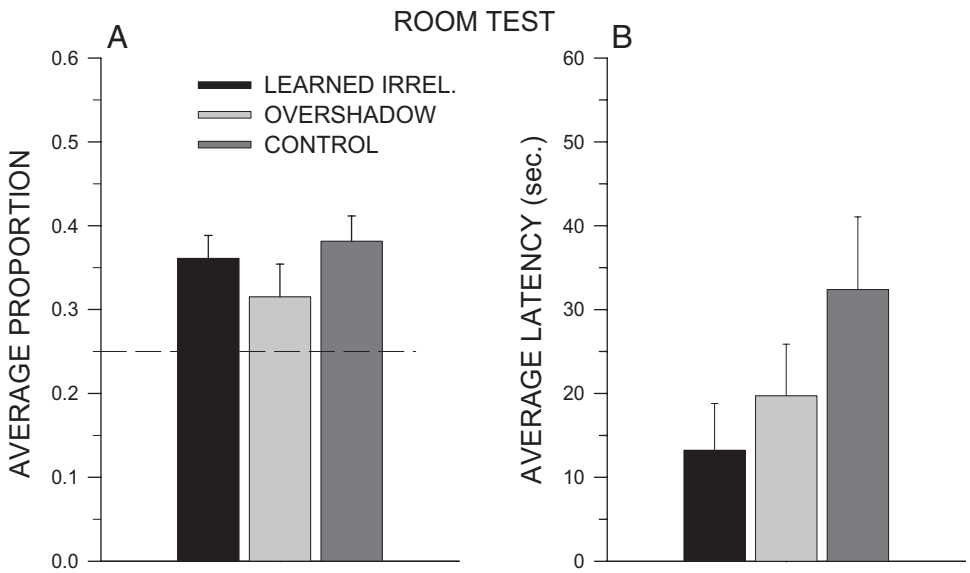

Figure 4. A: Average proportion of time (out of 60 s) spent by the learned-irrelevance (irrel.) group, the control group, and the overshadow-control group in the quadrant predicted by the landmarks to contain the safety platform. The dashed line represents the chance proportion of time spent in each quadrant. B: Average latency (in seconds) for the learned-irrelevance group, the control group, and the overshadow-control group to cross the platform location in the quadrant predicted by the landmark.

irrelevance group and the overshadow-control group were on average slightly quicker to cross the platform location than the control group, an ANOVA revealed no group effect, $F(2, 22) = 1.94$. The data on frequency of crossing the platform location showed the same nonsignificant pattern among the groups, $F(2, 22) = 2.69$.

Preference Test. The results of the Preference Test (data not shown), in terms of proportion of time spent (and latency to cross the platform location), were similar to those in Experiment 1, showing no effect among the learned-irrelevance group, the overshadow-control group, and the control group, but showing a significant quadrants effect, $F(2,42) = 7.22$. In the present case, the proportion of time spent in the beacon quadrant (.34) exceeded both the landmark (.25) and background cue (.22) proportions, which did not differ. (Only the learned-irrelevance group preferred the landmark to background cue quadrants.) Newman–Keul's tests also showed that the overshadow group was faster on average to cross the platform location predicted by the beacon than to cross the location predicted by the landmarks. Because this group had never seen the beacon before the Preference Test, this finding shows a strong unconditioned tendency for rats to rapidly approach a novel hanging beacon.

Discussion

The most important finding in Experiment 2 was that the overshadow-control and the control groups did not differ, thereby providing no support for the hypothesis that the facilitation effect and the absence of a cue-competition effect in Experiment 1 were due to the beacon overshadowing the landmarks in the Stage 1 training of the control group. Further, given that the learned-irrelevance group did not differ from either the control or the overshadow-control groups in proportion of time spent in the predicted platform quadrants in the Room or Preference Tests, we cannot attribute the absence of cue-competition effects to failure to train against the landmarks in Stage 1. Finally, the tendency of the learned-irrelevance group to cross the platform location in the Room Test faster and more frequently than the control groups supports the findings of Experiment 1 that any Stage 1 beacon training promotes searching in the center half of the pool during the Room Test and, thus, results in increased accidental crossings of the platform location.

Experiment 3: Pole Beacon With Fixed Versus Random Background Cues

In neither Experiments 1 nor 2 did we find the cue-competition/blocking results expected from previous literature (see Mackintosh, 2002; Roberts & Pearce, 1999; Rodrigo, 2002). Specifically, (a) we did not produce blocking relative to controls in any moving-beacon group in a Room Test following compound Stage 2 training; (b) it did not matter whether the moving-beacon group was trained in Stage 1 only against the background cues (Experiment 1) or against both landmarks and background cues (Experiment 2); (c) our failure to show blocking cannot be attributed to the beacon in Stage 2 overshadowing the control group learning about the landmarks, because the overshadow-control group trained with only the background cues in Stage 2 was not distinguishable from the control group trained with the background cues and beacon in Stage 2.

A clear difference remained between our experiments and those of Roberts and Pearce (1999); they used a pole beacon connected by a rod to the platform rather than a hanging beacon. The aim of the present experiment was to replicate the procedure of Experi-

ment 1 (training fixed- and moving-beacon groups in Stage 1 and adding a control group in Stage 2), but with a pole beacon. Our pole beacon was made by inverting the hanging beacon used in Experiments 1 and 2 and inserting the end of the black 1.5-cm rod (from which it had been suspended in Experiments 1 and 2) into a slot at the edge of the platform (as in Roberts & Pearce, 1999). Thus, we used the same beacon body in Experiments 1, 2, and 3, placed in the same location and orientation over the platform, and at the same height above the surface of the water. The only difference was the presence of a pole linking it to the platform in Experiment 3.

Pilot work indicated that the rats strongly attended to the pole when they found it, often grabbing it and hanging on during several trials before they began climbing onto the platform. Given this level of focus, it seemed that the pole beacon might well draw attention away from background cues in Stage 1 training and away from landmarks and background cues in Stage 2. Such a strong shift in attention relative to Experiments 1 and 2 makes it more likely to find cue competition in the Room Test for the moving beacon group and should decrease or eliminate facilitation for the fixed beacon group

Method

Twenty-seven naive male Sprague–Dawley rats (*Rattus norvegicus*) were divided into three groups of 9: the fixed-pole-beacon, moving-pole-beacon, and control groups. One rat was eliminated from the control group before the Room Test because of high variability of behavior from one trial to the next within each session. During Stage 1, the moving-pole-beacon group received eight sessions of three trials each, with the location of the predictive pole beacon and the location of the platform changed randomly with respect to the background cues. The fixed-pole-beacon group received the same treatment, except that the location of the predictive pole beacon and the location of the platform were fixed with respect to the background cues. Then, during the 6 days of Stage 2, the location of the beacon and the location of the platform were fixed with respect to all landmarks and background cues for all groups. The Room Test was administered on a fourth trial added on the final day of Stage 2. Following a retraining day and an additional trial, we gave the Preference Test, pitting against each other the platform locations predicted by the beacon, landmarks, and background cues. Note that we used a hanging beacon in this test to keep the rats from clinging to the pole during the whole trial. This should allow a better assessment of the degree of spatial learning related to landmarks and background cues. See the General Method section for other details.

Results

Acquisition. Figure 5 shows the latency to find the platform averaged over three daily trials across 2-day blocks during Stage 1 for the fixed- and moving-pole-beacon groups and during Stage 2 (compound training) for both the pole-beacon and control groups. Repeated measures ANOVAs applied across 2-day blocks of latencies showed significant acquisition effects in both Stages 1 and 2, $F(3, 48) = 133.0$ and $F(2, 46) = 62.1$, respectively. Stage 2 also showed better performance by the pole-beacon groups, $F(2, 23) = 44.1$, and a Groups × Blocks interaction, $F(4, 46) = 42.1$, that was due to the marked improvement of latency scores in the control group. Tukey's tests showed no difference among the pole-beacon groups and the control group during the last block of Stage 2.

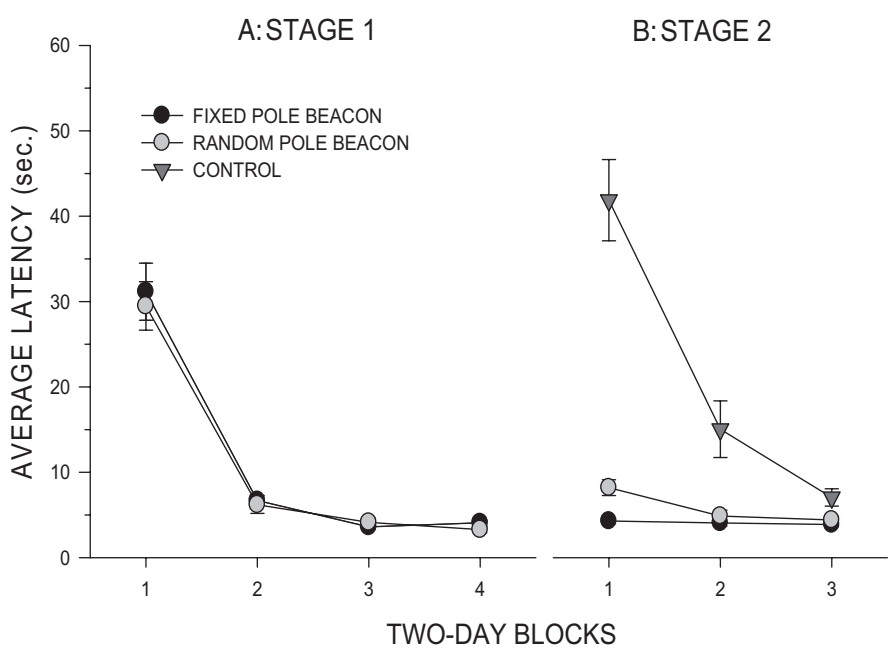

Figure 5. A: Latency (in seconds) averaged over three daily trials and 2-day blocks for the fixed-pole-beacon and moving-pole-beacon groups to find the submerged platform during Stage 1 training. B: Latency in seconds averaged over three daily trials and 2-day blocks for the fixed-pole-beacon group, the moving-pole-beacon group, and the control group to find the submerged platform during Stage 2 training.

Room Test. Figure 6A shows the proportion of time spent in the platform quadrant predicted by the landmarks for the moving-pole-beacon, fixed-pole-beacon, and control groups during the Room Test in the absence of the beacon and platform. The dashed line at .25 represents the chance level for proportion of time spent in a quadrant, assuming equal access to each quadrant. An ANOVA on proportion of time spent in the predicted platform quadrant with the variables of groups and trial half showed a significant effect for groups, $F(2, 23) = 3.62$, which Newman–Keul's tests showed was due to the moving-pole-beacon group (.25) showing significant blocking relative to the control group (.34) and the fixed-pole-beacon group (.36), which did not differ.

Figure 6B reveals that the moving-pole-beacon group also showed longer average latencies to cross the platform location than did the control and fixed-pole-beacon groups, although this difference did not reach significance, $F(2, 23) = 2.42$. A similar tendency was shown for frequency of crossing the platform location. It is worth noting that Roberts and Pearce (1999) also did not show significant latency differences between the moving-pole-beacon and control groups. Finally, an ANOVA on proportion of time in the center half of the pool (Table 1, Experiment 3) with the variables of groups and trial half showed no effect for groups or trial half, $F(2, 23) < 1$ and $F(1, 23) < 1$. An insignificant Groups × Trial Half interaction appeared, $F(2, 23) = 2.69$, influenced by an improvement in proportion of time in the center half of the pool by the moving-pole-beacon group from the first trial half (.55) to the second trial half (.67)

Preference Test. As in the first two experiments, an ANOVA on the proportion of time spent in the quadrants predicted by the different cues showed no effect of groups but showed significant effects of quadrant, $F(2, 44) = 26.9$. Newman–Keul's tests showed greater attention to the platform quadrant predicted by the hanging beacon (.38) than to the quadrants predicted by the landmarks (.22) or the background cues (.19). It is worth noting that this difference would likely have been much larger if we had not used the hanging beacon configuration to prevent the rats from going directly to the pole and clinging there until the test trial was over. Relative to the hanging beacon in Experiment 1, it seems likely that training with the pole beacon interfered with observation of the landmarks in Stage 2 in this experiment. The latency to cross the predicted platform locations also showed an effect of quadrant, $F(2, 44) = 16.0$, with the rats crossing faster in the beacon quadrant than in the landmark or background quadrants, which did not differ. Finally, an ANOVA on proportion of time searching the center half of the pool (Table 1, Experiment 3) showed no groups effect but showed a significant effect of test half, $F(1, 22) = 30.6$, with center search greater during the first 30 s (.70) than the second (.54).

Discussion

The central finding in this experiment was that the proportion of time spent by the moving-pole-beacon group in the platform quadrant during the Room Test showed cue competition relative to the control group, an effect similar to that reported by Roberts and Pearce (1999). The moving-pole-beacon group's cue-competition effect was also significant relative to the performance of the fixed-pole-beacon group, whereas the control and fixed-pole-

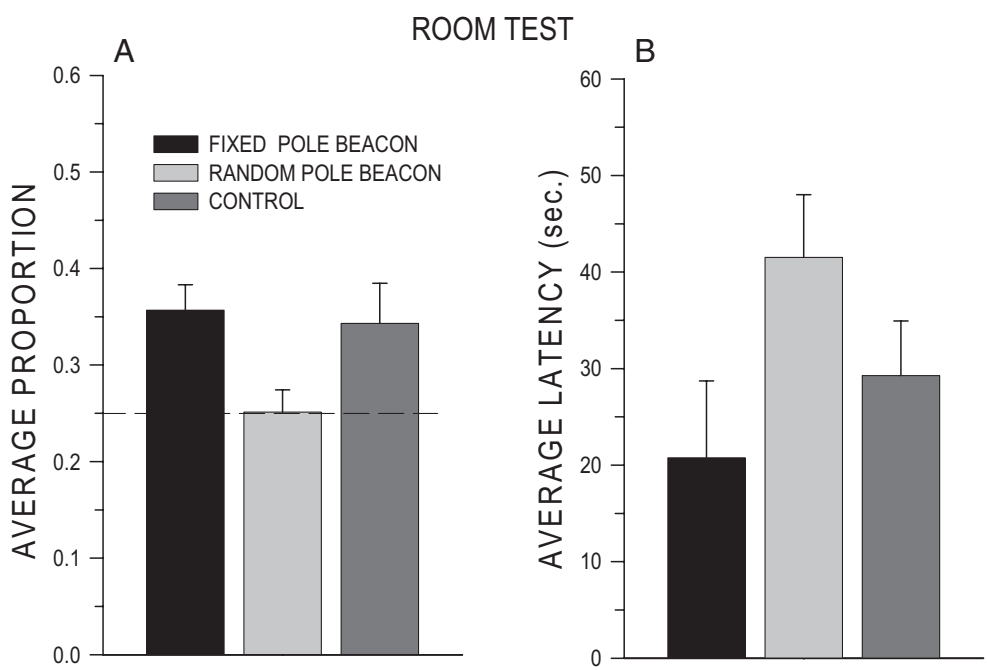

Figure 6. A: Average proportion of time (out of 60 s) spent by the fixed-pole-beacon group, the moving-pole-beacon group, and the control group in the quadrant predicted by the landmarks to contain the submerged platform. The dashed line represents the chance proportion of time spent in each quadrant. B: Average latency (in seconds) for the fixed-pole-beacon group, the moving-pole-beacon group, and the control group to cross the platform location in the quadrant predicted by the landmark.

beacon groups did not differ. A similar, though nonsignificant, pattern was shown in other measures. For example, the moving-pole-beacon group crossed the platform location more slowly and less often than the control group and the fixed-pole-beacon groups.

In contrast to group differences in responding in the Room Test, the Preference Test showed results similar to those of Experiments 1 and 2. It is worth pointing out that the Preference Test used the hanging rather than the pole beacon, because pilot work showed that animals simply clung to the pole for most of the test. As a result, the Preference Test did not accurately measure the attractiveness of the pole beacon. Finally, the trends in latency to cross the platform location and proportion of time spent in the center half of the pool in the Room and Preference Tests are compatible with the conclusion of Experiments 1 and 2: Namely, any beacon training in Stage 1 facilitates searching the center half of the pool in subsequent tests, relative to the behavior of a control group.

Experiment 4: Displaced (Hanging) Beacon With Random Background Cues

The primary aim of the final experiment was to explore the generality of the facilitation effects shown in the Experiment 1 Room Test, in which the presence of a stable background cue framework, beginning in Stage 1 training of the fixed-beacon group, appeared to facilitate Stage 2 learning of added, redundant landmarks. As noted earlier, it might be argued that the facilitated Room Test results for the fixed-beacon group in Experiment 1 did not depend on stable background cues facilitating the relation of the landmarks to the platform location in Stage 2, but depended solely on the fixed-beacon animals continuing to use the stable background cue framework learned in Stage 1 to locate the platform in the Room Test. It is important to note that the rest of our data were not consistent with this supposition, and some data were inconsistent with it. For example, in the Preference Test for Experiment 1, the landmarks were significantly more attention getting than the background cues, both according to the proportion of time spent in the platform quadrant predicted by the landmarks relative to the quadrant predicted by the background cues and according to the latency to cross the two predicted platform locations. Still, it would be of interest not only to test the effects of a different type of environmental framework, but to use a framework in Stages 1 and 2 that was not present during the Room Test, thereby ruling out any direct effect of Stage 1 training on the results of the Room Test.

To accomplish these aims, we established a within-pool geometric framework based on a moving displaced beacon suspended from the end of a sturdy and salient strip of unpainted sheet metal that was 10 cm wide × 24 cm long and edged with black tape. The strip of metal was located 23 cm above the surface of the water, was screwed to the top of a wooden brace that fit over the rim of the pool, and could be readily moved to any of four equally spaced locations around the rim (or removed completely). The beacon was similar in shape and appearance to the hanging beacon used in Experiments 1 and 2, although it was approximately 1 cm larger in height and maximum width. The major differences were that the beacon hung from the clearly visible metal strip (10 × 24 cm and 23 cm above the water) and the vertical edge of the triangular pie-slice shape pointed at the submerged platform 20 cm away.

In geometric terms, the suspending flat metal piece created a thick line at right angles to the pool wall, which connected the wall to the beacon and, if visually continued to the opposite side of the pool, passed through the location of the submerged platform and the center of the pool, bisecting its area. From the rat's point of view inside the pool, the sheet metal strip led directly from the wall to the beacon and pointed at the platform 20 cm away (and the middle of the pool beyond). Thus, after a few trials, the animals could locate the platform by following the metal strip or by going directly to the beacon and then continuing for 20 cm past its point toward the middle of the pool. Soon, many rats went relatively directly toward the platform. A critical advantage of using this moving displaced beacon to test the facilitating effects of training with an environmental framework in Stage 1 was that removing the displaced beacon for the Room Test also removed any basis for using an intrapool geometric framework in the Room Test.

Further, in Stage 1, the background cues were made irrelevant by randomly moving the positions of the displaced beacon and platform to one of four locations for each trial (sampling with replacement each day), while the starting location was also randomly and independently moved. In Stage 2, the position of the beacon was fixed for both the moving-displaced-beacon and the control groups. Because of the displacement of the beacon from the platform and the random location of both with respect to background cues, we anticipated slower learning of the platform location in both Stages 1 and 2, so we made Stages 1 and 2 both 12 days. Finally, to control for possible effects of overlearning in the moving-displaced-beacon group or the control group, and to investigate acquisition processes for both groups, we ran two Room Test trials, one after the last trial on Day 6 of Stage 2 and the second after the last trial of Day 12 of Stage 2. We also looked for and did not observe obvious search strategies like swimming in a circle at the distance of platforms from the pool walls.

Method

Eighteen naive male Sprague–Dawley Norway rats (*Rattus norvegicus*) were divided into two groups of 9: the moving-displaced-beacon group and control group. During Stage 1 beacon training, the animals were trained against the background cues by randomly rotating the beacon and platform together (and rotating the start location independently) on each trial. Both Stage 1 beacon training and Stage 2 compound training were run for 12 days. A Room Test was given at the end of both Days 6 and 12 of Stage 2. A Preference Test was given after the second Room Test following the usual procedure. See the General Method section for other details.

Results

Acquisition. Figure 7 shows the latency (averaged over three daily trials by 2-day training blocks) to find the platform during Stage 1 training for the moving-displaced-beacon group and during Stage 2 training for the beacon and control groups. Repeated measures ANOVAs applied to the 2-day blocks of latencies showed significant acquisition effects in both Stages 1 and 2, $F(5, 35) = 13.6$ and $F(5, 75) = 28.5$. Stage 2 also showed better performance by the beacon group, $F(1, 15) = 5.2$, and a Group × Day Blocks interaction, $F(5, 75) = 13.8$. The interaction was

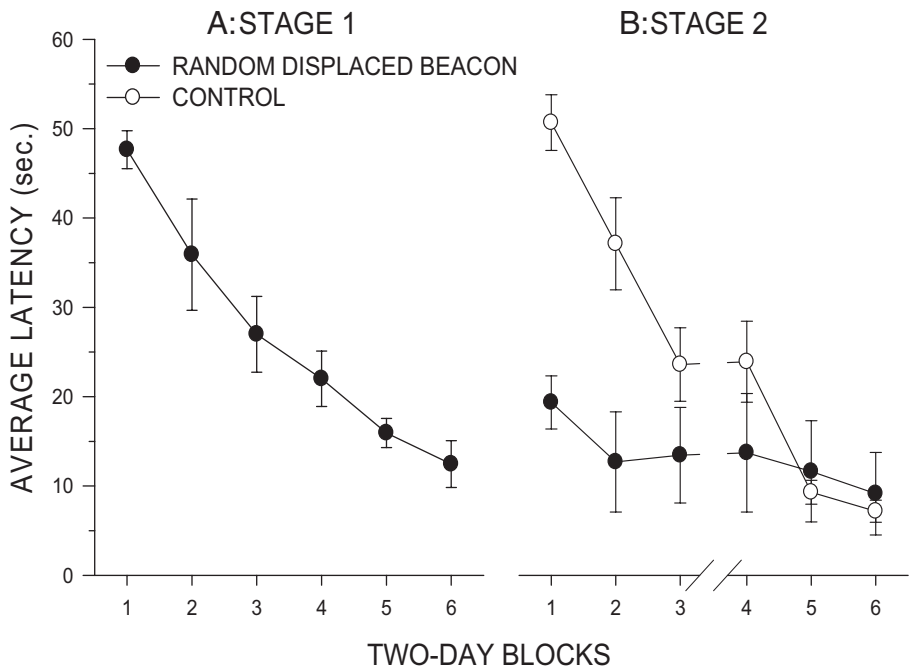

Figure 7. A: Latency (in seconds) averaged over three daily trials and 2-day blocks for the moving-displaced-beacon group to find the submerged platform during Stage 1 training. B: Latency (in seconds) averaged over three daily trials and 2-day blocks for the moving-displaced-beacon group and the control group to find the submerged platform during Stage 2 training. The break in the abscissa indicates a Room Test was run as an added fourth trial following 6 days (three 2-day blocks) of training.

caused by the marked improvement of latency scores by the control group. Tukey's tests showed no difference between the two groups during the last two blocks of Stage 2 training.

Room Tests. As expected on the hypothesis that the rats would develop a within-pool framework that promoted learning the location of the platform relative to the beacon in Stage 1 and relative to the landmarks in Stage 2, Figure 8 showed facilitation of proportion of time spent in the platform quadrant by the moving-displaced-beacon group relative to the control group in both Room Test 1 (following Day 6 of Stage 2 training) and Room Test 2 (following Day 12 of Stage 2 training). An ANOVA on proportion of time spent in the platform quadrant for groups by first versus second Room Test by test half showed an overall groups effect, $F(1, 15) = 9.62$, with the moving-displaced-beacon group (.53) greater than the control group (.38). The ANOVA also showed an effect of test half, $F(1, 15) = 5.24$, with the first-half proportion of time in the platform quadrant (.48) exceeding the second-half proportion (.42). There were no interactions.

An ANOVA on the proportion of search time in the center half of the pool (Table 1, Experiment 4) showed a similar main effect of group, $F(1, 15) = 7.64$, with the moving-displaced-beacon group (.81) spending more time overall in the center than the control group (.65). There was no effect of first versus second Room Test, $F(1, 15) < 1$, or test half, $F(1, 15) = 4.43$, although, on average, presence in the center half of the pool was greater during the first 30 s (.77) than during the second 30 s (.69). Figure 8B shows that the latency results in the two Room Tests were less consistent. An overall ANOVA on latency for groups and tests found no groups effect or interaction on latency to cross the platform location predicted by the landmarks. However, there was a significant improvement in latency to cross the platform location for both groups from Room Test 1 to Room Test 2, $F(1, 15) = 11.6$.

Preference Test. The mean proportion of time spent in different platform quadrants in the Preference Test (data not shown) once again revealed no effects of group but showed a marked effect of quadrant, $F(2, 48) = 17.1$. Newman–Keul's tests showed that, as in Experiment 1, the animals preferred the beacon quadrant (.38) and the landmarks quadrant (.29) to the background cue quadrant (.16). The latencies showed similar effects with only a main effect of quadrants, $F(2, 30) = 3.99$, and the slowest latency to cross the platform location was for the background cue quadrant. Finally, the proportion of time spent searching the center half of the pool during the Preference Test (Table 1, Experiment 4) showed no effect of groups or quadrants but showed an effect of trial half, $F(1, 15) = 5.22$, with a larger amount of time spent in the center half of the pool during the first half of the trial (.77) than during the second half (.69).

Discussion

The proportion of time spent in the platform quadrant for the first and second Room Cue Tests showed that the moving-displaced-beacon group was facilitated rather than blocked relative to the control group, an outcome we expected on the basis of the assumption that a within-pool framework created by the geometric characteristics of the circular pool combined with the 25 cm long × 10 cm wide flat metal hanger for the beacon,

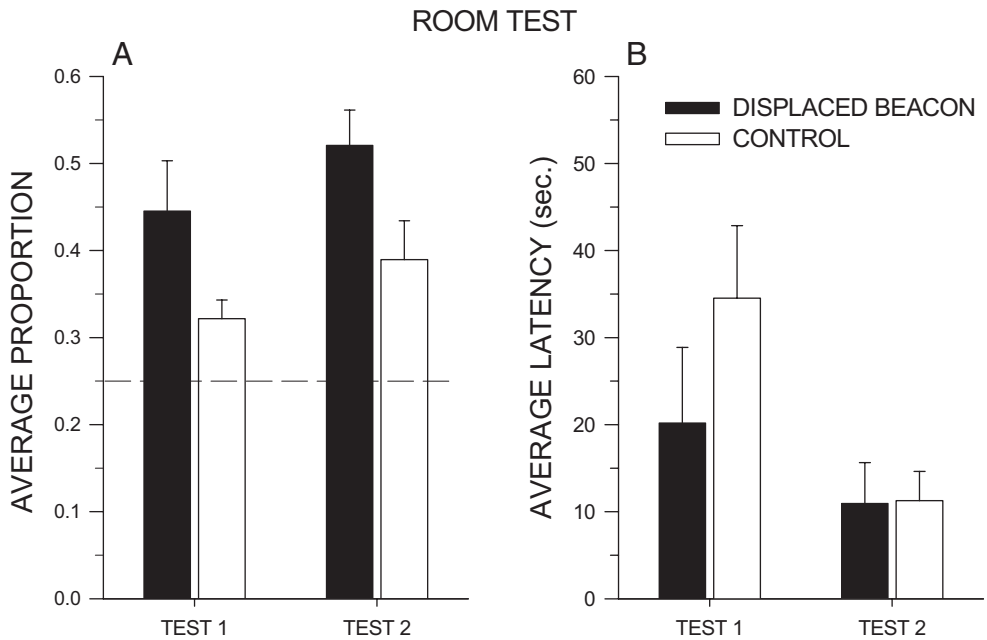

Figure 8. A: Average proportion of time (out of 60 s) spent by the moving-displaced-beacon group and the control group in the quadrant predicted by the landmarks to contain the safety platform. The dashed line represents the chance proportion of time spent in each quadrant. B: Average latency (in seconds) for the moving-displaced-beacon group and the control group to cross the specific platform location in the quadrant predicted by the landmark.

which followed a diameter of the pool. It is important to note that the Room Test facilitation effect was not due directly either to a framework acquired through differential training with the background cues (they were irrelevant in Stage 1) or to the presence of the geometry of the beacon assembly with the pool (it was absent in the Room Test). It appears to have been due to the training of an allocentric framework based on the relation of the platform location to the landmarks. Further, it appears that Stage 1 training with any kind of hanging beacon produces more attention to the landmarks than to the background cues when they predict different locations, an effect not shown with a pole beacon.

With regard to Room Test 1 (Day 6) versus Room Test 2 (Day 12), the additional training before Test 2 appeared to eliminate the Test 1 difference in latency to cross the platform between the moving-displaced-beacon and control groups. However, the additional Stage 2 training did not change the facilitation of time spent in the platform quadrant and in searching the center half of the pool for the displaced-beacon group relative to the control group. In short, it appears that learning a spatial framework relating the beacon and platform in Stage 1, whether it is based on extramaze or intramaze geometry, remains an appropriate explanation for the increased search persistence in the platform quadrant during the Room Test. Training in Stage 1 with a beacon promotes center search, and increasing the amount of training in Stage 2 appears only to eliminate differences in latency to cross the platform location without affecting the proportion of time spent in the platform quadrant.

General Discussion

The present four experiments used a two-stage associative-blocking procedure (see Roberts & Pearce, 1999) to analyze determinants of spatial learning in a water maze. Stage 1 training used several types of beacon (hanging, pole, and displaced) to predict the location of a submerged escape platform. In Experiments 1 and 3, Stage 1 beacon training was fixed or random with respect to background cues and occurred without the four landmarks. In Experiment 2, Stage 1 beacon training was random with respect to both background cues and the four landmarks. In Experiment 4, Stage 1 beacon training was random with respect to (extramaze) background cues but was fixed with respect to a within-pool geometry involving the beacon, and this training occurred without the four landmarks. In all experiments, Stage 2 training occurred with beacon, landmarks, and background cues all predicting the location of the platform for all groups. Spatial learning of the location of the platform was assessed with a subsequent Room Test with only landmarks and background cues present and with a Preference Test in which the beacon and the landmarks were moved with respect to background cues so that each cue type predicted a different platform location.

In the Room Test, we presented experimental and control groups with room cues (background cues and landmarks) in the absence of the beacon and platform. We used standard measures of water-maze learning: (a) proportion of time spent in the platform quadrant predicted by the landmarks and background cues in the absence of the beacon and the platform and (b) latency to cross the location of the platform in that quadrant. We also measured num-

ber of crosses of the platform location, proportion of time spent in the center half of the pool, and the first versus the second 30 s of the test trial. The measure of time spent in the center half of the pool was used to index the extent to which rats knew and persisted in searching for the platform in the most likely section of the pool, and we assumed that both cue competition and locale-learning effects would be strongest in the first 30 s.

Cue Competition Versus Locale Learning (Integration)

Associative theory predicts that Stage 1 training with a beacon predicting the location of the platform should compete with (block) Stage 2 learning about added (redundantly predictive) landmarks and background cues. This prediction rests on the assumption that the near asymptotic Stage 1 training of the beacon as a predictor of the platform location uses up nearly all the reinforcing abilities of the escape platform. As a result, very little reinforcing capacity remains to produce Stage 2 learning of the location of the platform relative to the redundant landmarks and background cues. Further, what little reinforcing capability remained should have been rapidly used up by any attempt to use previously irrelevant background cues or landmarks as predictive cues, as was the case for all moving beacon groups. Thus, from the cue-competition view, blocking should be the dominant outcome of the present experiments. In contrast, a locale-learning view suggests that training with a stable environmental (allocentric) framework in both Stages 1 and 2 (a framework based on either extramaze background cues or intramaze geometry) should help integrate the redundant landmarks added in Stage 2 with an existing allocentric framework, thus facilitating learning the relation of the added landmarks to the location of the platform.

On these grounds, we expected cue competition (relative to a control group) when the beacon in Stage 1 was notably more salient than the landmarks because of its intrinsic properties (especially the pole beacon in Experiment 3) or because it was trained randomly with respect to cues potentially forming an allocentric environmental framework (Experiment 2). On the other hand, we expected facilitation when a stable framework of background cues or of geometry involving the beacon and the walls of the pool was present in both Stages 1 and 2—as in the case of the fixed-hanging-beacon group (fixed with respect to background cues) in Experiment 1 and in the case of the moving-displaced-beacon group (fixed with respect to intrapool geometry but not background cues) in Experiment 4. In those groups mixing elements with opposite effects (the promotion vs. the destabilization of allocentric environmental frameworks), we expected they would tend to cancel each other and produce no effect relative to the control (e.g., the random-beacon group in Experiment 1 and the fixed-pole-beacon group in Experiment 3).

In general, the results followed predictions based on the presence of two processes: the process of cue competition (predicted by associative theories) and the process of cue integration (predicted by locale learning). The Room Test showed significant cue competition in learning the platform location relative to the Stage 2 landmarks only when the rats were trained in Stage 1 with a moving pole beacon and against an environmental framework (Experiment 3). This beacon was highly salient because of its physical proximity to the platform, its palpable attachment to the submerged platform by a metal rod, and its random training with respect to background cues. In contrast, groups with a hanging beacon and involvement with an allocentric environmental framework (the fixed-beacon group in Experiment 1 and the moving-displaced-beacon group in Experiment 4) showed facilitation relative to control groups. The remaining three beacon groups scattered through these experiments were trained in Stage 1 with one characteristic that promoted cue interference and another characteristic that promoted locale learning (the moving-hanging-beacon groups in Experiments 1 and 2 and the fixed-pole-beacon group in Experiment 3). As would be expected from a relative balance between opposing tendencies, these groups did not differ from control groups in proportion of time spent in the platform quadrant and latency to cross the platform location in the Room Test.

In summary, we obtained cue competition in learning the relation of the (redundant) Stage 2 landmarks to the platform location when we used a markedly attention-getting pole beacon trained to produce irrelevant background cues in Stage 1. We obtained facilitation of learning the relation of Stage 2 landmarks to the platform location when stable predictive background cues or within-pool geometry persisted into Stage 2. Simply fixing or randomizing the beacon with respect to the landmarks in Stage 1 was not the key to producing either facilitation or cue-competition effects; the key was an interaction of the type of beacon with fixed or random training and the presence versus absence of an effective allocentric environmental framework.

Additional Measures and Tests

We hoped to clarify further determinants of behavior in the water-maze blocking procedure by considering several other measures (latency to cross and number of crosses of the trained platform location, proportion of time spent searching the center half of the pool, and the first vs. the second 30 s of each test trial), and by adding a simultaneous Preference Test that separated the platform locations predicted by the beacon, landmarks, and background cues, we hoped to gain information about the relative control of behavior by each stimulus.

Many of these additional measures produced useful information. For example, in the Experiment 1 Room Test, both the moving- and fixed-beacon groups showed high levels of center-half search and short latencies to cross the platform location, relative to the control group, thus showing that the moving-beacon group also learned at least about the general location of the platform. However, this learning apparently lacked the same level of certainty shown by the fixed-beacon group. Not only did the moving-beacon group show significantly less persistence of searching the platform location in the Room Test, but the subsequent Preference Test showed that the moving-beacon group had fallen to the level of the control group on both latency to cross the platform location and proportion of center-half search. A parallel set of outcomes occurred in the case of the fixed-pole-beacon group in Experiment 3.

Considering all four experiments, we can conclude that all groups receiving training with a proximate beacon in Stage 1, or extensive displaced beacon training in Stage 2, tended to show shorter latencies in crossing the platform location and searching the center half of the pool in the Room Test. However, except for the fixed-(hanging)-beacon group in Experiment 1 and the moving-displaced-beacon group in Experiment 4, these groups did

not exceed the control groups in searching the platform quadrant in the Room Test and did not maintain their improved crossing latency and center-half search in the Preference Test (or in the second Room Test in Experiment 4). The simplest explanation of these effects is that the animals learned a general strategy directing search to the center half of the pool with greater experience in finding the platform in that area but that, without a stable allocentric framework, this strategy did not persist through multiple tests.

Finally, use of the Preference Test to compare the relative strength of attention to the platform quadrants predicted by the beacon, landmarks, and background cues was, at best, a limited success because of the overwhelming attractiveness of the beacon. Even the unlearned attractiveness of a hanging beacon never seen before (shown by the overshadow-control group in Experiment 2) was clearly much stronger than any learned attractiveness of platform locations predicted by landmarks and background cues in the Preference Test. A more effective preference test might be to compare the platform quadrants predicted by the landmarks versus the background cues, but in the absence of the beacon. However, even in the presence of the beacon, it was possible to see that the background cues were not as important as the landmarks in controlling behavior in Experiments 1 and 4, and we were able to discover that with further testing, some center-half and quadrant preference measures weakened.

Reconciling Our Results With Previous Water-Maze Work

Nearly all prior published work with a blocking procedure in the water maze using beacons or highly salient landmarks has reported learned cue-competition effects based on Stage 1 training (e.g., Diez-Chamizo, Blackman, & Thomas, 1985; Roberts & Pearce, 1999; Rodrigo et al., 1997; see also Biegler & Morris, 1999, in a land analogue). Seemingly in contrast, only one of our four experiments showed a blocking outcome, whereas all showed some form of facilitation (a) in proportion of time spent in the quadrant predicted for the platform location, (b) in latency or frequency of crossing the platform location, or (c) in proportion of searching the center half of the pool. Only Stage 1 training with a moving pole beacon produced unalloyed cue competition. Time spent in the center half of the pool showed a comparable decrement for this group. Differences in subjects, pool size, landmarks, and procedural details may have contributed to decreasing the occurrence of learned cue competition (e.g., see Wahlsten et al.'s, 2003, meta-analysis for mouse strain and laboratory differences in water mazes). However, our ability to systematically manipulate cue-competition versus cue-facilitation outcomes in these experiments strongly indicates that the water-maze blocking paradigm engages more than one spatial-learning mechanism.

Our results also appear compatible with the results of a number of recent studies showing that animals can learn the location of safety platforms, using both geometric frameworks and specific landmarks and beacons (see Graham et al., 2006; Hayward et al., 2003; Pearce et al., 2006). For example, Graham et al. (2006) showed that the presence of a proximate color cue on a geometric frame predicting the location of a platform within a water maze facilitated finding the platform in relation to the frame without the color cue. This suggests that the animals integrated information from the color cue and the geometric structure to improve learning the location of the platform relative to the geometry alone. In this context, our results can be seen as supporting the possibility that an environmental framework can facilitate transmission of location information in the opposite direction—from the environmental framework to redundant landmarks.

Our results also are partly compatible with the hypothesis that learned cue competition in the water maze is related to shifts in attentional strategies during conditioning (see Redhead et al., 1997). In Experiment 1, the fixed nature of the background cues with a hanging beacon perhaps drew attention outside the pool. In Experiment 3, the tactile pole beacon likely drew attention to the water surface, thus interfering with attention outside the pool in Stage 2. However, explanations based on simple attention seem incomplete. For example, in Experiment 2, it is not clear why learned inattention to landmarks and background cues did not produce competition for subsequent learning relative to controls. Also, Redhead et al. (1997) argued that an ambiguously predictive beacon in an experiment received more attention, thereby interfering with further learning. Our displaced beacon came closest to being ambiguous in its prediction, but it performed notably better than its control group in the Room Test, presumably because it was part of a geometric framework that in Stage 2 facilitated integrating landmarks with the location of the platform.

Finally, there is a long and rich history of viewing the phenomenon of learned cue competition as a diagnostic characteristic of Pavlovian conditioning, a stance that seems oversimplified here. It may be important to recall that classic temporal conditioning has shown both cue facilitation and competition. For example, although some taste-aversion studies have reported blocking of control by a second cue added to create a compound predicting an emetic US (Gillian & Domjan, 1977; Kalat & Rozin, 1972; Parker, 1986; Revusky, 1971; Willner, 1978), others have shown facilitation (augmentation) in learning the second cue added during compound training (see Batsell & Batson, 1999; Rusiniak, Hankins, Garcia, & Brett, 1979). Particularly when a taste ($A+$), aversively conditioned with an emetic US, is subsequently presented with an odor cue ($AX+$) predicting the same US, avoidance of the odor is facilitated relative to a control group receiving the odor alone paired with the emetic (Batsell, 2000). In the water maze, it appears possible that learned environmental frameworks facilitate both cue competition and integration of multiple predictive cues, and that both these processes are important in accounting for the full range of phenomena in Pavlovian procedures.

Control Groups

Finally, a particularly critical question in associative learning research is whether a control group is adequate to allow the experimenter to distinguish the effects of conditioning procedures. The present collection of experiments has a consistent compound control plus a number of defensible but less orthodox additions; thus, we think the answer here is *yes.* The fundamental issue for any control group is what effect it controls for. In a typical temporal-blocking study, there seem to be two related aims. The first is to avoid effects of overshadowing in the control group that might reduce its performance relative to the experimental group and, therefore, underestimate learned cue competition. The second is to provide the control group with the same level of training as the experimental group to avoid the possibility that relatively incomplete learning by the control group might result in effects

like failure to block. In this research, we attempted to avoid these difficulties: If performance in the control group is too low, then finding learned cue competition is too difficult, and facilitation is too easy. If performance in the control group is too high, then detecting facilitation is difficult, but finding learned cue competition is too easy.

In Experiments 1 (hanging beacon) and 3 (pole beacon), we included the same three groups: the fixed-beacon group, the moving-beacon group, and the compound-control group. This essentially provided us with two control groups in each experiment, the control group and the fixed- or moving-beacon group that we predicted would show no effect. As predicted, Experiment 1 showed facilitation of proportion of time spent in the platform quadrant by the fixed-beacon group relative to both the control group and the moving-beacon group, which did not differ. Experiment 3 showed cue-competition effects on proportion of time spent in the platform quadrant for the moving-beacon group relative to both the control group and the fixed-beacon group, which also did not differ. Finally, the control groups spent the same proportion of time in the platform quadrant in the Room Test. In other words, by simply changing the same beacon body from hanging above the platform to connecting to the platform via a pole, we were able to reverse the performance of the fixed- and moving-beacon groups with respect to each other and with respect to a common control group showing similar performance.

All experiments also provided evidence separating different measures of performance. All groups of animals that received training in Stage 1 tended to show decreased latency and increased frequency of crossing the platform locations relative to the control groups; however, only the predicted groups (the fixed-hanging-beacon group in Experiment 1 and the moving-pole-beacon group in Experiment 3) showed differences from their controls in the proportion of time spent in the platform quadrant in the Room Test. In other words, the type of Stage 1 experience, not the extent, was critical for producing both cue-competition and cue-facilitation effects.

We tested directly for the role of experience in Experiment 4 by imposing two Room Tests in Stage 2 (training with landmarks, background cues, and beacon present), one after Day 6 and a second after Day 12. The Room Test on Day 6 showed expected, experience-based differences of faster latency to cross the platform location and greater proportion of time spent in the center half of pool by the displaced-beacon group than by the control group; however, this difference disappeared by the Day 12 Room Test. If the proportion of time spent in the platform quadrant also had been determined by experience, we would expect a similar pattern of results. Instead, in both the first and second Room Tests, the displaced-beacon group showed a significantly greater proportion of time spent in the platform quadrant than did the control group. Finally, to ensure that our facilitation results in Experiment 1 were not due to overshadowing of the landmarks by the beacon in the compound-control group, Experiment 2 had an overshadow-control group that directly tested for overshadowing in the compound-control group. There was no evidence for it.

In summary, although beacon experience in Stage 1 training did affect the initial latency to cross the platform quadrant and the proportion of center half search in the Room Test, it did not affect either cue competition or facilitation in Stage 2 learning of the relation between added landmarks and the location of the platform. What appeared critical was the nature of the Stage 1 training in relating characteristics of the beacon and surrounding cues to the location of the submerged platform. In Experiment 3, the visual and especially tactile cues of the moving beacon were related to the submerged platform but not (or less so) to the irrelevant background cues. In Experiment 1, Stage 1 training related the visual cues of the hanging beacon and the context of stable background cues to the submerged platform and apparently incorporated the landmarks into this allocentric framework in Stage 2 training. Similarly, in Experiment 4, it appears that Stage 1 training related the intramaze geometry, incorporating the walls of the pool and the beacon and its 10 cm wide suspension piece, to the location of the submerged platform; it also appears that Stage 2 training transferred that relation to the landmarks and perhaps to the background cues.

A reasonable interpretation of the present results is that cue competition and cue facilitation are based on independent processes engaged by a blocking procedure in the water maze. The cue-competition effect depends on the presence of a tactile cue at water level, perhaps combined with a hanging visual cue (see Roberts & Pearce, 1999, Experiment 2). The cue-competition effect can be superseded by cue integration (locale learning) in the presence of a suitable beacon and the context of stable extra- and/or intrapool frameworks. When cues controlling both cue competition and cue facilitation are present in Stage 1 learning, the results appear to be a compromise, although caution in presuming a simple additive model seems appropriate.

Conclusions

Both cue-competition and cue-integration mechanisms appear to influence the results of using a familiar two-stage blocking procedure to study spatial learning in the water maze. Some of these mechanisms appear to compete (cue competition and cue integration), and others may operate in parallel (perhaps center search, latency, and persistence). It appears important to consider the circumstances producing and controlling these processes, their characteristics, and the form(s) of their interaction(s).

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Received July 14, 2006
Revision received February 15, 2007
Accepted February 15, 2007 ■

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