Latent inhibition in a navigation task: Evidence for the use of associative processes in spatial memory

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Rats were trained to find an invisible platform in a Morris water maze. One group was preexposed to the landmarks that subsequently defined the location of the platform while the control group was preexposed to the apparatus, without landmarks. Preexposed rats showed a retarded learning when swimming to the platform. These results provide little support for the notion of a cognitive map and are consistent with an associative analysis.

The water maze (Morris, 1981) provides a navigation task in which rats have to search for an invisible goal by orienting themselves with respect to stimuli that are at some distance from this goal but whose spatial relation with it is known. This navigation strategy has been named *piloting strategy* (Gallistel, 1990) or *locale learning* (O'Keefe & Nadel, 1978). After Tolman's work (1948) several authors have argued that rats use a truly map like representation of their environment when solving this kind of task, but the nature of the processes underlying the construction and uses of this representation remains unsolved.

On the one hand, map theories (e.g. O'keefe & Nadel, 1978) distinguished mapping strategies from taxon strategies, based in associative processes. The cognitive map involves the building of a complete

representation of the environment, in an all-or-none manner in response to novelty, and allows animals to plan routes and short cuts to navigate. Once the map is constructed, it will be updated if any change occurs in the animal's environment. On the contrary, Pavlovian and instrumental conditioning –the taxon strategies– are believed to be incremental, to have a slower acquisition, and to need standard reinforcement conditions (O'Keefe & Nadel, 1978; Nadel, 1992). On the other hand, some authors have pointed to the possibility of associative processes being involved in spatial learning, thus suggesting that learning to locate an invisible goal could be ruled by principles similar to those governing Pavlovian conditioning (e.g. Whishaw, 1991).

Morris (1981) suggested that if spatial navigation depends on associative learning processes common to those studied in Pavlovian conditioning experiments, then phenomena routinely found in such experiments should be readily demonstrable in spatial learning. Recently, some studies in the water maze have demonstrated that some of these effects, such as overshadowing and blocking, can also be observed in the spatial domain, confirming the suggestion that spatial learning in the swimming pool is governed by associative principles similar to those of classical conditioning (Redhead, Roberts, Good & Pearce, 1997; Rodrigo, Chamizo, McLaren & Mackintosh, 1997; Roberts & Pearce, 1999; Sánchez-Moreno, Rodrigo, Chamizo & Mackintosh, 1999).

The purpose of the present work is to assess how preexposure to the experimental environment can affect subsequent learning of a navigation task. Cognitive map theory and the associative framework make different predictions about how preexposure should affect learning to locate an invisible goal. According to the cognitive map theory (O'Keefe & Nadel, 1978; Nadel, 1992) prior exposure to the environment could be expected to benefit subsequent performance in locale learning, by ensuring that an accurate map has already been established. However, recent theories about cognitive map acquisition suggest that the construction of a cognitive map depends on rat's motor movements among the landmarks (e.g. Etienne, Maurer & Seguinot, 1996). If that is correct, a rat preexposed in a passive way to some landmarks would not show benefits on subsequent learning of a spatial task, but it certainly will not show an impairment of this learning.

On the other hand, it is well known that preexposure to a stimulus that is to serve as a conditioned stimulus (CS) in a Pavlovian paradigm typically retards subsequent learning (Lubow, 1989). This is the phenomenon of latent inhibition, often attributed to a decline in the salience of a stimulus produced by preexposure (Mackintosh, 1983). Applying standard associative theory to the swimming pool task, one could argue that, if spatial stimuli behave like other simple stimuli, preexposure to the array of cues surrounding the pool could be expected to produce latent inhibition, and make harder to learn the location of the invisible platform.

Nevertheless, changes in the associability of the CS are not the unique explanation proposed to account for the retarded conditioning typically observed after preexposure. Latent inhibition has also been described as a

consequence of interference between different memory stores – interference between what is learned during preexposure and what is learned during subsequent conditioning (e.g. Bouton, 1993; Aguado, Symmonds and Hall, 1994). Placing a rat in the pool during preexposure might have the effect of teaching it about a place or places of safety; so at the outset of testing it would prefer to search in these regions to find the platform. That could enhance subsequent performance when the rat is asked to swim to a platform located in the same place of preexposure. On the other hand, if the platform is located in a different area during the training, we can expect that the knowledge of a previous safe place would interfere with the learning of the new location, and thus result in a retarded learning.

Some works pointed to the fact that a brief –passive– exposure to the right location of the invisible platform in a Morris swimming pool enhances immediate subsequent performance when swimming to the platform (Sutherland & Linggard, 1982; Keith & McVetty, 1988; Whishaw, 1991). In a recent work, Pearce, Roberts, Redhead and Prados (1999) preexposed rats on a small platform in one quadrant of the pool before training them to swim toward the platform located in a new quadrant. The interference theory outlined above predicts that the learning of the location of the platform during preexposure would interfere with the learning of the new location during the swimming training, thus producing a retarded acquisition. However, Pearce et al. found the opposite result, that is, rats preexposed to the room cues from a single place were faster learning the new location of the invisible platform than control animals that were not preexposed to the room cues. Although this result cannot be accommodated by the interference view of latent inhibition, it could be well explained by the cognitive map theory.

Using a rather different preexposure procedure, Prados, Chamizo and Mackintosh (1999) found that exposure from a single place to the landmarks surrounding a swimming pool can either result in a facilitated or a retarded learning. Locating the invisible platform in our experiments requires the presence of at least two landmarks (Prados & Trobalon, 1998; Rodrigo et al., 1997), the inference being that rats use configurations of two or more landmarks to locate the platform. Therefore, anything that reduces the associability of these configural cues is expected to impair subsequent learning of a navigation task, whereas a treatment that increases discriminability between the configurations is supposed to facilitate it. Prados, Chamizo and Mackintosh (1999) assumed that the mere exposure to the spatial cues should reduce their associability. In their experiments, rats were trained to swim toward an invisible platform defined by four landmarks (A, B, C and D) after been preexposed to these landmarks in pairs (AB, BC, CD and DA) or to the individual landmarks (A, B, C and D). Preexposure to the pairs of landmarks, i.e. to the relevant configural cues, retarded subsequent learning, whereas preexposure to the individual landmarks facilitated it. Prados et al. suggested that the loss of associability of the preexposed configurations of landmarks was responsible for the retarded effect observed after preexposure to pairs of landmarks. Otherwise, loss of associability of the elements common to different configurations, i.e. the individual landmarks, was

supposed to increase the discriminability of the configural cues, thus facilitating subsequent learning.

The present experiment was designed to evaluate how preexposure from different locations inside a water maze could affect subsequent learning locating the invisible platform. Two groups of rats were trained to find an invisible platform defined by four landmarks in a swimming pool. The experimental group was given passive preexposure, from many points inside the pool, to the four landmarks, whereas a control group was preexposed to the apparatus without landmarks. Cognitive map theory predicts that the preexposed rats will learn faster the spatial task than the control nonpreexposed rats. If we assume that passive exposure to the landmarks prevents animals from building a cognitive map, then we can expect not to find differences between the two groups. On the contrary, if spatial stimuli are subject to latent inhibition, as could be expected from an associative view of spatial learning, animals in the preexposed group might learn slower the location of the invisible platform than animals in the control group.

METHOD

Subjects. Twelve Long Evans rats, 4 males and 8 females, between 3 and 4 months old, and experimentally naive, were housed in pairs on ad-lib food and water. They were subjected to a 12-hour light cycle (0800-2000), and the experiment was carried out between 1400 and 2000. The animals were divided at random in two groups of six (two males and four females).

Apparatus. The apparatus was a large circular pool, 158 cm in diameter and 65 cm deep. It was filled to a depth of 49 cm with water that was made opaque by adding 750 ml of polystyrene latex, a non-toxic substance that does not spoil. A constant temperature of $21\pm1°$ C was maintained. The pool was situated in the middle of a large room, mounted on a wooden platform 43 cm above the floor. A circular platform, 11 cm in diameter and made of transparent Perspex, was mounted on a rod and base, and could be placed in one quadrant of the pool, 38 cm from the side, with its top 1 cm below the surface of the water. Also, a saved aluminium compartment was used for preexposure. It was 10x15 cm on its base, with a 4-cm height wall, and could be placed in the pool over the water level. Thick black curtains reaching from ceiling to floor and forming a circular enclosure 240-cm in diameter surrounded the pool. A closed circuit video camera with a wide-angle lens was mounted 175 cm above the centre of the pool in a black false ceiling, and its picture was relayed to recording equipment in an adjacent room.

The four landmarks used in the present Experiment were as follows: A, a 40-W light placed inside a white plastic inverted cone 11 cm in height and 13 cm in diameter at the base; B, a plastic beach ball 30 cm in diameter with alternate blue-white, yellow-white, and orange-white vertical segments; C, an intermittent 1-W light flashing on and off at a frequency of 60-80 times per minute; D, a green plastic plant, approximately 35 cm in diameter and 30 cm

in height. The landmarks could be suspended from the ceiling, 35 cm above the surface of the water and with their mid-line directly above the wall of the pool. The location of the invisible platform was always in the centre of the quadrant between C and D (see figure 1). The entire false ceiling, with these landmarks suspended, could be rotated from trial to trial, as well as the platform.
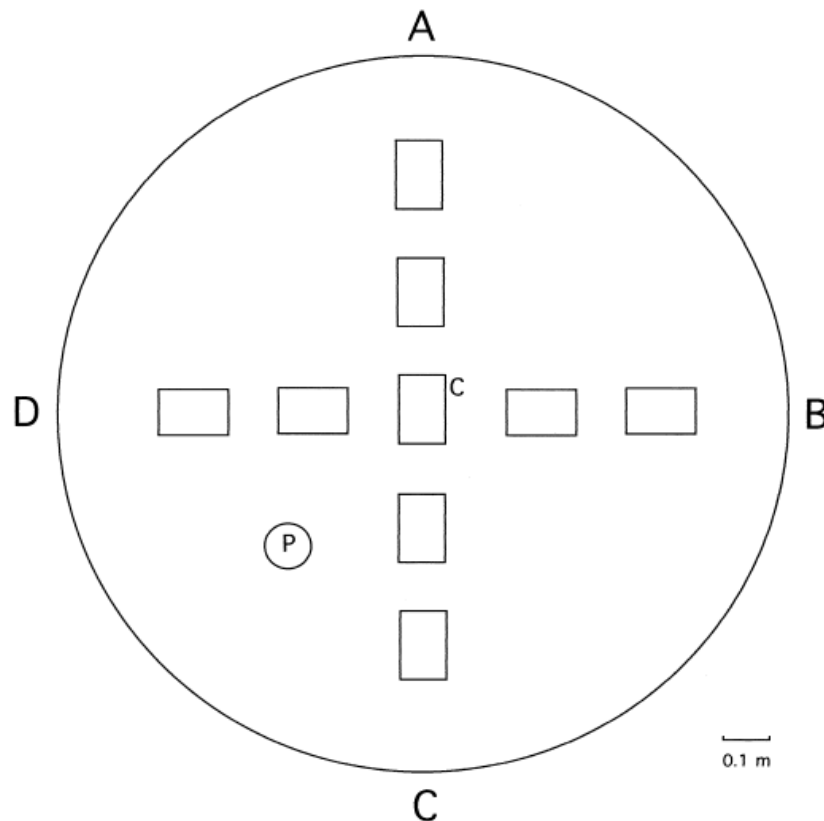
Figure 1. Schematic plan of the pool with the landmarks, the nine possible locations of the preexposure compartment (C) and the invisible platform (P).

Procedure. There were three phases in the present experiment: pretraining, preexposure and escape training.

The pretraining phase lasted three days at a rate of two trials per day. A pretraining trial consisted of placing the rat into the pool, without landmarks but with the platform present. The rat was given 120 s to find the platform, where it was allowed to stay for 60 s. If it had not found the platform within 120 s it was picked up, placed on it, and left there for 60 s. The platform was moved from one trial to the next, and the rat was placed in the pool in a

different location on each trial (at one of the 4 points, A, B, C and D, in figure 1) equally often as far as possible on the same or opposite side of the pool from the platform and with the platform to the right and to the left of where the rat was placed.

The preexposure phase lasted 8 days, at a rate of 8 trials per day. Preexposure trials involved placing the animal on the preexposure compartment for 1 min. This compartment was moved from one trial to the next (there were nine possible locations, see Figure 1), and the set of landmarks was rotated 90° between trials. Therefore, in each trial the animal was in a different part of the experimental environment. Animals in Preexposed group were preexposed always in the presence of the four landmarks while animals in Control group were preexposed only to the pool, without landmarks.

The procedure for escape training was exactly the same as for pretraining, except that four landmarks were always present and that the rats were given only 60 s to find the platform. This phase lasted 7 days, and there were four escape trials per day, with an average inter-trial (ITI) of 15-20 min. The landmarks and platform were rotated 90° anticlockwise between trials to insure that there were no other static rooms' cues affecting the performance of the rats. On each block of four trials the rat was placed in the pool twice at A and twice at B. The time spent by the rats in finding the platform (latency of escape) was recorded.

During the training phase, the animals received one test trial in days 2, 3, 5 and 7, after the four escape training trials. A test trial consisted of placing the rat in the pool, with landmarks present but without the platform, and leaving it there for 120 s. For purposes of recording the rat's behaviour, the pool was divided into four quadrants: the platform quadrant PT, between the landmarks C and D, the left quadrant LE, between A and D, the right quadrant RI, between B and C and the opposite quadrant OP, between A and B. The amount of time the rat spent in each quadrant was recorded.

RESULTS

All the animals found the platform on days 2 and 3 of pretraining within the 120-s time limit. An ANOVA was performed on the latency of escape with groups and pretraining trials as factors. The analysis revealed that the trials factor was significant, $F(5,50)=7.49$, $p<0.01$, MSe=1154,35, but there were no differences between groups, $F<1$, MSe=2064,32, and the interaction groups x trials was not significant, $F<1$, MSe=1154,35.

Figure 2 shows the mean escape latency in the escape training phase. Experimental animals in group Preexposed were slower to find the platform than controls. An ANOVA with groups and blocks of four trials as factors, confirmed that there were significant differences between groups, $F(1,10)=5.12$, $p<0.05$, MSe=49,68, and was significant the factor blocks of four trials $F(6,60)=4.27$, $p<0.01$, MSe=63,68. The interaction groups x blocks was not significant, $F(6,60)=1.03$, MSe=63,68.
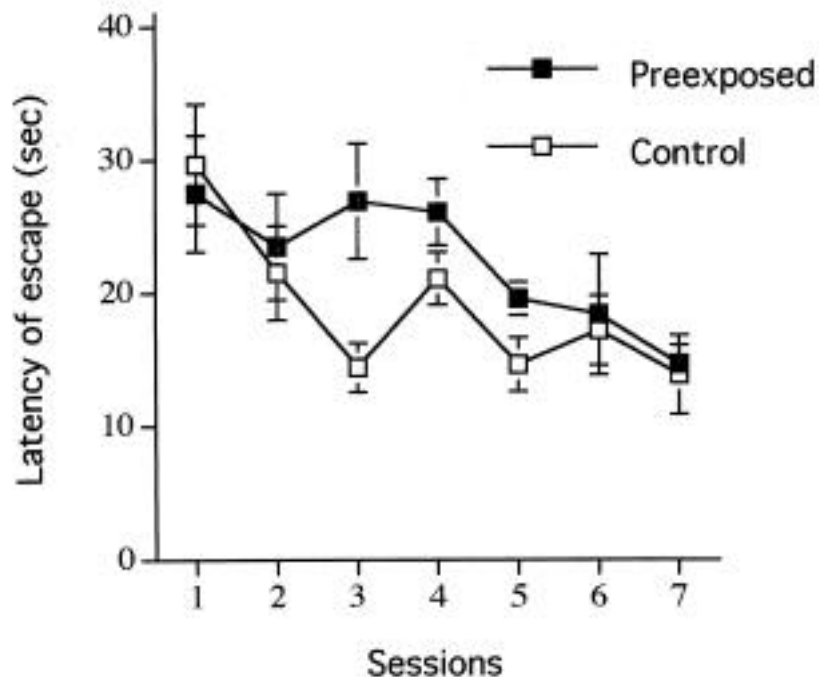
Figure 2. Mean latency to find the platform in the seven training sessions by the groups Preexposed and Control.

Figure 3 shows the mean percentage of time spent by the animals in groups Preexposed and Control in quadrants PT and the other three (RI-LE-OP) on two blocks of two test trials. A three-way analysis of variance, ANOVA, with the factors of group (Preexposed and Control), blocks of test and quadrant (PT and RI-LE-OP), revealed a significant groups x blocks interaction, $F(1,10)=5.00$, $p<0.05$, MSe=3,42, and a significant groups x blocks x quadrant three-way interaction, $F(1,10)=5.00$, $p<0.05$, MSe=13,71. There was a significant effect of quadrant, $F(1,10)=8,69$, $p<0.05$, MSe=31,52, but the effects of group, $F(1,10)=1,35$, MSe=7,87, block, $F(1,10)=3,53$, MSe=3,42 and the remaining interactions (groups x quadrant, $F(1,10)=1,35$, MSe=31,52, blocks x quadrant, $F(1,10)=3,52$, MSe=13,71, were all not significant.

The analysis of the groups x blocks interaction (simple main effects) revealed that differences existed between groups in Block 1, $F(1,10)=14.64$, $p<0.01$, MSe=1,87, but not in Block 2, $F<1$, MSe=9,42. Also there were differences between the two blocks in Preexposed group, $F(1,10)=8.46$, $p<0.05$, MSe=3,42, but not in the control group, $F<1$, MSe=3,42.

Additional analyses were carried out to study thoroughly the three-way interaction groups x blocks x quadrants of test trials. An ANOVA of the percentage of time spent by the animals in the Block 1 of tests, with groups

and quadrants (PT and RI-LE-OP) as factors, showed differences between groups, $F(1,10)=14.64$, $p<0.01$, MSe=1,87, been significant the difference between the quadrants, $F(1,10)=6.15$, $p<0.05$, MSe=7,51, and the interaction group x quadrants $F(1,10)=14.64$, $p<0.01$, MSe=7,51. The analysis of this interaction (simple main effects) showed that animals in Control group spent more time in the PT quadrant than the animals in the Preexposed group, $F(1,10)=14,63$, $p<0.01$, MSe=8,44, and that the group Preexposed spent more time in the areas RI-LE-OP than the Control group, $F(1,10)=14,64$, $p<0.01$, MSe=0.93. Moreover, animals in the Preexposed group spent the same time in the four quadrants, $F<1$, MSe=7,51, while rats in Control group spent more time in the PT quadrant than in the other three (RI-LE-OP), $F(1,10)=19,87$, $p<0.01$, MSe=7,51. The same analysis in Block 2 revealed no differences between groups, $F<1$, MSe=9,42, been significant the difference between the quadrants -all the animals spent more time in the PT quadrant than in the other three, $F(1,10)=7.33$, $p<0.05$, MSe=7,72. The interaction groups x quadrants was not significant $F<1$, MSe=37,72.
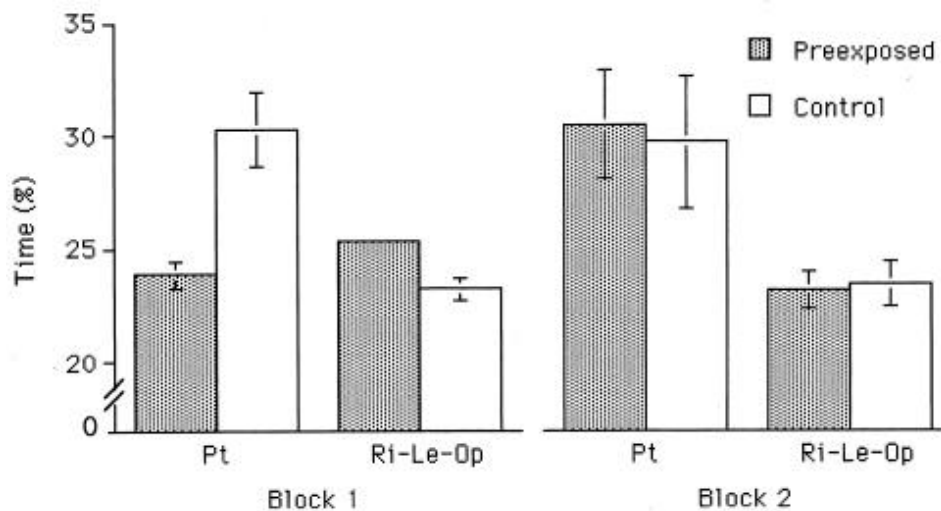
Figure 3. Mean percentage of time spent by the groups Preexposed and Control in the PT quadrant and the other three (RI-LE-OP) in the two blocks of test trials.

DISCUSSION

The present experiment showed a retarded learning of a spatial task by previous exposure to the experimental environment: preexposed rats were slower finding the invisible platform than control animals. Also, in test trials, preexposed animals' performance was initially at random level while control animals showed a significant preference for the PT quadrant, but later on all the animals performed well.

Cognitive map theories (O'Keefe & Nadel, 1978; Nadel, 1992; Etienne et al., 1996) assume that prior exposure to the environment should benefit subsequent performance in locale learning, by ensuring that an accurate map has already been established. This map is consider to be a powerful and flexible representation of the environment, and should be updated whenever any changes –new landmarks or goals– are detected by the animal in the environment. Even if the ideal conditions to build the map are not provided, these theories would never expect preexposure to impair subsequent learning.

The associative view which assumes that spatial cues surrounding the pool are subject to latent inhibition, could provide a simple explanation for the present results. Latent inhibition is normally regarded as being consequence of a loss of salience by the preexposed cues (e.g. Pearce & Hall, 1980; McLaren, Kaye and Mackintosh, 1989). It has been suggested that the mere exposure to the array of landmarks surrounding the pool could reduce their associability, making harder to learn where the platform is during the escape training (Prados, Chamizo & Mackintosh, 1999). This associative view implies that preexposure from one single place as well as from many different locations from the pool should disrupt subsequent learning. Such a prediction contrasts with the known latent learning observed when rats are given brief preexposure to the room cues from the right location of the invisible platform immediately before swimming to it (Sutherland & Linggard, 1982; Keith & McVetty, 1988; Whishaw, 1991; see also Rodrigo et al., 1997). We might deduce that latent inhibition of the spatial cues requires a long preexposure phase. However, Pearce et al. (1999) found the opposite result: rats that were given long preexposure (36 min) from a single place, showed a facilitated learning when required to swim toward the invisible platform located in a new position.

An alternative explanation would take into account the relevance of the preexposed cues to find the platform. Prados, Redhead and Pearce (1999) proposed that the different effects of preexposure in the swimming pool place task could be understood in terms of the theory of attention proposed by Sutherland and Mackintosh (1971, see also Mackintosh, 1975). According to these authors, the associability of a Pavlovian CS will be high when it is relevant to the occurrence of a US, and low when it is irrelevant to the delivery of a US. Conceivably, a similar principle governs the associability of the configuration of landmarks that surround the water maze. Therefore, when preexposure involves placing the rat at different locations in the pool the landmarks are irrelevant to where the platform can be found and this would result in a loss of associability. But when the rat is kept in the same place throughout the preexposure phase, the room cues are relevant to find the platform and their associability would be increased. This account is able to explain the latent inhibition effect observed in the present experiment after preexposure to the spatial cues from many points inside the pool, as well as the facilitated learning frequently reported when preexposure takes place from a single location (Pearce et al., 1999; Sutherland & Linggard, 1982; Keith & McVetty, 1989; Whishaw, 1991).

This attentional account is consistent with the original demonstration of latent inhibition and perceptual learning reported by Prados, Chamizo and Mackintosh (1999) after preexposure to four landmarks from the centre of the pool. In the experiments in which a retarded effect was found, rats were given preexposure to pairs of adjacent landmarks, in such a way that in each preexposure trial the animals could see a different pair. That is to say that on the first preexposure trial of a session, rats may have seen, for example, the pair AB, with A to the left of B; on the next trial they may have seen BC, with B to the left of C, and so forth. As a result of this treatment, therefore, the spatial relationship between each landmark and the platform varied from trial to trial, which might have led to the landmarks being ignored in the test phase. On the other hand, in the experiments in which a facilitated effect was observed, rats were exposed to a single landmark always placed in the centre of the field of view from the observation compartment. Each landmark can therefore be said to have been presented at the same location relative to the platform, and this stable relationship might have led to attention to the landmarks been enhanced for the test stage.

However, the facilitator effect reported by Prados, Chamizo and Mackintosh (1999), was observed only under a restricted set of conditions –when all the four landmarks shared an explicit common element. When rats were given preexposure to simple landmarks without explicit common elements, although these spatial cues were always presented in a stable relationship with the platform, and contrary to what could be expected from the attentional theory, no effect was found. Moreover, in a related study, Prados (1999) found that increasing the amount of preexposure to individual landmarks always presented at the same place related to the animal, far from enhancing subsequent learning retarded it. Alternative explanations, based in the assumption that the mere exposure to the landmarks reduces their associability, or the inference that inhibitory learning takes place when rats are given alternated preexposure to individual landmarks sharing common features, seems more appropriate to account for these results.

We can conclude that most of the preexposure effects reported in the swimming pool place task seems to be influenced by the spatial relationship between the platform on which the preexposure takes place and the cues surrounding the pool. When this spatial relationship is stable rats learn to attend to the landmarks, whereas when this relation is unstable rats learn to ignore them. However, in the absence of more empirical evidence, this conclusion must remain tentative.

Finally, the present results agree with those of other studies (Redhead et al., 1997; Rodrigo et al., 1997; Prados, Chamizo & Mackintosh 1999; Roberts & Pearce, 1999; Sánchez-Moreno et al., 1999; Prados, Redhead & Pearce, 1999; Pearce et al., 1999) claiming that spatial learning seems to be ruled by principles similar to those governing Pavlovian conditioning.

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