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Spatial Learning: Conditions and Basic Effects

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A growing body of evidence suggests that the spatial and the temporal domains seem to share the same or similar conditions, basic effects, and mechanisms. The blocking, unblocking and overshadowing experiments (and also those of latent inhibition and perceptual learning reviewed by Prados and Redhead in this issue) show that to exclude associative learning as a basic mechanism responsible for spatial learning is quite inappropriate. All these results, especially those obtained with strictly spatial tasks, seem inconsistent with O'Keefe and Nadel's account of true spatial learning or locale learning. Their theory claims that this kind of learning is fundamentally different and develops with total independence from other ways of learning (like classical and instrumental conditioning -taxon learning). In fact, the results reviewed can be explained appealing on to a sophisticated guidance system, like for example the one proposed by Leonard and McNaughton (1990; see also McNaughton and cols, 1996). Such a system would allow that an animal generates new space information: given the distance and address from of A to B and from A to C, being able to infer the distance and the address from B to C, even when C is invisible from B (see Chapuis and Varlet, 1987 -the contribution by McLaren in this issue constitutes a good example of a sophisticated guidance system).

1. Introduction.

Are both the "when to respond" problem and the "where to respond" one governed by the same, general associative laws? Or are they not? To debate the idea of a general learning mechanism is not new. Experiments by Garcia and his colleagues on taste aversion (Garcia, Kimmeldorf and Koelling, 1955; and Garcia and Koelling, 1966) are a good example of this kind of question (Rozin and Kalat, 1971, 1972). When an internal illness is artificially induced in a rat after having eaten or drunk a substance with a novel taste (normally by means of a Lithium Chloride injection) the rat will subsequently avoid eating or drinking a substance with such a taste. This conditioning can happen after a single pairing of the taste and the illness, and even when several hours may elapse between these events. Is taste aversion a

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rat's specific kind of conditioning which adapts it to the demands of its environment? It was argued that because this kind of learning is not arbitrary but instead highly adaptative, this suggested a new learning mechanism, which had very little in common with that responsible for traditional forms of learning, like classical and instrumental conditioning. And the rapidity with which these aversions are learned, provided evidence in favour of such a claim. But later research has demonstrated that taste aversion conditioning is indeed associative learning: practically all the basic phenomena which normally occur when traditional preparations of conditioning are used, are also observed when using a taste aversion procedure (Revusky, 1977). As Dickinson (1980) has indicated, what taste aversion studies have really done is to modify and enrich our conception of the general learning mechanism. Are the present controversies related to spatial learning and navigation a sign that we are facing a similar case? Time will tell. And always we should keep in mind Lloyd Morgan's canon: "in no case may we interpret an action as the outcome of the exercise of a higher psychological faculty, if it can be interpreted as the outcome of one which stands lower in the psychological scale" (cited from Pearce, 1997, p. 15).

2. Spatial learning and navigation

As we have seen in Chapter 1 animals have a varied range of strategies, some innate and others learned, that help them to navigate, and when faced with a specific spatial task, the one they choose will depend both on their sensorial capacities and on the nature of the stimuli that are available. Spatial learning makes us think of Tolman (1948) and maze experiments. How does a rat solve a T-maze problem? (see Figure 1). Usually, food is placed in one of the two goal-boxes (GB+) and not in the other one (GB-), and the subject has to choose between one arm and the other at the choice point. This is a spatial discrimination task, and traditionally it has had two alternative explanations. According to Tolman (1932, 1948), the rat learns to associate the correct goal-box, GB+, with food and the incorrect one, GB-, with its absence, so that after a certain number of trials it chooses the correct goal-box and avoids the incorrect one. On the other hand, according to Hull (1943), what the rat learns is to execute a certain response instead of another at the choice point, because the first one is followed by food while the second one is not. In both cases we say that the animal has been conditioned, although for Tolman it is a case of classical conditioning, "place" conditioning (the rats learn associations between places and rewards), and for Hull it is a case of instrumental conditioning, "response" conditioning (the rats learn associations between responses and rewards).

The most typical way to discover which is the strategy that the rats use in a T-maze consists of rotating the maze 180° (test of the maze in cross form). If the animal has learned the task leaving from start-box 1 (SB-1) in Figure 1, the test trial is carried out from start-box 2 (SB-2) and its performance is registered when choosing a goal-arm at the choice point. Place learning would direct the rat through the maze independently of the turn

response learned, and therefore to the correct goal-box, GB+. On the contrary, response learning would predict that the rat will continue making the same turn that it initially learned, and therefore that it would choose the incorrect goal-arm, GB-. When both goal-arms are identical, the most frequent result has been that when several extra-maze cues or landmarks are present and there is abundant light, place learning prevails (Tolman, Ritchie and Kalish, 1946), while in the absence of landmarks and with little light, response learning prevails (Blodgett and McCutchan, 1948). Other methods have also been used (for example the test of the solar maze), with results generally in favour of place learning (see Tolman et al., 1946).

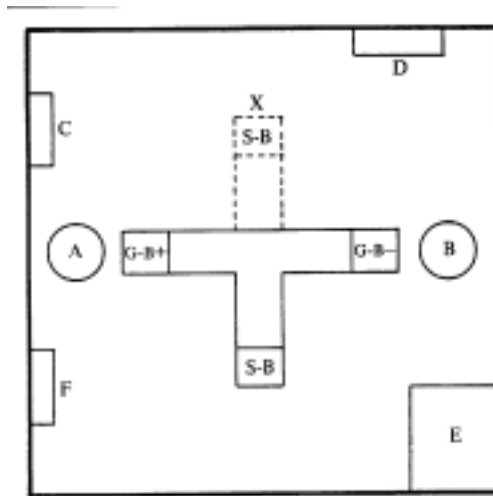


Figure 1. A schematic diagram of a T-maze. S-B = start-box, G-B+ and G-B- the rewarded and unrewarded goal-boxes. A and B, represent distinctive objects immediately adjacent to the goal-boxes, and C, D, E, and F are various landmarks (doors, windows, tables) in the room. The dotted start-box and arm at X represent a new location for the start of a test trial. (After Mackintosh, 1983 –with permission.)

3. The legacy of Tolman

Tolman regarded conditioning as the acquisition of new knowledge about the world, instead of the acquisition of new responses or new reflexes. He considered that as a result of conditioning, animals acquire knowledge about their environment (for example, that a specific stimulus, like a tone, signals food; or that a specific response, like a lever-press, causes food to appear). Thus, the function of conditioning becomes that of allowing animals to discover the causal structure of the world (Tolman and Brunswick, 1935). For Tolman, what a rat learned as it ran through a maze was a map of the spatial relationships among the maze arms, the rewarded goal-arm and diverse landmarks. As Mackintosh indicates (1983), “the translation of this

knowledge into performance cannot simply be a matter of activating a response tendency. It would seem to require some more elaborated and less easily specified processes, including combination with further knowledge about the values assigned to some of the events or places so associated, and some process of inference to produce a decision” (p. 12). Tolman argued that the rats arrived at the correct goal-arm by using a cognitive map of the experimental room. But he never explained the specific properties of the cognitive maps, and consequently his theory lost credibility (O’Keefe and Nadel, 1978). In fact, in an important review of maze learning (Restle, 1957), the conclusion was reached that there was no need to talk of cognitive maps or of qualitative differences between place learning and response learning.

Tolman was also the first author to insist on the importance of making a clear distinction between learning and performance (Tolman, 1932, 1948, 1949). And to such an end he carried out experiments to demonstrate that what an animal had learned could not be shown in its behaviour immediately. The classic experiments were those of “latent learning” (see Tolman and Honzik, 1930). In these experiments hungry rats were allowed to run freely in a complex maze for several trials for a few days. On these trials, food was never present in the maze. Then, food was introduced on a certain day, and the rats showed an abrupt change of behaviour as soon as this happened, running significantly faster than before and making few errors on their way to the goal. Even on the trial immediately after food was introduced the first time, the animals made no more errors than animals that had been rewarded with food from the beginning of training. Therefore, the rats must have learned the correct trajectory to the goal-box during the unrewarded trials, and this learning was behaviourally silent until they had an appropriate incentive. At present, Tolman’s visionary ideas are considered of great value. Nowadays, it is widely accepted that conditioning can be understood as the acquisition of knowledge about relationships among events, and that the best way to consider a behavioural change that an experimenter might register is as an index of that knowledge (Dickinson, 1980; Mackintosh, 1983).

4. The proposal by O’Keefe and Nadel (1978)

We know that rats typically solve maze problems by learning to approach the place where the goal is. But how is this place defined? After many years of silence, O’Keefe and Nadel (1978) resurrected Tolman’s idea of a cognitive map. Two findings were decisive in the elaboration of a new theory. The first was that certain complex cells of the rats’ hippocampus, “place cells”, are activated in a selective way when animals are in specific places in a familiar environment (O’Keefe and Dostrovsky, 1971; O’Keefe and Conway, 1978; O’Keefe and Speakman, 1987). The second was that hippocampal lesions have a profound effect on spatial learning. Animals with hippocampal lesions have no difficulty in navigating toward a goal that they can see, but they are completely disoriented when the goal is hidden (Morris, Garrud, Rawlins and O’Keefe, 1982; Sutherland, Whishaw, and Kolb, 1983; Pearce, Roberts and Good, 1998).

In their very influential book, O'Keefe and Nadel (1978) claimed that rats can learn the correct trajectory to reach a goal in a maze in two ways. The main one, "true spatial learning", they label locale learning (or the "hypothesis of the cognitive map"). A rat solving a problem by locale learning would form a cognitive map of the environment where the maze is located, and of the specific location of the rewarded goal-arm within that environment. A crucial feature of their account was that O'Keefe and Nadel (1978) consider that such a learning is non-associative; that it happens in an all-or-nothing way; and that it implies the formation and readjustment of a complete representation of the environment in response to novelty. They also claimed that this kind of learning is highly flexible, and that the hippocampus is the responsible cerebral structure. The second way to approach a goal they termed guidance learning. Learning by guidance implies approaching one specific cue or set of cues (a particular colour, shape, odor or texture in the rewarded goal arm, for example, or a particular landmark or configuration of landmarks just behind the correct arm). Guidance learning was regarded as one form of taxon learning, the other being orientation learning, which is basically the same as Hull's response learning. Guidance learning is associative and can be regarded as a form of Pavlovian conditioning, that does not depend on the hippocampus. It is also less flexible than true locale learning. These two strategies, locale and guidance, proposed by these authors to solve spatial tasks were traditionally understood as only one form of learning, place learning (Tolman, 1948; Restle, 1957). However, O'Keefe and Nadel emphasize that locale and guidance strategies are two fundamentally different and independent forms of learning, each of them controlled by a different cerebral structure, and that only the taxon strategy, the guidance one, is controlled by associative laws. Are these two ways of learning really different and independent?

5. Spatial and temporal domains: Common basic effects

One way to appeal this question is to consider whether it is possible to find parallels between spatial learning and other forms of learning. I start with an analysis of spatial and non-spatial stimuli. When spatial location is analysed in a manner similar to what is normal with other properties or dimensions of the stimuli (such as wavelength and auditory frequency), the control exerted by the location of stimuli appears to be similar to that exerted by other properties or dimensions of the stimuli. Absolute spatial proximity and both generalization and peak shift effects have been observed with variations in spatial location.

5.1. Absolute spatial proximity between a landmark and a goal.

The effect of absolute temporal proximity of the conditioned stimulus (CS) to the unconditioned stimulus (US) in a Pavlovian preparation is well known (Revusky, 1971). Normally, conditioning improves as the interval between CS and US decreases, although at very short intervals conditioning may be worse (Ost and Lauer, 1965; Schneiderman and Gormezano, 1964). In a parallel

way, it has been found that the control acquired by a single landmark is different depending on its relative distance or its absolute spatial proximity from a goal (Cheng, 1989; Spetch and Wilkie, 1994; Chamizo, in preparation). In this study two groups of rats were trained in a Morris pool to find a hidden platform in the presence of a single landmark. Circular black curtains surrounded the pool, with the single landmark inside this enclosure, so that no other room cues could provide additional information to find the platform. This landmark was hung from a false ceiling and rotated from trial to trial, and the position of the platform also changed on each trial, thus preserving a constant relation between the platform and the landmark.

For one group the position of the landmark was relatively close to the hidden platform (Group Near), while for the second group it was relatively further away from it (Group Far) -see Figure 2. Test trials, without the platform, revealed a difference between the groups. Although a preference for searching in the correct quadrant of the pool was found in both groups, this preference was significantly higher for near rats. Then, in a second experiment, new rats (Group Near), were compared to rats for which the position of the landmark was exactly above the hidden platform, like a beacon (Group Above). Again, a preference for searching in the correct quadrant of the pool was found in both groups, but now this preference was significantly higher for beacon rats. The implication is that the control acquired by a single landmark is different depending on its relative distance from the goal, a hidden platform: Closer landmarks acquire a better control than further away ones - the limiting case being a clearly visible platform (Morris, 1981). There is thus a clear parallelism in comparison with the effect of absolute temporal proximity of the CS to the US in classical conditioning.

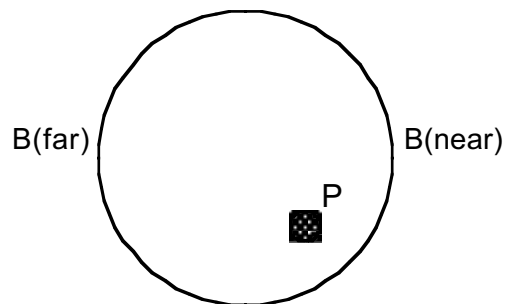


Figure 2. A schematic representation of a pool and two landmarks (B-near, and B-far), as well as the platform. Landmark B could also be above the platform. (After Chamizo, in preparation.)

5.2. Spatial generalization. Stimulus generalization is said to exist whenever the subject responds in a similar way to various stimuli (Pavlov, 1927; Guttman and Kalish, 1956). In the study by Guttman and Kalish (1956), pigeons were trained to peck at a key which was illuminated by a light of a specific wavelength. After training, the animals were tested with a variety of other wavelengths presented on the key. The results showed a gradient of responding as a function of how similar each test stimulus was to the original stimulus. This result is called a stimulus generalization gradient. Spatial generalization gradients have also been found in a touch-screen task with either pigeons or humans as subjects (Spetch, Cheng and McDonald, 1996; Cheng, Spetch and Johnston, 1997; Spetch, Cheng, McDonald, Linkenhoker, Kelly, and Doerkson, 1997). In Experiment 1 of the study by Cheng et al. (1997), pigeons were trained on a fixed-interval schedule for pecking at a computer screen following presentations of a small square in a fixed screen location (S+). Then unrewarded test trials at a range of locations were intermixed to the previous trials. The results showed a gradient of responding as a function of the relative proximity of the test locations to the location of the original stimulus (S+): the pigeons showed higher responding to S+, which decreased symmetrically with distance from S+. The same results were found with human subjects. They showed a Gaussian distribution over a linear scale of space. Similar spatial generalization gradients have also been found with honeybees (Cheng, 1999, 2000), thus demonstrating an important cross-species generality.

5.3. The peak shift effect. In a classical study by Hanson (1959), three groups of pigeons were trained to peck at a key illuminated with light of 550 nm (S+). A control group received no other training, but for two other groups, reinforced trials to S+ alternated with nonreinforced trials to S-, which was either 555 or 590 nm. The results of the control animals showed the expected stimulus generalization gradient around S+. But birds trained on the 550-590 discrimination showed a higher rate of pecking to S+, and surprisingly their rate of responding was even higher to shorter wavelengths—like 540, away from S-. This shift of the peak responding away from the original S+ is called the peak shift phenomenon, and it was even more pronounced in birds trained on the 550-555 nm discrimination. The peak shift effect occurs when working with intradimensional discriminations, and as a function of the similarity between S+ and S-.

Recently Cheng, Spetch and Johnston (1997, Experiments 2, 3, and 4) have reported the peak shift manipulation (training with S+ and S-) in the spatial domain, with pigeons. During training one location (S+) indicated reward on half of the trials, and for the rest of the trials a second location (S-), indicated no reward. Then unrewarded test trials at a range of locations were intermixed to the previous trials. The generalization gradient obtained showed higher responding on the side of S+ away from S-. This effect was stronger when S- was closer to S+. This effect has been called area shift (Rilling, 1977). The results of the experiments by Cheng et al. (1997) showed an exponential gradient over a linear scale of space. This shape was also found

along the orthogonal vertical dimension. As the authors claim, these results clearly parallel the pattern found for similar discrimination training in other dimensions of experience.

6. First tests in favour of O'Keefe and Nadel's proposal

Morris (1981) was the first author to demonstrate that rats could locate an object that they were not able to see, hear, or touch, whenever it maintained a fixed relationship with respect to distal landmarks. In his work he used a circular pool full of opaque water from which the animals could escape by climbing to a platform which was a centimetre below the level of the water. The platform always maintained a constant relationship with the landmarks of the room. The rats, good swimmers but not very fond of water, quickly learned to escape from the water by swimming directly to the platform from different points of the pool. Ingenious additional tests, search tasks, corroborated these data. Morris interpreted his results as showing that the animals learned how to locate the position of the platform being guided by the position that it maintained regarding the context in which the experiment was carried out, the room and the objects that it contained, and he considered that they supported O'Keefe and Nadel's theory of locale learning or cognitive map (1978). However, Morris (1981) also indicated that his results did not offer information regarding the mechanism responsible for the acquisition of such a map. He suggested that one way to address this question would be to see whether phenomena characteristic of classical and instrumental conditioning, such as blocking and latent inhibition, might also be observed in experiments in which rats apparently acquired a spatial map. Well controlled laboratory experiments were clearly needed to solve this puzzle.

7. Evidence against O'Keefe and Nadel (1978) proposal

Does locale learning consist of the conditioning of approach responses to a goal that is defined in terms of the spatial relationship that it maintains regarding a number of landmarks (i.e., an associative point of view) or alternatively, is this a kind of learning different and independent of the traditional ways of learning, as O'Keefe and Nadel claim? It is one thing to show that spatial location can act as a dimension or continuum like other physical dimensions. But the critical question has always been whether knowledge about spatial location is acquired in the same way as knowledge about other relations between events.

7.1. Blocking and overshadowing: rats.

Chamizo, Stereo and Mackintosh (1985) were the first authors to test Morris' proposals (1981) in a series of experiments of blocking and overshadowing. The purpose of Chamizo et al. (1985) study was to check whether locale learning could be blocked (Experiments 1 and 2) and overshadowed (Experiment 3) by guidance learning, and vice-versa. Blocking is observed when prior establishment of one element of a compound cue as a

signal for reinforcement reduces or blocks the amount learned about a second (Kamin, 1969). The term overshadowing refers to the finding that the presence of a second relevant cue will cause animals to learn less about a first than they would have done if trained on the first cue in isolation (Pavlov, 1927; Kamin, 1969). Experiment 1 consisted of four groups of animals, two pre-trained ones (Intra and Extra), and the other two without pretraining (Compound groups). The experiment examined whether prior training with either intra-maze or extra-maze cues alone relevant would block learning about the other class of cue when, in a second phase of the experiment, both sets of cues simultaneously signalled the location of reward. An elevated radial maze, used as a three-arm maze, and a discriminative task were used in this study. One of the arms was used as a start-arm, and the other two as goal-arms. The maze was located in the middle of a big, well illuminated room, that contained many and diverse objects strategically dispersed, landmarks, that made the walls clearly distinctive. The reinforced and non-reinforced arms could be defined in terms of intra-maze stimuli (the floor of one of the arms was covered with black rubber and that of the other with yellow sandpaper), in terms of extra-maze stimuli (the arms could point in different directions: north, north-east, east, south-east, south, south-west, west, and north-west), or these alternatives were defined by both sources of information simultaneously present (the correct arm was covered with black rubber and always pointed to the north-east corner of the room). It was supposed that the rats would learn a guidance strategy when they had to use intra-maze stimuli to find the food, and a locale one when they had to use the landmarks or extra-maze stimuli to find the food. Test results showed an effect of reciprocal blocking: pre-training with intra-maze stimuli blocked conditioning based on extra-maze stimuli, and vice-versa. If food had been found on the basis of intra-maze stimuli in the first phase, the rats did not learn that in the second phase it could also be found on the basis of landmarks or extra-maze cues; if it had first been found on the basis of extra-maze cues, they did not learn that it could now be found by intra-maze cues. (For an additional demonstration of blocking between locale and guidance learning, using a circular pool and rats as subjects, see Redhead, Roberts, Good and Pearce, 1997, Experiment 4). Experiment 2 of this study was carried out to eliminate an alternative explanation of spatial blocking in terms of learned irrelevance (Mackintosh, 1973, Baker and Mackintosh, 1977). The results showed a clear interaction between intra-maze cues and landmarks that could not be attributed to a learned irrelevance explanation (for an additional demonstration to eliminate an explanation of spatial blocking in terms of learned irrelevance, with rats and a circular pool, see the study by Roberts and Pearce, 1999). Finally, Experiment 3 was designed to see whether training with intra- and extra-maze cues simultaneously would overshadow each other. The experiment consisted of four groups of rats, two trained with intra- and extra-maze cues relevant, and the other two with only one of these cues relevant, one intra and the second one extra. It was found that the extra-maze stimuli could overshadow the intra-maze ones, but not vice-versa. However, a subsequent study (March,

Chamizo and Mackintosh, 1992) provided a demonstration of reciprocal overshadowing between intra- and extra-maze cues in the radial maze.

7.2. Landmark-based blocking, unblocking, and overshadowing: rats.

An even more critical test to evaluate O'Keefe and Nadel's proposal (1978) –that locale learning occurs non-associatively in an all-or-none manner, and that animals constantly update their cognitive map of their environment– would be to see whether blocking and overshadowing occur entirely within the spatial domain. For example, if rats learned to navigate toward a goal defined by reference to a particular set of landmarks (A, B, and C), would they fail to use a new landmark (X) when it was subsequently added to the original set? The studies by Rodrigo, Chamizo, McLaren and Mackintosh (1997) and by Sánchez-Moreno, Rodrigo, Chamizo and Mackintosh (1999), both with the Morris pool, were designed to test blocking (Rodrigo et al.) and overshadowing (Sánchez-Moreno et al.) among landmarks. A final study (Rodrigo, 2001) was designed to test unblocking. In these studies, one major innovation was introduced in comparison to Morris's work (1981). We attempted to control, more precisely than he did, the landmarks which could be used to define the location of the platform. The swimming pool was surrounded by circular black curtains in order to eliminate the use of any static directional cues, and a fixed number of objects, landmarks, were placed at particular positions relative to the platform, inside this enclosure. These landmarks were hung from a false ceiling and rotated from trial to trial, and the position of the platform also changed on each trial, thus preserving a constant relation between the platform and the landmarks.

7.2.1. Blocking. The experiments of Rodrigo et al.'s (1997) study show, first, that rats use configurations of landmarks to locate a hidden platform (Experiments 1A and 1B), and secondly that previous established landmarks may block learning about newly introduced ones (Experiments 2 and 3). In Experiment 1C a placement training procedure was developed (see Whishaw, 1991) in order to equate, as far as possible, the experience of the rats with the different landmarks during training. This experiment showed that after extensive placement training and a few escape trials, animals could solve the test task in the presence of three landmarks, but not in the presence of two or one landmark only. The following experiments, Experiments 2 and 3, were carried out with the placement procedure. The rationale for these experiments was that if locale and taxon systems represent quite independent modes of solution, as O'Keefe and Nadel (1978) claim, one would not expect to see any of the interactions typically found in the taxon solution (where both classical and instrumental learning belong to) in the locale way of solving problems. Therefore, the two experiments were designed to see whether rats initially trained to use three landmarks to find the platform, learned less about a fourth landmark when it was added than did rats trained from the outset with all four landmarks. Experiment 2 consisted of two groups of rats. One group had

initial training with a set of three landmarks, A, B, and C (a fixed light, a beach ball, and an intermittent light, respectively), and then both groups had a second phase of training with A, B, C, and X. Thus, a new landmark, X (a plastic plant), was added to the previous set of landmarks. On the basis of the results of Experiment 1C, it was expected that animals would show good performance only when tested with three landmarks. Therefore control by X was assessed by testing animals with A, C, and X. Rats were also tested with A, B, and C, to see whether they had learned the basic spatial discrimination. A clear blocking effect was found: rats that had already learned to locate the hidden platform by reference to three landmarks, A, B, and C, learned less about a fourth landmark, X, when it was added than did a control group trained with all four landmarks from the outset. And the same results were replicated in Experiment 3, where control animals also received placement trials in the first phase but with a different set of landmarks (a string of colored Christmas tree lights, a cone, and a cube, respectively). The implication of Experiments 2 and 3 is that when a new landmark is added to a familiar configuration of landmarks, rats do not *immediately* update their cognitive map. But O'Keefe and Nadel's (1978) proposal implies that they should: they claim that an unexpected landmark would engage a novelty detector which would trigger exploratory behaviour which would update their map (either by integrating new features into or by deleting removed ones from it); in other words, that once the map has been created, updating should proceed automatically, and more rapidly than would building a new map. On the contrary, these results imply that rats do not immediately learn about a newly added landmark when other familiar landmarks are still available. The result is that expected by any standard associative learning theory. As the authors suggested, any version of the cognitive map hypothesis that hopes to accommodate these data must find a more suitable analogy than the rat as a cartographer.

A possible reason why the blocking groups failed to learn about the added landmark, X, is this: because they already knew the location of the platform on the basis of A, B, and C, they simply did not look toward the position of the new landmark and therefore failed to incorporate it into their map. Biegler and Morris (1999) ruled out this explanation in an experiment on spatial blocking among an array of discrete objects, landmarks, in an open field arena (the Manhattan maze). Rats were trained to find food using a set of landmarks. Then a new landmark was added, and although the animals noticed and explored this new object, they failed to use it subsequently as a landmark when searching for the hidden food.

7.2.2. Unblocking. Sometimes blocking does not occur: A change in the conditions of reinforcement between the two training phases can produce an attenuation or even a total elimination of this effect. This is called unblocking (Kamin, 1969). Unblocking has been recently addressed in the spatial domain (Rodrigo, 2001). This work replicates the finding that previously established landmarks block learning about a new subsequently introduced landmark and, most important, that a change in the position of the

platform between the two phases of the experiment can eliminate this effect. The study by Rodrigo (2001) consisted of three groups of rats. Two of the groups, Blocking and Unblocking, had initial training with a particular set of landmarks, A, B, and C, while the third group, Control, had initial training with a different set of landmarks, L, M, and N (the landmarks in this experiment were identical to those in Rodrigo et al., 1997). Then, a new landmark, X, was added to the first set of landmarks and the three groups had a second phase of training with A, B, C, and X. A new platform position was introduced between the first and the second phases of the experiment for both the Control and the Unblocking groups. As in the Rodrigo et al. (1997, Experiment 3) study, a clear blocking effect was found: rats that had already learned to locate the hidden platform by reference to three landmarks, A, B, and C, learned less about a fourth landmark, X, when it was added than did the control group initially trained with a different set of landmarks; and most important, those animals initially trained with A, B, and C, and for which a new platform position was introduced in the second phase of the experiment in addition to the added landmark, X, showed an absence of the blocking effect. These rats, the Unblocking group, learned about landmark X as well as did animals from the Control group. These results show unblocking of learning about a new landmark when a change in the location of reinforcement was introduced between the first and the second phases of the experiment - a result expected by any standard associative learning theory.

7.2.3. Overshadowing. A subsequent study by Sánchez-Moreno et al. (1999) reported overshadowing between landmarks working in a circular pool with rats, thus complementing the results by Rodrigo et al. (1997). The experiments by Sánchez-Moreno et al. (1999) were designed to see whether two landmarks placed in the same location would overshadow each other. Rats were trained in a Morris pool to locate a hidden platform, whose location was defined by four visual landmarks A, B, C and D (a fixed light, a beach ball, an intermittent light, and a plastic plant, respectively), spaced at equal intervals round the edge of the pool. Control animals were trained with these four visual landmarks only. But for animals in overshadowing groups, an auditory component, X, was added to landmark D. Control by D was assessed by testing animals with A, C, and D, and control by X by testing animals with A, C, and X. Rats were also tested with A, B, and C, to see whether they had learned the basic spatial discrimination. In Experiment 1, the overshadowing group spent less time in the platform quadrant than controls when tested with D, but the two groups performed equally well on test trials which did not use D. The auditory component X overshadowed the visual landmark D. In Experiment 2, evidence of reciprocal overshadowing, of D by X and of X by D was obtained. Then Experiment 3 suggested that an appeal to generalization decrement was insufficient to explain the previous results. These results are those expected by any standard associative learning theory; they clearly complement those by Rodrigo et al. (1997).

In Pavlovian conditioning overshadowing depends on the relative salience of both overshadowing and overshadowed stimuli (Mackintosh,

1976), on their relative temporal proximity to reinforcement (Revusky, 1971), and on their relative validity (Wagner, 1969) –i.e., whether the reinforcer is also signalled by other events. Biegler and Morris (1993; see also 1996), however, claimed that in spatial learning a relatively less valid predictor of reinforcement was more likely to acquire control over behavior than a relatively valid predictor. In both cases, the cue in question was a small vertical tower, placed in a large arena, with food available at a fixed distance and direction from the tower. In the variable condition, the tower (and food) moved around from trial to trial; in the fixed condition, it always stayed in exactly the same location in the arena. Biegler and Morris (1993) argued that in the fixed condition, the tower was a more valid predictor than in the variable condition. If tower and food were always in the same position in the arena, then the food could be located by reference to its fixed location with respect to the walls of the arena in addition to its location by reference to the tower. But when tower and food moved from trial to trial, the tower provided the only cue to the location of the food. Nevertheless, in this variable condition, the tower apparently acquired less control over the rats' search behaviour. Biegler and Morris argued that learning about landmarks must be subject to at least one special constrain: an object that moves around from trial to trial cannot be a landmark; only a stationary, fixed object will be used as a landmark to direct search towards a goal. However, other authors (Cartwright and Collet, 1982, 1983; Collet, Cartwright and Smith, 1986; Collett, 1987) have reported experiments favouring the opposite result: an object that moves around from trial to trial can be a good landmark.

Roberts and Pearce (1998) carried out a further series of experiments to compare the control by a stationary landmark with that of a moving one on rats' performance. In Experiments 1, 2, and 3, rats had to find a hidden platform which was both at a certain distance and specific direction with respect to a moving object, a beacon. The platform position varied from one session to the next, although the spatial relationship between the landmark and the platform was kept constant. The results demonstrated that in order to obtain information of both the direction and the distance of a hidden goal, rats could use an intra-pool landmark that moves from session to session as a reference point. Then, in Experiments 4 and 5 different groups of rats were asked to navigate to a hidden platform by using a reference point that could be either stationary or that moved from session to session. According to Biegler and Morris (1996), the control acquired by a fixed point of reference should be always higher than that acquired by a moving one. An associative explanation in terms of relative validity predicts exactly the opposite result. The results showed that the control acquired by a point of reference that moved from one session to the next was superior to that obtained by a stationary one (Experiment 4). And when a subsequent experiment, Experiment 5, was carried out in order to eliminate an alternative explanation in terms of generalization decrement, the same results were replicated. In conclusion, the study by Roberts and Pearce (1998) do not offer any support to the initial claim by Biegler and Morris (1993; see also 1996) that the stability of a reference point is a requirement for successful navigation. The

authors concluded that the conditions for spatial learning are not necessarily different from those observed when non-spatial tasks are used (but see Pearce, Ward-Robinson, Good, Fussell, and Aydin, 2001.)

Pearce et al. (2001) have recently carried out a series of experiments in the Morris pool to assess if a beacon could overshadow (Experiments 1-4) or block (Experiment 5) learning about the position of a platform with reference to the shape of a pool. The pool had a distinctive triangular shape and the question of interest was to see whether the presence of the beacon above a submerged platform would detract from learning about the position of the platform with respect to the shape of the pool. The results showed that presence of the beacon either had no effect on such spatial learning (although see Experiment 1, where the presence of the beacon overshadowed learning based on the shape of the pool) or had a beneficial effect. The authors concluded that the results of this series of experiments favour the proposal by Cheng (1986) and Gallistel (1990) that spatial learning based on the shape of the test environment is unaffected by the presence of other landmarks. Thus suggesting that the conditions for spatial learning can be different from those observed when non-spatial tasks are used.

7.3. Configural and elemental learning.

Experiments with spatial tasks and rats as subjects have demonstrated that when several landmarks are simultaneously present in a given environment, all the landmarks, including the ones which are proximal to a goal, participate in configural and not elemental learning (for a demonstration in a Morris pool, see Rodrigo, Chamizo, McLaren and Mackintosh, 1997, and Prados and Trobalon, 1998; and in maze experiments, Suzuki, Augerinos and Black, 1980, and O'Keefe and Conway, 1978). In Experiments 1A and 1B of the study by Rodrigo et al. (1997), rats were trained to find an invisible platform which was defined by a set of four landmarks. After acquisition, rats were tested, without the platform, in the presence of two or three landmarks only (Experiment 1A). The results showed that rats performance on test trials did not differ in the presence of two or three landmarks: with any configuration of landmarks animals preferred that quadrant of the pool where the platform should have been. Equally important was the demonstration that no specific landmark was necessary for successful performance: any set of two or three landmarks used in the swimming pool environment was equally effective in controlling the animals behaviour when searching for the platform. In Experiment 1B, with a shorter acquisition phase, test trials were in the presence of one or two landmarks only. In this case, the rats' performance clearly did differ: rats tested with two landmarks preferred that quadrant of the pool where the platform should have been, and this preference disappeared in the presence of one landmark only. All these experiments clearly imply that the rats were solving these spatial tasks by using configurations of landmarks, rather than by learning, elementally, about individual landmarks.

But in a recent study in the Morris pool by Manteiga and Chamizo (2001), elemental and not configural learning was found in spite of presenting

a set of simultaneous landmarks during training. In this study rats were required to escape from a circular pool by swimming to an invisible platform that was located in the same place relative to two sets of two landmarks each. The two configurations shared a landmark in common. This landmark was always relatively close to a hidden platform. Test trials, without the platform, revealed a preference for searching in the correct quadrant of the pool in the presence of the common landmark, either by itself or when it was accompanied by any of the other landmarks. But when tested with any of the other landmarks, either one at a time or in pairs, the rats performed at chance. It was concluded that after such configural training, navigation towards an invisible platform was controlled by elemental learning, specifically by the common landmark, which overshadowed the other landmarks, and therefore a configural way of learning. (For an additional demonstration of overshadowing between locale or configural learning and simple guidance learning, using a circular pool and rats as subjects, see Morris, 1981, Experiment 1). Would this preference in the presence of the common landmark be the same if this landmark had been farther away from the platform? Chamizo, Manteiga, García and Baradad (2001) tested this prediction. In a set of experiments the effects of the relative distance from the hidden platform (relatively near vs. further away from it) were examined (see Figure 3).

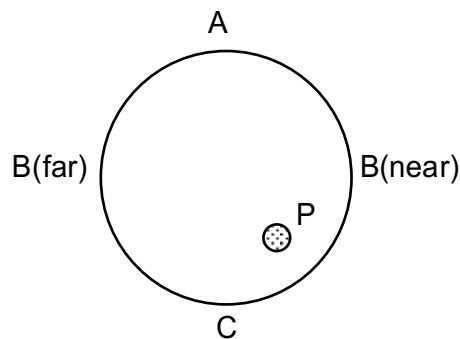


Figure 3. A schematic representation of a pool and four landmarks (A, B(near), B(far) and C), as well as the platform. Landmark B could be either relatively near from the platform or further away from it. (After Chamizo et al., 2001.)

The results showed an overshadowing effect by relative spatial proximity of the common landmark: only near animals revealed a preference for searching in the correct quadrant of the pool in the presence of the common landmark, both when it was presented alone or when it was accompanied by any of the other landmarks. In the absence of this near,

common landmark, animals consistently performed at chance. The implication is that the relative distance of a landmark, which is common to several configurations of landmarks, from a goal, seems to be a crucial determinant of the kind of strategy, elemental or configural, that an animal might learn.

It is well accepted that both mammals and birds can represent stimuli either elementally or configurally or, in other words, that both simple and configural representations are possible (and for a demonstration in a reptilian species, with turtles, see López, Rodríguez, Gómez, Vargas, Broglio, and Salas, 2000). The results by Manteiga and Chamizo (2001) are easily explained by the Rescorla and Wagner (1972) model, a model that allows that individual stimuli when presented in compound become differentially associated with the US or with the outcome of a trial. In this model it is assumed that the associative strength of a compound stimulus is the algebraic sum of the associative strength of its elements. If these elements have different relative intensities, then it predicts an overshadowing effect; the stimulus or event which is more intense will be the one to gain the greater associative strength and therefore the one to overshadow the less intense one. However, the results by Rodrigo et al. (1997) showing that rats tested with two or three landmarks preferred that quadrant of the pool where the platform should have been, and that this preference disappeared in the presence of one landmark only, support a configural explanation. According to a configural account (Pearce, 1987, 1994; Sutherland and Rudy, 1989), the set of stimuli presented prior to the unconditioned stimulus, US, or to the outcome, on a given trial, is able to activate a single representation of the configuration of stimuli, and this representation is associated with the US or outcome of the ongoing trial. As Shettleworth (1998) has pointed out, it is far from clear how and why animals performance is governed by a single landmark or by a configuration of landmarks. Is the position of the common landmark a crucial determinant of the kind of strategy that will prevail? So that when the common landmark is close to the goal, the strategy learned will be elemental, based on the common landmark, and when it is farther away from it, configural? We have just seen that these strategies compete. Can they be learned simultaneously, in parallel? To both inquests, research in progress suggests a positive answer (see Chamizo, Manteiga, García, and Baradad, 2001). More research is certainly needed to understand these and other questions, so to untangle the complex topic of the so called “cognitive maps”.

7.4. Blocking and overshadowing: Cross species-generality

The generality of spatial blocking and overshadowing, basic Pavlovian phenomena, has been expanded to other species.

7.4.1. Pigeons and humans. Spetch (1995) tested pigeons and humans using a touch-screen procedure and computer-generated landmarks. An invisible target was placed at the same place for both species, at a small distance from one or more landmarks. In both species Spetch found that the control over the response (pecking for pigeons and pressing for humans)

acquired by a landmark a given distance from the target was reduced by the presence of another landmark closer to the target. These results are a clear demonstration of overshadowing by relative spatial proximity.

A blocking effect has also been found in humans using virtual navigation (Hamilton and Sutherland, 1999), specifically a computerized version of the Morris water task which is called VMWT (virtual Morris water task). Measures of human performance by means of this task indicate that students can locate a hidden goal by using virtual landmarks in much the same way that rats do (Astur, Ortiz, and Sutherland, 1998). In the study by Hamilton and Sutherland (1999), students initially trained to locate an invisible goal with a particular set of landmarks, were poor at locating the goal when tested with a new set of subsequently added landmarks. The authors argue that this blocking effect is inconsistent with the cognitive mapping theory proposed by O'Keefe and Nadel (1978), and also with a Hebbian explanation, which is merely based on the contiguity of events (in fact, the two accounts predict the absence of blocking), and consistent with an error-correcting associative rule (Mackintosh, 1975; Pearce and Hall, 1980; and Rescorla and Wagner, 1972).

An overshadowing effect has also been found in humans using virtual navigation¹ (Chamizo, Aznar-Casanova, and Artigas, 2002). In Experiment 1, the students were trained to locate a platform in the presence of four landmarks. Following this, they had a test trial in the presence of the landmarks, without the platform. For half of the subjects the platform was visible (Overshadowing Group), and for the other half it was invisible (Control Group). On the test trial, a clear overshadowing effect was found: the Overshadowing group spent significantly less time in the platform quadrant than the Control group. Landmark-based learning was overshadowed by simple guidance. Then, Experiment 2 eliminated an alternative explanation in terms of generalization decrement.

7.4.2. Honeybees. Blocking and overshadowing have been extensively studied with honeybees (for a review of the blocking literature see Hammer and Menzel, 1995; and for a review of the overshadowing literature, Bitterman, 1996). For our purposes we are more interested in landmark-based search tasks, which only recently have been studied with these animals (Cheng and Spetch, 2001). In the study by Cheng and Spetch (2001), in two experiments honeybees were tested using a task where the animals had to search at the right place with respect to one or more landmarks. The landmarks used were identical objects, although with different colours, which indicated the position of a cup filled with sugar water (the reward). In both experiments the blocking groups were trained with a single landmark in the first phase. Then, in the second phase, a new landmark was added so that both landmarks were relevant for finding the reward. The spatial relation of the added landmark with the first landmark remained constant across the phases. In Experiment 1,

¹ The software for this study was designed by Jose Antonio Aznar Casanova.

the control group only had the second phase of training, while in Experiment 2 these animals also received training but with a different landmark (an irrelevant landmark in an irrelevant position). A blocking effect was found in both experiments: final tests trials in the presence of the new landmark on its own showed that the blocking group searched less in the target area than did control animals. Cheng and Spetch (2001) concluded that their results of blocking using a landmark-based search task with honeybees extends the range of parallel phenomena found in searching both in space and in time, thus suggesting common underlying neurophysiological mechanisms for coding both spatial and temporal information.

The clear general implication of all the blocking, unblocking, and overshadowing studies that we have just reviewed is that the mechanism responsible for locale learning seems to be clearly associative, since it interacts with other forms of learning in the same way as the conditioning of a light interacts with the conditioning of a tone (Kamin, 1969). [Latent inhibition and perceptual learning effects were also addressed in the eighties (see Chamizo and Mackintosh, 1989; and Chamizo, 1992). These effects have also been repeatedly found with rats, both in the radial maze and in the Morris swimming pool, and will be extensively discussed in Chapter 3].

8. Spatial integration.

According to O'Keefe and Nadel (1978), a configuration of distal landmarks would form a cognitive map, and such a representation will not obey associative principles. But the results of a recent study on spatial integration by Chamizo and Mackintosh (in preparation) do not give any support to such a claim. In the Chamizo and Mackintosh study, rats were trained to find a submerged platform whose location was defined by reference to several external landmarks. All rats were trained with two sets of three landmarks; for group integration there was a landmark common to the two sets; for nonintegration animals the two sets of landmarks shared no landmark in common. Each configuration could be either relatively near or relatively far from the hidden platform. Test trials in the presence of a new configuration formed by two non-common landmarks, each of them coming from a different training configuration, found evidence of spatial integration: rats initially trained to find the platform using the two configurations that shared a common landmark showed better performance when searching for the platform than did rats trained to use the two configurations that did not share a common object. This integration effect was clearly facilitated when the platform had been located relatively far away from the landmarks. When the platform had been located close to the landmarks the integration effect was weaker. The main implication of this study is that the processes operating to integrate information about separate but relevant associations when using spatial landmarks work in the same way as in conditioning experiments with non-spatial stimuli (Holland & Straub, 1979; Leyland, 1977; Rashotte, Griffin and Sisk, 1977).

The results reported by Chamizo and Mankintosh (in preparation) are hard to reconcile with O'Keefe and Nadel's (1978) claims. This study (see also Manteiga and Chamizo, 2001; and Chamizo, Manteiga, García and Baradad, 2001), also suggest that the relative distance of a common landmark might be an important determinant of the kind of strategy, elemental or configural, that an animal would preferentially learn when training consists of two configurations of landmarks that share a landmark in common.

9. Conclusions.

Spatial information clearly seems to interact during learning: landmarks compete according to an error-correcting rule like that in the Rescorla-Wagner (1972) model. Blocking, unblocking, and overshadowing in the spatial domain are a demonstration that different kinds of spatial information interact competitively. But as Shettleworth (1998) indicates, well controlled experiments from behavioural neuroscience and ethology also suggest that rather than competing during learning, distinct spatial memory systems acquire information simultaneously, in parallel (Keeton, 1974; Chapuis, Thinus-Blanc, and Poucet, 1983; Fiset, Gagnon, and Beaulieu, 2000). For example, there seems to be three different mechanisms used by birds to navigate. These mechanisms imply the use of the sun, the stars, and magnetic fields. Pigeons can return to their nests from places which are hundreds of kilometers away, beginning their flights in a place that they had never been before, and that in relation to their nests is in a direction towards which they had never flown before. If the place where they are freed is East of their nest, they fly West; if it is West, they fly East. If two groups from different nests are freed together in the same place, each group will fly in the appropriate direction. According to a guidance strategy, a bird will detect a discrepancy between the conditions where it is freed and those of its natural habitat; and the purpose of its movement would be to reduce this discrepancy. The position of the sun in the sky and the speed of its apparent movement will be important sources of information for the bird. But nowadays we know that the sun is not indispensable in order that pigeons can find their way back to their nests, because these birds can return to their nests in cloudy weather both from a familiar and unfamiliar starting point. In experiments with pigeons where their internal clocks have been changed because they have been exposed to an altered day-night cycle, it has been observed that when it is sunny they begin flying in the wrong direction, while in cloudy conditions they fly in the right direction (Keeton, 1974). This implies that pigeons have an alternative system of orientation, probably a magnetic system. Because when a little magnet is placed on a pigeon's head, it has difficulties returning to its nest on a cloudy day, but not on a sunny one. The fact that they can interchange sun and magnetism implies that birds have an alternative compass. It has been suggested that if pigeons have a compass, they must also have a map, because a compass by itself is useless. Kramer's (1953) map and compass hypothesis, previously introduced by Rodrigo in this issue, does not fit in with any of the taxon strategies, but it does so with a locale one (O'Keefe and Nadel, 1978). Unfortunately the basis of cognitive maps, if they

do indeed exist, is something unknown and requires very well controlled experiments.

The hypothesis of the cognitive map proposed by O'Keefe and Nadel (1978) also faces other problems. Although it is certain that the hippocampus plays an important role in many spatial tasks (Sutherland, Kolb and Whishaw, 1982; Sutherland, Whishaw and Kolb, 1982), it is also true that it also does so with many other non-spatial tasks, whenever they require a highly relational representation (Sutherland and Rudy, 1989; Eichenbaum, Fagan and Cohen, 1986; Eichenbaum, Mathews and Cohen, 1989; Otto, Schottler, Staubli, Eichenbaum and Lynch, 1991). Therefore, at the moment, no agreement has been reached about which are the functions of the hippocampus (see Eichenbaum, 1994; and Bunsey and Eichenbaum, 1996). Moreover, it is known that some important neuronal circuits, which are implied in complex locale learning, are outside this structure (Alyan and McNaughton 1999; Smith-Roe, Sadeghian and Kelley, 1999). This state of affairs has led some investigators to recognize that the proposal by O'Keefe and Nadel is more a metaphor than a theory (Sherry and Healy, 1998).

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