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Area and peak shift effects in a navigation task with rats

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Abstract

In two experiments in a Morris pool rats were trained with a successive discrimination procedure in the presence of two objects or landmarks. The angular separation between the two landmarks signalled either the presence (0 degrees, S+ trials) or the absence (90 degrees, S- trials) of the platform. After training the rats received unrewarded test trials in which one of the landmarks was presented at a range of places in relation to the second landmark. The generalization gradient obtained in Experiment 1 showed higher responding on the side of S+ away from S-. This effect has been called area shift. In Experiment 2, with a slightly different discrimination training, a moderate peak shift effect was obtained. The present experiments show for the first time area and peak shift effects with rats across spatial locations when working with a navigation task.
Keywords: Morris pool, rats, peak and area shift effects, landmarks, navigation.

Resumen

Efectos de desplazamiento del área y del máximo en una tarea de navegación con ratas. En dos experimentos en una piscina de Morris a unas ratas se las entrenó mediante un procedimiento de discriminación sucesiva en presencia de dos objetos o puntos de referencia. La separación angular entre los dos puntos de referencia indicaba la presencia (0 grados, ensayos E+) o la ausencia (90 grados, ensayos E-) de la plataforma. Tras el entrenamiento, las ratas recibieron ensayos no reforzados en los que uno de los puntos de referencia se presentaba en un rango de localizaciones en relación con el segundo punto de referencia. El gradiente de generalización que se obtuvo en el Experimento 1 mostró más insistencia en la respuesta en el lado del E+ que estaba situado en dirección opuesta al E-. A este efecto se le ha denominado desplazamiento del área. En el Experimento 2, con un entrenamiento discriminativo ligeramente diferente, se obtuvo un efecto moderado de desplazamiento del máximo. Estos experimentos con ratas muestran por primera vez los efectos de desplazamiento del área y del máximo cuando se manipulan localizaciones espaciales trabajando en una tarea de navegación.
Palabras clave: piscina de Morris, ratas, efectos de desplazamiento del área y del máximo, puntos de referencia, navegación.

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When the two stimuli of a discrimination, S+ and S-, are similar except for one single feature that is called an intradimensional discrimination. An important characteristic of these discriminations is that often they show interesting interactions between the subjects' performance observed in the presence of these stimulus (Hanson, 1959).

In the classical study by Hanson (1959), three groups of pigeons were trained to peck at a key illuminated with a 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 (i.e., the biggest peak shift) in birds trained on the 550-555 nm discrimination. Therefore, as S- comes closer to S+ during discrimination training between two stimuli along a single dimension, there is a progressive distortion in the shape of the post-discrimination gradient, with a higher proportion of responses occurring to stimuli on the other side of S+, and the peak of the gradient falling at stimulus values further removed from S+, in a direction away from S- (for other examples of the peak shift effect, using different species, stimuli dimensions and preparations, see Dougherty & Lewis, 1991; Moye & Thomas, 1982; Terrace, 1964; Weiss & Weissman, 1992; Wills & Mackintosh, 1998).

Hanson's results seem to provide an excellent confirmation of Spence's (1937) conditioning-extinction theory of discrimination learning. According to this theory, both excitation and inhibition are conditioned to the absolute properties of S+ and S- during discrimination training. Spence suggested that the two tendencies would generalize to other stimuli (including S+ and S-), according to their similarity to S+ and S- and that responding to the different stimuli on test would be related to the algebraic sum of these tendencies. An alternative explanation to Spence's theory (i.e., that does not rely on the absolute properties of S+ and S-), mainly when simultaneous discriminations are used, refers to a relational way of learning. The animals can learn that one stimulus is larger or wider than a second stimulus, for example (Kohler, 1939; Thomas, 1974).

Is the peak shift effect also observed in the spatial domain? When the 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 (for a few examples see Chamizo & Rodrigo, 2004; Cheng, Spetch, & Johnston, 1997; Cheng & Spetch, 2002; Rodrigo, Sansa, Baradad, & Chamizo, 2006).

In the study by Cheng *et al.* (1997, Experiments 2 and 3) with pigeons and a touch-screen task, 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 has been called area shift (Rilling, 1977). When S- was closer to

S+ (i.e., as the discrimination became more difficult), then a peak effect was obtained.

The aim of the present study was to expand the findings of Cheng *et al*. (1997) with pigeons and a computer screen to a new species, rats, and a new spatial task, the Morris pool (Morris, 1981; Stewart & Morris, 1993), in order to complement the results of a previous study showing generalization gradients with rats and the circular pool (Rodrigo, Sansa, Baradad, & Chamizo, 2006).

The circular pool or Morris pool is an apparatus in which rats are trained to escape from water by swimming to a hidden platform whose location can only be identified using distal extra-maze cues or landmarks. In the study by Rodrigo *et al*. (2006), circular black curtains surrounded the pool, with only two objects, landmarks, inside this enclosure, so that no other room cues could provide additional information about the location of the hidden platform. These objects, B and F, were hung from a false ceiling and rotated from trial to trial; the position of the platform changed on each trial, thus preserving a constant relation between the platform and the two objects. Object B was just above the platform (i.e., a beacon for the hidden goal), and the second object, F, also a landmark, was in front of B, directly above the wall of the pool, 38-cm from both the beacon and the hidden platform). The function of F was to behave as a frame of reference, which was crucial when moving B from F on test trials (which were without the platform).

Thus, a real frame of reference was replaced by a discrete landmark that we could easily control. The test results of this study (Rodrigo *et al*., 2006) showed a generalization gradient as a function of the relative distance of the two objects: more time searching in the B segment, where the platform should have been, when B was in the original position (i.e., in front of F), which decreased symmetrically with distance of B from F. But because rats tend to solve spatial tasks by using configurations of landmarks, rather than by learning elementally, about individual landmarks (for a demonstration in a Morris pool, see Rodrigo, Chamizo, McLaren, & Mackintosh, 1997, and Prados & Trobalon, 1998; and in maze experiments, Suzuki, Augerinos, & Black, 1980, and O'Keefe & Conway, 1978), several manipulations were needed to promote elemental learning. One was a different salience of the two landmarks, B and F, and was accomplished in several ways. For example, with a different distance to the platform, much shorter for B, a beacon for the platform, the target landmark, than for F (see Chamizo, Rodrigo, Peris, & Grau, 2006, for a demonstration that proximity to the goal is an important factor to determine the salience or intensity of a landmark -and for a related study, Chamizo & Rodrigo, 2004).

Would it be possible to find a peak shift effect or an area effect, after successive discrimination training, when manipulating the angular separation between two landmarks, their spatial location, on the two types of trial, S+ and S-?

The purpose of this study was to answer this question working in a circular pool with rats, thus complementing the results by Rodrigo *et al*. (2006). Following Cheng *et al*. (1997), the two experiments of the present study had an intra-group design. A significance level of $p<.05$ was adopted for the statistical tests reported in the two experiments.

Experiment 1

A peak shift effect is observed when subjects show a displacement of the highest rate of responding in a stimulus-generalization gradient away from the S+ in a direction opposite the S- after intradimensional discrimination training (Hanson, 1959). Experiment 1 examined whether a discrimination training where the two types of trial, S+ and S-, were defined by a different angular separation between two and the same landmarks (i.e., the absolute properties of the two landmarks were identical), would eventually show, on the test trials (trials without platform, where the two landmarks are presented with a range of different angular separations between them), a displacement of the highest time searching in the expected stimulus-generalization gradient away from the S+, in a direction opposite the S-. This demonstration would show that the rats can respond to the relationship between S+ and S-, even when trained with a successive discrimination (i.e., without a simultaneous comparison of S+ and S-) and a navigation task.

Method

Subjects

The subjects were 18 naive rats, Long Evans, 9 males and 9 females, approximately four months old at the beginning of the experiment. They were maintained on ad lib food and water, in a colony room which had a 12:12-hr light-dark cycle, and were tested within the first 8 hrs of the light cycle.

Apparatus

The apparatus was a circular swimming pool, made of plastic and fibre glass, modelled after that used by Morris (1981). It measured 1.60-m in diameter and 0.41-m deep, with water rendered opaque by the addition of 1 cl/l of latex. The water temperature was maintained at 22 + 1°C. The pool was situated in the middle of a large room, mounted on a wooden platform 0.43-m above the floor, and it was surrounded by black curtains reaching from ceiling to nearly the base of the pool and forming a circular enclosure 2.4-m in diameter. Inside the black curtain enclosure, two objects were suspended from the false ceiling, 30-cm above the surface of the water. For all rats, the two objects, B and F, were: B- a 9,5-cm diameter yellow plastic ball; and F- a white cardboard inverted cone 16-cm in diameter and 59-cm in height, with 1-cm thick black horizontal stripe spaced 3.5-cm apart. In order to ensure that the rats used these objects, rather than any inadvertently remaining static room cues, to locate the platform, B, F and the platform were semi-randomly rotated with respect to the room (90°,180°, 270° or 360°), with the restriction that all parts of the room were used equally often each day. A closed-circuit video camera with a wide angle lens was mounted 1.75-m above the center of the pool inside the false ceiling, and its picture was relayed to recording equipment in a corner of the room. A circular platform, 0.11-m in

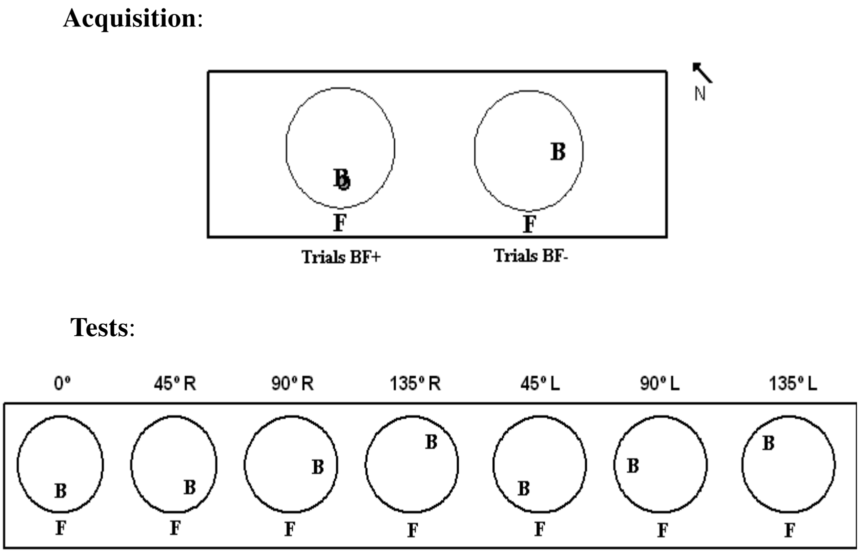

Figure 1. Top.- A schematic representation of the pool and the position of the two objects used in Experiment 1, B and F, both on trials BF+ (as well as the platform), and BF- during discrimination training. On trials BF+ (trials with platform, S+ trials) object B was exactly above the platform (i.e., a beacon for the goal, the hidden platform), while object F was outside the pool, approximately 30 cm behind its wall (i.e., a frame of reference). On trials BF- (trials without platform, S- trials), landmark B was displaced from F, although always maintaining the same distance to the wall of the pool (in Experiment 2, on trials S-, the two objects present were W, instead of B, and F. Also in Experiment 2, the position of F differed in comparison to Experiment 1; it was above the wall of the pool). Bottom.- a schematic representation of the test trials: 0°, 45ºR, 90ºR, 135ºR, 45ºL, 90ºL, and 135ºL (i.e., when manipulating the angular separation between the two landmarks, B and F).

diameter, could be placed in one segment of the pool, 0.38-m from the side, with its top 1-cm below the surface of the water. The platform and objects were always situated as shown in Figure 1 (top panel) for the two types of trial, S+ (trials with the platform) and S- (trials without the platform).

Procedure

There were three types of trial: pretraining, escape training, and test trials.

Pretraining consisted of placing a rat into the pool, without landmarks but with the platform present. The rat was given 120 s to find the platform, and once it had found it, it was allowed to stay on it for 30 s. If it had not found the platform within the 120 s, it was picked up, placed on it and left there for 30 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 North, South, East, and West in Figure 1 -top panel), as far as possible equally often on the same or opposite side of the pool from the platform and with the platform to the right or to the left of where the rat was placed. Rats were given five such pretraining trials during two days, at a rate of two trials the first day, and three trials the second day.

The procedure for the acquisition phase was similar as for pretraining although with a few main exceptions. First, in this phase two landmarks were always present, B and F. Secondly, there were two types of trial: trials with platform (i.e., trials BF+), in which the angular separation between the two landmarks was 0 degrees, and trials without the platform (i.e., trials BF-), in which the angular separation between the two landmarks was 90 degrees (as shown in Figure 1, top panel). On trials BF+, trials with the platform, landmark B, the ball, was exactly above the platform (i.e., a beacon for the goal) while object F, the inverted cone, was outside the pool, 32 cm from its apex to the wall of the pool (i.e., a frame of reference). On trials BF-, trials without the platform, landmark B was displaced from F, although always maintaining the same distance to the wall of the pool. This displacement of B from F was to the right for fifty per cent of the rats, and to the left for the remaining animals. Therefore, the task was a discrimination one in which one angle of separation of 0º degrees between the two objects or landmarks indicated the availability of the platform on half of the trials, and for the rest of the trials a second angle of separation of 90º between the two landmarks indicated the absence of the platform (i.e., S+ and S- trials, respectively). Animals were given eight trials per day during twenty four days (a total of 192 trials), four trials with the platform and four without the platform (i.e., a total of 96 BF+ trials, and 96 BF- trials).

The platform and the landmarks were rotated between trials. At trials BF+ the rat was given 120 s to find the platform, and once it had found it, it was allowed to stay on it for 30 s. If it had not found the platform within the 120 s, it was picked up, placed on it and left there for 30 s. At trials BF- the rat was allowed to swim for 30 s. The two types of trial had an average ITI of approximately 8-10 min.

After the training phase, the test phase lasted seven days. Each of these days contained six trials in total. The first trial each day was without the platform (i.e., a BF- trial); then, trials 2-5 were escape trials, trials with the platform (i.e., trials BF+); and finally, the last trial of each day was the test trial, without the platform. Test trials were always in the presence of landmark B and landmark F and lasted one minute. For each rat test trials were always Test 0º, Test 45º R, Test 90º R, Test 135º R, Test 45º L, Test 90º L, and Test 135º L (as shown in Figure 1, bottom panel). The order of these trials was counterbalanced. For fifty per cent of the rats, S- coincided with Test 90º L, and for the remaining animals with Test 90º R.

For purposes of recording the rat's behaviour, on test trials the pool was divided into eight sectors (i.e., octants) of 45º each, and rats were, as much as possible, placed equally in the four starting positions, North, South, East, and West, in Figure 1. The amount of time was recorded that the rat spent in the sector where object B was.

Results and Discussion

Figure 2 shows the mean escape latencies of rats during the BF+ trials on both the training phase (days 1-24 -with 4 escape trials per day) and the retraining escape trials of the test phase (days 25-31 -with 4 escape trials per day). An ANOVA was used to analyse the training latencies. It took into account the variables Sex and Days (days 1-24). The results showed that the variable Days was significant, F (23,368)= 14.28. No other main effect or interaction was significant (Fs< 1.5). The performance of the rats improved as days went on. An ANOVA of the escape trials during the test phase, taking into account the same variables, Sex and Days (days 25-31), found that no main effect or interaction was significant (Fs< 1.5).

Figure 3 shows the mean time searching in the sector where B (the critical landmark) was during the test trials. T tests were used to compare rats' performance with chance (i.e., 7.5 s searching in the segment where B was) in order to evaluate whether the test results reflected significant spatial learning. The rats' performance differed from chance on the following test trials, test 0 (S+), t (15)= 6.96; test -45, t (15)= 3.53, test -90 (S-), t (15)= 2.25; test +45, t (15)= 4.27; test +90, t (15)= 3.5; test +135, t (15)= 2.79. Thus, the performance of the rats reflected significant spatial learning

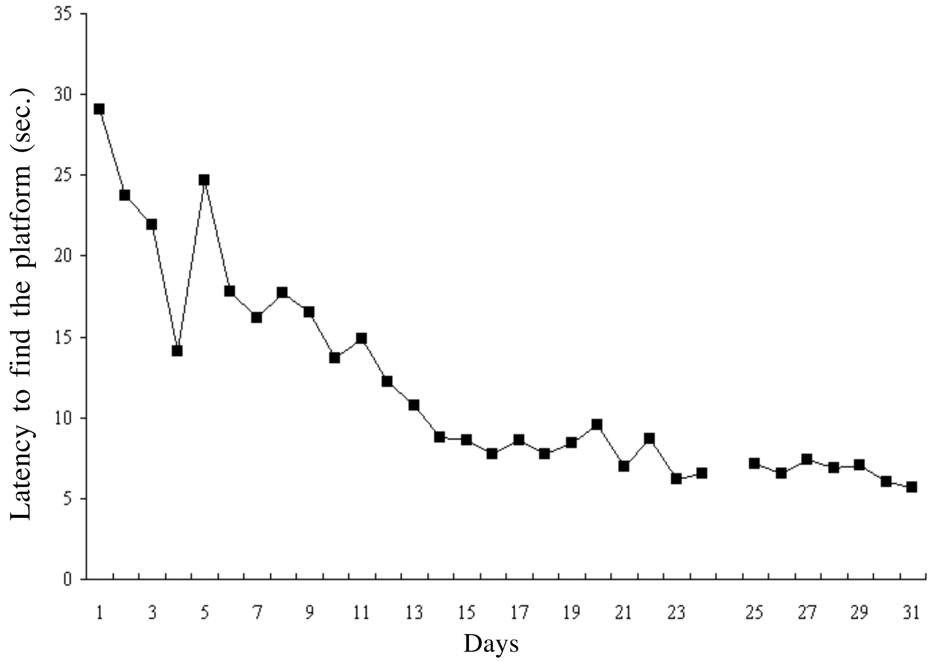

Figure 2. Mean escape latencies for the rats of Experiment 1 on the BF+ trials (trials with platform) during discrimination training, and also during the retraining trials on the test phase.

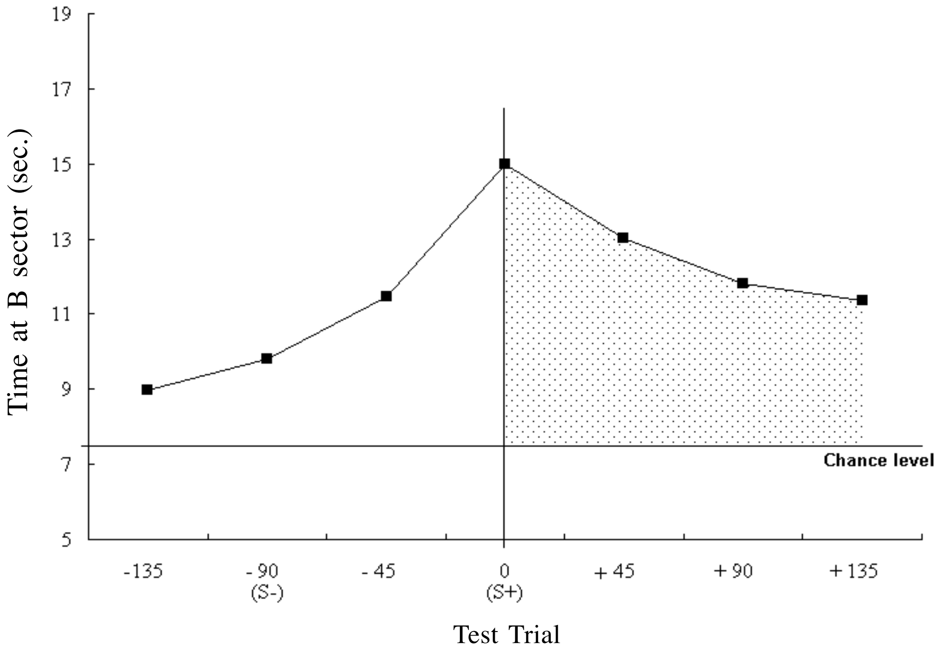

Figure 3. Mean time spent in the B segments by rats of Experiment 1 during the test trials.

on these test trials. Following Cheng *et al*. (1997), two types of statistical tests were conducted by using within-subject analysis of variance. The first ANOVA, taking into account the variables Sex, Laterality (right and left), and Tests (-135, -90 [S-], -45, 0 [S+], +45, +90, +135), showed that the only significant variable was Tests, F (6,84)= 4.81. No other main effect or interaction was significant (Fs< 2). The second ANOVA examined the symmetry of the results. The time searching in the sector where B (the critical landmark) was during six test trials (i.e., Test -135, Test -90 [S-], Test -45, Test +45, Test +90, and Test +135), in relation to Test 0º [S+] was measured. Specifically, the time searching in each sector where B was (i.e., in each of the previous test trials), was divided by the time searching in Test 0º. Then, a further analysis, taking into account the variables Sex, Laterality (right and left), Side (side with S-, side without S-), and Tests (45, 90, 135), showed that the variable Side was significant, F (1,14)= 5.65. No other effect or interaction was significant (Fs< 2.5).

The present results clearly indicate an asymmetric generalization gradient away from the original S-, an area shift (i.e., more time searching on the side of S+ away from S-), thus replicating Cheng *et al*. (1997).

Experiment 2

Experiment 2 examined whether the asymmetric generalization gradient found in Experiment 1, an area shift effect, could be modulated by a slightly different discrimination training in which the two types of trial during the training phase, S+ and S-, were defined not only by a different angular separation between the two landmarks (0 and 90 degrees, respectively), but also by one of the two landmarks in the S- trials, trials without the platform, in comparison to Experiment 1. Specifically, in this experiment, the trials without the platform were in the presence of landmark W and landmark F, trials WF-, instead of in the presence of landmark B and landmark F, trials BF-, as in Experiment 1. With this manipulation we intended to reduce the proportion of common elements shared by the two types of trial, S+ and S-.

We know that spatial discriminations are more difficult if the same landmarks enter into the definition of both S+ and S- (for demonstrations in the radial maze see Sansa, Chamizo, & Mackintosh, 1996; Trobalon, Sansa, Chamizo, & Mackintosh, 1991). Therefore, by reducing the amount of common elements between the two types of trial, S+ and S-, in the present discrimination, we assumed that we were facilitating the discrimination. The test phase was identical to Experiment 1 (i.e., with B and F presented with a range of different angular separations between them). Would the different angular separation between these two landmarks still control the subjects' performance on the test phase in spite of the different landmarks present in the test phase in comparison with the training phase? A relational account predicts so in spite of the new pair of landmarks on the test phase (i.e., W and F instead of the training landmarks, B and F). But if the discrimination was learned in terms of the absolute properties of the landmarks present on a given trial, then the prediction is a bad control of the subjects' performance on the test trials (i.e., with the new pair of landmarks, B and F). Finally, it could be the case that rats had used both sources of information, absolute and relational, to solve the task, in which case an intermediate performance is expected.

Method

Subjects and Apparatus

The subjects were 8 naive rats, Long Evans, 4 males and 4 females, approximately four months old at the beginning of the experiment. They were maintained on ad lib food and water, in a colony room which had a 12:12 hr light-dark cycle, and were tested within the first 8 hrs of the light cycle. The apparatus and the experimental room were the same as in Experiment 1. In this experiment three objects, B, W, and F (instead of two, B and F, the yellow plastic ball and the inverted cone, as in Experiment 1), were used. The third object, W, was a plastic bottle completely covered in silver foil, 17 cm high and 5.7 cm diameter at the base.

Procedure

As in the previous experiment, there were three types of trial: pretraining, escape training, and test trials. The general procedure was very similar to that on Experiment 1, with two main exceptions. The first one is that in this experiment during the training phase three landmarks could be present, B, W and F (instead of two, as in Experiment 1, landmarks B and F); trials S+ were exactly the same as in Experiment 1 (i.e., in the presence of landmarks B and F, with an angle of separation of 0 degrees) but trials S- were in the presence of landmarks W and F (with an angle of separation of 90 degrees). The second main difference (by human mistake) refers to the position of landmark F. This landmark was directly above the wall of the pool (instead of approximately 30 cm behind its wall, as in Experiment 1). There were two other minor differences during the training phase in comparison to Experiment 1. Firstly, animals were given twelve trials per day during sixteen days (instead of eight trials per day during twenty four days, as in Experiment 1), six trials with the platform, in the presence of landmarks B and F, and six trials without the platform, in the presence of landmarks W and F (i.e., a total of 96 BF+ trials, and 96 WF- trials, as in Experiment 1). The platform and the landmarks were rotated between trials. At trials BF+ the rat was given 120 s to find the platform, and once it had found it, it was allowed to stay on it for 30 s. If it had not found the platform within the 120 s, it was picked up, placed on it and left there for 30 s. The second minor difference was that at trials WF- the rat was allowed to swim for 60 s (instead of 30 s, as in Experiment 1). The two types of trial had an average ITI of approximately 10-12 min.

After the training phase, the test phase lasted seven days. This phase was very similar to Experiment 1, although with one minor difference. The five trials previous to the test trial had a different order of presentation in comparison to Experiment 1. Each test day contained six trials in total; four of them, trials 1-4 (instead of 2-5, as in Experiment 1), were always with platform (i.e., BF+ trials); then, trial five (instead of trial one, as in Experiment 1), was a trial without the platform (i.e., a WF- trial); and the final sixth trial was the test trial, also without the platform. Test trials were always in the presence of landmark B and landmark F and lasted one minute. For each rat, test trials were always Test 0º, Test 45º R, Test 90º R, Test 135º R, Test 45º L, Test 90º L, and Test 135º L (as shown in Figure 1, bottom panel). The order of these trials was counterbalanced. For fifty per cent of the rats, S- coincided with Test 90º R, and for the remaining animals with Test 90ºL. For purposes of recording the rat's behaviour, on test trials the pool was divided into eight sectors (i.e., octants) of 45º each, and rats were, as much as possible, placed equally in the four starting positions, North, South, East, and West, in Figure 1. The amount of time was recorded that the rat spent in the sector where object B was.

Results and Discussion

Figure 4 shows the mean escape latencies of rats during the BF+ trials on both the training phase (days 1-16 -with 6 escape trials per day) and the test phase (days 17-23 -with 4 escape trials per day). An ANOVA was used to analyse the training latencies. It took into account the variables Sex and Days (days 1-16). Only the variable Days was significant, F (15,90)= 8.65. No other main effect or interaction was significant (Fs< 1.0). The performance of the rats improved as days went on. An ANOVA of the

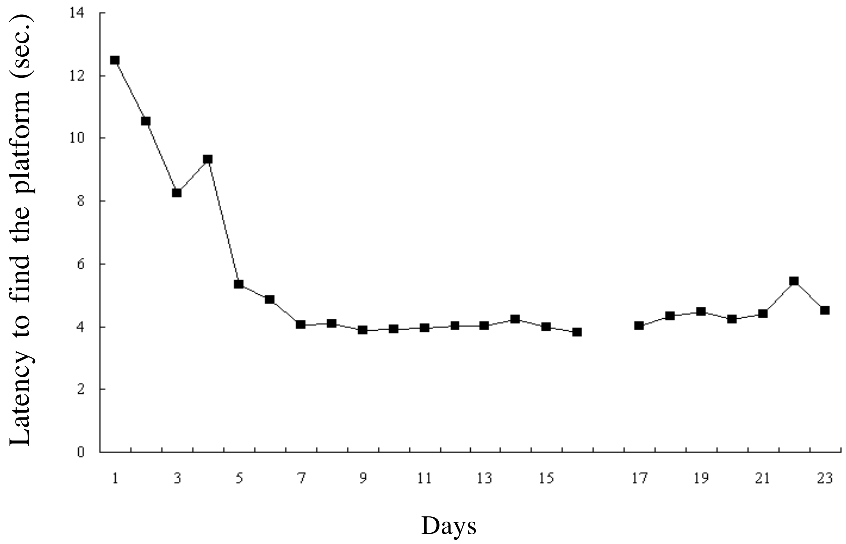

Figure 4. Mean escape latencies for the rats of Experiment 2 on the BF+ trials (trials with platform) during discrimination training, and also during the retraining trials on the test phase.

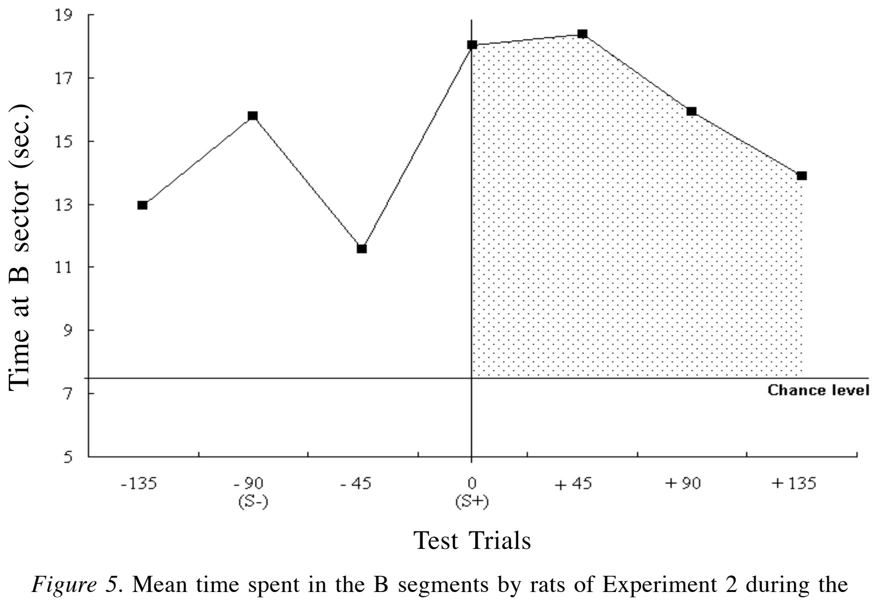

Figure 5. Mean time spent in the B segments by rats of Experiment 2 during the test trials.

escape trials during the test phase, taking into account the same variables, Sex and Days (days 17-23), found that no main effect or interaction was significant (*F*s< 4.5).

Figure 5 shows the mean time searching in the sector where B (the critical landmark) was during the test trials. T tests were used to compare rats' performance with chance (i.e., 7.5 s searching in the segment where B was) in order to evaluate whether the test results reflected significant spatial learning. The rats' performance differed from chance on test trials, test 0 (S+), *t* (15)= 2.98; test -45, *t* (15)= 2.15; test +45, *t* (15)= 5.3; test +90, *t* (15)= 4.05; and test +135, *t* (15)= 2.98.

As in Experiment 1, two types of statistical tests were conducted by using within-subject analysis of variance. The first ANOVA, taking into account the variables Sex, Laterality (right and left), and Tests (-135, -90 [S-], -45, 0 [S+], +45, +90, +135), showed that the only significant variable was Tests, *F* (6,24)= 8.03. No other main effect or interaction was significant (*F*s< 2.5). The second ANOVA examined the symmetry of the results. In this analysis the time searching in the sector where B (the critical landmark) was during six test trials (i.e., Test -135, Test -90 [S-], Test -45, Test +45, Test +90, and Test +135) in relation to Test 0º [S+] was measured. Specifically, the time searching in each sector where B was (i.e., in each of the previous test trials), was divided by the time searching in Test 0º. This second analysis took into account the variables Sex, Laterality (right and left), Side (side with S- and side without S-), and Tests (45, 90, and 135).

The results showed that the variable Side was significant, *F* (1.4)= 18.13, as well as the interaction Side x Tests, *F* (2.8)= 58.39. No other main effect or interaction was significant (*F*s< 7.0). These results clearly indicate an asymmetric gradient away from the original S-, an area shift effect in which a moderate peak shift effect was obtained.

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General Discussion

The results of the present experiments establish that an area shift effect, as well as a moderate peak shift effect, can occur after discrimination training with S+ (being S+ defined as a specific configuration between two landmarks, with an angular separation of 0 degrees) and S- (being S- defined as a second specific configuration between two landmarks, with an angular separation of 90 degrees), with rats, in a standard spatial navigation task. These results show that on trials S+ an excitatory tendency was developed, while on trials S- an inhibitory tendency was developed, thus complementing the results of Rodrigo *et al*. (2006), who reported generalization gradients in a similar navigation task.

Specifically, Experiment 1 shows that when the angular separation between two and the same landmarks, B and F, is of 0 degrees on some trials (S+) and of 90 degrees on other trials (S-), the initial discrimination was learned rather slowly (the average latency to find the platform in the first twelve S+ trials was 24.90 s.); then, in the test phase, when B and F were presented at a range of angular separations, an area shift effect was found. This experiment is a clear example of relational learning. The relationship between two and the same landmarks, B and F, during acquisition (i.e., on trials BF+

and BF-) was the only information available for rats to solve the discrimination task. Figure 3, although asymmetrical, indicates a rather good generalization in the test phase (i.e., the gradient of responding obtained is a function of how similar each angular separation, the test "stimulus", between landmarks B and F was to the training S+ stimulus, with the highest amount of responding to S+).

In Experiment 2, although during acquisition S+ trials (i.e., BF+ trials) were identical to those in Experiment 1, when the platform was not present (i.e., WF- trials), two dimensions informed the rats of this type of trial, the shape of one landmark, object W, as well as the angular separation between F and this landmark, W. Then, test trials were always in the presence of B and F (as in Experiment 1). The results of this experiment showed two differences in comparison with Experiment 1 which are worth mentioning. First, in Experiment 2 the initial discrimination seems to have been learned more rapidly than in Experiment 1 (the average latency to find the platform in the first twelve BF+ trials was 11.51 s. -instead of 24.90 s., as in Experiment 1). Secondly, in the test phase, a moderate peak shift was found, as can be seen in Figure 5 (instead of an area shift, as in Experiment 1). This last result indicates a poorer generalization in this phase in comparison to Experiment 1 (i.e., in the gradient of responding obtained, the highest amount of responding was not to S+ but to a test stimulus close to S+, slightly away from S-). How can the different results of these two experiments be explained?

The main manipulation in Experiment 2 (S- trials being in the presence of landmarks W and F, instead of B and F as in Experiment 1) intended to reduce the proportion of common elements shared by the two types of trial, S+ and S-, in order to facilitate the discrimination. As McLaren, Kaye, & Mackintosh (1989) have claimed, reducing the associability of landmarks or features common to S+ and S- in a discrimination problem should facilitate the learning of that discrimination. In fact, this is what was found in Experiment 2, where the average latency to find the platform in the first twelve BF+ trials was 11.51 s. instead of 24.90 s., as in Experiment 1. But it is also possible that the previous manipulation has affected the discrimination in a different way. Specifically, in Experiment 2 both the angular separation between the two landmarks present on a given trial, as well as the shape of the landmarks (i.e., the two dimensions) participated in the definition of the two types of trial, S+ and S-, with the consequence of both gaining control over the subjects performance. In fact it seems that the animals had learned something of the absolute values of the training landmarks because, otherwise, the test change in the landmarks would have gone undetected, with the result of an area shift effect, as in Experiment 1.

In Experiment 1 only one dimension, the angular separation between the two landmarks, informed the rats of the type of trial, either S+ or S-, and therefore gained control over the subjects performance. If the two modalities behave as spatial landmarks do within a standard learning or attentional model (i.e., Rescorla & Wagner, 1972; Mackintosh, 1973, respectively), competition between them is expected (for competition or overshadowing between spatial landmarks see Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006; Sánchez-Moreno, Rodrigo, Chamizo, & Mackintosh, 1999; Spetch, 1995). Such a competition clearly predicts a worse performance (i.e., a poorer generalization gradient, a peak shift effect) on the test trials by rats from Experiment 2 in comparison with Experiment 1. The reasoning being that the presence of one source of information (specifically, the presence of landmark W), could have overshadowed learning about the other (i.e., the angular separation between the two landmarks), with the consequence of a smaller control of the rats' performance by the angular separation between the two landmarks than if this source of information were separately presented (i.e., like in Experiment 1). If this line of reasoning is correct, it makes possible that the moderate peak shift effect observed in Experiment 2 could be, at least partly, a case of competition between sources of information. Besides, generalization decrement is also a possible explanation for the results of Experiment 2 considering the landmark changes from training to test in comparison to Experiment 1.

Experiment 2 contains a factor that perhaps could explain the results obtained. Specifically, the position of landmark F was different in comparison to Experiment 1. In Experiment 1, landmark F was always outside the pool, approximately 30 cm. behind its wall; while in Experiment 2 it was directly above the wall of the pool. It could be argued that the different position of landmark F in the two experiments could be responsible, somehow, for the different results (see Rodrigo *et al.*, 2006, for a demonstration that this position of F allows this landmark to compete with B). An unpublished experiment from our laboratory (see Figure 6) can be useful to solve this doubt. In this experiment the position of landmark F was identical to Experiment 2 (i.e., directly above the wall

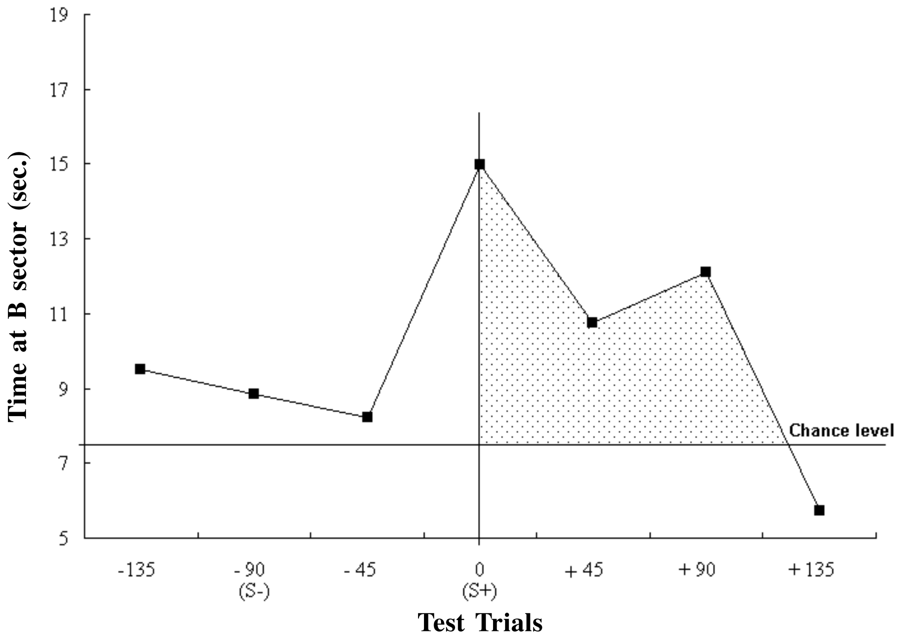

Figure 6. Mean time spent in the B segments by rats of an additional experiment during the test trials.

of the pool), while discrimination training was essentially identical to Experiment 1 (i.e., in the presence of two and the same landmarks, B and F, with an angular separation between them of 0 or 90 degrees, S+ and S-, respectively).

No evidence of peak shift in this new experiment, but instead an area shift effect was found (although an ANOVA examining the symmetry of the results did not reach the accepted level of significance). Thus, it could be concluded that the two positions of landmark F do not seem to be a crucial determinant to obtain one or the other result (i.e., an area or a moderate peak shift effect).

According to Spence (1937) animals learn about the *absolute* properties of the stimuli. Therefore, when they are presented with a discrimination between S+ and S-, both stimuli from the same dimension, there will be a measure of generalization between them, with the consequence that the excitatory tendency to approach S+ will also be elicited by S- (and by other stimuli), but to a weaker extent; and for the same reason, the inhibitory tendency to avoid S- will be aroused by S+ (and by other stimuli), but to a weaker extent. The strength of approach to either stimulus will then be determined by the interaction between these sources of generalization. Subsequent research by Hanson (1959), the peak shift effect, absolutely confirmed Spence's prediction. But the peak shift effect also has alternative explanations in terms of relational learning (Kohler, 1939; Thomas, 1974).

In experiments with human participants, Thomas (1974; and for a revision see Thomas, Mood, Morrison, & Wiertelak, 1991) interpreted the peak shift effect in a perceptual way (instead of a learning way), according to Helson's (1964) theory of adaptation level. Following these authors, organisms learn response tendencies between stimuli values. The adaptation level account (originally developed to explain the "central tendency effect") may be thought of as a frame of reference based on an average of all relevant stimuli experienced by the subject.

In the case of a discrimination training, the adaptation level is presumably established approximately midway between the training stimuli, S+ and S-, thus forming an adaptation level or frame of reference, so that subjects learn to respond to one stimulus, S+, which is "X" units greater than the adaptation level, and to a second stimulus, S-, which is "X" units smaller than the adaptation level. In the test phase, the adaptation level moves towards the average of the range values being tested. If the stimuli are tested in a symmetrical way (which is the normal thing to do) then the adaptation level moves towards S+, with the consequence that the highest rate of responding moves "X" units in relation to what the subject learned during training, and a peak shift effect is observed. But as Thomas (1974) indicates, such a peak shift effect is found in humans but not when non-human subjects are used, perhaps due to the length of the training discrimination -which is normally much longer in non-human than in human participants (Thomas *et al*., 1991). Such a longer discrimination could have caused a more stable adaptation level, one more resistant to the change experienced in the test phase, when new values are presented in the test trials. Cheng *et al*. (1997) have tested the range effects following the generalization test phase by presenting those values belonging to either one or another side of the gradient although with negative results. These authors argued that the fact that the test trials were intermixed with retraining trials could have had the consequence that the level of adaptation will not move.

Although in the present experiments the range effects have not been tested (our values were symmetrical round S+), we did not expect any range effects considering our previous results (Rodrigo *et al*., 2006). In the Rodrigo *et al*. study, half the rats were tested with values belonging to a side of the S+ (0, -45, -90, -135), and the remaining rats with values belonging to other side of the S+ (0, +45, +90, +135). If the range effects had been effective, we should have found the highest level of responding between test trials 45 and 90, which was not the case. Following Cheng *et al*. (1997), the fact that the test trials were, also in our case, intermixed with re-training trials could have had the consequence that the level of adaptation will not move. Because in the present experiments test trials were identical to those in the Rodrigo *et al*. (2006) study, the arguments also apply to the present experiments.

No doubt, more research is needed to clarify what exact conditions are crucial to obtain in the Morris pool the results just seen, an area shift and a moderate peak shift effect..

In conclusion, in the present study area and peak shift effects were found when varying the location of two stimuli in a navigation task. We believe that these results contribute to demonstrate a cross-species generality while showing a clear parallelism between spatial learning and other forms of learning.

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