

Encoding of Geometric and Featural Spatial Information by Goldfish (*Carassius auratus*)

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Goldfish (*Carassius auratus*) were trained in different place-finding tasks as a means of analyzing their ability to encode the geometric and the featural properties of the environment. Results showed that goldfish could encode and use both geometric and featural information to navigate. Goldfish trained in a maplike, or relational, procedure encoded both types of information in a single representation. In contrast, fish trained in a directly cued procedure developed 2 independent and competing strategies. These results suggest that the geometric properties of the spatial arrangement and discrete landmarks are sensitive to encoding in a maplike or relational system, whereas different sources of spatial information are encoded in a single and flexible representation of the environment.

Several works have shown that vertebrates are able to encode the geometric properties of spaces and surfaces. Rats trained to locate a goal in a rectangular environment, where each corner was distinctly signaled by a panel with particular features, consistently confused geometrically equivalent places, despite the fact that each corner of the apparatus presented distinct featural properties, for example, different color and brightness (Cheng, 1986; Margules & Gallistel, 1988). In a reference memory task, rats were able to partially use featural information to locate a goal; however, they were not able to combine featural and geometric information: As the high number of rotational errors suggests, they mainly relied on the geometrical properties provided by the surfaces that defined the environment (Cheng, 1986; Gallistel & Cheng, 1985). It has been suggested that rats encode the geometrical properties of the configuration of spaces and surfaces in a distinct cognitive module, which Cheng (1986) called *metric frame*. This representation of the geometrical properties of space would be characterized by two main properties. On one side, it would provide a global framework for spatial orientation, and on the other, it would be impervious to nongeometric information such as texture, color, or odor (Cheng, 1986; Fodor, 1983; Gallistel, 1990). Gallistel (1990) defined *geo-*

metric information as the property that a surface, line, or point possesses relative to the position of other objects or surfaces present in the same environment. In contrast, *nongeometric information* is defined as the property that cannot be defined by relative position alone (p. 212).

Results consistent with the idea that rats encode geometric information in a distinct cognitive module have been reported in other works (Benhamou & Poucet, 1998; Biegler & Morris, 1993, 1996; Cheng & Gallistel, 1984; Margules & Gallistel, 1988). Also, similar results have been reported for young children. In a task similar to that used by Cheng (1986), 18–24-month-old children were trained to find a goal in a rectangular room with either uniformly painted walls or a distinctive wall painted blue (Hermer & Spelke, 1994). In both tasks, children used the geometry of the apparatus to find the goal, but they were unable to use the featural information (blue wall). Children, like rats, failed to combine geometric information with any other spatial information to reorient (Gouteux & Spelke, 2001; Hermer, 1997; Hermer & Spelke, 1996; Wang, Hermer, & Spelke, 1999). In contrast with these results, recent studies have reported the use of nongeometric information by children (Garrad-Cole, Lew, Bremmer, & Whittaker, 2001; Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, & Huttenlocher, 2001) and by rats (Golob & Taube, 2002). In summary, although there are some contradictory results, a larger number of studies have evidenced that several species are able to encode geometric information but that they do not use it jointly with featural cues when the latter would have permitted them to disambiguate symmetrical situations and, consequently, to reach optimal performance levels.

However, other studies have shown that adult humans (Hermer & Spelke, 1994), chicks (Vallortigara, Zanforlin, & Pasti, 1990), pigeons (Kelly & Spetch, 2001; Kelly, Spetch, & Heth, 1998), nonhuman primates (Gouteux, Thinus-Blanc, & Vauclair, 2001), and fish (Sovrano, Bisazza, & Vallortigara, 2002; Vargas, 2000) are able to make a joint use of geometrical and featural information for goal location using similar procedures.

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Such discrepant data, in particular the exclusive use of geometry, may be accounted for in terms of species (rats vs. pigeons and monkeys; cf. above); maturation and mastery of spatial language (young children vs. adults; Hermer & Spelke, 1994); previous experience (Kelly et al., 1998); and methodological aspects such as the size of the experimental set-up (Learmonth et al., 2002), the disorientation method (Gouteux & Spelke, 2001), the size of the featural cues (Gouteux et al., 2001), and the task to perform (Golob & Taube, 2002).

The possibility that animals could process and use the geometry of the experimental space to locate places in the environment has promoted considerable interest. However, little is known about the mechanisms underlying this capacity or the way in which this information is encoded. In opposition to the idea proposed by Cheng (1986)—that geometric information is encoded in a separate cognitive module—the idea that geometric spatial and surface information might be included in cartographic representations has been considered. This hypothesis comes from works that examined the simultaneous use of geometric and featural cues. The fact that rats and children use basically geometric information to solve spatial tasks (Benhamou & Poucet, 1998; Cheng, 1986; Greene & Cook, 1997; Hermer & Spelke, 1994; Margules & Gallistel, 1988), whereas chicks use primarily featural information (Vallortigara et al., 1990), and pigeons one or another according to their previous experience (Kelly et al., 1998), suggests the possibility that both kinds of spatial information might be encoded independently as separate spatial representations. However, the possibility that animals develop two competing strategies based on geometric and featural information has not been tested. The parallel encoding of spatial information in different learning and memory systems, allowing animals to possess redundant information about their environment, has been considered a suprastrategy phenomenon for the spatial adjustment of an organism to the environment (Able, 1991; Reese, 1989). The cognitive mapping theory (O'Keefe & Nadel, 1978) is in agreement with the combined use of allocentric and egocentric strategies, indicating that the taxon and the cartographic hippocampus-dependent spatial memory systems are not mutually exclusive but rather complementary (Nadel, 1990; Schacter & Tulving, 1994; Sherry & Schacter, 1987; Shettleworth, 1993; Tulving, 1984, 1985).

An increasing number of laboratory studies have indicated that teleost fish, like other vertebrates, use at least two types of spatial strategies with distinct behavioral properties and different neural bases for navigation (see, e.g., Salas, Rodríguez, Vargas, Durán, & Torres, 1996). Thus, fish are able to adapt their behavior to specific situational requirements on the basis of processing and encoding the environmental features in a unique allocentric memory representation or in simple egocentric representations of particular objects associated with particular responses, or on the basis of the combined action of the two (López, Bingman, Rodríguez, Gómez, & Salas, 2000; López, Broglio, Rodríguez, Thinus-Blanc, & Salas, 1999; Reese, 1989; Rodríguez, Durán, Vargas, Torres, & Salas, 1994; Rodríguez et al., 2002; Roitblat, Tham, & Golub, 1982; Salas, Broglio, et al., 1996; Salas, Rodríguez, et al., 1996). In addition, some experimental evidence suggests that the modification of the geometry of the environment does not alter the performance of fish trained in a directly cued procedure when the cues associated with the goal are maintained (López et al., 1999).

Nevertheless, a change in the geometry of the apparatus in a relational or allocentric procedure produces a strong deficit in locating a goal (López et al., 1999). This result suggests that the configuration of the cues with respect to the geometry of the apparatus may influence different spatial strategies with different properties. If this hypothesis is true, one could expect that the geometric properties of the environment and nongeometric information can be codified either jointly in a maplike representation or in two independent and competing strategies.

In this study, we tested goldfish under different spatial configurations of cues to determine their capacity to encode and use geometric and featural information. We did this to analyze the possible similarities and differences in relation to those described in mammals and birds. We also tested the characteristics of the codification of geometric information with different configurations of featural information to analyze whether geometric information could be included in cartographic representations based on encoding the reciprocal spatial relationships among the different geographical landmarks.

Experiment 1

We designed the first experiment to study whether goldfish are able to encode and use the geometric information of the environment in place-finding tasks in a manner similar to that of mammals and birds. For this purpose, fish were trained to find a goal placed in a corner of a rectangular environment on the basis of the geometrical information provided by the apparatus (similar to that used by Cheng, 1986). In this task, locating the goal required fish to determine the spatial relationships between the geometrical properties of the apparatus and the goal. Because of the geometric properties of the apparatus, the correct corner was indistinguishable from the diagonally opposite (180°) corner.

Method

Subjects. Ten experimentally naive goldfish (*Carassius auratus*), 12–14 cm in body length, obtained from a local supplier, served as subjects. Prior to the experiment, the fish were maintained for 2 months in small groups in glass aquaria with aerated and filtered water at 20 ± 2 °C, on a 14:10-hr light–dark cycle. Goldfish were fed once a day after the experimental session with Tetrapond Pondsticks (Ulrich Baensch GmbH, Melle, Germany). At the end of each experimental session, the fish were returned to the home aquaria. Use and handling of the subjects were in accordance with the European Communities Council Directive of 24 November 1986 (Council of the European Communities, 1986).

Apparatus. The experimental apparatus consisted of a dark gray rectangular enclosure made out of rigid polyvinyl chloride (PVC; 70 cm wide \times 35 cm deep \times 24 cm high), placed in the center of a large circular aquarium (120 cm in diameter and 30 cm high) made out of flexible PVC. The aquarium was filled to a depth of 20 cm with aerated and filtered water at 20 ± 1 °C. The experimental enclosure contained four openings (6 cm wide \times 20 cm high), one in each corner, that served as exit doors. In the training phase, three of these doors were blocked by a transparent glass barrier, the fourth door remaining open as the only exit (goal; see Figure 1A). So that no salient cues were available except those provided by the experimental setting, the floor and the walls of the aquarium were made of homogeneous opaque white plastic and the walls of the experimental room were of a homogeneous brown color. The enclosure was illuminated by a 40-W lightbulb placed at a height of 30 cm over the center of the apparatus,

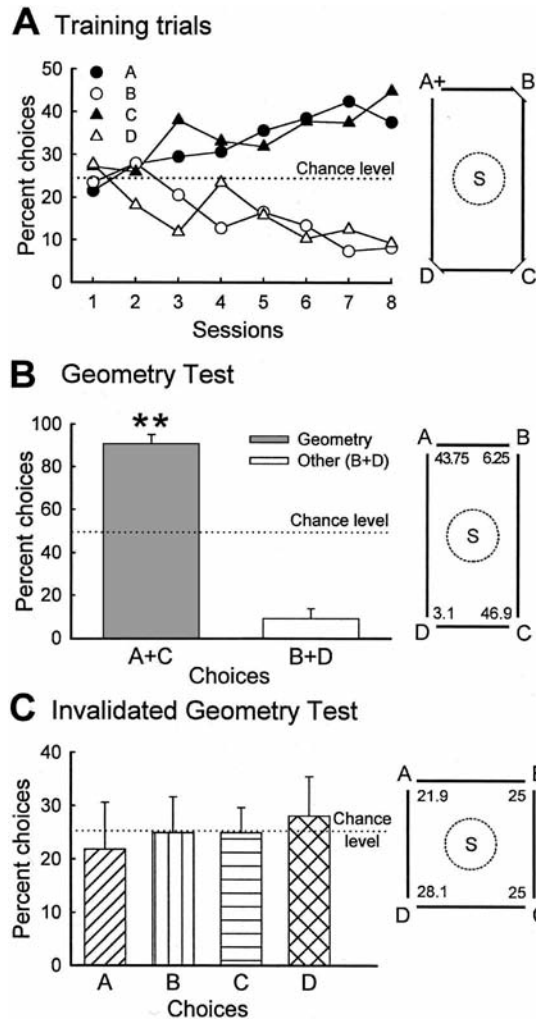


Figure 1. A: Percentage of choices during the eight training sessions in Experiment 1. On the right are diagrams of the experimental conditions, showing the start cylinder (S), the position of the glass barriers, and the location of the goal. The position of the reinforced door is indicated by the plus sign. Data are shown with the reinforced door in A; however, the actual reinforced door was counterbalanced across fish. B: Results and schematic representation of the geometry test. C: Results and schematic representation of Type II probe trials. Numbers in diagrams indicate the percentage of choices to each door; error bars denote standard errors of the means. Asterisks denote significant differences between choices ($p < .01$).

keeping the experimental room in the dark during training and test sessions. The fish's movements were monitored by means of a video camera mounted in the center of the experimental room.

A glass cylinder (20 cm in diameter and 22 cm high) placed in the center of the rectangular enclosure served as the start point. Fish were placed in the cylinder, and the cylinder was raised by a hand-operated device, releasing the fish into the enclosure. Fish were trained in groups of 4, but each trial was performed individually. Two glass enclosures placed in the aquarium adjacent to the two long walls of the experimental enclosure served as waiting areas during the intertrial intervals. The subject within the experimental enclosure could not see the others until they had passed through the exit and completed the trial.

Training. Prior to training, the fish were preexposed to the apparatus by being allowed to swim 10 times from the start cylinder and make spontaneous exits through the four open doors. The glass barriers were not used during preexposure trials. The training period began the following day and consisted of 20-trial sessions on consecutive days until the fish reached the acquisition criterion (see below). For each fish, the goal location occupied a constant spatial position relative to the apparatus's geometry. However, the location of the goal was counterbalanced such that different fish were rewarded in each one of the four possible goal locations.

To begin each trial, the fish was carefully placed in the glass cylinder. After 15 s, the cylinder was raised, releasing the fish into the enclosure. The fish could then freely swim to the goal to escape from the enclosure and exit to the open space of the aquarium. An error was scored when the fish bumped against a glass barrier, and a correct choice was scored when its head passed through the exit. A trial was considered successful only when the initial choice was correct. The relative position of the correct door with respect to the apparatus remained constant throughout the experiment, but the enclosure was rotated pseudorandomly as a whole within the aquarium between trials to ensure that the enclosure's geometry was the only relevant and spatially invariant information. An acquisition criterion of 70% geometrically correct choices in one session (14 correct trials of 20) was established.

Once the fish reached the acquisition criterion, two additional post-criterion 24-trial sessions were conducted; in each session, there were 20 training trials with 4 probe test trials interspersed. The two different types of probe tests were presented in a pseudorandom order. By the end of Experiment 1, each fish had performed a total of eight probe trials, four of each type. A choice was recorded when the fish's head passed through one of the doors.

Probe test. Two different probe trials were carried out: geometry test and invalidated geometry test. During the probe trials, the glass barriers were not used, so that fish could exit freely through any door. For the geometry test, the apparatus was the same as during training, but during these test trials the four exits (one in each corner of the rectangular apparatus) were open. The objective of these probe tests was to verify whether the fish used the geometric information provided by the surfaces of enclosure or whether, on the contrary, their performance was based on the direct detection of the presence of the glass barriers.

For the invalidated geometry test, a new apparatus was used, which modified the geometric properties of the experimental enclosure used during training. This new apparatus consisted of a square enclosure (49.5 × 49.5 × 24.0 cm) built of the same dark gray PVC as the training apparatus. The apparatus contained four openings, one in each corner. The dimensions of the four openings and the area of the apparatus were the same as those of the training enclosure (Figure 1C). The purpose of this test was to analyze the performance of the fish when the geometric information provided by the enclosure was not relevant to solution of the task.

Results

Training trials. Figure 1A shows the mean percentages of choices for each of the four doors during the training trials. No statistically significant differences were observed in any of the analyzed variables between the counterbalanced conditions (Kruskal-Wallis, all $\chi^2(3, N = 8) < 5.70$, all $ps > .12$; consequently, the data of the fish were pooled in the group mean. Two fish that had not reached the criterion by the seventh session were excluded from the analysis. Therefore, the final size of the group was 8. At the onset of the training, during the first 10 trials of Session 1, the choices of the fish were distributed at random between the exit door and the three doors blocked by the glass barriers, all $\chi^2(3, N = 8) \leq 2.00$, all $ps > .57$. With more training,

the fish progressively chose more frequently the correct door and the geometrically equivalent door, increasing their accuracy (Friedman), $\chi^2(7, N = 8) = 26.02, p < .01$, for the eight sessions. All fish reached the criterion on Session 6, maintaining it until the end of the experiment.

Probe tests. Figure 1B shows the percentage of choices during the geometry test when the glass barriers were removed. The percentage of geometrically correct choices (90%) was significantly higher than that expected by chance, $\chi^2(1, N = 8) = 21.13, p < .01$. No statistically significant differences were observed between the percentage of choices to the goal door and the percentage of choices to the geometrically equivalent door, $\chi^2(1, N = 8) = 0.00, p = .85$. The results of the invalidated geometry test, in which the geometric cues were removed, are reported in Figure 1C. During these trials, no significant differences were observed in the percentage of choices between the four doors, $\chi^2(3, N = 8) = 0.30, p = .97$.

Discussion

The results of Experiment 1 show that goldfish were able to locate a place in an environment that lacked relevant featural information by encoding the goal location with respect to the geometrical properties of the experimental space. Thus, fish made systematic rotational errors by confusing geometrically equivalent places (Figure 1A). These results suggest that the fish relied on the geometric information provided by the surfaces of the experimental apparatus to orient. Thus, when the geometric characteristics of the apparatus were modified such that they were made ambiguous, the performance was significantly impaired, suggesting that the fish used no other landmark but the shape of the rectangular arena (Figure 1C). In addition, the results of the geometry test indicate that the observed pattern of responses was not due to the direct detection of the glass barrier that blocked the error doors (Figure 1B).

Experiment 2

Many experiments have shown that rats and young children use predominantly geometrical information to orient, and when geometrical information is irrelevant to solve the task, they do not use featural information to orient (Benhamou & Poucet, 1998; Biegler & Morris, 1993, 1996; Wang et al., 1999). Experiment 2 was aimed at determining whether fish are able to use the featural information of the environment to solve a task in which the use of geometric information is irrelevant. For this purpose, in Experiment 2, fish were trained in the spatial constancy task. This task was used previously to test the spatial capabilities of fish (Ingle & Sahagian, 1973) and mammals (Thinus-Blanc & Ingle, 1985). In this spatial test, locating the goal required fish to determine the spatial relationship between cues within the test environment and the goal.

Method

Subjects. Eight experimentally naive goldfish, 12–14 cm in body length, obtained from a local supplier, served as subjects. They were maintained in the same condition as those described in Experiment 1.

Apparatus. The experimental apparatus used during training in Experiment 2 was a square box (the same used in the invalidated geometry test of Experiment 1). Two removable panels with alternate dark gray and white 2-cm vertical stripes provided the featural cues. These panels were placed on two adjacent walls of the square box. The goal was situated at one of the doors between a striped wall and an unstriped wall (see Figure 2A). The apparatus was placed in the same experimental room used in Experiment 1.

Training procedure. Training consisted of 20-trial sessions on consecutive days. An acquisition criterion of 13 trials out of 20 (65% correct in a session) for one session was established. As in Experiment 1, once the

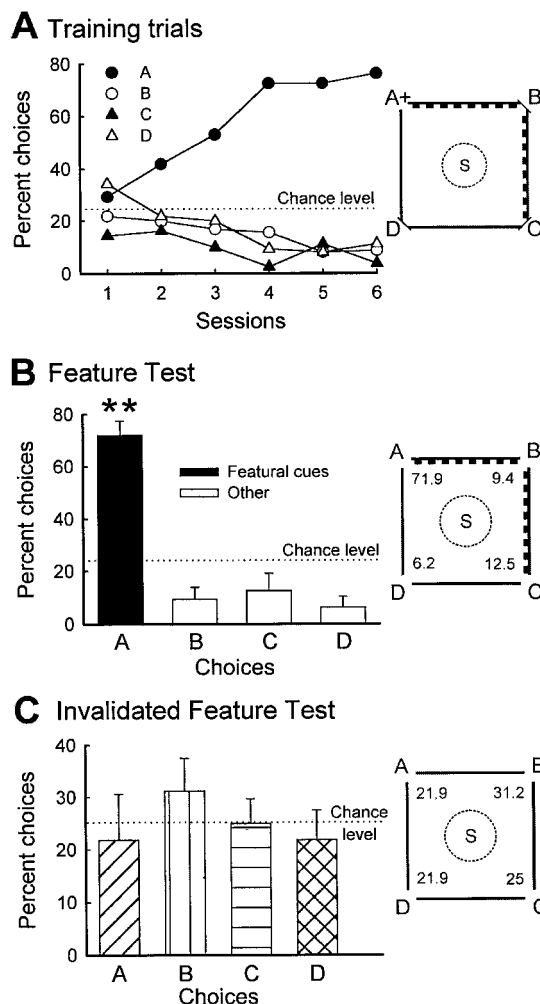


Figure 2. A: Percentage of choices during the training sessions in Experiment 2. The first six sessions were included because some fish had completed the training by that time. On the right are diagrams of the experimental conditions, showing the start cylinder (S), the position of the glass barriers, the location of the featural cues (striped walls), and the goal. The position of the reinforced door is indicated by the plus sign. Data are shown with the reinforced door in A; however, the actual reinforced door was counterbalanced between Doors A and C across fish. B: Results and schematic representation of the geometry test. C: Results and schematic representation of Type II probe trials. Numbers in diagrams indicate the percentage of choices to each door; error bars denote standard errors of the means. Asterisks denote significant differences between choices ($p < .01$).

fish reached the acquisition criterion, two additional 20-trial postcriterion sessions were conducted; in each session, four probe tests trials were interspersed. By the end of Experiment 2, each fish had performed a total of eight probe trials, four of each type.

Probe test. To examine whether the fish were using the featural cues to solve the task, we arranged two types of probe trials. The feature test was similar to training trials, but the glass barriers that occluded the three incorrect doors were removed, and therefore fish could exit freely through any door (Figure 2B). In the invalidated feature test, the striped walls were removed from the enclosure (Figure 2C). The objective of these probe tests was to verify that the fish did not detect the presence of the glass barriers and that they were using the information provided by the constant spatial relationships between the featural cues and the goal location to solve the task.

Results

Training trials. Figure 2A shows the performance of the fish trained in the square experimental environment. No significant differences were observed between the counterbalanced conditions (Mann–Whitney U test; all U s ≥ 3.5 , all p s $\geq .20$); consequently, the data were pooled. At the onset of training, during the first 10 trials of the first session, the choices of the fish were distributed randomly among the four exits, all $\chi^2(3, N = 8) \leq 3.60$, all p s $> .30$. With more training, the fish increased choice accuracy (Friedman), $\chi^2(5, N = 8) = 36.19$, $p < .01$, for the six sessions. Seven fish reached the learning criterion on Session 4, and 1 fish on Session 5. Performance was maintained at a steady level on post-criterion sessions.

Probe tests. The performance in the feature test, in which the glass barriers were removed, is shown in Figure 2B. Fish consistently continued to select the correct door in the probe trials. During these trials, the percentage of choices to the correct exit was significantly higher than that expected by chance, $\chi^2(3, N = 8) = 37.75$, $p < .01$. Figure 2C shows the performance in the invalidated feature test, in which the striped panels were removed from the walls. The percentage of choices did not differ from that expected by chance, $\chi^2(3, N = 8) = 0.75$, $p = .86$. Thus, the results of the probe trials showed that the accurate performance of the fish in this task was not based on the direct detection of the glass barriers, but rather, the fish used the featural information on the walls to solve the spatial task.

Discussion

The results of Experiment 2 indicate that goldfish can locate a place by using the featural information of an environment where geometric properties do not provide distinctive spatial information (Figure 2A). The dramatic performance decline to random levels during the invalidated feature test (Figure 2C), when the featural cues were removed, indicate that the fish relied on the information provided by the distinctive walls. The possibility that the fish could have used other types of strategies to solve this task—for instance, a guidance strategy based on the use of geomagnetic cues or other directional cues—can be disregarded, as the apparatus was systematically rotated as a whole within the aquarium between trials. Thus, the only relevant and invariant information was provided by the featural cues. In this sense, performance decreased to random level when the featural information was eliminated (Figure 2C). In

addition, the results of the probe trials when the glass barriers blocking the incorrect doors were removed demonstrate that the performance of the fish could not be due to the direct detection of the glass barrier (Figure 2B).

Experiment 3

A great deal of data suggest that, with the possible exception of rats and young children, all the vertebrates species studied are able to encode the geometric and featural information of the environment simultaneously. All these studies have focused their interest on the primacy of control of these two different types of information. Nevertheless, the possibility that geometric information may be included in a cartographic representation of environmental space has not been tested. We performed Experiment 3 to analyze the orientation strategies of fish when the experimental environment simultaneously provided geometrical and featural information. Moreover, the purpose of this experiment was to identify the reliance on both types of information and whether geometric information is included in a cartographic representation, or whether this kind of information is kept as a separate module in the way postulated by Cheng (1986). For this purpose, fish were trained in a rectangular box in which featural information was provided. The configuration of featural cues with respect to the goal was similar to the spatial constancy task used in Experiment 2.

Method

Subjects. Eight experimentally naive goldfish, 12–14 cm in body length, obtained from a local supplier, served as subjects. The fish were maintained in the same conditions as those described in Experiment 1.

Apparatus. The apparatus used during training trials was a rectangular box (the same used in Experiment 1). Two removable gray PVC panels (cues) with 2-cm wide white vertical stripes were placed on two adjacent walls of the cage. The goal was situated in one of the doors, which was marked by different featured walls in a similar way to that of Experiment 2 (see Figure 3A).

Training procedure. The training procedure was similar to that used in Experiment 1. An acquisition criterion of 13 correct trials out of 20 (65% correct in a session) was established. Once the fish reached the acquisition criterion, two additional 20-trial postcriterion sessions were conducted; in each session, 6 probe tests trials were interspersed. By the end of Experiment 3, each fish had performed a total of 12 probe trials, 4 of each type.

Probe test. Three different types of probe trials were performed. In the geometry test, the featural cues (striped walls) were removed from the enclosure (Figure 3B). The purpose of this test was to verify whether the fish had encoded the geometrical information provided by the surfaces of the enclosure during the training phase even when featural information was simultaneously available. In the feature test, a square enclosure (the same used in the invalidated geometry test of Experiment 1 and during training in Experiment 2) with striped panels in adjacent walls was used (Figure 3C). The purpose of this test was to make irrelevant the geometrical information to assess to what extent fish encoded the featural information when geometrical information was simultaneously available. In the dissociation test, the striped walls were rotated 90° in the enclosure (Figure 3D). The purpose of this test was to create a situation in which the two sources of information were set in conflict.

Results

Training trials. The percentage of choices during training for each door is shown in Figure 3A. No significant differences were

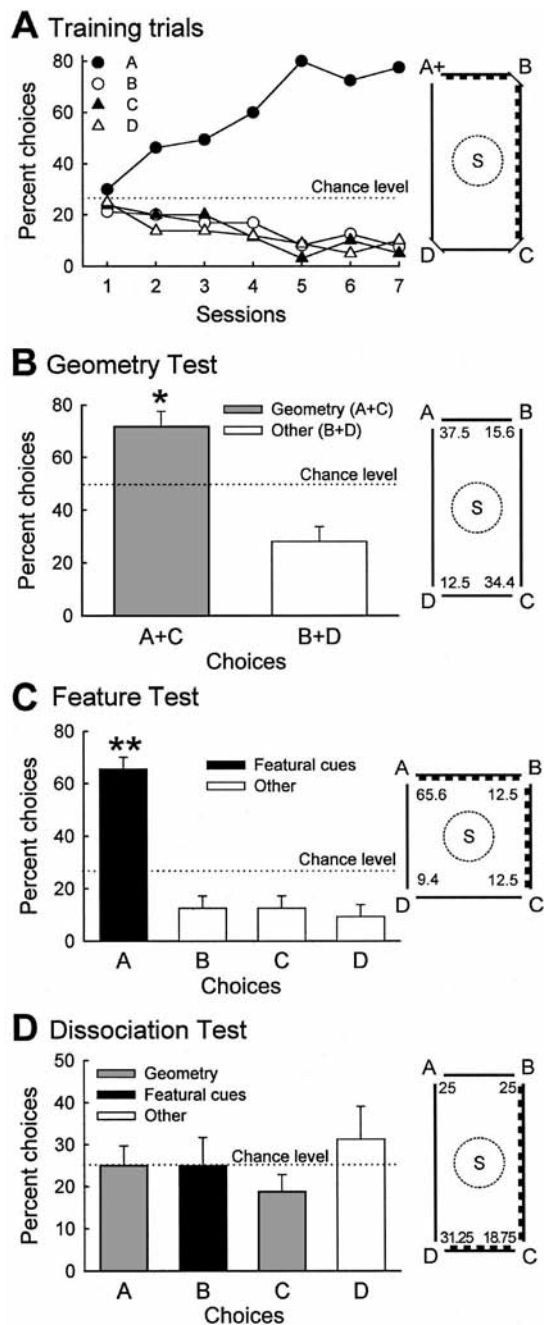


Figure 3. A: Percentage of choices during the training sessions in Experiment 3. The first seven sessions were included because some fish had completed the training by that time. On the right are diagrams of the experimental conditions, showing the start cylinder (S), the position of the glass barriers, the location of the featural cues (striped walls), and the goal. The position of the reinforced door is indicated by the plus sign. Data are shown with the reinforced door in A; however, the actual reinforced door was counterbalanced between Doors A and C across fish. B: Results and schematic representation of the geometry test. C: Results and schematic representation of Type II probe trials. D: Results and schematic representation of Type III probe trials. Numbers in diagrams indicate the percentage of choices to each door; error bars denote standard errors of the means. Asterisks denote significant differences between choices (* $p < .05$; ** $p < .01$).

observed between the counterbalanced conditions (Mann–Whitney U test; all U s ≥ 3.5 , all $ps \geq .20$); consequently, the data were pooled. At the onset of the training, during the first 10 trials of the first sessions, the fish chose at random between the four exits, all $\chi^2(3, N = 8) \leq 3.60$, all $ps > .30$. With additional training, the fish increased choice accuracy (Friedman, $\chi^2(6, N = 8) = 40.36, p < .01$, for the seven sessions. Six fish reached the learning criterion on Session 5, and 2 on Session 6. The performance level remained steady during postcriterion sessions.

Probe tests. Figure 3B shows the performance during the geometry test, in which the featural information was removed. The percentage of geometrical choices (71.88%) was significantly higher than that expected by chance, $\chi^2(1, N = 8) = 6.13, p > .01$. However, the percentage of choices to the correct door was not significantly different from the percentage of choices to the geometrically equivalent door, $\chi^2(1, N = 8) = 0.04, p = .84$. Figure 3C shows the performance during the feature test. The percentage of choices to the correct door (65.60%) was significantly higher than expected by chance when only the featural information was available, $\chi^2(3, N = 8) = 28.25, p < .01$. The performance during the dissociation test, in which the geometrical and featural information was set in conflict, is shown in Figure 3D. Fish did not show a preference for any particular door; neither the percentage of geometrical choices nor the featural choices were significantly different from that expected by chance, $\chi^2(3, N = 8) = 1.00, p = .80$.

Discussion

The results of Experiment 3 show that fish were able to simultaneously encode featural and geometrical information when the environment provided both kinds of information. Furthermore, fish were able to use both geometric and featural information when access to the other type of information was restricted. Fish had codified the geometric properties of the environment even when this information was not necessary to solve the task because of the presence of featural information.

The results of the dissociation test show that goldfish did not use featural or geometric information when these two types of information were placed in conflict. They solved the task successfully by using either the geometrical cues (Figure 3B) or the featural cues (Figure 3C) but chose at random between the possible exits when the information provided by both types of cues was dissociated and made contradictory (Figure 3D). This suggests that the goldfish may have elaborated a complex representation of the environment, in which the different elements of the experimental space (including both the featural cues and the general shape of the apparatus) were not only simultaneously encoded but probably encoded as one configural representation integrating the two sources of information (Eichenbaum, Otto, & Cohen, 1994; Eichenbaum, Stewart, & Morris, 1990; O’Keefe & Nadel, 1978; Poucet, 1993; Thinus-Blanc, 1996). It has been suggested that major changes introduced in the spatial relationship among stimuli in an experimental environment induce animals to consider that they are in a novel learning situation (Nadel & Willner, 1980; Nadel, Willner, & Kurz, 1985). The results of the present experiment indicate, on one hand, that fish’s representation of the environment is flexible and resistant to losses of redundant but

relevant spatial information but, on the other hand, is disrupted by alterations in the metric and topological relationships among the composing elements (López et al., 1999; O'Keefe & Nadel, 1978).

Experiment 4

The results of Experiment 3 showed that goldfish trained in a place-finding task with geometric and featural information simultaneously available were able to use either of these two kinds of information, in the absence of the other, to orient. Nevertheless, when both kinds of information were placed in conflict, the performance dropped to random levels. In contrast, in an equivalent situation, adult primates and birds chose one or another, suggesting that these animals encoded both types of information in a way different from goldfish. The differences between fish (Experiment 3) and adult primates and birds may be explained by experimental differences in the relationship between the cues and the goal in the present experiment versus the experiments with primates and birds. In Experiment 3, the goal was not directly marked by any of the cues; however, in experiments with birds (Kelly et al., 1998; Vallortigara et al., 1990) and adult primates (Gouteux et al., 2001; Hermer & Spelke, 1994) one conspicuous cue directly marked the goal. López et al. (1999) found that for goldfish trained in a place-learning task, the geometrical properties of the environment prevailed over conspicuous local cues. In contrast, a massive change in the geometry of the apparatus did not alter the performance of goldfish trained in a cue task. This result suggests that a maplike, or relational, representation of the environment may contain geometric information. In contrast, a cue-directed, or guidance, strategy would be independent of the geometric information of the environment. In this case, the geometric information could be codified as a separate, independent representation.

To test this possibility in Experiment 4, we trained goldfish in a directly cued procedure in a rectangular apparatus. To ensure a good level of similarity with Experiment 3, we used the same apparatus, and the only difference was the relationship of the goal with respect to the featural cues. In Experiment 3, locating the goal required fish to determine the spatial relationship between the cues and the goal; in Experiment 4, the goal was directly signaled by the featural cues.

Method

Subjects. Eight experimentally naive goldfish, 12–14 cm in body length, obtained from a local supplier, served as subjects. The fish were maintained in the same conditions described in Experiment 1.

Apparatus. The apparatus described in Experiment 3 was used during this experiment; the only difference was the position of the goal with respect to the featural cues. In Experiment 4, the goal was situated in one of the doors flanked by two identical walls (Figure 4A).

Training procedure. The training procedure was similar to that used in the Experiment 1. An acquisition criterion of 13 correct trials out of 20 (65% correct in a session) was established. Once the fish reached the acquisition criterion, two additional 20-trial postcriterion sessions were conducted; in each of these, 6 probe tests trials were interspersed. By the end of Experiment 4, each fish had performed a total of 12 probe trials, 4 of each type.

Probe test. The probe trials described in Experiment 3 were used during this experiment. In the geometry test, the featural cues were removed from the enclosure (see Figure 4B). In the feature test, the square

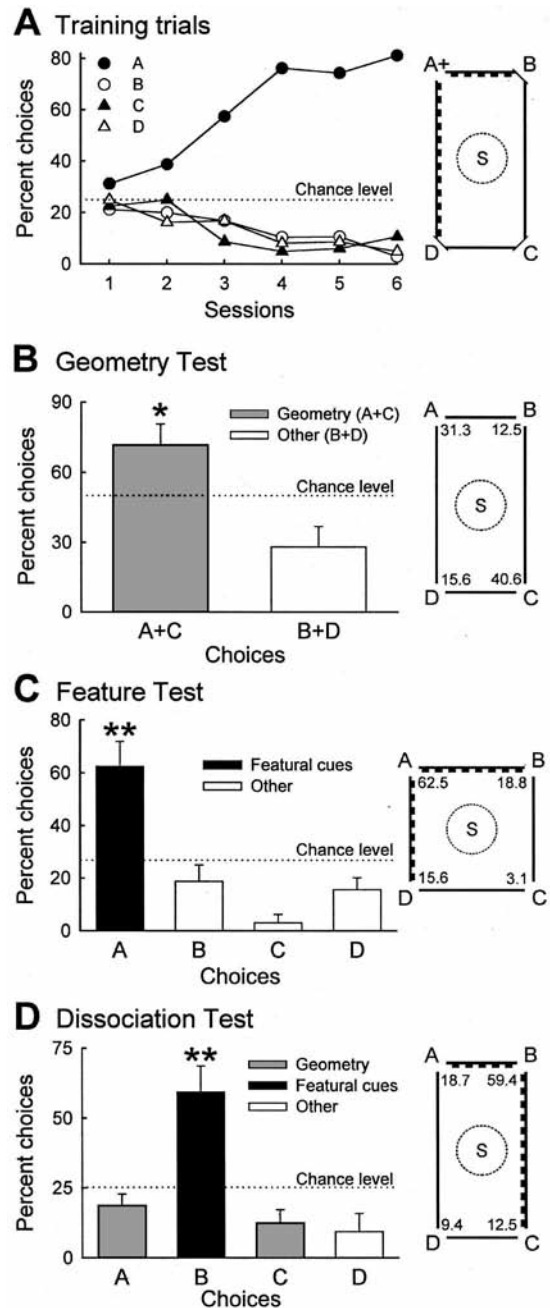


Figure 4. A: Percentage of choices during the training sessions in Experiment 4. The first six sessions were included because some fish had completed the training by that time. On the right are diagrams of the experimental conditions, showing the start cylinder (S), the position of the glass barriers, the location of the featural cues (striped walls), and the goal. The position of the reinforced door is indicated by the plus sign. Data are shown with the reinforced door in A; however, the actual reinforced door was counterbalanced between Doors A and C across fish. B: Results and schematic representation of the geometry test. C: Results and schematic representation of Type II probe trials. D: Results and schematic representation of Type III probe trials. Numbers in diagrams indicate the percentage of choices to each door; error bars denote standard errors of the means. Asterisks denote significant differences between choices (* $p < .05$; ** $p < .01$).

enclosure with striped panels in adjacent walls was used (see Figure 4C). In the dissociation test, in which the striped walls were rotated 90° in the enclosure, for the case represented in Figure 4D, Door B was featurally correct, Doors A and C were geometrically correct, and Door D was incorrect on the basis of both geometric and featural information.

Results

Training trials. The percentage of choices for each door during training is shown in Figure 4A. No significant differences were observed between the counterbalanced conditions (Mann–Whitney U test; all $U_s \geq 5.0$, all $p_s > .48$); consequently, the data were pooled. At the onset of training, during the first 10 trials of the first session, the fish chose at random between the four exits, all $\chi^2(3, N = 8) \leq 4.40$, all $p_s > .22$. With additional training, the fish increased choice accuracy, (Friedman), $\chi^2(5, N = 8) = 34.62, p < .01$, for the six sessions. Seven fish reached the criterion on Session 4, and 1 on Session 5. The performance level remained steady during postcriterion sessions.

Probe tests. Figure 4B shows the performance during the geometry test, in which the featural information was removed. The percentage of geometrical choices (71.9%) was significantly higher than that expected by chance, $\chi^2(1, N = 8) = 6.13, p > .01$. However, the percentage of choices to the correct door and the geometrically equivalent door were not significantly different from each other, $\chi^2(1, N = 8) = 0.39, p = .53$. Figure 4C shows the fish's performance during the feature test. The percentage of choices to the correct door when only the featural information was available (62.5%) was significantly higher than that expected by chance, $\chi^2(3, N = 8) = 25.75, p < .01$. The performance during the dissociation test, in which the geometrical and featural information was set in conflict, is shown in Figure 4D. The fish showed a greater preference for the door corresponding to the correct door according to the featural cues, $\chi^2(3, N = 8) = 20.75, p < .01$.

Discussion

Taken together, the results of Experiments 3 and 4 show that goldfish trained in environments where featural and geometric information were simultaneously provided were able to use both types of spatial information for place location. The performance during training trials shows that the fish used the featural information to locate the goal. Furthermore, the results of the probe trials in which the geometrical cues were eliminated demonstrate that the fish were able to locate the goal on the basis of the featural cues exclusively (Figures 3C and 4C). In addition, the results of the probe trials in which the featural information was removed indicate that the goldfish encoded the geometrical characteristics of the experimental apparatus, even though the featural information was sufficient to solve the task (Figures 3B and 4B). The fact that fish encoded the geometrical information conveyed by the environment even when the featural cues provided enough information to locate the goal indicates that they could discriminate, encode, and use a variety of diverse and redundant sources of spatial information for goal location.

In the dissociation test, when the featural cues were rotated 90° relative to the geometrical cues within the experimental apparatus (Figure 4D), the two sources of spatial information conveyed contradictory information about the location of the goal, making

the simultaneous use of both sources of information impossible. In this test, goldfish in Experiment 4 preferentially chose on the basis of the featural information, suggesting that the fish had encoded geometric and featural cues as two independent, competing strategies. In fact, the data indicate that these fish demonstrated primary stimulus control by the featural information. The differences found between Experiment 3 and Experiment 4 in this test may be explained by the differences in the procedure. Fish solved the task used in Experiment 3 by means of a maplike, or relational, strategy, and the task used in Experiment 4 by a cue guidance strategy (López et al., 1999; López, Broglio, Rodríguez, Thinus-Blanc, & Salas, 2000). Previous experiments have shown that a directly cued procedure facilitates a very local representation of the situation (the exit door surrounded by the featural information), whereas the need to use more complex relationships induces a more global processing of the environmental cues. Consequently, the configuration of the featural cues within the experimental environment might promote the use of different spatial strategies (López et al., 1999; López, Broglio, et al., 2000). In this sense, when the featural cues signaled the goal directly, the fish appeared to encode separately the geometric characteristics of the apparatus. In contrast, when the goal was not signaled by any particular cue, but by the arrangement of featural cues, the fish encoded the geometric characteristics of the apparatus and the featural cues jointly in a maplike, or relational, representation (López et al., 1999; Lopez, Broglio, et al., 2000).

It has been suggested that the capability to elaborate cartographic representations of the environment may be associated with the capacity to process and encode geometric information. Thus, a cartographic representation would encode the geometric relationships between points, lines, and surfaces that define the macroscopic structure of the space (Gallistel, 1990). However, it has been also pointed out that the global shape of the environment (the geometric properties) does not provide enough information by itself, and for this reason, a spatial representation should also encode the array of proximal and distal discrete cues or elements (Poucet, 1993).

General Discussion

The results of the experiments presented here show that goldfish are able to use different kinds of spatial information to orient and navigate. Thus, fish encoded the geometrical properties of the experimental environment, in both the absence (Experiment 1) and the presence (Experiments 3 and 4) of featural information. Moreover, the results of Experiment 3 and 4 suggest that goldfish encoded geometrical information even when it was not strictly required to locate the goal. Also, when the geometric information was insufficient or not relevant to goal location, goldfish used featural information (Experiment 2). Results of Experiments 3 and 4 suggest that goldfish can encode geometrical and featural information in two independent strategies, or in a complex representation of the environment that includes both types of spatial information. Our discussion about the pattern of performance in goldfish addresses two issues: the codification of featural and geometrical information by goldfish and the characteristics of the representation that goldfish elaborate when both geometrical and featural information are available.

Codification of Featural and Geometric Information by Goldfish

Goldfish can encode geometric information in a manner similar to that of rats (Cheng, 1986), chicks (Vallortigara et al., 1990), pigeons (Kelly et al., 1998), monkeys (Gouteux & Spelke, 2001; Tinklepaugh, 1932), humans (Hermer & Spelke, 1994), and other species of fish (Sovrano et al., 2002). Also, goldfish can use featural information to orient in both the absence and the presence of geometrical information. These results are consistent with those observed in birds (Kelly et al., 1998; Vallortigara et al., 1990), monkeys (Gouteux & Spelke, 2001), and adult humans (Hermer & Spelke, 1994), which are capable of using featural information to orient in a rectangular environment containing discrete visual cues. In contrast, both rats (Biegler & Morris, 1993, 1996; Cheng, 1986) and children (Hermer & Spelke, 1994; Wang et al., 1999) appear to be unable to use featural information to locate a goal in a square or a rectangular experimental environment. Taken as a whole, the available data suggest that the ability to encode the geometric properties of the environment is quite a general phenomenon in vertebrates; however, when geometric information is joined with featural information, some interspecies differences appear.

It has been suggested that the simultaneous use of geometric and nongeometric spatial information might constitute a problem-solving capacity unique and distinctive to adult humans and that this ability is linked to linguistic processes (Hermer & Spelke, 1994, 1996). Nevertheless, it should be noted that the available experimental data of every vertebrate group studied indicate a remarkable similarity both in the neural and behavioral mechanisms of spatial navigation and in the simultaneous use of geometric and nongeometric environmental information. The differences in the encoding processes of geometric and nongeometric spatial information observed in the vertebrate groups studied to date are limited on one hand to those observed in children and rats, which encode mainly the geometric features of the environment, and on the other hand to birds, monkeys, adult humans, and fish, which encode both types of information simultaneously and use them with high flexibility. Although these differences may indicate that there are at least two different ways to encode spatial information, recent studies have indicated that the size of the room (Learmonth et al., 2001, 2002), the disorientation method (Gouteux & Spelke, 2001), and the position of the featural cues with respect to the goal (Garrad-Cole et al., 2001) influence the use of featural information by children and that the type of task required influences the use of featural information in rats (Golob & Taube, 2002). It should be noted that an aversive procedure was used in this study. Compared with rats trained in an appetitive procedure, rats trained in an aversive procedure showed an improvement in the use of featural cues when geometric information was available (Golob & Taube, 2002). Nevertheless, no other species have ever been studied with appetitive and aversive procedures to describe the codification of featural versus geometric information, so we could not affirm if this difference is specific to the rat or can be found in other animals.

The inability of rats and children to use featural information in the presence of geometrical information appears similar to the well-described phenomena of blocking and overshadowing in Pavlovian and instrumental conditioning and would interfere with the

learning of some cues over others in a situation that provides redundant spatial information (Chamizo, 2003; Mackintosh, 1974; Pavlov, 1927; Rodrigo, Chamizo, McLaren, & Mackintosh, 1997). Consequently, it could be expected that the different types of spatial cues would induce in the animals a competitive-like encoding process, such that the control by one group or set of cues could interfere with the potential power of other cues to control behavior, or such that a source of information would be overshadowed by another, more salient, cue, but both having the same predictive potential. For instance, in an environment providing discrete featural cues and geometric cues simultaneously, rats and children might encode more readily (or exclusively) the geometric information, whereas the latter might overshadow both visual and olfactory nongeometric cues. In this regard, sensory, or even cognitive, differences in the salience of the different stimuli for different species could underlie the observed differences. However, the possibility that the salience of the different types of stimuli might be due mainly to procedural differences rather than to sensory or cognitive capabilities of the studied groups should be seriously considered. The spatial stability of environmental objects has been pointed out as an important requirement for cues to be considered as reliable sources of spatial information (Biegler & Morris, 1993, 1996). In fact, the use of featural cues by children was enhanced when Hermer and Spelke's (1994) study was replicated with more stable visual cues, that is, when the children did not witness cue manipulation (Learmonth et al., 2001).

Therefore, the differences found in the processing of spatial information might be due to genuine species differences in the nature of spatial systems, but, more probably, they might be due to procedural differences. For instance, factors such as the relative size of the discrete visual cues or their position, occupying one whole wall or marking exclusively the corners (see, for instance, Gouteux et al., 2001); the relative stability or instability of the discrete visual cues; the size of the experimental room or the type of task that might determine whether or not the animals encode; and the discrete visual cues in their representation of the environment have not been specifically equalized in the still-scarce studies regarding the use of environmental geometric information. Consequently, because of the differences among the procedures used according to the species and the differences found in experiments with rats and children, more research is necessary to clarify the capacity of these species to encode and use nongeometrical information to orient.

Simultaneous Codification of Geometric and Featural Information

The results of Experiments 3 and 4 indicate that fish encoded the geometric information in different ways depending of the strategy used to solve the task. These differences appeared though response requirements and visual cues in both experiments were exactly the same, and the two situations differed only in the position of the featural cues in relation to the goal. The results of studies intended to analyze the learning strategies used by goldfish in the spatial constancy and in the directly cued tasks showed that fish solve both tasks by means of different strategies, with different characteristics based on distinct neural substrates (López et al., 1999; López, Broglio, et al., 2000; Salas, Broglio, et al., 1996). Goldfish

solve the spatial constancy task, used in Experiment 3, by a maplike, or relational, representation that includes the relationships of the goal and a large number of cues, including the geometric information of the experimental apparatus. In this sense, no one cue is essential to solve the task. Also, this kind of representation has a high level of flexibility, and fish can readily transfer the initial learning to a reversal learning situation (López et al., 1999; López, Broglio, et al., 2000). On the other hand, fish solve the directly cued task by means of a guidance strategy. The performance of these animals relies on information closely associated with the goal and is independent of the geometry of the enclosure, and no positive learning transfer is observed during reversal of the task. Moreover, telencephalic ablation in fish produces selective impairments in a spatial constancy task, whereas it has no significant effect on a directly cued task (López, Broglio, et al., 2000; Salas, Broglio, et al., 1996).

In Experiment 3, fish trained in the spatial constancy task probably encoded the geometric and the nongeometric information in the same representation of the environment. In this sense, they were able to locate the goal by relying on the available source of spatial information, whether featural or geometrical, and neither the visual nor the geometric cues prevailed in controlling spatial choices. But when the geometric and the featural cues were placed in conflict, altering the metric and topological relationships between the different elements of the environment, fish were unable to use any of the strategies to solve the task. In contrast, results of Experiment 4 suggest that fish trained in a directly cued task learned two independent and competitive strategies and that they could use one or the other even when both sets of cues were placed in conflict. These data are similar to those observed in mice and in rats, where the presence of a conspicuous intramaze visual cue signaling the hidden platform directly in a Morris maze did not interfere with encoding the array of extramaze visual cues (Brown, Yang, & Digian, 2002; Chapillon & Roulet, 1996) or the shape of the arena (Hayward, McGregor, Good, & Pearce, 2003). Therefore, the results of Experiments 3 and 4 suggest that geometric and nongeometric information is capable of being encoded together in a single representation or in different and competitive representations depending on the characteristics of the task (global vs. local processing).

In summary, the present work reveals that goldfish, similar to mammals and birds, can encode the geometrical properties of the environment. Goldfish use both featural and geometrical information for navigation. When both geometric and featural information are presented together, fish can encode both types of information in separate, competitive strategies or in a single and cooperative strategy, depending on the initial training procedure. In addition, these results suggest that the geometric information is likely to be incorporated into maplike, or relational, representations of the environment, together with featural information.

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