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Time-place learning in the zebrafish (*Danio rerio*)

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ABSTRACT

Animals exhibit activity cycles that repeat over days. The most noteworthy cyclical behaviors are related to forraging, which generally occur at the same times and locations. The synchronization of animal activities via the association of different places at different times for the occurrence of relevant biological events is known as time-place learning (TPL). In the present study, we used zebrafish (*Danio rerio*) to test time-place learning based on a different stimulus: social reinforcement. Fish were not only able to associate time and place of the social stimulus, but also displayed anticipatory activity prior to the arrival of the stimulus. Furthermore, we show that the group of conspecifics is an relevant stimulus for time-place learning tasks, while other studies have only used food.

1. Introduction

Animals exhibit activity cycles that repeat over days, seasons, and years. Among the most noticeable cyclical behaviors are foraging and resting, which generally appear at established times and places (Carr and Wilkie, 1997; Dunlap, 1999). The processes by which the animals synchronize its activities to occur at different locations and different times is known as time-place learning (TPL) (Wilkie, 1995; Widman et al., 2000). For this type of learning to occur, the time domain and spatial awareness are the most important aspects. Moreover, the ability of TPL can be considered adaptive, since it provides advantages for exploiting resources that are not continuously available (Enright, 1970).

Groundbreaking TPL studies were conducted with bees, suggesting their ability to flexibilize foraging to find food at specific times and locations (Wahl, 1932; Finke, 1958; Koltermann, 1974). After bees, TPL was also observed in other insects (Breed et al., 2002), birds (Wilkie et al., 1996), and rodents (Means et al., 2000; Thorpe and Wilkie, 2002). In fish, this cognitive ability has received little attention, and the available studies focus on the time-place learning of social animals as a response to food resources that vary over time and in space (Reebs, 1993, 1996, 1999; Gómez-Laplaza and Morgan, 2005, Barreto et al., 2006; Brannas, 2014). Considering that food availability changes daily, seasonally and annually, it is believed that TPL is functional in optimizing the location and exploitation of the resource, as well as in avoiding predators in an environment of predictable cyclical change, allowing a decrease in energy costs and consequent increase in survival (Mulder et al., 2013).

Although studies on fish reveal the ability of food-related TPL, learning in groups of animals may have been masked by the copy phenomenon, whereby leaders of a group make the decisions while other individuals follow their behavioral patterns (Reebs, 2000). Indeed, for social animals, grouping has advantages in terms of locating food resources, foraging time and protection against predators (Pitcher et al., 1982; Krause and Ruxton, 2002; Brown and Laland, 2003; McRobert, 2004; Luchiari and Freire, 2009). In addition, the possibility of grouping is understood as a reward (Al-Imari and Gerlai, 2008), promoting a sensation of well-being and increasing dopamine secretion in the brain (Saif et al., 2013). In this respect, conspecific groups may act as a stimulus for markedly social animals, favoring time-place learning.

Therefore, the highly social zebrafish (Engeszer et al., 2007a; Pritchard et al., 2001; Spence et al., 2008) can be considered a study model for TPL based on social reinforcement. Social behavior in zebrafish is innate and appers immediately after hatching (Engeszer et al., 2007b). If held isolated, zebrafish shows a fast regrouping when placed together (Kerr, 1963), indicating the social group has a positive effect on motivation to shoal. Thus, this study aimed at assessing whether the zebrafish (*Danio rerio*), when tested individually, is capable of associating place with specific times of the day in which a group of conspecifics is presented. First, the results of this study contribute to increasing knowledge regarding the cognitive ability of fish, primarily TPL, increasing the variety of fish tested for this phenomenon, as well as adding new tasks to the behavioral investigation of this species. Furthermore, since it is a

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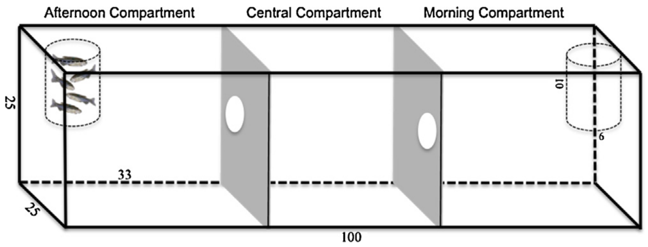

Fig. 1. Schematic diagram of the tank used to test time-place learning. On the right, the morning compartment, on the left, the afternoon compartment. The central compartment allows passage through the two 8 cm-diameter round windows, one located on the right, the other on the left, preventing the animal from seeing all the compartments at the same time. The values refer to the areas of the tank in cm.

strong stimulus for the species, the social stimulus used indicates that other events relevant for the species can be considered during learning, in addition to those closely associated with survival (for example, food).

2. Material and methods

2.1. Animals and procedures

Zebrafish *D. rerio* (Hamilton, 1822) were obtained from a fish farm (Natal, Rio Grande do Norte state) and kept in stocking tanks (2 fish/L) with aired and filtered water. Four 50 L tanks make up one stocking unit in the closed water circulation system, with mechanical, biological and chemical filtration, in addition to UV disinfection. Water was maintained at 28 ± 1 °C, with pH 7.2 and low levels of ammonium and nitrite. The light cycle (fluorescent light, 150 lx) was fixed at light-dark (LD), with the start of the light phase at 7 am. The fish were fed commercial pellets twice a day (38% protein, 4% lipids, Nutricom Pet) and *Artemia salina*.

Ten zebrafish (adults of both sexes) from the aforementioned stock were used to test time-place learning. All the procedures with the animals were authorized by the Animal Ethics Committee of Universidade Federal do Rio Grande do Norte (CEUA 039/2015).

2.2. Experimental design

The experimental animals were individually transferred to test tanks (100 × 25 × 25 cm; length × width × height), divided horizontally into three same-size compartments (33 cm long): one central and two lateral (Fig. 1). The compartments were separated by opaque dividers, each with an 8 cm-diameter circular passage that allowed the fish to swim between the compartments. The passage was located on the right of the right side divider and on the left of the left side divider, such that the fish could not visualize more than two compartments at the same time (Fig. 1), thereby preventing the stimulus placed in one of the side compartments from being seen when the animal was in the opposite side compartment. A cylindrical open-front receptacle (10 cm in diameter and 10 cm high) was fixed to the upper part of the wall, and used to offer the stimulus (conspecific group) at specific times. The side compartments were denominated morning compartment and afternoon compartment. The tanks were positioned on two multiple-layers shelf, placed one in front of the other, in a way that the morning compartment of some tanks were equivalent to the afternoon compartment of some other tanks, in a way that the position of the tanks did not allow for side bias to the fish. Each tank was constantly aerated through an external filter (JEBO 50, 250 L/h) located in the central compartment and porous rocks in the side compartments.

Animals were kept for 5 days in experimental tanks for acclimatization and for a further 30 days of the experimental phase. A 12 h light-dark (LD) cycle (7 am–7 pm) was used. A group of 5 zebrafish (same size and age) were introduced every day into the receptacle located in the morning compartment at 8 am and removed at 9 am, and into the receptacle of the afternoon compartment at 5 pm and removed at 6 pm, acting as a stimulus for the experimental fish to occupy the compartment where the group was placed. The group was introduced through a receptacle (500 mL) connected to a handle (2 m) so that the experimenter could not be seen by the animals, which were separated by an opaque curtain. The stimulus was introduced 1 h after the onset of the morning light and 2 h before the end of the light phase. Food (artemia) was offered daily (once a day) at random times, always in the central compartment so they would not be associated with any other stimulus. The fish was also checked from behind the curtain many times a day, thus providing cues of the experimenter presence to the fish that could not be associated to any other cues.

On days 15 and 30 of the experimental period, the behavior of the animals was recorded on video for 1 h and 15 min, starting at 7:45 am and 4:45 pm, in order to observe animals for 15 min before the arrival of the group (stimulus) and during their entire presence. Behavior on day 15 was recorded in the presence of the group to estimate the strength of this stimulus. However, on day 30, the animals were filmed without the presence of the group, in order to assess time-place learning in the zebrafish.

Video records were made with Sony DCR-SX45 Digital Video Camera Recorders placed in front of the tanks. Analysis of behavioral records was conducted using the ZebTrack tracking program, developed at MatLab. The following parameters were assessed: residence time and entry frequency in the morning and afternoon compartments, average swimming speed, and total distance travelled. The distance of the centre point of the fish from the previous sample frame to the following sample frame indicated the distance travelled between frames. The ZebTrack calculates the total distance travelled by summing the distances from the previous and current frames along the total period of recording. The average speed takes into account the distance travelled by the time spent to cover that specific distance, also calculated by the ZebTrack software.

2.3. Statistical analysis

Behavioral data for time spent in the compartments and frequency of entry into each compartment were compared in the morning and afternoon, on days 15 and 30, using the paired Student's *t*-test. We also assessed speed and total distance travelled in the compartments with respect to the presence of the stimulus. These data were compared for the period prior to group arrival (15 min before) and that related to the presence of this stimulus, on days 15 and 30. The same parameters were also compared between the morning and afternoon in both windows of time (15 min before the group and 60 min with the group). The paired Student's *t*-test was used for both comparisons, in order to determine behavioral changes caused by the presence/absence of the stimulus, and at different times of the day. We disregarded all data from the central compartment, since it was a passage area and feeding site at random times. Thus, the animal could visit this area to pass from the right compartment to the left or to search for food. Moreover, we did not compare day 15 versus day 30 because the experimental conditions were different (presence of the shoal vs. absence of the shoal), and the shoal presence is a biased condition.

3. Results

3.1. Responsiveness on day 15

During the 15 min before the group of conspecifics arrived, there was no significant difference in residence time between the com-

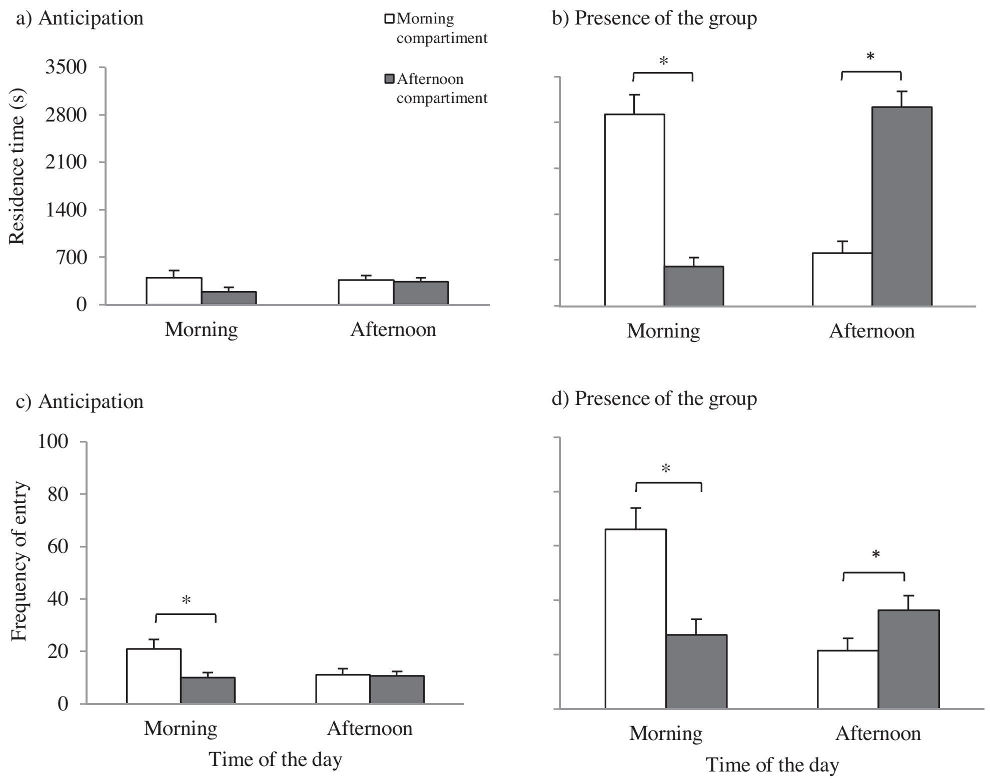

Fig. 2. Residence time (a and b) and frequency of entry (c and d) in the morning and afternoon compartments on day 15 of the experiment with zebrafish (n = 10) in a TPL test. Observations were made between 7:45 and 9:00 am, and 4:45 and 6:00 pm The first 15 min of observation indicate their ability of anticipating the arrival of the social stimulus (a and c). During the following 60 min, the social stimulus (group with 5 conspecifics) was maintained in the experimental tank (b and d). * indicates statistical significance (Student's *t*-test, $p < 0.05$) between the compartments corresponding to each experimental period.

partments in the morning (Student's *t*-test, df = 9 $t = 1.29$ $p = 0.23$) or afternoon (Student's *t*-test, df = 9 $t = 0.72$ $p = 0.49$) (Fig. 2a). The frequency of entry into the morning compartment was higher in the morning (Student's *t*-test, df = 9 $t = 2.46$ $p < 0.001$; Fig. 2c), but did not differ in the afternoon (Student's *t*-test, df = 9 $t = 0.15$ $p = 0.88$).

During the presence of the group, residence time in the morning compartment was higher in the morning (Student's *t*-test, df = 9 $t = 5.19$ $p < 0.001$), and in the afternoon compartment in the afternoon (Student's *t*-test, df = 9$t = -3.18$ $p = 0.01$) (Fig. 2b). We obtained a similar result for frequency of entry into the compartments in the morning (Student's *t*-test, df = 9 $t = 5.22$ $p < 0.001$), and afternoon (Student's *t*-test, df = 9 $t = -2.93$ $p = 0.02$) (Fig. 2d).

The average speed recorded was lower in the 60 min in which the group was present, when compared to the 15 min before their arrival, in both the morning (Student's *t*-test, df = 9 $t = 8.18$ $p < 0.001$) and the afternoon (Student's *t*-test, df = 9 $t = 2.33$ $p = 0.04$; Fig. 3a). The total distance travelled by the individuals was greater during exposure to the group, only in the afternoon (Student's *t*-test, morning df = 9 $t = -0.72$ $p = 0.49$; afternoon df = 9 $t = -2.36$ $p = 0.04$; Fig. 3b). When the parameters were compared between the morning and afternoon for each time period (15 min before the group and 60 min with the group), there was no significant difference in average speed (Student's *t*-test, df = 9 $t = 0.17$ $p = 0.87$; Fig. 3a) or total distance travelled (Student's *t*-test, df = 9 $t = 0.59$ $p = 0.57$; Fig. 3b) in the 15 min before the group arrived, or during the 60 min of exposure to them (Student's *t*-test, average speed df = 9 $t = -1.65$ $p = 0.14$; total distance travelled df = 9 $t = 0.48$ $p = 0.64$; Fig. 3).

3.2. Determination of learning on day 30

In the 15 min before the group was introduced into the tank, the fish remained mostly in the morning compartment in the morning (Student's *t*-test, df = 9 $t = 6.68$ $p < 0.001$; Fig. 4a), but in the afternoon there was no difference between the time spent in each compartment (Student's *t*-test, df = 9 $t = -1.95$ $p = 0.08$). The frequency of entry was also higher in the morning compartment in the morning (Student's *t*-test, df = 9 $t = 2.55$ $p = 0.03$) and the afternoon compartment in the afternoon (Student's *t*-test, df = 9 $t = -2.18$ $p = 0.05$) (Fig. 4c).

During the 60 min that the group was expected to arrive, even in the absence of a stimulus, the fish remained for a longer time in the morning compartment in the morning (Student's *t*-test, df = 9 $t = 3.41$ $p = 0.01$) and the afternoon compartment in the afternoon (Student's *t*-test, df = 9 $t = -3.28$ $p = 0.01$) (Fig. 4b). The frequency of entry into the compartments was higher in the morning (Student's *t*-test, df = 9 $t = 5.83$ $p < 0.001$) and afternoon (Student's *t*-test, df = 9 $t = -3.73$ $p = 0.01$) (Fig. 4d).

There was no significant difference in average speed between the 15 min preceding the group's arrival and the 60 min where it was present, in both the morning and afternoon (Student's *t*-test, morning df = 9 $t = -0.31$ $p = 0.77$, afternoon df = 9 $t = -0.59$ $p = 0.57$; Fig. 5a). The total distance travelled also did not differ between the 15 min prior to the group's arrival and the time it was usually in the tank, in the morning (Student's *t*-test, df = 9 $t = -0.97$ $p = 0.36$), or the afternoon (Student's *t*-test, df = 9 $t = 0.67$ $p = 0.52$) (Fig. 5b). The parameters also did not differ when the morning and afternoon were compared for each time period (15 min before the arrival of the group and 60 min without it), both during the 15 previous minutes (Student's *t*-test, average speed df = 9 $t = -1.31$ $p = 0.22$; total distance travelled df = 9 $t = 0.09$ $p = 0.93$), and in the 60 min without the presence of the group (Student's *t*-test, average speed $t = -1.64$ $p = 0.13$; total distance travelled df = 9 $t = 0.53$ $p = 0.61$) (Fig. 5).

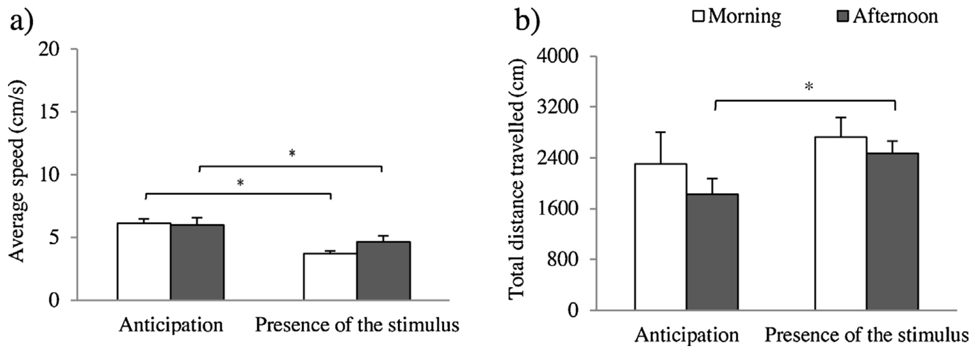

Fig. 3. Average speed (a) and total distance travelled (b) by the zebrafish (n = 10) on day 15 of the experimental test for TPL. The animals were observed for 15 min before presentation of the social stimulus (from 7:45 to 8:00 am, and from 4:45 and 6:00 pm) and for the 60 min that the stimulus was present (from 8:00 to 9:00 am, and from 5:00 to 6:00 pm). * indicates statistical significance (Student's *t*-test, $p < 0.05$) between the period before presentation of the stimulus and during the presence of the social stimulus.

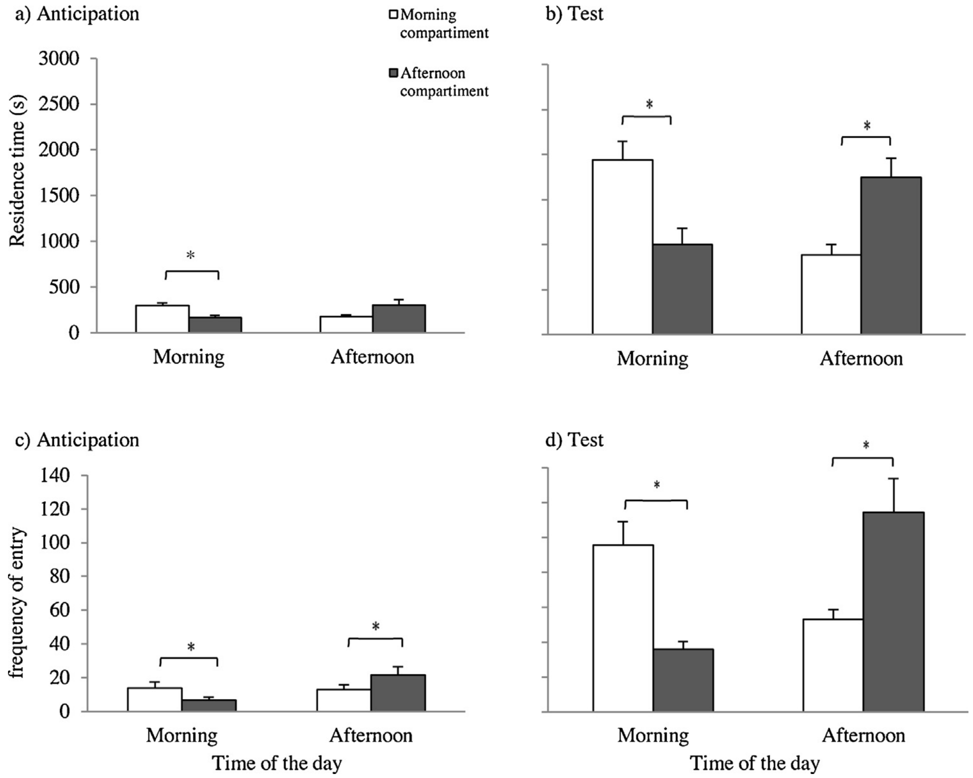

Fig. 4. Residence time (a and b) and frequency of entry (c and d) in the morning and afternoon compartments on day 30 of the experiment with zebrafish (n = 10) in the TPL test. Observations were made from 7:45 to 9:00 am, and from 4:45 to 6:00 pm The first 15 min of observation indicate the ability to anticipate the arrival of the social stimulus (a and c). During the next 60 min, the social stimulus was not introduced into the experimental tank (b and d). * indicates statistical significance (Student's *t*-test, $p < 0.05$) between the compartments corresponds to each experimental period.

4. Discussion

Our results show that zebrafish not only stayed longer where conspecifics were present at predetermined times, but also exhibited anticipatory ability, remaining longer and visiting more frequently the compartment of the tank where the group of conspecifics was present, for 15 min before the stimulus itself was offered. These results are relevant, since they indicate that zebrafish are not only able to associate environmental cues (time and space) with important events (social stimulus), but also suggests the ability to anticipate relevant signs.

Few studies have discussed the ability of time-place association in fish, and to the best of our knowledge, there are only 10 studies in the literature on the issue (Reebs, 1993, 1996, 1999; Gómez-Laplaza and Morgan, 2005; Delicio et al., 2006; Barreto et al., 2006; Delicio and Barreto, 2008; Heydarnejad and Purser, 2008; Ebrahimi et al., 2013; Brannas, 2014), most of which use groups of fish and all of them use food as the learning stimulus.

In our study, we used a group of 5 zebrafish as a time-place learning stimulus. In the 15 min before the group arrived, the zebrafish entered the correct compartment more frequently only in the morning. Although the time spent in the compartments did not differ between the morning and afternoon (Fig. 2a), the greater frequency observed in the morning (Fig. 2c) indicates anticipation of the stimulus. Anticipatory activity has previously been demonstrated in groups of Arctic char (*Salvelinus alpinus)* when faced with a food stimulus (Brannas et al., 2005). Anticipating a temporal event may be advantageous, providing benefits in terms of food, partners, or refuge acquisition (Davis and Bardach, 1965; Reebs and Gallant, 1997). However, this did not occur in the afternoon, pos-

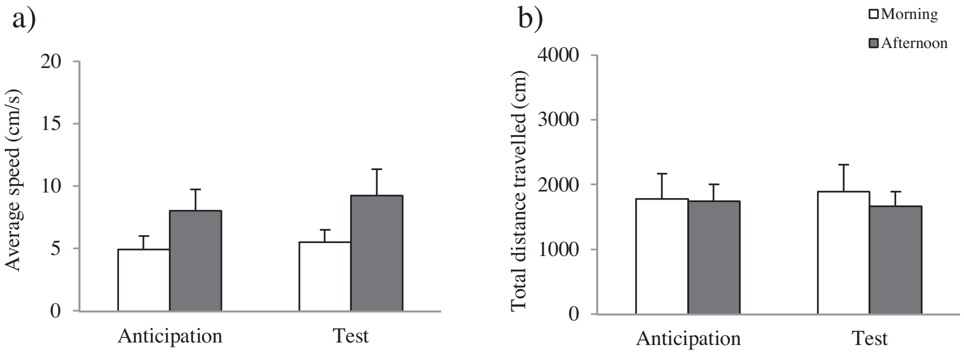

Fig. 5. Average speed (a) and total distance travelled (b) by the zebrafish (n = 10) on day 30 of the TPL experimental test. The animals were observed for 15 min before presentation of the social stimulus (from 7:45 to 8:00 am, and from 4:45 to 6:00 pm) and during the period in which the stimulus was present, but without the presence of social stimulus (from 8:00 to 9:00 am, and from 5:00 to 6:00 pm). * indicates statistical significance (Student's *t*-test, $p < 0.05$) between the periods prior to presentation of the stimulation and the presence of the stimulus.

sibly because a 15-day period may not have been sufficient for individuals to memorize the exact time of stimulus presentation. Moreover, light may have been used to predict the group's arrival, favoring the perception of the time in the morning that this took place, since the stimulus occurred 1 h after the onset of the light phase (7 am). In the afternoon, the stimulus occurred 1 h before lights off (7 pm), such that the animals must have had more difficulty in associating the group's arrival with the subsequent light cue.

On day 15 of behavioral records, the experimental animals remained significantly longer near the group of conspecifics during the exposure time in the morning and afternoon (Fig. 2a and b). This reinforced the importance of conspecifics for zebrafish, confirming the social behavior reported in other studies (Wright et al., 2003; McRobert, 2004; Ruhl and McRobert, 2005; Engeszer et al., 2007a; Paciorek and McRobert, 2012). With respect to the average speed, it was higher in the 15 min before the group's arrival, both during the morning and the afternoon (Fig. 3a), indicating fish decreased swimming speed and stayed longer with the group during both presentation time periods.

Studies on time-place learning usually used long testing times (Reebs, 1996; Widman et al., 2000; Delicio et al., 2006; Ebrahimi et al., 2013), since they report on learning that involves not only entrainment of the internal oscillator, but also the daily routine of time and place association (Biebach, 1989). Thus, after 30 days of the experiment we observed that in the 15 min before the presence of the stimulus, the animals entered more frequently (Fig. 4c) and spent more time in the correct compartments (Fig. 4a), in both the morning and afternoon. These results corroborate the hypothesis of a circadian strategy in the time-place learning process. According to Carr and Wilkie (1999), animals that use circadian strategy learn that the time of the event has fixed periodicity, which is associated with different stages of endogenous circadian phases. Thus, animals can use this information to predict the exact time that an event must occur. Indeed, studies with rats show anticipation of time-place learning in a T-maze with food reward (Deibel and Thorpe, 2013).

How some animals learn to associate time-place stimuli and others do not, remains largely unknown. Many animals live in environments in which food resources, sexual partners and predators vary periodically and predictably over time (Rijnsdorp et al., 1981; Silver and Bittman, 1984; Becker et al., 1993; Wilkie et al., 1996). When individuals predict events and learn to associate them with the place and time of occurrence, they may obtain advantages, which are likely linked to the evolution of cognitive and circadian systems (Enright, 1970; Daan, 1981; Aschoff, 1989; Reebs, 1996; Carr and Wilkie, 1999). Evidence that time-place learning is associated with endogenous circadian rhythm was proposed by Van der Zee et al. (2008). These authors showed that Cry1 and Cry2 knockout mice were unable to learn time-place association, while wild mice learned in both circadian cycle and under constant light. The biological clock includes an auto-regulated and oscillating temporizing system with defined anatomical structures and DNA coded oscillators (Marques and Menna-Barreto, 2003). Even though only few studies approach the system structure in zebrafish, it is known that this species presents a biological clock (Cahill et al., 1998).

One could argue that instead of time-place learning based on the circadian timing, fish may have shown win-stay, lose-shift strategy. This possibility, however, may be discarded in the present study because win-stay, lose-shift strategy use to occur within a shorter than 8 h period of time and the absence of the shoal in the morning compartment in the morning period would lead to an increase in the time spent in the afternoon compartment, or, at least a higher frequency of entries in the afternoon compartment, indicating the fish were checking the afternoon compartment. However, we observed fish stayed longer in the morning compartment during the morning and in the afternoon compartment during the afternoon (Fig. 4b and d).

Therefore, our results regarding the time zebrafish spent on day 30 in each compartment as a function of the stimulus (Fig. 4b), in which learning was tested without the presence of a social stimulus, shows the time-place learning ability of this animal. Thus, we corroborated earlier studies with fish (Reebs, 1993, 1996, 1999; Gómez-Laplaza and Morgan, 2005; Barreto et al., 2006; Delicio et al., 2006; Delicio and Barreto, 2008; Heydarnejad and Purser, 2008; Ebrahimi et al., 2013; Brannas, 2014) and found that time-place learning ability may be involved with relevant stimuli for the species under study, in this case, the social signal. We did not found significant differences in both average speed and total distance travelled before and during the 60 min of test on the 30° day, possibly due the absence of the stimulus fish did not change swimming behavior pattern on this probe day.

Finally, it is important to emphasize that in the present study, the sight of a group of conspecifics was effective as a stimulus for the learning task proposed. A social stimulus can be effectively used due to the highly social characteristic of zebrafish (Wright et al., 2003; Engeszer et al., 2004; Luchiari et al., 2015). Other studies with social signals as a learning stimulus indicate the validity of this signal, such as the study by Karnik and Gerlai (2012) using a conspecific image for conditioning of place, Silveira et al. (2015) using conspecifics in associative conditioning tasks, and Luchiari et al. (2015) using a group of conspecifics in a latent learning task.

Due to the high sociability of zebrafish, future studies on time-place learning in groups submitted to a stimulus, whether social or food, may contribute to a better understanding of the animal's behavior and learning copy strategies. Furthermore, since our study does not discuss the day-to-day development of the time-place association, additional studies are needed to follow the behavior patterns throughout the entire experimental period. Other points for future investigation that could not be covered in the present study are the offer of food in a different part of the tank, which forced us to eliminate the central compartment from TPL analyses, and the baseline behavioral analysis in order to cover the distribution of the fish before training. Despite not using this compartment or following the animal for the 30 days of the test, our results are robust in that they show the time-place association ability of zebrafish, as demonstrated by data on day 30 of the test (Fig. 4).

In our study, *D. rerio* exhibited time-place learning, as well as anticipated the arrival of the stimulus. Moreover, we showed that the group of conspecifics is an revevant stimulus for time-place learning tasks, in which there are no records of studies using this type of stimulus. Here, we used a circadian photoperiod (LD), but time-place learning studies in the absence of light zeitgebers are needed to investigate TPL without light signals to indicate time. Studies with molecular analyses must also be conducted to indicate the association between the biological clock and this type of task, essential for understanding the endogenous mechanisms involved in TPL.

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