

Light-oriented swimming of schooling fish in continuous channels

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Synopsis

Fish groups were tested both in a circular and in a figure eight-shaped channel. In both cases fish showed a long lasting, constant direction swimming provided that illumination was maintained at a constant angle around the channel. In the circular channel, fish did not reverse direction, as would be expected, when light angle was shifted from one side to the other in the channel. However, direction reversals did occur when these illumination shifts were performed on the eight-shaped channel. We suggest that constant-oriented swimming reflects a sun-compass oriented behavior, but swimming at a constant angle in the circular channel produces an irreversible disarrangement of the inertial-orientation system, which does not occur in the eight-shaped channel due to the geometrical relationship between the light and the shape of the channel.

Introduction

One of the major problems for the study of orientation in fish is the difficulty of providing an experimental setup which allows the fish to swim uninterruptedly in a fixed direction without barriers or influence of any moving stimuli. Laboratory devices that promote constant swimming in fishes have been used to measure metabolism (Puckett & Dill 1984), 3-D structure of schools (Partridge et al. 1980), ontogeny of schooling behavior (Shaw 1960), and orientation to external cues (Hoar 1958). In all these experiments the fish movements were either promoted by a moving stimulus or constrained to short trajectories in straight alleys. Previous observations (Levin & Belmonte 1988), indicated that groups of schooling fish showed a long-lasting, constant-oriented swimming, when placed in a circular channel provided that illumination

angle was constant along the channel. We hypothesized that the sustained constant-direction swimming in the circular channel reflected a sun-compass oriented behavior. According to this interpretation, it should be expected that the swimming direction in the circular channel would be reversed if the illumination angle was the same, but at the opposite side of the channel. To test this hypothesis we used both a previously described circular channel (the light-centered circular channel) and a new channel design, the light-centered infinite channel.

The apparatus

The light-centered circular channel was an annular-shaped channel of 100 cm of external diameter and 15 cm width, in which two symmetrical sources of light were used (for a full description of the appara-

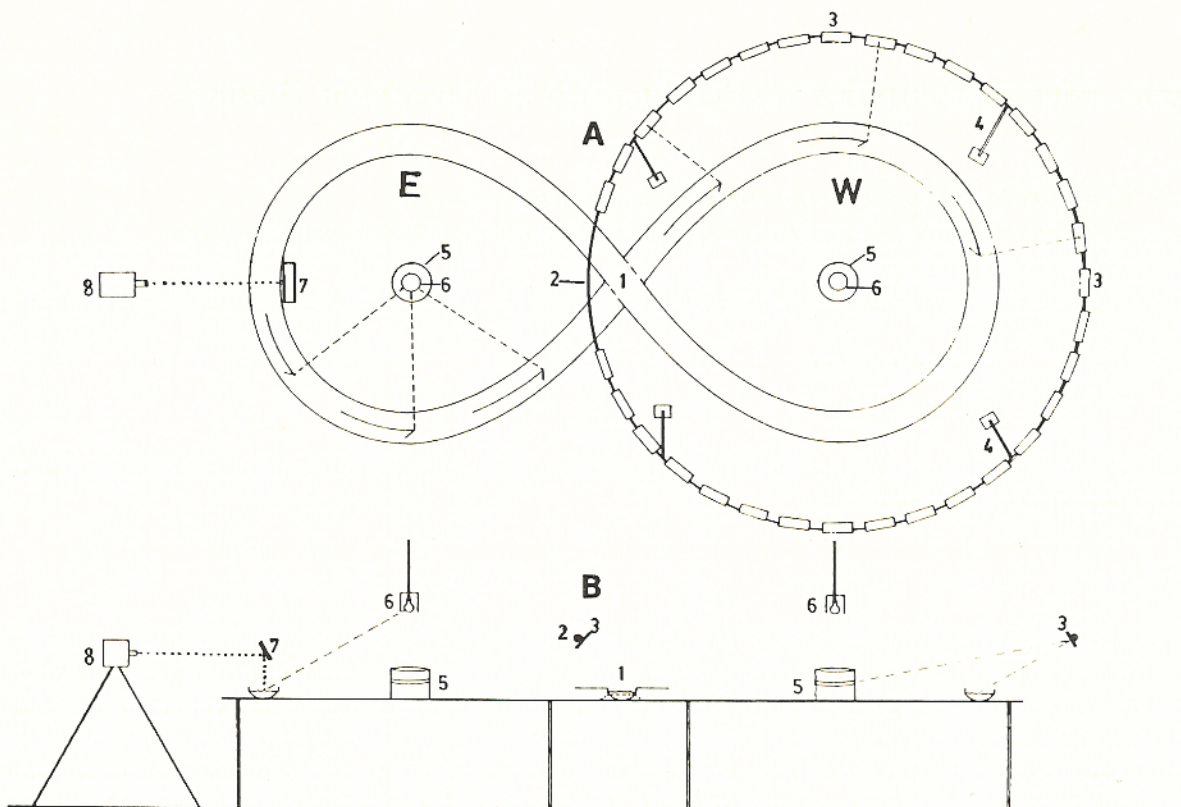


Fig. 1. Top (A) and lateral (B) view of the light-centered infinite channel. The channel consisted of two cycles (E: east; W: west): (1) crossing point of the channel; one arm ran under the other without connection (see detail in Fig. 2); (2) supporting ring for the peripheral light mirrors; (3) mirrors; (4) supporting base for the ring; (5) peripheral light source: the bulb was enclosed into an opaque container; the light came out through a circular opening 1.7 cm width; (6) central light source: the bulbs were collimated using a 17 cm diameter opaque cylinder; (7) observation mirror; (8) TV camera. In the infinite channel fish swam uninterruptedly in a fixed direction when they received light at a constant angle from one side (exemplified by arrows), because there was always a different illumination system at each cycle. These systems could be exchanged in position. The light course of central and peripheral lights is shown by dotted lines.

tus see Levin & Belmonte 1988). The first light source, central light, consisted of a clear light incandescent bulb (G.E. 75 W) placed 36 cm above the water surface over the geometric center of the channel. The second source of light was a set of 18 incandescent bulbs (Sylvania 30 W) placed around the channel at a height of 59 cm above the water surface. These lamps had radially directed collimators which restrict the number of light sources to a maximum of two at any given point of the channel. Both sources projected light at an angle of 40° on the water surface throughout the channel. Thus, unlike other methods that employ asymmetric light sources, the light-centered circular channel (henceforth, circular channel) provided the fish with the

possibility of swimming uninterruptedly without perceiving changes in the angle of incidence of light.

The light-centered infinite channel (henceforth infinite channel) consisted of an eight-shaped double circular channel (Fig. 1). The channel was built using a 10 cm diameter plastic pipe (PVC) cut longitudinally in half. Each circle was 106 cm in external diameter, 10 cm wide, and had a maximum depth of 5 cm. The total length of the channel was 647 cm. The two circles of this eight-shaped device were named according to their relative position as east and west cycles. The crossing point was built in such a way that fish travelling along one arm could not deviate to the other one (Fig. 2). A 25×20 cm

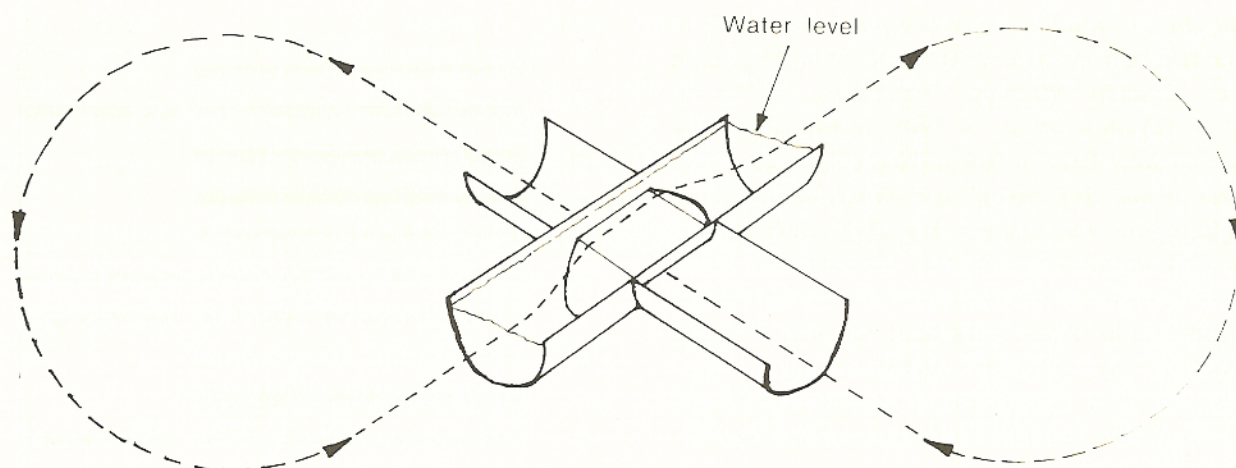


Fig. 2. Detail of the crossing point of the channel: One of the arms was opened at both sides and a transparent platform covered this place so a tunnel for the other arm was formed. The height of the platform was half the water level so fish passing by one arm went over and those passing by the other one went under. The broken arrows indicate the fish path when swimming in one direction.

mirror was placed at 45° over the extreme east end to allow observations in a horizontal plane. The two central light bulbs (G.E. 75 W) were collimated using a 17 cm – diameter cylinder. For peripheral illumination, a bulb (G.E. 100 W) enclosed in an opaque container with a circular slit was placed at the geometric center of each cycle. There were 36 (5×12 cm) mirrors attached with rubber bands to a ring (163 cm diameter) placed on four movable supporting bases. Thus, the light was directed onto the water surface at a constant angle of 40° . The main difference between the circular channel and the infinite channel was that the latter provided no accumulation of turns when fish swam in a constant direction.

The experiments

Previous observations (Levin & Belmonte 1988) indicated that groups of approximately 100 *Moenkhausia dichroua*, a schooling characid, showed a constant-oriented swimming when placed in the circular channel. When the light angle was fixed, swimming direction was constant for several months and then changed. When the light angle was systematically varied between horizontal and vertical, fish reversed direction, and the reversal

angle was different at different times of the year. In view of these observations we hypothesized that the sustained constant-direction swimming in the circular channel reflected a sun-compass oriented behavior. Were our hypothesis correct, it should be expected that the swimming direction of fish in the circular channel would be reversed if the light system was shifted from peripheral light to central light or vice versa.

Since we did not find specimens of *M. dichroua* in the field, we used groups of the abundant species *Cheirodon pulcher*, a small schooling characid with similar distribution in the flood plains of southern Venezuela. Preliminary observations showed that groups of around 100 *C. pulcher* maintained, as well as *M. dichroua*, a long-lasting constant swimming direction. But, when the lights were shifted in successive days, they did not reverse swimming direction as expected, even with a whole 12 h light period with asymmetric light. This light source was an incandescent light bulb (75 W) placed at one side of the channel, 1 m away, and at water level. Oriented swimming did not occur under this illumination. Under the assumption that the lack of response to light shifts was due to some kind of learning of the curvature of the channel, we performed the experiments described herein.

Experiments were performed with groups of the

schooling characid *Cheirodon pulcher* ranging in total length from 20 to 30 mm, caught in the Guapo river, Estado Miranda, Venezuela (10° 15' N; 66° 17' W) on February 8, 1985. In the laboratory the fish were held in 60 l tanks receiving dry food every other day except for experimental days. Light regime was 12 h per day (0600–1800 h). Water temperature was 25–28°C. Groups were transferred from the common tank to the corresponding channel under asymmetric light between 1754 and 1800 h the day before the experiment began. Swimming direction (clockwise or counter-clockwise) was continuously monitored and recorded on time-lapse videotape.

Experiment in the circular channel

In experiment EI, 15 groups of 10 naive (not previously exposed to any kind of experimental procedure) fish were independently tested in the circular channel under central light or peripheral light during the morning. Nine of these groups continued under the same light during the rest of the daylight period, and the other six received a light shift from central to peripheral light or vice versa at 1200 h. (Light shifts are indicated in Figure 3 by breaks between bars; before the new light was lit, fish were left in darkness during 15 min.) Four of the groups subjected to light shifts remained in the channel, and received during the next morning the same type of light as in the previous afternoon.

For all groups, the initial swimming direction displayed in the morning did not reverse during the day (Fig. 3) (binomial (B) test 15/15, $p < 0.001$), even with a light shift at noon (B: 9/9, $p < 0.01$), or after a 12 h dark period (B: 4/4, $p = 0.06$). On the other hand, swimming direction was not correlated with the type of light used in the first morning (under central light: 5 clockwise and 5 counter-clockwise ($p = 0.22$); under peripheral light: 2 clockwise and 5 counter-clockwise, $p = 0.16$).

Experiments in the infinite channel

In experiment EII, a new group of 20 naive *C.*

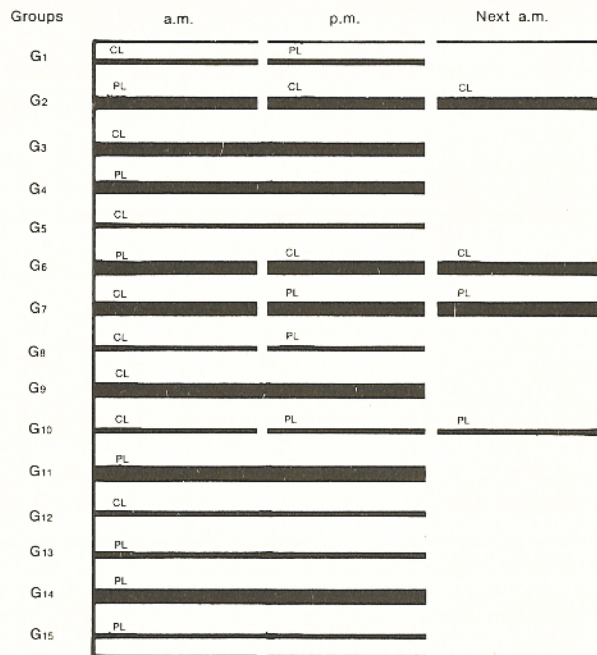


Fig. 3. Experiment EI in the circular channel. Swimming direction (narrow bars = clockwise; wide bars = counter-clockwise) of the 15 groups of *C. pulcher* during the first day and where indicated for the next morning. The morning light [central (CL) or peripheral light (PL)] was shifted at noon for 6 of the groups. (The breaks between bars indicate a light shift or the night interval).

pulcher was placed in the infinite channel. Since this channel was twice as long than the one used in EI, a double number of fish was used for practical purposes. The central light was shifted in successive days from east to west and vice versa, with the peripheral light always at the opposite side. Direction reversals within the session appeared in the four first sessions. In the infinite channel, in which no 'anchoring' to the curvature is possible, direction reversals persisted during an extended period. In the following three sessions, swimming direction remained constant during each session, but each light system promoted a specific direction (central light west: left, central light east: right) (Fig. 4). Once the direction reversals extinguished, the light angle dependency showed up. Since the main difference between the circular channel and the infinite channel is the lack of cumulative curvature in the second, the reluctance to respond to light shifts in the circular channel could be interpreted in

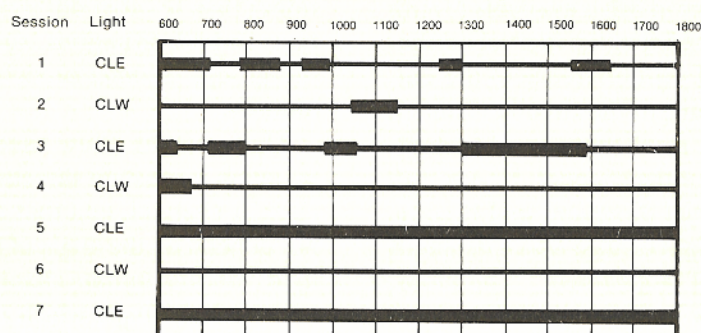


Fig. 4. Experiment EII in the infinite channel. Swimming direction (narrow bars = clockwise; wide bars = counter-clockwise) of a group of 20 *C. pulcher* from 0800 to 1700 h during 7 consecutive days. The lights were shifted in consecutive days from CLE (central light at the eastern cycle) to CLW (central light at the western cycle).

terms of the mentioned anchoring to the curvature.

In order to determine whether the anchoring in one direction in the circular, but not in the infinite channel, was dependent on the shape of the channel and not on any other factor, one cycle of the infinite channel was transformed into a circular channel by blocking the connections to the other cycle. The corresponding central light and peripheral light were used. In experiment EIII a new group of 20 naive fish was tested during 7 days in the halved infinite channel. The lights were shifted between successive days. This group showed swimming direction reversals during the first day and a half, but during the rest of the experimental period swimming direction was always clockwise inde-

pendently of the light used (Fig. 5). Thus, as well as in the circular channel, anchoring develops in this halved infinite channel which, except for the shape, is in all aspects similar to the infinite channel.

Discussion

The outcome of EI may suggest that swimming in a constant direction is triggered and maintained by a light falling at a constant angle, although direction itself is not determined, as would be the case if y-axis orientation would have been in operation (Goodyear & Bennett 1979). Nevertheless, we propose that the lack of consistency between type of light and swimming direction of the groups in the circular channel is because when recently installed, the mechanism for constant light-orientation is not in operation. Instead, random exploratory movements associated with escaping from an unfamiliar confinement dominate. Once this 'escape response' extinguishes, two orientation mechanisms compete in this fish. One of them is the maintenance of a constant angle with the light source. A second one is an inertial guidance mechanism which, in natural conditions and in the absence of external cues, allows for straight course navigation by equating the amount of turns to the right and to the left (Kleerekoper et al. 1969). The balance between the two directions could be, in part, mediated through the vestibular system as has been suggested for other vertebrates (Barlow 1964), al-

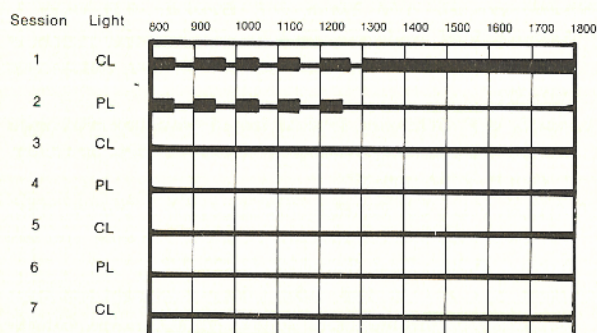


Fig. 5. Experiment EIII in the halved infinite channel. Swimming direction (narrow bars = clockwise; wide bars = counter-clockwise) of a group of 20 *C. pulcher* from 0800 to 1700 h during 7 consecutive days. The lights were shifted in successive days from CL (central light) to PL (peripheral light).

though no direct evidence in fish is available (Smith 1985). It could be assumed that the inertial mechanism is normally zeroed with reference to the sun. After some time swimming in the circular channel, the zero of the inertial mechanism would be adjusted to the curvature of the channel. Hence, fish would fix a random initial direction, and become unable to respond to a light change which demands a discrete double fold adjustment. Therefore, swimming would anchor in the original direction.

The tests performed in the infinite and in the halved infinite channel suggest that this interpretation may be correct. Swimming direction reversals occurred during the first session in the halved infinite channel while in the circular channel a single direction was apparent from the start. This may indicate that the escape response is more enduring in the halved infinite channel, perhaps because of its lower water level and smaller cross section. But once a unique direction is maintained for some time, there is no response to light shifts.

The infinite channel allows fish to swim at a constant angle with light, in a constant direction, and with no accumulation of turns to one particular side. In this condition no systematic bias in the inertial mechanism would develop. Therefore no reluctance to direction reversals as a response to light angle shifts should appear. In fact, the infinite channel promoted in a group of *C. pulcher* a constant oriented swimming with direction depending upon the angle of incidence of light. This behavior was displayed after several days during which direction reversals under constant illumination occurred. As discussed for the halved infinite channel, this may probably represent attempts to escape from confinement and as expected would be more enduring since no anchoring develops in the infinite channel.

In the halved infinite channel a mixed situation appeared: fish changed direction during the first days (as in the infinite channel), but once a constant direction was shown, it persisted independently of the light used (as in the circular channel). Therefore the light dependency of swimming direction in the infinite, and not in the circular channel, should be attributed to the shape of the channels

rather than to other differences between the conditions in both situations, such as number of fish in the group, channel section, temperature or light intensity.

These results show that groups of *C. pulcher* maintain a constant direction in the light centered circular channel, and that the direction itself does not depend on the angle of light. In contrast, in the light centered infinite channel, fish show a dependence on light angle which might be a factor in the seasonal migrations of this flood plain species (Levin & Belmonte 1988). An inertial guidance system seems to be implicated in the orientation of this fish.

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