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USE OF AN EGOCENTRIC FRAME OF REFERENCE BY GROUPED FISH (*Aphyocharax erithrurus*) IN A SPATIAL DISCRIMINATION

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ABSTRACT: Small groups of fish of a schooling species (*Aphyocharax erithrurus*) were trained to turn right or left in order to avoid being temporarily swept out of the water. This was achieved by a rotating avoidance paddle approaching them with one door (right or left) open. Once a learning criterion was attained, the direction of the paddle was reversed and both doors were opened. During these inversion trials, fish chose the door which was at the same side in relation to their body, showing that egocentric clues were used when facing the problem from an opposite viewpoint. When vertical black and white stripes were present at one side of the tank, a different response appeared during the inversion trials: fish passed through the door nearest to the stripes regardless of which door was open during training. It is concluded that these fish use egocentric references when the spatial problem is reversed by 180°, and that this response is overridden by a tendency to swim near a vertically striped background.

INTRODUCTION

Spatial orientation of animals and humans may be based on a reference system centred on their own body (egocentric orientation) or may rely on environmental stimuli (allocentric orientation) such as sun, stars, landmarks, odours or geomagnetic clues. Landmarks may be used simply as corrective feedback clues to orient movements by approaching it, avoiding it or maintaining a constant angle to it while travelling (Etienne et al., 1990b; Morris, 1981; Collet, 1987). But several landmarks may be taken together so that relational information may be used to construct a spatial representation or map (O'Keefe & Nadel, 1978; Nadel, 1990). This enables the subject to direct its movements to

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a particular place, even when approaching it from an unfamiliar viewpoint.

An experimental strategy used to discover the reference system in which spatial relations are punctuated while a subject contacts the environment, is to probe its response in different, altered ways after a learned spatial task has been solved (Nadel, 1990). One procedure is to compare the path during the outward and returning journey of a homing animal. Using this approach, gerbils appear to use an external or allocentric frame of reference to solve a spatial memory task (Thinus-Blanc & Ingle, 1985). Dogs trained in a "returning" task, initially base their orientation on a variety of external clues. But once criterion is reached, kinaesthetic (egocentric) clues predominate (Chapuis & Melin, 1979).

Other authors tested the spatial system of their subjects by introducing them into the experimental arena from a viewpoint different to the one available during learning (Acredolo, 1978; Thinus-Blanc & Ingle, 1985; Thinus-Blanc, Durup & Poucet, 1992). For instance, Acredolo (1978) found that after being rotated by 180° , spatial orientation in 6-months and 11-months-old children depends on an egocentric frame of reference when discriminating locations of objects within a familiar arena. In contrast, 16-months-old infants are able to keep track of their movements in space, showing an allocentric (objective) rule of orientation. The presence of a landmark did not change this situation. An objection to this changing viewpoint technique is that uncontrolled stimulation (internal and external) may occur during the passive relocation of the subject.

Fishes represent a low evolutionary stage of living vertebrates. Thus, the evaluation of their behavioural competence is interesting for comparative studies. Many studies have been performed on how fish handle space in large (Smith, 1985) and medium scale (Levin et al., 1989) migrations, but little is known about their ability for solving particular spatial discrimination problems. Several years ago, we designed and used the avoidance paddle to train fish on spatial discrimination problems. This technique is a one-way alternative to the shuttle-box that produces a large increase in the rate of spatial discriminated avoidance behaviour (Levin et al., 1982). This technique was used to compare the performance of individuals and groups in a spatial reversal learning task. The outcome was that only groups improved along reversals (Levin & Vergara, 1987). The avoidance paddle direction of rotation may be inverted at any time during training without changing any other aspect of the situation, and without manipulating the subject between trials. Thus, it offers a good method to study the reference system in which spatial responses are learned.

The purpose of the present experiment was to establish the spatial relationships that occur when groups of schooling fish are confronted with a 180° reversal of a learned spatial discrimination. This is evaluated in absence or in presence of external conspicuous references. Since our experimental subjects are extremely social because they are obligate schoolers (Shaw, 1970; Smith, 1985), small groups rather than individuals were used as experimental units.

METHODS

Subjects

Sixteen *Aphyocharax erithrurus* (Teleostei: Characidae) "rubicandela" ranging from 28 to 33 mm were used in this experiment. The fish were caught in shallow streams at Mantecal, Estado Apure, in Southern Venezuela with a thin mesh net, and were taken to the laboratory in plastic bags where water and oxygen was added. The specimens were kept for about two months before the experiment, in a 40-liter common tank filled with dechlorinated tap water that was maintained at 24°C, and were fed daily with dry food. They were randomly assigned to four groups of four individuals each. Each group was assigned to a different semicircular tank, where training and test trials were conducted.

Apparatus

The experiments were performed with the avoidance paddle, which has been fully described elsewhere (Levin, et al., 1982; Levin & Vergara, 1987). The paddle was a light plastic framework covered by a nylon net, which could be rotated in a semicircular tank (radius of 25 cm, wide of 10 cm) where the fish were kept. The paddle borders accurately adjusted to the tank walls (Fig. 1). The paddle was progressively moved through the water reducing the space where the fish were. The fish could surpass the approaching paddle and escape the space reduction by fleeing through a lateral doorway to avoid being temporarily swept out of the water (an error). The doorways were small corridors (6 x 11 mm) located at the end of two hollow pyramidal funnels placed side-by-side at the paddle extreme. This structure was symmetrically repeated at the opposite side of the paddle, so that its shape was the same regardless of its turning direction. The corridors could be closed with sliding transparent doors. A flat-black partition projected forward in the vertical midline. This barrier made left-right movements of the subjects

difficult while near the paddle. The barrier was opaque because previous observations showed that fish were unable to detour around a transparent partition (Levin, 1986). Thin plastic flappers shielded the space between the paddle and the tank walls.

The passage angle of the group was considered as follows: the curved bottom of the tanks was marked at 10° intervals. When the first fish of the group passed the door, the position of the paddle against the marks was recorded. The angular values increased in the direction of the turning paddle from 10 degrees, where the paddle made contact with the water surface, to 170 degrees where it left the water.

Groups of fish remained in separate semicircular tanks throughout the experimental period. The paddle was placed in each tank when performing each session. Illumination was provided by a 40-W incandescent reflector placed 20 cm above the water level.

For the asymmetric condition, a conspicuous landmark in the panorama was introduced by placing a white card with black 5-mm-wide vertical stripes 10 mm apart, against the glass on the right hand side.

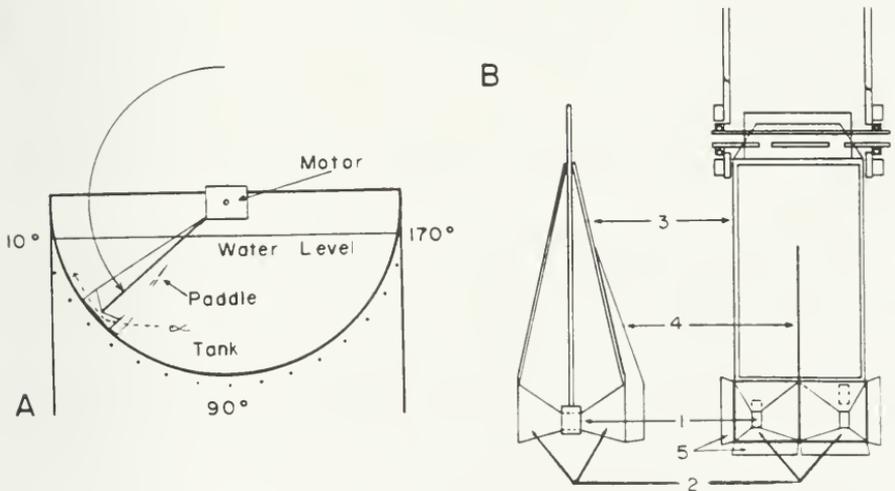


Figure 1. A, Diagram of the avoidance paddle. The paddle sweeps through the semicircular tank, entering the water at 10° and emerging at 170°. Fish may escape the space reduction or avoid an emergence from the water by passing through the open door (dashed line). B, Lateral (left) and frontal (right) view of the turning paddle. 1, corridors, one door open (the right one), one closed (the left one); 2, funnels; 3, framework; 4, partition; 5, flappers (modified from Levin et al. 1982).

Procedure

Each trial consisted of a 360° turn of the paddle (one turn in 25 s) starting at a high vertical position. One session per day of 40 trials with an inter-trial interval (ITI) of 30s was administered to each group until the criterion (10 successive trials with no errors) was obtained. Once this criterion was reached, and after the normal ITI, the inversion test was performed. That is, during four trials (inversion trials) the paddle turning direction was reversed and both doors remained open. The same ITI was applied.

Observations were made through a one-way mirror placed at an angle to the tank wall, so that the fish would not see their own reflected image. On each training trial, the number of errors was recorded. During the inversion trials, the number of passages through each door was recorded. The passage angle was also recorded.

The experiment consisted of 4 phases in which the same procedure was followed except that, in phase I, there was a symmetrical panorama: with identical one-way mirrors placed at both sides of the tank (only one was actually used). In phases II and III, a marked asymmetry was introduced into the panorama by placing the vertically striped card against the glass on the right hand side. In phase IV, the striped card was removed. Once again the panorama became symmetrical as in phase I. During phases I and II, training for groups G1 and G2 was performed with the left door open (left or right relative to the fish body when heading towards the approaching paddle), and with the right one open for groups G3 and G4. At the end of phase II, the open door was shifted right-left for the four groups.

Phase I was intended to show how fish orientation was shifted when the spatial problem presentation was rotated by 180°. The effect of strong asymmetrical clues on this transfer was tested in phase II. With the aim of balancing order effects, phases III and IV were performed. At the end of phase II, the open door was shifted right-left, with the striped card remaining at the right side of the tank. Hence, training began "de novo" under asymmetrical conditions.

RESULTS

The number of fish that passed through the door opposite to the training door during the four trials of each inversion test was expressed as the percentage of the total number of passages during the test (%EGO). The %EGO for each successive inversion test was plotted for

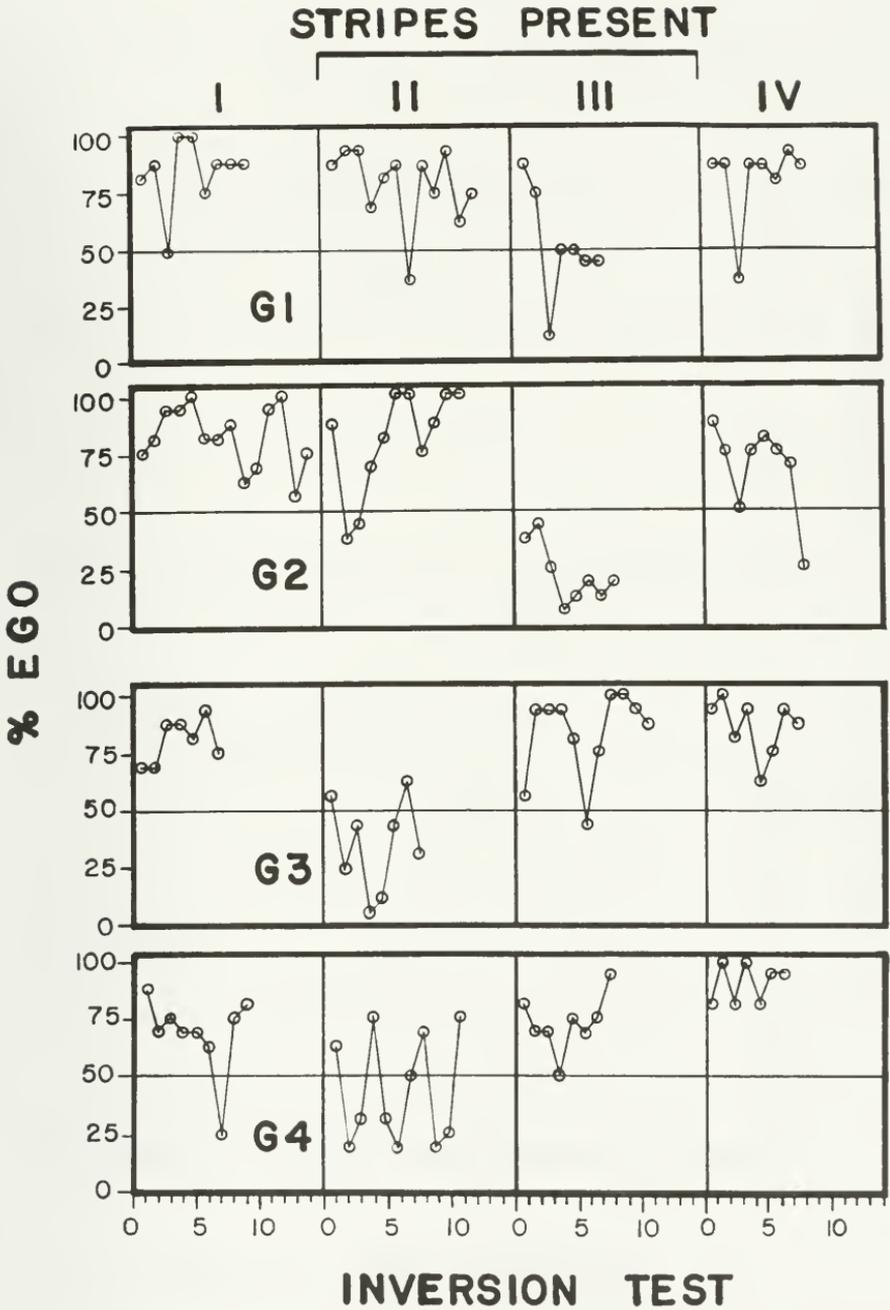


Figure 2. Percentage of individuals which passed through the door opposite to the training one with respect to the number of passages through both doors (%EGO), during each successive inversion trial along the four experimental phases, for groups G1-G4.

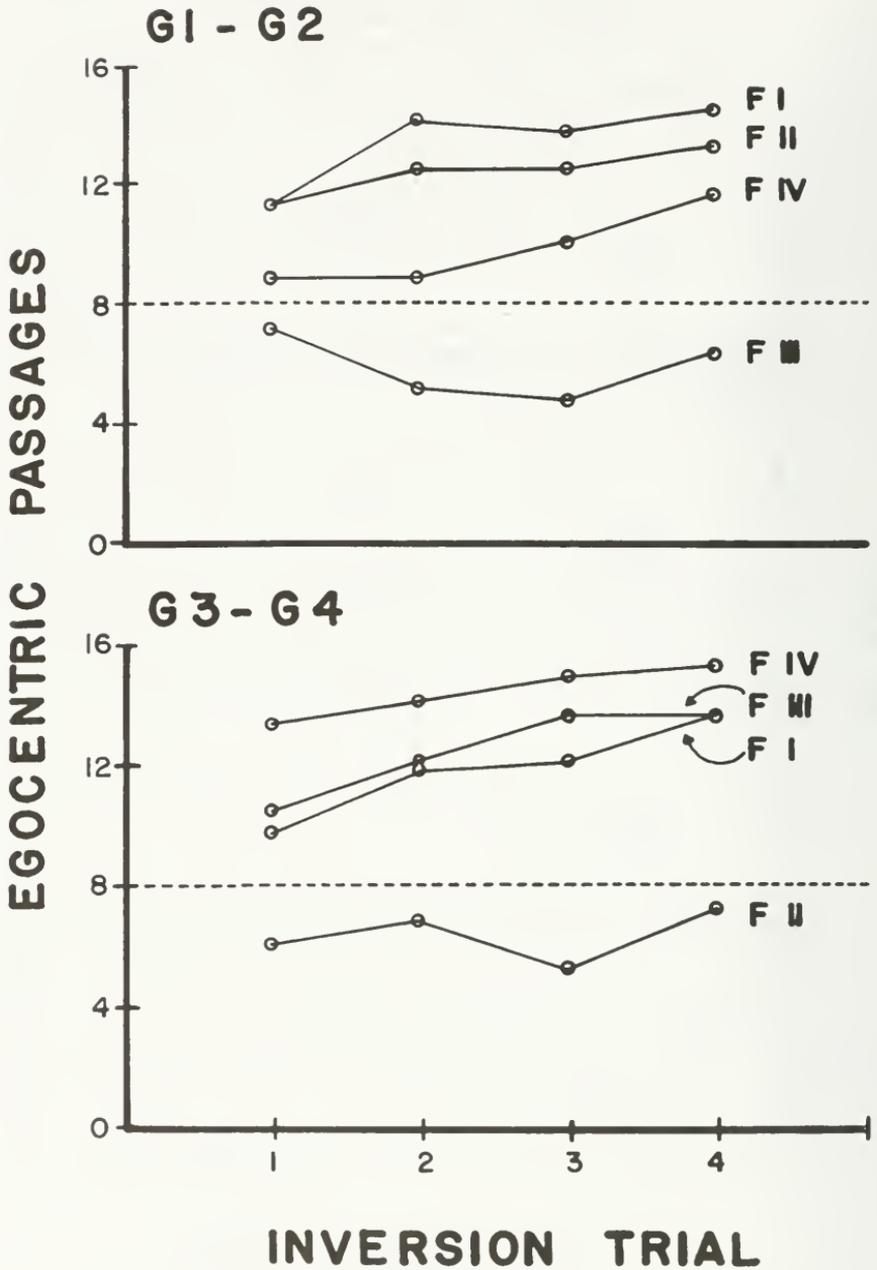


Figure 3. Mean number of fish which passed through the door opposite to the training one during each of the four inversion trials in the four phases (P). Replicate groups (G1-G2 and G3-G4) are pooled together. The horizontal line at 8 indicates an equal number of passages through both doors.

the four groups along the four phases (Fig. 2). During phases I and IV, the %EGO for all the groups were over 50% (binomial test: 68 cases out of 74, $p < .001$). When there were stripes, the outcome was also over 50% but only for groups G1-G2 in phase II (21 out of 23, $p < .001$) and for G3-G4 in phase III (18 out of 19, $p < .001$). On the other hand, groups G1-G2 in phase III were under 50% (11 out of 15, $p \leq .05$) and groups G3-G4 in phase II were not different from 50% (12 out of 19, $p = .1$). Such apparently non-egocentric cases were those in which training proceeded with the door nearer to the stripes open, so that egocentric orientation would result in fish passing at a distance from the stripes during the inversion trials.

Figure 3 shows the number of fish that passed through the door opposite to the training one, during each of the four successive inversion trials in each of the four phases. Replicate groups (G1-G2 and G3-G4) were pooled. It can be seen that, there are two cases in which the plots fall below the horizontal line at 8 (which indicates an equal number of fish by each door). These correspond to phase III for groups G1-G2 and to phase II for groups G3-G4, which are the above mentioned apparently non-egocentric cases. All the other curves are over the horizontal line, and their value increases with trials ($F(3, 20) = 3.40$, $p < .05$).

The passage angles of the four trials immediately before (Mean = 68.4, SD = 4.8), and during (Mean = 93.6, SD = 24) the four inversion test trials, pooled for all the inversion tests, were compared. The "during" angle was larger than the "before" angle (Mann Whitney "U" = 28.5, $p < .01$) ($n = n = 16$). This means that when the paddle turning direction was reversed, the fish passage through the door was delayed, even though, during the test, both doors were open. The difference between the mean passage "during" and "before" angles, was larger when there was a vertically striped card in one side of the tank (phases II and III: 36.3°, SD = 25°) than when it was absent (phases I and IV: 15.3°, SD = 5°; Mann Whitney "U" = 47, $p < .02$, $n = n = 8$).

The number of errors per session during training in phase II for G1-G2 was larger than for G3-G4. During phase III the reverse was true (Kolmogorov-Smirnov, $p < .05$ in both cases).

DISCUSSION

Once a group of fish learnt to swim through one of the lateral doors of the paddle, the reversal of the paddle direction with both doors open provided a test for the frame of references used by fish when facing the problem from the new viewpoint. Without conspicuous landmarks, fish responded egocentrically. That is, they passed through the door located

at the same side in relation to their own body, which is opposite to the one used during training. Mammals respond in a different way in what seems to be a similar situation. Lukaszewska (1961) suggested that the successful return journey made by rats in a T-maze must be based on the reversal of the direction taken on the outward path: a right-hand turn when the outward path involved a left-hand turn and vice-versa. Blind rats perform as well as normal ones indicating that kinaesthetic information is used in this task. Golden hamsters also base their homing trajectory in self-generated, route-based signals collected during their outward path when returning from a feeding place to their nest (Etienne et al., 1985; 1990a). In dogs, returning behaviour can be based upon a wide range of cues early during training but when the problem is mastered, they mainly rely on kinaesthetic cues (Chapuis & Melin, 1979). This kind of "route reversal" homing has been also described in pigeons (Wiltschko & Wiltschko, 1987).

The present results show that, at least when no external cues are present (phases I and IV), the fish do not return using the same route. The opposite door is used, which means that fish adopt a strictly egocentric solution, without correcting their response in accordance with the reversal of the problem. The likelihood that fish did not notice the paddle reversion is ruled out by the significant increase in the delay of the passages (larger passage angle) during the four inversion test trials. This suggests that the fish perceived the reversal direction of the paddle as a novel situation (Missilin & Ropartz, 1981; Save et al., 1992). Mechanical noises and the timing of the experimental events did not change with the change in paddle direction, and no conspicuous asymmetric clues were present. Thus, the change in paddle direction could be only detected by the fish by keeping track of their movements during the ITI, perhaps by kinaesthetic cues (Chapuis, 1982) or inertial integration (Barlow, 1964; Levin et al., 1989; Levin & González, 1994). In fact, when external asymmetric clues were available, an increase in angle retardation was measured during the inversion trials. This indicates that the novelty of the situation was perceived by the fish. In fact, when the inversion test was performed with landmarks present, two dimensions change: the inertial (or kinaesthetic) one, and the landmark side, relative to the responding fish axis. The egocentric tendency increased along the four successive test trials, suggesting that habituation of the disruptive effects of the novel situation had occurred.

However, when asymmetric landmarks were available, egocentric responses appeared only if they corresponded with approaching the stripes (groups G1 and G2 in phase II, and groups G3 and G4 in phase III). When the egocentric response would compel the fish away from the stripes during the test, an opposite reaction appeared: the fish again

passed the door nearest to the stripes (groups G1 and G2 in phase III and groups G3 and G4 in phase II). Two alternative explanations could account for these cases: either an "environmental" or absolute frame of reference is used in orienting the response, or superimposed with egocentricity, there is a tendency to pass the door as near as possible to the stripes. If an environmental rule was the case, groups G1 and G2 in phase II and groups G3 and G4 in phase III should also give an environmental response, which did not occur. Thus, a "visual discontinuity" taxis (Benhamou & Bovet, 1992) is validated. If this taxis is operative during the inversion trials, it should also be present during training. In fact, this was the case. The number of errors were larger when training proceeded through the furthest door rather than through the nearest one to the stripes.

This "visual discontinuity" taxis may be based on an optokinetic response (Bayliss, 1966). The body moves tending to stabilize the stripes in the visual field. This results in a slowing of the side of the fish nearest to the stripes. Thus, the fish turns and reduces the distance to the stripes. This response may have the adaptive advantage of directing the escape reaction towards discontinuities as those offered by the many aquatic reeds and plants that may provide refuge in the natural habitat of this fish. Another freshwater fish *Coreoperca kawamebari* has been found which prefers a vertically striped background rather than a horizontally striped or all white one (Yasutoshi & Watanabe, 1986).

Longitudinal studies of orientation rules in children have shown a shift from (strict) egocentric to an external frame of reference in localizing expected objects (Acredolo, 1978; 1990). Different specialized structures of the brain of mammals are responsible for these different functions (Buzsáki et al., 1982; Nadel, 1990) and they have different ontogenetic timecourses (Acredolo et al., 1975). A general picture of an increasing scale of sophistication and adaptivity has grown from these evidences. Some authors have considered that allocentric orientation involves a more "abstract" function than the apparently more simple egocentric orientation (Thinus-Blanc & Ingle, 1985). O'Keefe and Nadel (1978) considered three different kinds of behavioural strategies or hypothesis: "orientation", based on body-turns, "guidance"; based on individual landmarks; and "place" based on a set of landmarks relationally taken. Our finding of a strict egocentric rule for fish solving a spatial reversal task may suggest that these primitive vertebrates can achieve only the lowest degree of spatial differentiation. However, fish can perform outstanding homing trips of thousands of miles with extraordinary precision (Smith, 1985), where highly sophisticated orientation mechanisms are evident (Northcote, 1984; Levin et al., 1989). Today, there is a growing accumulation of evidence in favour of

the idea that all metazoans possess multiple orientation capabilities which interact hierarchically with one another (Able, 1991). How the egocentric response shown here relates to other orientation mechanisms, needs to be further examined.

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