Cognition 85 (2002) B51–B59

COGNITION

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Brief article

Modularity and spatial reorientation in a simple mind: encoding of geometric and nongeometric properties of a spatial environment by fish

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Received 14 November 2001; received in revised form 12 March 2002; accepted 29 May 2002

Abstract

When disoriented in environments with distinctive geometry, such as a closed rectangular arena, human infants and adult rats reorient in accord with the large-scale shape of the environment, but not in accord with nongeometric properties such as the colour of a wall. Human adults, however, conjoined geometric and nongeometric information to reorient themselves, which has led to the suggestion that spatial processing tends to become more flexible over development and evolution. We here show that fish tested in the same tasks perform like human adults and surpass rats and human infants. These findings suggest that the ability to make use of geometry for spatial reorientation is an ancient evolutionary tract and that flexibility and accessibility to multiple sources of information to reorient in space is more a matter of ecological adaptations than phylogenetic distance from humans. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Modularity; Spatial reorientation; Geometric and nongeometric properties; Spatial environment; Fish; Spatial cognition

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1. Introduction

Developmental research on spatial reorientation mechanisms has shown that geometric features are spontaneously taken into account by young children and predominate over local, nongeometric cues, even when the latter would allow the organisms to make the distinction between geometrically similar places (Hermer & Spelke, 1996). For instance, when disoriented in a familiar rectangular room, perfectly homogeneous and without

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PII: S0010-0277(02)00110-5

distinctive featural information, young children rely on the large-scale geometry of the room to reorient themselves (Hermer & Spelke, 1994). Similar results have been reported previously for several other vertebrate species (Cheng, 1986; Kelly, Spetch, & Heth, 1998; Vallortigara, Zanforlin, & Pasti, 1990). Much more surprisingly, however, young children (Hermer & Spelke, 1994) failed to reorient by nongeometric information, such as a distinctive differently coloured wall in the rectangular cage, in spite of the fact that this featural information would have allowed fully successful reorientation. Rats also have been proved to rely almost exclusively on geometric cues in a working memory version of the reorientation task in the rectangular environment (Cheng, 1986). In a reference memory version of the task rats eventually used featural information to distinguish between geometrically equivalent locations, but geometric shape still dominated over features because rats did not follow the correct feature when it was moved to a geometrically incorrect corner (Cheng, 1986). Given that rats have been proved able to use nongeometric information for solving spatial tasks that do not involve spatial disorientation (e.g. Morris, 1981; Suzuki, Augerinos, & Black, 1980), these findings have been interpreted to suggest that spatial reorientation depends on an encapsulated, task-specific mechanism, a "geometric module" (Cheng, 1986; Cheng & Gallistel, 1984; see also Fodor, 1983). The module would encode only the geometric properties in the arrangement of surfaces as surfaces: in the case of the spatial reorientation task in the rectangular environment, for instance, the geometric module would use only "metric properties" (i.e. distinction between a long and a short wall) and what is known in geometry as "sense" (i.e. distinction between right and left).

Human adults, in contrast to young children and rats, readily solved the blue-wall version of the reorientation task in the rectangular environment (Hermer & Spelke, 1994), suggesting that the most striking limitations of the geometric module are overcome during human development. Hermer and Spelke (1994, 1996) also went on with a more specific and strong hypothesis: namely that the performance of human adults, when compared with that of rats and young children, would suggest that some representational systems become more accessible and flexible over development and evolution. Research has suggested that language could be necessary to human beings for combining geometric and nongeometric information (Hermer-Vasquez, Spelke, & Katsnelson, 1999).

The aim of this paper is twofold. Firstly, we want to check whether reliance on purely geometric information for spatial reorientation could be observed even in a vertebrate species which is very distantly related to humans, such as fish. If so, that would provide quite convincing evidence for an ancient evolutionary origin of the geometric module in vertebrates. Secondly, we want to check whether the combined use of geometric and nongeometric information is indeed out of reach for (supposed-to-be) less advanced species (see e.g. Hodos & Campbell, 1969 for the difficulties associated with comparing cognitive abilities and phylogenetic histories in different, current-living organisms).

We tested fish (*Xenotoca eiseni*), a species that live in shallow, transparent water with pebbles and rich vegetation (Meyer, Wischnath, & Foerster, 1985), in the same task used with humans. In the first experiment fish were tested in a closed rectangular tank, lacking any distinctive landmark, with uniform white-coloured walls. Fish could escape from the tank by pressing small flexible opaque doors of similar appearance, located at the corners (Fig. 1, top). We were interested to check whether fish proved able to discriminate between

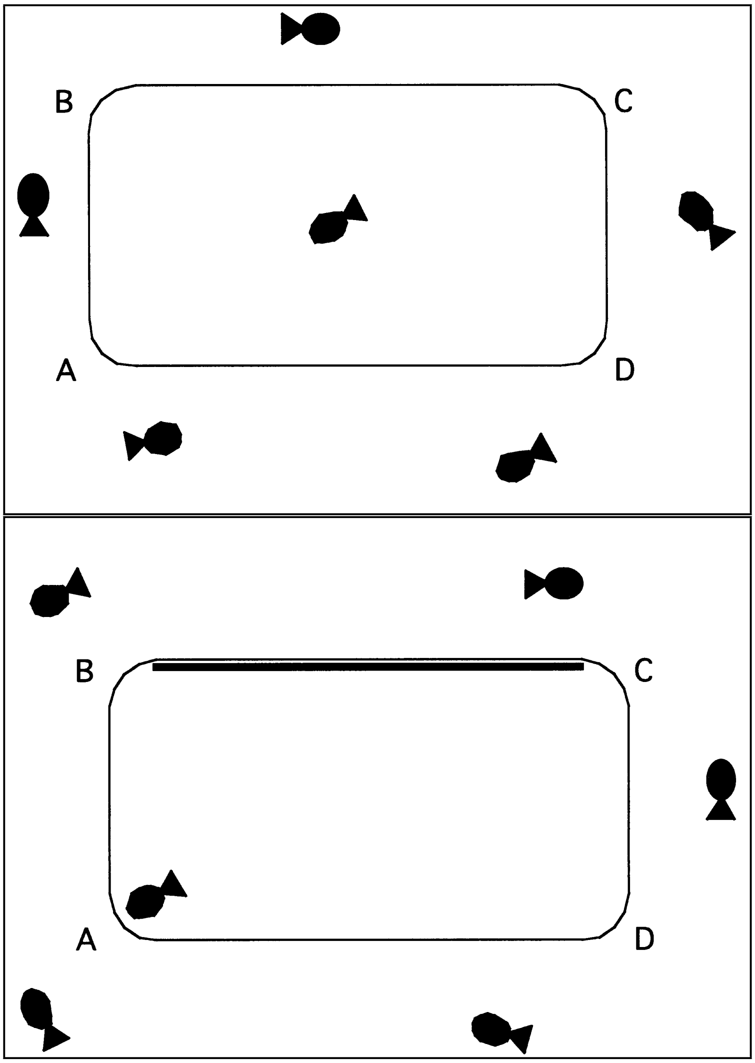

Fig. 1. Schematic representation of the test apparatus. The test fish could escape from the inner rectangular shape pushing moveable opaque doors placed at the corners A, B, C and D and rejoin its companions in the annular region of the outer tank. In Experiment 1 (top) the walls of the testing tank were all white and the task for the fish was to distinguish between corners A, C and corners B, D using purely geometric information (corner A and its rotational equivalent, corner C, are in fact indistinguishable on the basis of purely geometric information, but can be distinguished from corners B and D, which, in turn, are geometrically equivalent and cannot be distinguished from each other). In one testing condition doors A and C were both reinforced (i.e. they could be opened) and in another condition only door A was reinforced; if fish were orienting by purely geometric information then they should have confused geometrically equivalent locations A and C in both testing conditions. In Experiment 2 one wall was made of a different colour, i.e. blue (indicated by the line in bold in Fig. 1, bottom). Only the door at corner A could be opened, the others being blocked. Fish could disambiguate between the two geometrically equivalent corners A and C using the nongeometric information provided by the blue wall.

the two geometrically equivalent locations, A–C, and the other two, geometrically different, locations B–D. Such a behavioural performance requires the combined use of "metric properties" and "sense" (above), which are the distinctive computations performed by the geometric module. To check that fish were orienting using only geometric information, and therefore chose geometrically equivalent corners with the same frequency, two testing conditions were devised. For some fish only one door (e.g. at corner A) and its geometric equivalent (e.g. at corner C) could be opened, the other two doors being blocked; for some other fish only one door (e.g. at corner A) could be opened, the other three doors being blocked.

In the second experiment another group of fish was tested in a similar apparatus, but this time with one wall with a distinctive colour, i.e. blue. Only one door could be opened (A in Fig. 1, bottom), the others being blocked. We were interested to check whether in this case fish could distinguish between the two geometrically equivalent corners, A and C, choosing correctly corner A. This would demonstrate that fish conjoined geometric and nongeometric information to reorient themselves.

2. Methods

Subjects were 18 mature fish (ranging 3–5 cm in length) of the species *X. eiseni* from a stock maintained in our laboratory within vegetation rich (*Ceratophillum* sp.) large tanks (55–120 l) provided with artificial illumination 16 h per day.

The apparatus consisted of a rectangular tank (31 cm long, 14 cm wide and 16 cm high), with uniform white walls in Experiment 1 (Fig. 1, top) and a distinctive blue wall in Experiment 2 (Fig. 1, bottom), covered with a one-way screen to eliminate extra-tank cues and lit centrally with a 75 W light bulb. The testing tank was inserted in a larger tank (60 × 36 × 25 cm) so as to create an annular region with vegetation and food where the test fish was located together with five other conspecifics (not tested) that provided motivation for social reinstatement. In each trial, the fish was inserted in the test tank where four identical opaque doors (2 × 3 cm; 5 cm from the floor) made of a flexible plastic material were located at the corners (which were smoothed to allow insertion of the doors, see Fig. 1). In Experiment 1, in one testing condition ($N = 6$) only two doors, geometrically equivalent, could be opened, the others being blocked (the correct doors are conventionally indicated with A and C in Fig. 1, but different animals were tested with different pairs of corners); in the other testing condition ($N = 4$) only one door could be opened, the other being blocked (the correct door is conventionally indicated with A in Fig. 1, but different animals were tested with different corners). In Experiment 2 ($N = 8$), with the blue wall, only one door (conventionally indicated with A, though different doors were used as the reinforced one for different fish) could be opened. Fish could open the correct door to escape by pressing on it with the snout; attempts to escape were clearly visible from videorecording because of characteristic movements of the tail and body of the fish. Before testing, fish underwent a shaping procedure in their hometank (30 × 40 × 20 cm) for 10 days, using a partition that divided their hometank in two halves, one ('comfortable') with food and vegetation and the other ('uncomfortable') without any food and vegetation. Two moveable doors identical to those subsequently used at test were positioned on the partition, allowing the fish to move between the two compartments. In this way fish were accustomed to the use of the moveable doors before testing. At test, fish were given five daily sessions of ten trials. In each trial the number of attempts to escape through the four doors was videorecorded, until the fish was able to exit and rejoin conspecifics in the annular region (in each trial, the maximum time allowed to escape was 20 min). The inter-trial interval was 10 min, during which the fish was allowed to remain in the annular region (reinforcement time). After that, the tank was rotated 90° and the fish was placed in a closed, opaque container and slowly rotated on a rotating chair in order to eliminate the use of compass and inertial information before being tested again.

3. Results

Frequencies of escape attempts in the white-walls task (Experiment 1) are shown in Fig. 2a,b. Data were analyzed by analysis of variance (ANOVA) with testing conditions (two doors reinforced vs. one door reinforced) as a between-subjects factor, and geometry (AC vs. BD) and sessions as within-subjects factors. The ANOVA revealed significant effects of geometry ($F(1,8) = 263.30$, $P = 0.0001$), testing conditions ($F(1,8) = 98.152$, $P = 0.0001$), sessions ($F(4,32) = 3.902$, $P = 0.011$) and a geometry × testing conditions interaction ($F(1,8) = 41.709$, $P = 0.0001$). There were no other statistically significant effects (sessions × testing conditions $F(4,32) = 0.416$; geometry × sessions conditions $F(4,32) = 1.957$; geometry × sessions × testing conditions $F(4,32) = 0.133$).

Fish proved able to direct escape responses predominantly on corners A and C in both testing conditions (two doors reinforced: $F(1,5) = 79.919$, $P = 0.0001$; Fig. 2a; only one door reinforced: $F(1,3) = 150.682$, $P = 0.001$; Fig. 2b). As expected, escape attempts tended to decrease with testing sessions, but there were no significant interactions associated with geometry and testing conditions. Moreover, escape attempts tended to be higher in the condition with only one door reinforced, because of partial reinforcement effect, but fish chose corners A and C with identical frequency in both testing conditions (two doors reinforced: $F(1,5) = 0.307$, n.s.; see Fig. 2a; only one door reinforced: $F(1,3) = 0.001$, n.s.; see Fig. 2b). This demonstrates that fish were orienting only by the geometry of the enclosure and thus confused geometrically equivalent locations.

Frequencies of escape attempts in the blue-wall task (Experiment 2) are shown in Fig. 3. Data were analyzed by ANOVA with locations (A, B, C and D) and sessions as within-subjects factors. The ANOVA revealed a significant effect of locations ($F(3,21) = 41.896$, $P = 0.0001$); as in Experiment 1 escape responses tended to decrease with time (sessions $F(4,29) = 5.143$, $P = 0.003$), but there was no significant interaction ($F(12,84) = 0.728$, n.s.). There were no statistically significant differences between locations B, C and D ($F(2,14) = 2.192$, $P > 0.15$). Fish thus proved able to completely disambiguate the problem, choosing predominantly corner A over corners B, C and D.

4. Discussion

In Experiment 1 geometric information alone could not specify unambiguously single locations, but was sufficient for a partial disambiguation of the reorientation task. Fish

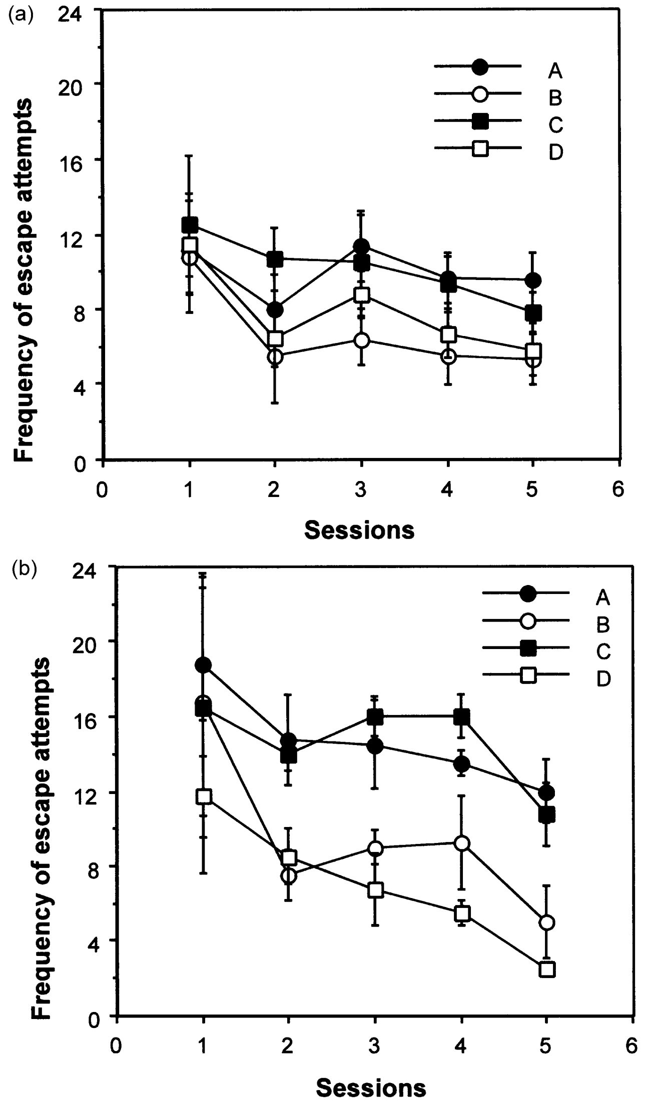

Fig. 2. Frequency of escape attempts (group means with SEM are shown) in Experiment 1 (a: doors A and C could both be opened; b: only door A could be opened).

chose the two geometrically equivalent locations (A and C) with equal frequency, even when only one of them was reinforced (Fig. 2b); this proves that fish did not have access to some other means of orientation. Results showed that fish could distinguish between locations A–C and locations B–D, thus revealing their ability to use purely geometric information. These findings, together with those obtained with birds (Kelly et al., 1998; Tommasi & Vallortigara, 2000; Vallortigara et al., 1990) and mammals (Cheng, 1986), suggest that the ability to use purely geometric information for reorientation is widespread among vertebrates, likely representing an evolutionarily ancient trait and a very basic cognitive mechanism. Use of geometric information for spatial reorientation makes sense ecologically. The large-scale shape of the landscape does not change across seasons, whereas there are important seasonal changes in the nongeometric properties of the landscape (e.g. appearance of grass and vegetation, snowfall and melting and so on; see also Cheng & Gallistel, 1984).

In the second, crucial, experiment fish were tested in the presence of a distinctive nongeometric feature, i.e. one wall of the tank was blue coloured. The nongeometric cue provided the animal with the possibility of a complete disambiguation of the reorientation task. Results showed that fish could distinguish between the two geometrically equivalent corners A and C, choosing correctly corner A. This demonstrates that fish conjoined geometric and nongeometric information to reorient themselves.

It has been suggested that language, and more specifically spatial language, may provide the medium for representing conjunctions of geometric and nongeometric properties of the environment (Hermer-Vasquez et al., 1999). Indeed, the ability to correctly orient in the blue-wall task (Hermer & Spelke, 1994) correlated with the ability of children to produce and use phrases involving “left” and “right” when describing the locations of hidden objects (MacWhinney, 1991). The developmental time course of the ability to conjoin geometric and nongeometric information thus suggests that language acquired by children (starting at 2–3 years of age) would allow them to perform as well as adults (at about 5–7 years of age) (see Hermer-Vasquez, Moffet, & Munkholm, 2001).

Gouteux, Thinus-Blanc, and Vauclair (2001) recently demonstrated, however, that rhesus monkeys also combine geometric and nongeometric information; these authors

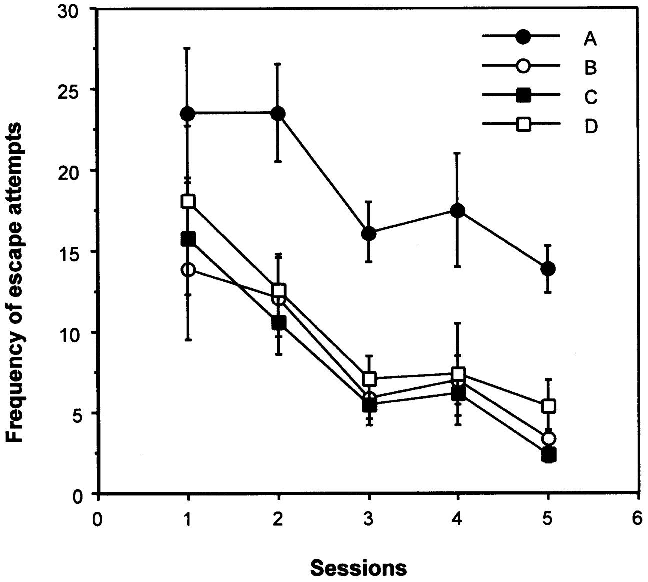

Fig. 3. Frequency of escape attempts (group means with SEM are shown) in Experiment 2.

thus proposed a less strong version of the original Hermer and Spelke claim according to which joint use of geometric and nongeometric information, though not strictly dependent on language, nonetheless would become accessible only to advanced mammalian species. It is also worth noting that Learmonth, Newcombe, and Huttenlocher (2001) recently provided evidence that in certain conditions children can use nongeometric information for reorientation, though systematic rotational errors were made as well (see also Learmonth, Nadel & Newcombe, in press).

Our findings clearly confirm that language is not necessary for solving the blue-wall task. Obviously, it is possible that humans do encode the available information linguistically; if so, it will be important for comparative research trying to establish what sort of advantages such an encoding could offer with respect to the non-linguistic encoding which is the only available to non-human species.

Our results indicate that the ability to make joint use of geometric and nongeometric information does not appear to be related in any simple ways with the complexity of the brain and/or phylogenetic distance with humans. Recent work has revealed dissociation between place and cue learning by telencephalic ablation in fish (Lopez, Bingman, Rodriguez, Gomez, & Salas, 2000) and the pallial region of the telencephalon may contain subdivisions that are homologous to the medial pallium or hippocampus of mammals (Northcutt, 1995). Like other biological characteristics, not all cognitive and neural features change over the course of evolution: the brains of all living vertebrates are likely a mosaic of both primitive and advanced characteristics (see also Hauser, 2000). This appears to be in agreement with the idea that the evolution of intelligence cannot be regarded as a simple unilinear process: sometimes fish do easily what is out of reach for young children and rats.

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