The Geometric World of Fishes

Subjects: Psychology

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Spatial orientation may be led by the distinctive geometry of an environment: fish can use metric and left-right direction to reach convenient locations, such as a foraging site. This remarkable capacity requires to handle the macrostructural characteristics of space, which are based on the Euclidean concepts of point, surface, and boundary.

navigation	spatial geometry	reorientation	teleosts	fishes

1. History

Ecological habitats share spatial characteristics that allow animals to find useful supplies such as food, shelter, and companions, for survival. The ability to make use of these characteristics falls within "spatial cognition", which embraces a set of orientation strategies used by animals to better adapt in life spaces. One of these strategies relies on geometric spatial information, such as metric (length, distance, angular magnitudes) and positional sense (left-right direction), so representing stable cues animals can rely on to efficiently navigate through an environment.

The classic example of geometric reorientation is the following. You are standing in the center of a perfectly rectangular room where in one corner there is a prize. You are blindfolded and turned in place, during which time the prize is removed. Afterwards, you are asked to take the blindfold off and identify the corner where you saw the prize before. Rather than choosing one of the four corners at random or always choosing the correct corner (i.e., the position where there was the prize), you will also choose the symmetric corner on the diagonal at 180°, since it was characterized by the same geometric cues (e.g., a short wall on the left) as the correct corner position.

Freshwater and seawater species of fish make use of several orientation strategies for adaptative behavior^[1]. Some of these strategies request to detect, process, and memorize specific sets of spatial cues, according to self-based coordinates, while others involve spatial relationships in world-based coordinates^[2]. Spatial orientation based on the environmental geometry has been widely investigated across species, starting from Cheng's original observations with rats^{[3][4][5][6][7]}. His findings led him to advance the hypothesis that a "geometric module" might exist in the brain of animals to encode metric and sense properties of surfaces.

Traditionally, experiments to investigate the use of metric and sense spatial cues have been carried out in arenas with a geometric shape that is defined well (most of all, rectangular, but also diamond-, parallelogram-, or trapezoid-shaped arenas^{[8][9][10]}). Animals are required to identify the position of a reward that is usually hidden at the level of one of the four corners. In the case of perfectly rectangular environments, two corners have the shorter

wall on the left (and the longer wall on the right), while two corners have the shorter wall on the right (and the longer wall on the left). Thus, it is possible to draw two diagonals, which are characterized by opposite geometric cues. If one corner only is rewarded, animals will make "rotational errors" towards the other corner on the diagonal, proper due to these spatial contingencies. However, the use of nongeometric cues, such as conspicuous or local landmarks, allows animals to discriminate the equivalent corners, significantly reducing rotational errors. For example, if one of the four wall is painted with a different color, it is possible to conjoin geometry and such a landmark to resolve the two-way symmetry and choose the correct corner position. Another relevant geometric cue is that provided by relative or absolute distances, from the arena's center to the corners, or considering the goal-position as a reference.

2. Research in fish

Fish possess excellent capacities in spatial mapping and navigation: they can plan and execute adaptive movements to remembered goals^[11], by means of learning and memory processes comparable to those displayed by land tetrapods. Beyond that, fish can resolve spatial reorientation tasks in which:

- 1. environmental geometries are interlaced with featural information, such as conspicuous (blue wall, blue 3D cylinder) or local landmarks (corner panels);
- different behavioral methodologies and memory systems are engaged, those based on spontaneous ("socialcued memory task") or acquired ("rewarded exit task") behavior;
- 3. nonvisual transparent environments or blindness conditions request to use other sensory systems or motion patterns in alternative to sight.

An example of acquired reorientation behavior of fish under nonvisual conditions is that performed within a rectangular transparent arena. To resolve the geometric task, the fish had to choose one of the two target corners on the geometrically correct diagonal allowing it to leave the arena. These two corners share the same geometry, having a short wall on the right and a long wall on the left. The transparency of the rectangular space requests the fish to use other sensory channels than vision to properly reorient. The behavioral pattern became increasingly consistent with repeated experience, as the fish is typically rewarded with food in the case of correct choices. Original unpublished data are revealing that different species of fish reoriented similarly through transparent surfaces, which defined a distinctive global shape, supporting spatial reorientation under undefined situations (e.g., seek out food within a visually lacking environment) as a shared skill among teleosts, despite ecological specificities. Moreover, this spatial capacity would be highly dependent on task's demands: actually, fish show no reorientation in the case of spontaneous behavior, where attentional factors (rather than motivational states driven by food) seem to determine short-term ("working") memories.

During geometric spatial reorientation, the involvement of other sensory channels than sight, as well as the use of alternative orientation strategies based on motion patterns, would have a twofold implication. First, it would increase the ecological relevance of metric and sense relationships, which could also be detected through sensory systems that are assigned to other functions (e.g., the lateral line to detect hydrodynamic gradients^{[12][13]}), or developing intelligent solutions based on adaptive behaviors (e.g., "wall-following" strategies^{[14][15]}). Second, it

would lead to consider the recruitment of modalities driven by touch for determining spatial geometric characteristics during reorientation. As such, a promising link between other vertebrates and humans takes place, in consideration of the orientation mechanisms used to face situations of visual deprivation or impairments^[16].

3. Conclusions

Behavioral observations with blind fishes^[17], and eyed fishes in visual transparency contexts^[18], have suggested that the shape of an environment can be experienced through multiple sensory systems (e.g., the lateral line, the sense of touch), thus supporting the ecological importance of geometric information. More than other animal groups, teleosts are increasingly emerging as a powerful model to explore spatial memory and its neural correlates, starting from their precision at navigating through underwater environments. The geometric world of fish has been sculpted by ecological pressures to use macrostructural spatial cues for survival purposes.

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