Comparing geometric models for orientation
Medial vs. principal axes

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Research examining the encoding of geometry for orientation has received considerable attention in the past 25 years with the proposition of a geometric module.¹ Supporting the importance of geometry in the formation of a spatial representation, to date the majority of species studied show an encoding of geometry, even when presumably more salient and reliable features could be used. Although studies have shown that animals encode geometric information such as distance, direction or angular amplitude from the environment, few have tested the assumption that geometry is encoded using global properties such as the major principal axis, a strongly supported proposition. Here we present an alternative model to principal axis, specifically medial axis. In addition we describe the straight skeleton model, which may also offer insights into the understanding of geometric encoding by orienting animals.

Comparing Geometric Models for Orientation: Medial vs. Principal Axes

An important ability for a mobile animal is to navigate from one location to another. The first step necessary for successful navigation is the determination of the direction in which to begin traveling—a process known as orienting. Since the pioneering work of Cheng,¹ many researchers have been interested in understanding how animals orient and reorient using the geometric properties of their environment.²⁻⁵ Many of these studies have sought to examine this problem using rectilinear spaces within a controlled laboratory environment. Notably, the vast majority of animals studied to date show an encoding of geometry. Yet, how an environment’s shape is represented by the animal, and which geometric properties are relevant, remains to be solved. Although theoretical models have been proposed to describe how geometry might be processed, few studies have attempted to empirically examine which geometric properties of an environment are encoded and how this information is represented.

Principal Axis

Until recently, the common supposition was that animals were using the principal axes of an environment.⁴ Cheng⁵ provides a clear definition of principal axes:

_The principal axes of a shape go through the centroid (centre of mass). [...] The first or major principal axis goes roughly through the length of the space. Mechanically, it minimizes the angular momentum when the space is spun around it. [...] It is the line through the space for which perpendicular distances from points in the space to the axis are minimized, by the least-squares criterion. [...] Except for spaces with multiple axes of symmetry, the principal axes are unique._ (pp. 8–9).

Recently two studies have attempted to evaluate whether animals use the major principal axis to orient within an enclosed space. Pearce et al.⁶ during Experiment 1, used a traditional rectangular environment to train rats to find a submerged platform at one corner of a water maze. Once the rats were accurately swimming directly to the platform, the researchers tested

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the rats in a kite-shaped environment. Even though this manipulation changed the shape from that of the training environment, the rats’ choice behavior was robust—they continued to search at the correct corner according to local geometric cues and sense information (turning left or right). The authors concluded that the rats must have learned to use local geometric cues coupled with a sensorimotor program during training and transferred this learning to the novel testing environment.

However, in reply to Pearce et al. Cheng and Gallistel provided an alternative and more parsimonious explanation for the results; they showed that the choice behavior of the rats could also be explained by the use of a major principal axis strategy—and thus argued that a more complex strategy of the use of local cues coupled with a sensorimotor program was not needed.

Tommasi and Polli also reported evidence for the use of local geometry for orientation. Moving beyond the traditional rectangular environment, they trained chicks to search for a hidden goal in a parallelogram-shaped environment. One group of birds found the hidden food at a corner with a 60° amplitude whereas another group found the hidden food at a corner with a 120° amplitude. At testing, the researchers provided the birds with transformed environments that would elucidate what geometric properties the birds had encoded. Modifying the shape of the environment showed that the birds encoded wall length information and the corner angle amplitudes (by making the environment either rectangular or rhombus-shaped, respectively)—both of these properties were considered as local geometric cues by the authors. However, modifying the environment such as by placing wall length information in conflict with corner angle amplitudes (a mirror reflection of the parallelogram) revealed interesting group differences. The chicks trained to go to the 60° corner showed control by angular information, whereas the chicks trained to go to the 120° corner showed reliance on wall length information. The authors explained these results by arguing that the birds were using local geometric cues, but that the acute angles were more salient than obtuse angles; thus the chicks trained on acute angles would be expected to rely on angular amplitude whereas chicks trained on obtuse angles would rely on wall length. However, Cheng and Gallistel showed that searching at the acute corner would be expected, by both groups, had the birds been relying on the major principal axis—a more parsimonious explanation than that offered by Tommasi and Polli.

Thus, Cheng and Gallistel’s work questions the necessity of explaining orienting behavior, at least in these two studies, using more complex strategies. However, the use of the principal axes is not without its own problems. As can be seen from the definition provided above, the principal axes are defined globally. In a rectangular space, the principal axes equate to two perpendicular lines bisecting the environment. Even at an intuitive level, it is clear that two perpendicular lines do not provide sufficient information about the shape of an environment. Although the major principal axis may be well defined in simple experimental environments, it is not necessarily uniquely defined in more complex (and arguably more realistic) environments as it depends on exactly which set of obstacles are included (Fig. 1). For example, the position and orientation of the major principal axis differ, in general, if one considers all obstacles within 10 m, all within 100 m, or all within 1,000 m. Finally, depending on which obstacles are included in its definition, the principal axis may be located arbitrarily far from the observer’s current position and, furthermore, its orientation may be independent of that of the observer’s local environment.

**Medial Axis**

An alternative model for examining geometric encoding by animals is the use of medial axis. Devadoss and O’Rourke (2011) define the medial axis as follows (where $\partial P$ denotes the boundary of $P$):

The medial axis $M(P)$ of a polygon $P$ (also known as the cut locus of $\partial P$) is the closure of the set of points in $P$ that have two or more closest points among the points of $\partial P$. (p.118).

The first study to empirically examine the use of the medial axis, conducted by Kelly, Chiandetti and Vallortigara, indeed showed that the orientation data from chicks and pigeons support a medial axis model. In this study, pigeons and chicks were trained to locate food hidden in a fully enclosed rectangular environment. Once the birds were responding accurately, they were tested in an L-shaped arena. The search behavior of the pigeons supported a medial axis model, and the chicks’ search behavior supported the primary use of local geometry coupled with a secondary medial axis model. This study is important as the L-shaped environment allowed the researchers to evaluate whether the birds’ search behavior was best modeled by the use of principal axis, medial axis or local geometric cues.

As explained above, the principal axis defines only one major axis (along with a corresponding minor axis perpendicular to it). In contrast, the medial axis defines a collection of axes. Informally, the medial axis is a backbone whose segments correspond to the respective orientations of a shape’s constituent components. This backbone is the locus of points that are locally central relative to the shape’s boundary. In a polygon, this locus corresponds to a tree structure, i.e., a set of vertices joined by arcs such that for any pair of vertices there is a unique sequence of arcs connecting them.

Unlike the principal axis, the medial axis is defined locally. From the point of view of an observer, the definition of the medial axis depends only on nearby obstacles; its position and orientation remain unchanged regardless of whether or not distant obstacles are considered (see Fig. 1). Thus, distant features can be included or ignored without affecting the medial axis. Furthermore, the medial axis of any subregion remains consistent with that of any larger region containing it. As mentioned earlier, the principal axis’ definition in more complex environments depends on which subset of obstacles is considered; the medial axis’ definition, however, is independent of the complexity or the extent of the environment.

**Other Models: Straight Skeleton**

In addition to principal and medial axes, other models remain to be explored. In particular, Aichholzer et al. introduced
the straight skeleton as a geometrically simpler alternative to the medial axis. In some cases the straight skeleton and the medial axis are identical (e.g., for all convex polygons). A key difference between the two is manifested at reflex vertices (each of which is identified with a curve in the medial axis): the straight skeleton of a polygon does not include any curves. Unlike the tree structure of the medial axis which has a leaf vertex for each convex vertex, the straight skeleton has one leaf vertex for every vertex. Further research is required to determine whether the movement paths of animals around reflex vertices are better characterized by the medial axis or the straight skeleton.

**Importance of Theoretical Models**

Geometric techniques for characterizing, simplifying and comparing shapes, including the principal axis and the medial axis,\(^1,\)\(^2\) provide models to better understand geometric encoding, including the search behavior shown by pigeons and chicks. These models are not necessarily intended to interpret an animal’s ability to understand geometric properties of its environment; rather, these models may be used to accurately explain and predict specific spatially-guided behaviors. It is possible that the medial axis (or another model) may best explain spatial search behavior while an individual is obtaining information for orientation, but once oriented, local geometric cues (such as distance, angular amplitude or sense information) may be used to more accurately identify a goal position. This supposition would be supported by some current theories of spatial orientation.\(^3,\)\(^4\) Developing models that better predict goal-directed search behavior is an important step for the design of empirically-based studies to understand how animals use environmental geometry for orientation.

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