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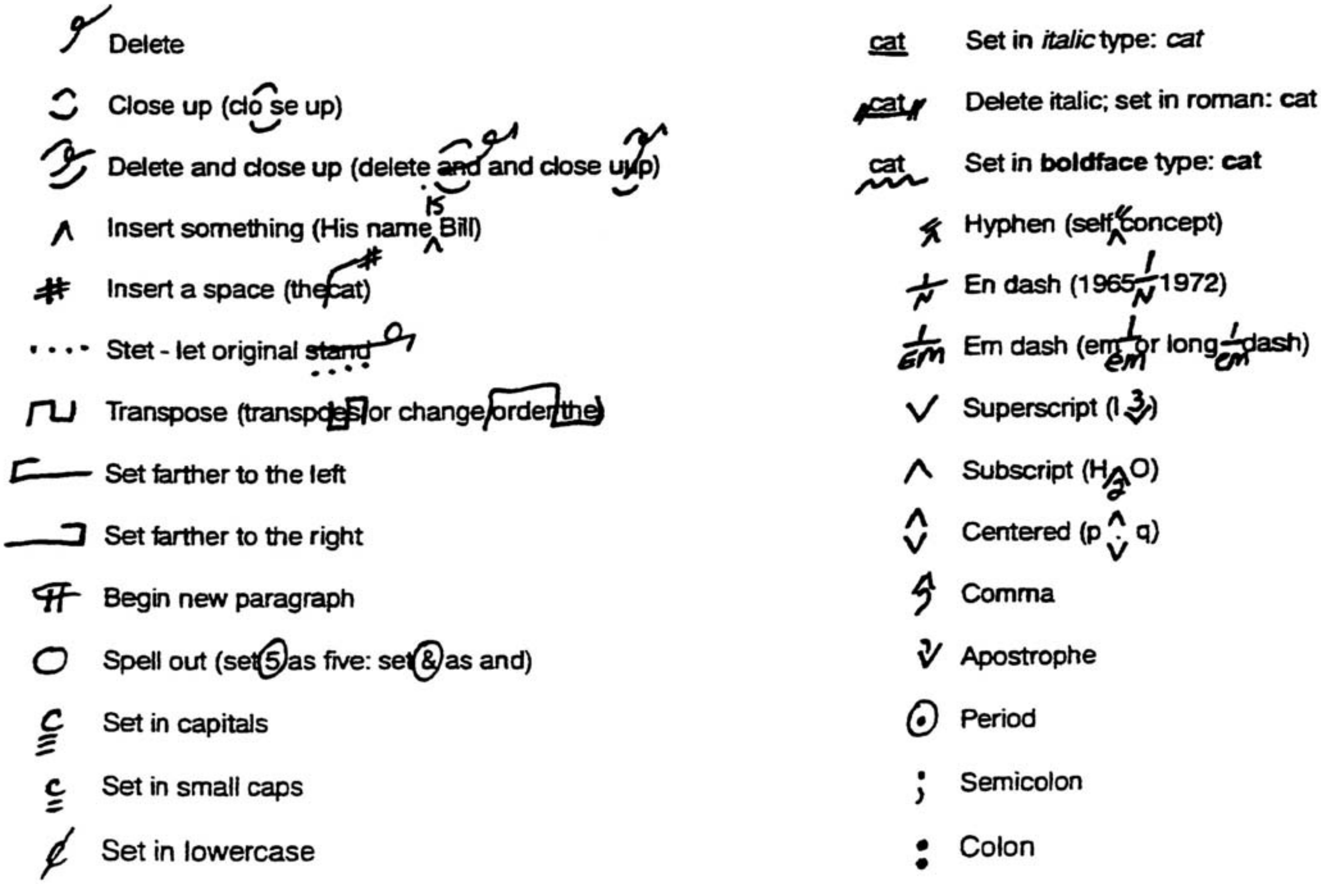

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Shape Parameters Explain Data From Spatial Transformations: Comment on Pearce et al. (2004) and Tommasi & Polli (2004)

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In 2 recent studies on rats (J. M. Pearce, M. A. Good, P. M. Jones, & A. McGregor, 2004) and chicks (L. Tommasi & C. Polli, 2004), the animals were trained to search in 1 corner of a rectilinear space. When tested in transformed spaces of different shapes, the animals still showed systematic choices. Both articles rejected the global matching of shape in favor of local matching processes. The present authors show that although matching by shape congruence is unlikely, matching by the shape parameter of the 1st principal axis can explain all the data. Other shape parameters, such as symmetry axes, may do even better. Animals are likely to use some global matching to constrain and guide the use of local cues; such use keeps local matching processes from exploding in complexity.

In the past 2 decades, research on how diverse vertebrate animals orient and reorient in enclosed rectilinear spaces has flourished (Cheng & Newcombe, in press). Of particular interest is the use of geometric information. This is the information contained in the broad shape of an environment. Cheng and Newcombe's (in press) review showed that all the vertebrate animals tested to date learn to use geometric information; these include human adults and children (Hermer & Spelke, 1996; Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, & Huttenlocher, 2001), rhesus monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001), rats (Benhamou & Poucet, 1998; Cheng, 1986; Margules & Gallistel, 1988), pigeons (Kelly & Spetch, 2001, 2004b; Kelly, Spetch, & Heth, 1998), chicks (Vallortigara, Pagni, & Sovrano, 2004; Vallortigara, Zanforlin, & Pasti, 1990), and fish (*Xenotoca eiseni*; Sovrano, Bisazza, & Vallortigara, 2003; goldfish; Vargas, López, Salas, & Thinus-Blanc, 2004). Under some circumstances, all these species also use nongeometric or featural information for reorientation, and it is debated how much and in what way the processing of geometric information is modular (Cheng, 1986; Cheng & Newcombe, in press; Gallistel, 1990; Newcombe, 2002; Wang & Spelke, 2002, 2003).

Although the use of geometric information is undisputed, the question of what and how geometric information is used has not been addressed empirically, except for two recent articles on rats (Pearce, Good, Jones, & McGregor, 2004) and chicks (Tommasi & Polli, 2004), which made imaginative use of the transformational strategy (Cheng & Spetch, 1998) and produced significant and interesting results. In both species, the animals were trained to go to one corner in a space of one shape and were tested in transformed spaces. The test spaces did not preserve the euclidean shapes of the training spaces. Because the animals nevertheless made nonrandom choices among the corners of the test spaces, both Pearce et al. (2004) and Tommasi and Polli (2004) concluded that the overall shape was not the basis of matching. Both articles suggest as explanation a suite of local strategies, including matching angles, lengths of sides, and sensorimotor programs. On this point, we disagree on grounds of parsimony, which Pearce et al. invoked to reject all forms of global matching. Rather, one global matching process, based on one parameter of shape, the major or first principal axis, explains all the data in both articles. In this comment, we show how this is the case. Our point is not as much to champion the hypothesis that animals rely on this particular parameter as it is to call attention to the possibility that they rely on one or more global parameters.

Data

The key data are best presented in graphic fashion. Pearce et al. (2004) trained rats to swim to one corner of a rectangular pool to find a submerged escape platform (Experiment 1A; see Figure 1A). The walls were all white. Cues around the pool were excluded. The platform gave the rats no cues; in learning the task, the rats went first just as often to the geometrically equivalent diagonal opposite corner (a rotational error) as to the correct corner. After sufficient training, the rats were tested in a kite-shaped pool (see Figure 1B). The transformation from rectangle to kite destroys the euclidean shape. The rats' choices were clear (see Figure 1B). They went first to either the top right corner (the correct corner) or the acute-angled corner (the apex). Experiment 1B reversed the training and test spaces of Experiment 1A. Rats were trained in the kite-shaped pool, with the target at one of the right angles. When tested in the rectangle, they transferred to the appropriate corners that matched in relative lengths of walls and sense (i.e., which wall, the long or the short, was to the right of the other).

In Experiment 2, hippocampal lesions were performed on some rats trained and tested in the all-white space and on some rats trained and tested in a black-and-white space, with long walls black and short walls white. The training space was rectangular,

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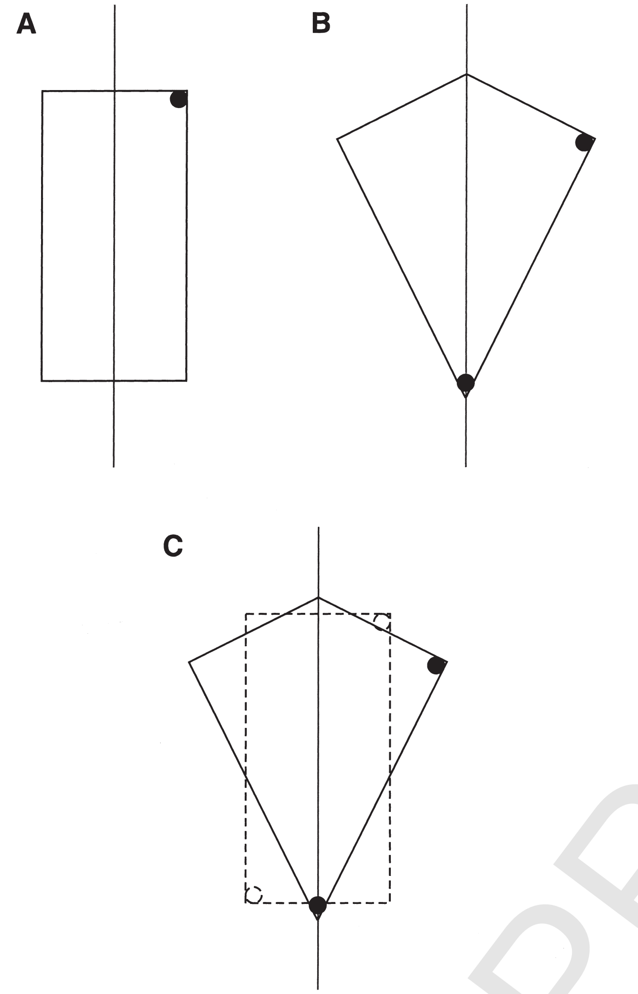

Figure 1. Results and explanation of Pearce et al.'s (2004) Experiment 1A. A: Training situation, with the circle indicating the target location. The rats searched at the diagonally opposite corner as well as this target location. B: Results when rats were transferred to a kite-shaped pool. Rats searched most at the two corners indicated by circles. C: Explaining this performance. The training space (dashed rectangle) is superimposed on the test space, lined up along the principal axis (vertical line in the middle). If the rats chose corners at the end of the principal axis and as far to the right as possible, the choice of the two corners they did choose is explained.

and the test space was a kite (as in Experiment 1A). The lesioned animals in the all-white space performed barely above chance through training. The other groups performed above chance. Having black-and-white walls improved performance in both sham and lesioned animals. In terms of first corner chosen on the transfer tests in the kite-shaped space, all groups showed nonrandom responding. Hippocamal-lesioned rats in the all-white space chose the apex most, the obtuse angle least, and the two right angles (mirror reflections of one another) at equivalent levels. This is what it looks like on Pearce et al.'s (2004) Figure 7, but no statistical comparisons across all four corners are given. The hippocampal-lesioned rats in the black-and-white space behaved like the rats in Experiment 1A. They chose the correct corner and the apex about equally often, at least for a number of sessions. By Session 7, they started to choose the correct corner, which was rewarded, over the apex. The sham rats in the black-and-white space chose the correct corner and the apex equally often for two sessions and then chose the correct corner progressively more. The sham rats in the all-white space persisted in choosing the correct corner and the apex equivalently through eight sessions.

Tommasi and Polli's (2004) data are shown in Figure 2. The F2

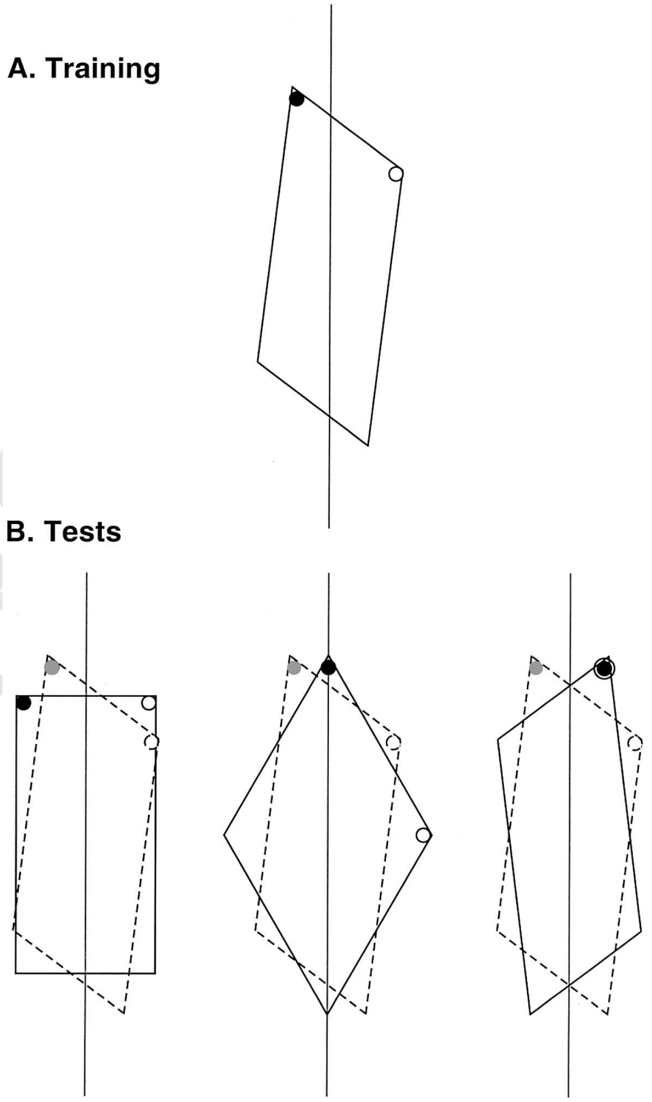

Figure 2. Results and explanation of Tommasi and Polli's (2004) data. A: Training condition for the chicks. The two circles indicate two different target locations for two different groups of animals. The chicks searched at their target location and its diagonal opposite equally often. B: Results from transformations and explanation of the data. Chicks were tested in a rectangle (left), a rhombus (middle), and a reflected parallelogram (right). The circles indicate where each group searched the most, up to rotational error. In the reflected parallelogram, both groups searched most at the acute angle. In the explanation of the data, the training situation (dashed parallelogram) is superimposed on the test spaces, lined up along the principal axis (line in the middle). Training targets are the gray and dashed circles for the filled-circle and open-circle groups, respectively. The chicks search at the nearest corner specified by this imperfect match.

training and testing spaces are drawn in solid lines. The dotted lines show the training space superimposed on the test spaces (discussed below). During training (see Figure 2A), a feeder was found at each of the four corners of a parallelogram. The feeder at one corner contained the food. It is important to note that two different groups were trained, with the food at geometrically different corners. These groups are represented by the open and filled circles. The disoriented chicks solved the problem up to rotational ambiguity—that is, they chose the correct corner and the diagonal opposite about equally often. Chicks were then tested in three transformed spaces. One was a rectangle; this preserved the relative lengths of walls of the parallelogram but made the angles equal. Another was a rhombus; this preserved the corner angles of the parallelogram but made all walls of equal length. Both of these are affine transformations; they destroy the global euclidean property of shape. The third transformation was a mirror reflection. This preserved all euclidean properties but reversed right and left. At an acute angle, the long wall was to the left of the short wall in the training space; the long wall was to the right of the short wall in the mirror-reflected space. The responses of the chicks, again up to rotational ambiguity, are shown by the corresponding symbols in Figure 2B. In the rectangular space, the chicks matched the relative lengths of walls and sense (i.e., which wall was to the right of which). In the rhombus, the chicks matched the corner angle. The reflected parallelogram produced the most interesting results. The two groups provided asymmetric results by choosing the same acute angle. Thus, the filled circles matched the corner angle, whereas the open circles matched the relative lengths of walls and sense.

Explanations

Various local processes were invoked by both Pearce et al. (2004) and Tommasi and Polli (2004). We use the word *local* with some reservation because one of the local matching processes invoked is matching lengths of walls and sense, a process that takes in half the perimeter of the space. To Tommasi and Polli, the corner angle is another local geometric feature that chicks can use for matching. Explaining the results from the reflected parallelogram (see Figure 2B) takes an extra assumption. An acute angle is assumed to be more salient than an obtuse angle. As a result, chicks trained to go to an acute angle stick to an acute angle in the reflected space, whereas chicks trained with an obtuse angle abandon matching by angle and go with relative lengths of walls plus sense. Pearce et al. (2004) also invoked matching by local geometry—lengths of walls plus sense. In addition, they explained the persistent and oft-found searching at the apex of the kite by a process we call a sensorimotor program. Roughly, the strategy is to find a long wall and go to its left end. Depending on which long wall the animal picks, it can end up at the correct corner or the apex. The length of wall chosen for this strategy is crucial. A priori, the rat can solve the problem in Experiment 1 (see Figure 1A) equally well by picking a short wall and swimming to its right end. Adopting this strategy would lead the rat to pick the obtuse angle some of the time, but the rats rarely did this. An added principle is needed to explain why the long-wall sensorimotor program was chosen, perhaps another principle of salience, with a long wall being more salient than a short wall.

Although the sensorimotor program was not well defined by Pearce et al. (2004), one project in artificial intelligence has provided an explicit program for solving Cheng's (1986, Experiment 2) reference memory problem (Nolfi, 2002). The starting points are limited, for example, to the middle of the sides. The goal is to get to one of the geometrically correct corners. Solutions evolved through artificial selection. A simple strategy to solve the problem illustrated in Figure 1A is to have the agent move with a systematic veer to the left. The veer is of such an extent that whether it starts at the middle of a long wall or the middle of a short wall, it runs into a long wall. On encountering a wall, the agent turns to the left and hugs the wall until it reaches a corner. The agent does not distinguish walls. It always reacts to bumping into a wall in the same way. Nolfi proposed such a solution to show the powers of reactive strategies (strategies without internal representations), not as a proposal for how rats or any other animals solve this task. Whether some such explicit program can work in the tests of Pearce et al. (2004) and whether rats actually adopt some such strategy remain uncertain.

Alternative Global Explanations

When a map is used to navigate, the navigating system must align the map with the environment that it represents before it can use the map to identify motivationally important locations. The interesting data from Pearce et al. (2004) and Tommasi and Polli (2004) show that shape congruence is not necessary for this process. The alignment process in the animal brain is robust; it can align two shapes that are seriously incongruent. In image processing, two encodings of the shape of the same object are often not congruent because of encoding errors. Thus, robust alignment algorithms do not demand perfect congruence (Fritsch, Pizer, Morse, Eberly, & Liu, 1994; Pizer, Fritsch, Yushkevich, Johnson, & Chaney, 1999). The most commonly used shape-alignment algorithms rely on global shape parameters. We argue that animals probably use alignment processes based on global shape parameters precisely because they are robust.

The simplest such schemes superpose the centroids and align the principal axes of the two shapes. More complex but also more powerful schemes often use axial skeletons, computed by a medial axis transform, which transforms a shape with area into a stick drawing lacking area (Fritsch et al., 1994). The medial axis is an axis of symmetry; it is the locus of points equidistant from the nearest shape boundaries. One reason to think that it plays an important role in the brain's encoding of shape is that it explains the perceptual salience of symmetry. It leads readily to a hierarchical part–whole decomposition of complex shapes (Leyton, 1992) and to the representation of the boundary locus by means of a radius function, specifying for each point along the medial axis skeleton the magnitude of and angle between the two vectors from that point and normal to the boundary points. In medial-axis alignment schemes, the medial axes are aligned and their branch points and other attributes warped to maximize overall congruence, as measured in some way. This might provide a model of how the animal integrates error-prone shape information across repeated experiences with the same environment (how it improves its map on the basis of further experience). The essential point of similarity between a simple approach based on principal axes and more sophisticated approaches based on medial axis skeletons is that the entities used to effect the alignment (centroids, principal axes, axial skeletons) are derived from transformations (computations) that act on and capture properties of the entire shape.

Although we suspect that the alignment algorithm used by animal brains is more like the medial axis skeleton algorithms than the principal axes algorithms, we show in what follows that the results so far obtained are consistent with a scheme based simply on the first principal axis.

Principal Axis

In this treatment, we take the space to be two-dimensional. Although space is clearly three-dimensional, almost all the place-finding problems in the geometry literature involve finding a location on a two-dimensional surface. When a vertical surface has been used, gravity seems to define a privileged or prepotent up–down axis (Kelly & Spetch, 2004a, 2004b), so our analysis does not apply. The first principal axis of a two-dimensional bounded figure or array of points is colloquially called the long axis. In mechanics, it is the axis around which the figure (conceived of as a two-dimensional array of point masses) rotates without wobbling and with minimal angular inertia (resistance to angular acceleration). Principal axes go through the centroid. In linear algebra, the principal axes are the eigenvectors of the form, which is conceived of as a dense point cloud bounded by the boundaries of the shape. In statistics, the first principal axis is called the first principal component. It is the line of mutual regression, the line through the points that minimizes the sum of the squares of the perpendicular distances of the points from the line (hence, the angular moment). Except in figures with multilateral symmetries, the set of principal axes is unique, and there are as many axes as there are dimensions to the figure. In highly symmetrical figures (e.g., circles, spheres, squares), there may be more than one set of principal axes (in circles and spheres there are infinitely many). For our account, we only need to invoke the first principal axis. (A custom MATLAB [MathWorks, 1998] function for computing and plotting the principal axes of a polygon specified by the coordinates of its vertices is available from C. R. Gallistel.)

In Figures 1C and 2B, we superimpose the training space on the test spaces, lining up the first principal axes at the center of the axis. The training space is in dotted lines. In Figure 1C, the superimposed training target is a little nearer to the obtuse angle than to the top right corner. We suppose, however, that rats are, in good part, looking for a corner far from the principal axis, in effect searching for a corner at one end of the principal axis and as far out to the right as possible. This explains the choice of corners in the kite-shaped space. In this scenario, the choice of the apex is a rotational error. The rat gets to this region of space and discovers that this is the only corner to choose. The persistence of this choice in Experiment 2 for rats in the all-white space suggests that the geometry learned in Phase 1 continued to guide behavior for quite a while. It is as if learning of the geometric information in Phase 1 blocked the learning of new geometric information in Phase 2. If so, this is a significant finding, because beacons do not block the learning of geometry (Hayward, McGregor, Good, & Pearce, 2003; Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001; Wall, Botly, Black, & Shettleworth, 2004; for a review, see Cheng & Newcombe, in press). This interpretation is, however, based on the dubious comparison of intact rats in Experiment 1B, Phase 1 (in which they learned the kite geometry for the first time), with sham lesioned rats in transfer tests in Experiment 2. Although proper comparisons are needed, the data are nevertheless suggestive.

A glance at Figure 2B, with the superimposed training spaces, should show immediately that the hypothesis of matching by principal axis explains Tommasi and Polli's (2004) data. No added assumptions are needed. The only local cue needed in both cases is the identification of a corner. No characteristics of the corner are needed except its global location.

In short, one principle explains all the transformation data in these two articles, without invoking relative saliences, matching of local geometry, or sensorimotor programs. The data underconstrain the theory by far, but, by Occam's razor, invoked by Pearce et al. (2004), the principal axis is parsimonious in doing away with a host of what, to us, are ad hoc local explanations.

Explanations: The Bigger Picture

This discussion of a global alignment process should not be taken to rule out local processes. Animals undoubtedly use local cues for localization. Pigeons and other birds use truly local geometry (Cheng, 1988, 1989, 1990, 1994, 1995; Cheng & Sherry, 1992; Cheng & Spetch, 1995; Gould-Beierle & Kamil, 1998; Lechelt & Spetch, 1997; Spetch, 1995; Spetch, Cheng, & MacDonald, 1996; Spetch et al., 1997; Spetch, Cheng, & Mondloch, 1992; Spetch & Wilkie, 1994). In these studies, the birds were oriented in space. They encoded and used vectors from the target to nearby landmarks, such as corners, walls, edges of blocks, features such as a colored stripe on a wall, discrete three-dimensional objects, and graphic objects on a monitor. Besides these processes, beacon learning has been amply demonstrated. Thus, in Morris's (1981) classic article demonstrating rats' spatial abilities in the swimming pool, the animals could learn readily to head to a visible platform whose location in the pool varied from trial to trial.

In this light, the kinds of local processes invoked by Pearce et al. (2004) and by Tommasi and Polli (2004) seem to us new invocations to explain just their data. It is parsimonious to stick to truly local geometry and beacons. Matching by principal axis or axes of symmetry allows us to invoke only these already needed kinds of local processes to do the job of explanation. Functionally, this global matching process points the animal to the approximate region in which local processes can take over. Relying solely on local information may tax the powers of discrimination. Imagine discriminating one tree from all others in a forest, without referring to the locations of trees. Computing and matching a principal axis or an axis of symmetry is a determinate process that does not explode in complexity with the complexity of the shape of space. A scheme of judiciously combining global and local processes serves to minimize computational explosions in both.

Methodologically, the transformational strategy is the way to go. The idea is to train animals in one space and test them in a transformed space. A large number of observations of behavior in transformed spaces can help determine the mechanisms of localization. Further discussion of research strategies is provided in the Discussion section of Cheng and Newcombe (in press; see especially Figure 5).

Hippocampus and Geometry

Finally, we speculate briefly on the results with hippocampal-lesioned rats in Pearce et al. (2004). The literature on the hippocampus is voluminous, and a detailed review is out of the question here. Suffice it to say that the hippocampus has been implicated in spatial processes in rats (Jeffery, 2003; O'Keefe & Nadel, 1978) and in birds (Bingman & Able, 2002; Bingman, Hough, Kahn, & Siegel, 2003). In birds, the effect of hippocampal lesions on the Cheng (1986) reference memory task is clear. Vargas, Petruso, and Bingman (2004) found that hippocampal-lesioned pigeons were still able to use featural information (a wall of a different color) but failed the task completely (performance was on a chance level) when only geometric information was available. Recent work on chicks implicates the right side of the brain (Vallortigara et al., 2004) and the right hippocampus (Tommasi, Gagliardo, Andrew, & Vallortigara, 2003) in processing geometric information. Earlier work on food-storing birds showed that a hippocampal lesion leads to decrements in relocating stored food but not in storing food (Sherry & Vaccarino, 1989).

Identifying a corner in a rectangle up to rotational ambiguity requires the use of both metric information (lengths of walls) and sense (whether the long wall is to the right or left of the short wall; Cheng & Gallistel, 1984). Failure to use either of these characteristics leads to the chance performance exhibited by Vargas et al.'s (2004) hippocampal-lesioned pigeons or the near chance performance exhibited by Pearce et al.'s (2004) hippocampal-lesioned rats in the all-white space. The performance of the lesioned rats in the all-white kite space suggests a problem of conjoining sense with metric information. It is as if the code consisted of the following instructions: Go to the end of the principal axis and find a corner far from the principal axis. It is not specified whether the animal should to go to the right or left of the principal axis. This strategy should produce most searching at the apex, because once the animal heads that way, there is only one corner to go to, and equivalent but intermediate levels of searching at the correct corner and its mirror reflection, with low searching at the obtuse angle. When one looks at Pearce et al.'s Figure 7, one sees that this is roughly the pattern. In this light, the problem might be one of configuring two kinds of information, a suggestion that Pearce et al. (2004) made.

In the black-and-white rectangular space, the rats might use the principal axis or a symmetry axis and local featural information, basically a beacon where the black wall meets a white wall, with the black wall on the right. Having local featural information improves performance, as indicated by the data. The animal apparently does not use this beacon when transferred to the kite space. Localization by principal axis or symmetry axis dominates for two sessions in the sham rats and for longer in the lesioned rats. It is as if the rats need to learn to rely on the beacon again, with learning proceeding faster in sham rats than in lesioned rats. Sometimes, a previously stably located beacon fails to control behavior when it is moved to a different location that is still within view of the approaching animal (Devenport & Devenport, 1994; Graham, Fauria, & Collett, 2003; Shettleworth & Sutton, 2005).

Conclusions

Pearce et al. (2004) and Tommasi and Polli (2004) have provided exciting data on the basis of geometric encoding, using the transformational strategy (Cheng & Spetch, 1998). In the transformed spaces, although euclidean properties (or sense) of the space changed, the rats and chicks still made nonrandom choices of locations. The authors therefore rejected matching on the basis of global shape, a point with which we agree only in part. We believe that the data rule out matching by global shape congruence. We maintain, however, that matching on the basis of the principal axis of space, a global shape parameter, accounts for all the transformational data in both articles. It is likely that other axes, notably symmetry axes, may do a still better job. This explanation dispenses with all the local processes proposed by Pearce et al. and by Tommasi and Polli and is thus parsimonious. We are not against local processes. Clear evidence exists for the use of local geometry and beacons. A combination of a determinate global process, such as matching by an axis of symmetry, and local processes is likely because it keeps both processes from exploding in computational complexity.

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