Animal Spatial Cognition:

Comparative, Neural & Computational Approaches

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Geometry, Features, and Orientation in Vertebrate Animals: A Pictorial Review

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Abstract

With much pictorial support, we review research on how vertebrate animals orient in enclosed rectilinear spaces. The phenomenon of the rotational error is introduced, along with the distinction between geometric and featural information. The circumstances under which a number of species use geometric and featural information for relocating a target place are reviewed. Other sections examine cue competition (actually lack thereof) between geometric information and landmark cues, artificial intelligence, and the neurophysiological bases underlying the coding of geometric information. We then examine two theoretical issues: 1) how geometry is encoded and used, 2) the modularity of mind.

Chapter Outline & Navigation

I. Chapter Orientation

We recently reviewed this literature in print (Cheng & Newcombe, 2005). Here we present an updated and far more pictorial review. To take full advantage of the web format, results and theory are discussed briefly in words, in 'nugget form'. Each section is illustrated by appropriate pictures and other visual presentations. The basic phenomenon (Rat section) and the distinction between geometric and featural information are crucial for understanding the entire literature. We suggest that you read this section first. Otherwise, the following sections on data can be read in any order as you wish. We suggest, however, that you read at least a few of them before proceeding to the theoretical sections.

II. Basic Phenomena

2.1 Rats

The idea of the use of the geometry of surfaces started with the doctoral work of Ken Cheng. Below is a picture of the rectangular arena used to test the animals, male white rats (see Figure 1). The photo was taken outside, not in lab conditions. The arena measured 120 cm by 60 cm. Not easy to notice in the photos are two additional kinds of cues: different textures on the corner panels and smells emanating from two of the corners. In the experiments, the bottom of the arena was filled with saw dust (wood chips used for rat bedding). A grid was drawn on the bottom for the purposes of scoring where the rats dug.

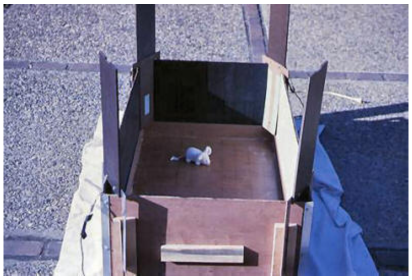


Figure 1. A view of the rectangular arena used to test male white rats..

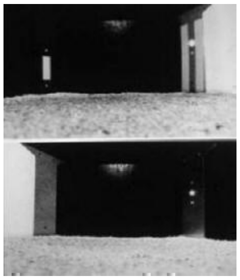


Figure 2. These photos, of the two ends of the rectangular arena, were taken in the lab, from the floor of the box.

The task was a working memory find-the-treasure-again task. Figure 2 represents roughly what a rat saw in the tasks. A box (12 X 6 cm) was put on the bottom of the arena at a randomly chosen location (Figure 3). In the exposure phase, the box was exposed, revealing 7 pellets of sweet cereal. The rat got to eat 3 pellets, and then was removed outside the room. The arena (actually an identical looking replica) was rotated at random, the remaining food was buried under saw dust, and the rat was returned to the arena 90 s later to dig up the remaining food.

The rotational error is crucial to understanding this entire corpus of work (Figure 4). In Figure 5, A. shows a plan view of the task situation, with the location of the food indicated by the filled dot. The open dot shows the rotational error, located at 180 degrees rotation through the center from the correct location. B. A record or representation of the geometric properties, with the food location indicated by the dot. This representation contains only the broad shape of the space, called the geometric properties. Missing are smells, textures, colors of walls, the information shown in C. Using a record such as B. can lead to rotational errors. This happens when the top wall of B. is matched to the bottom wall of of A., with the box in B. rotated 180 degrees. Using a record of the nongeometric information, called featural information, shown in C. results in an unambiguous match. Systematic rotational errors thus indicate a record such as that shown in B. We will argue later that far less than the entire geometric shape is represented by rats.

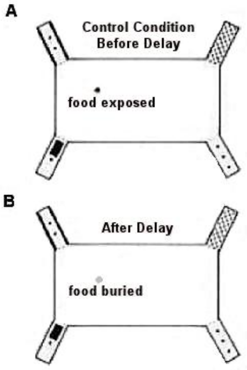


Figure 3. Schematic illustration of the basic task.

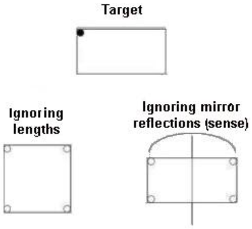


Figure 4. Rotational error.

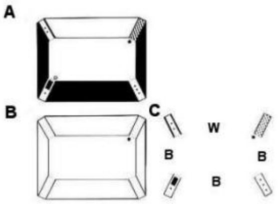


Figure 5. Geometry and rotational error.

Figures 6 and 7 show results of individual rats in the working memory task in Cheng (1986). C stands for correct choices, R stands for rotational errors, and E stands for everything else (other nonsystematic wrong choices or no digging at all). Each rat made a significant number of rotational errors. The advantage of correct choices over rotational errors (not statistically significant in any rat) is attributed to the fact that the rats were not disoriented during the delay. Margules and Gallistel (1988) repeated this experiment with disorientation during the delay period. The rats then make approximately equal numbers of correct choices and rotational errors.

In a reference memory task (Cheng, 1986, Experiment 2), the food stayed in one of the corners on every trial (Figure 8). The rats then learned to choose the correct corner over the rotational error (diagonal opposite). The rats as a group, however, still made systematic rotational errors (see Figure 9). This pattern (correct choice over rotational error, but systematic rotational errors still) is also found in young children and rhesus monkeys.

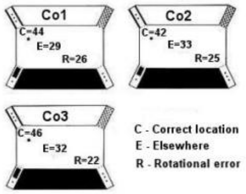


Figure 6. Results from Cheng (1986).

Figure 7. Cheng (1986) results averaged over the three rats.

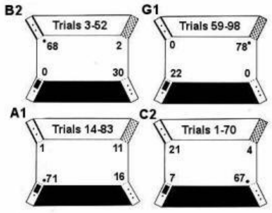


Figure 8. Results from reference memory task.

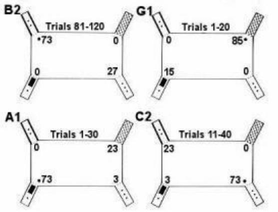


Figure 9. Cheng's rats chose the correct corner over the rotational error even when the white wall was made black, making the colors of walls nondiagnostic for locating the food. Again, they still made systematic rotational errors.

Benhamou and Poucet (1998) introduced two differences in the reference memory paradigm. 1) Their task was aversive rather than appetitive. Others have noted differences in performance between appetitive and aversive tasks. Golob and Taube (2002) found that in a rectangular swimming pool, rats did not make systematic rotational errors. In a dry, appetitive task in the same arena, rotational errors were prevalent. 2) The geometry was defined by an array of objects, not by surfaces. The pool was round and surrounded by a ring of curtains, rendering its geometry useless for the task.

In Figure 10, the blue dot at the bottoms of the panels shows the target position. The landmarks were different from one another perceptually. In the left panel, the configuration of landmarks specified the target unambiguously, and the rats learned to searched preferentially around the target. In the right panel, the configuration of landmarks left a threefold ambiguity as to target position. Individual perceptual identities of the landmarks needed to be used to resolve the ambiguity. The rats did not learn to resolve this ambiguity in 75 trials.

This task (Figures 10 and 11) is much harder than a standard pool task with lots of room cues, which supply both geometric and featural cues (Poucet, Lenck-Santini, & Save, 2003). This manipulation shows that it is the configuration of landmarks, rather than the individual identities of landmarks, that was important for the rats. The blue dot at the bottoms of the panels again shows the target (see Figure 11). When the landmarks swapped position (right panel), the configuration of landmarks and the individual identity of the nearest landmark dictated different responses. Rats mostly 'went with' the configuration, although their performance was slightly (and significantly) worse than under standard testing conditions (Benhamou & Poucet, 1998).

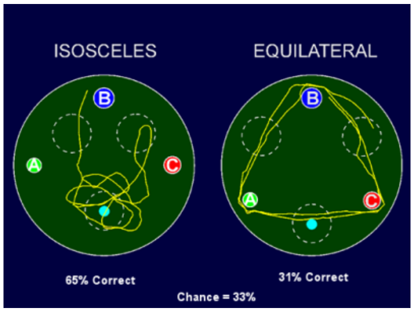


Figure 10. Benhamou and Poucet's swimming pool task. (Thanks to Simon Benhamou for providing this picture.)

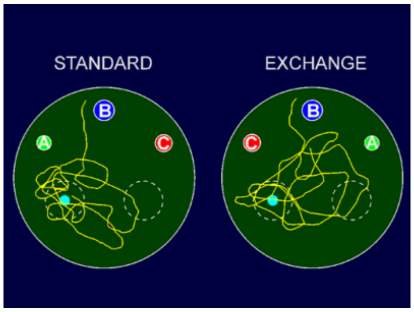


Figure 11. Landmarks vs. Configuration. (Thanks to Simon Benhamou for providing this picture.)

2.2 Chicks

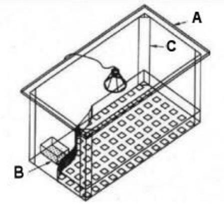


Figure 12. Apparatus used by Vallortigara et al., 1990.
a: One-way glass over the top of the arena.
b: Food box.
c: Panel in the corner, used in many of the experiments from Vallortigara's group. (Thanks to Giorgio Vallortigara for supplying this and the following five pictures.)

Vallortigara, Zanforlin, and Pasti (1990) tested chicks in the reference memory paradigm, and found that the birds used both geometric and featural properties readily. Figure 12 shows a schematic drawing of their rectangular test apparatus. In all the experiments, the food remained in one corner throughout training. The animals were disoriented between trials, so that they had to use cues within the arena to orient (see Figures 13-15).

Figure 13. Overhead view of a test situation. The blue wall is a featural cue, the rectangular shape a geometric cue.

Figure 14. Overhead view of another test situation with panels in the corners serving as featural cues.

When features and geometry were provided (Figure 16, left), the chicks were mostly correct (results not shown). The chicks showed no systematic rotational errors, unlike rats, young children, and rhesus monkeys. This meant that they used featural cues. That the chicks learned geometry as well is shown on the right (Figure 16), when all featural cues were removed for a test. The chicks concentrated their searching in the correct corner and the diagonal opposite, the rotational error. Without featural cues, it is in principle impossible to distinguish these two locations. Note that having the featural cues during training did not overshadow the learning of geometric cues. This is a theme found in most studies. See the cue competition section.

Figure 15. Examples of panels in the corner, with a chick at work on the task.

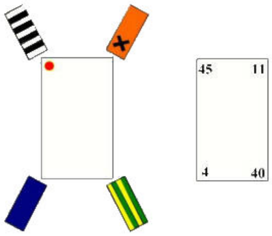


Figure 16. Results from Vallortigara et al., 1990.

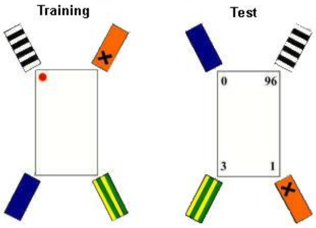


Figure 17. Results of featural/configuration conflict test from Vallortigara et al., 1990.

In the test shown in Figure 17, featural and geometric cues were put in conflict. This was done by moving the nearest feature, a beacon at the target, to a geometrically different corner on a test (right, Figure 17). Chicks overwhelmingly opted to 'go with' the beacon. Results of transformations of the size of the training arena came later (Tommasi, Vallortigara, & Zanforlin, 1997; Tommasi & Vallortigara, 2000). Chicks were trained to search at the center of a square space. When the square was expanded on a test, chicks showed tendencies to both search at the center and to search at the correct absolute distance from a wall (Figure 18). This suggests that both absolute and relative distances, two kinds of geometric cues, are encoded.

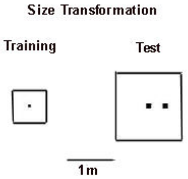


Figure 18. Size transformation test.

Information on the neurophysiology underlying the encoding of geometric and featural cues is given in the neurophysiological section.

2.3 Pigeons

The results from pigeons resemble those from chicks (Kelly & Spetch, 2001; Kelly, Spetch, & Heth, 1998). Pigeons, however, were also tested on a vertically oriented computer monitor. Figure 19A shows an overhead view of an 'open field' arena used by Kelly et al. (1998). Panels in the corner served as featural cues, with the food always at one of the corners (reference memory task). The birds were disoriented between trials.

Aside from two-dimensional panels, three-dimensional objects in the corners were also used as featural cues (Figure 19B). The results were similar in the two cases. In the standard task, the birds were nearly perfect; they did not make systematic rotational errors. Thus, pigeons use features in the relocation task. Systematic rotational errors did appear when the features were degraded in any of the manipulations that Kelly et al. tried.

- Removing the colors of features by making them all the same color.
- Removing the shapes of the features by making them all identical in shape.
- Removing the feature at the target and the diagonal opposite.

Some birds were also tested with no features (Figure 19C). Identical landmarks in the corners make them non-diagnostic for locating the food.

Figure 19A. Kelly et al. apparatus.
(Thanks to Debbie Kelly for the pictures in this section.)

Figure 19B. Kelly et al. apparatus with object cues.

Figure 19C. Kelly et al. apparatus with no featural cues.

Birds might be trained without features, or trained with features and then tested without features. In both cases, the pigeons used the geometric cues of the rectangle. They searched mostly at the correct corner or its diagonal opposite. Thus, as in chicks, having features during training did not overshadow the learning of geometry.

More on overshadowing in the section on cue competition.

Pigeons were also tested with size transformations of the training arena (Kelly & Spetch, 2001, Figures 20, 21). Figure 20 shows a smaller test arena made by blocking off a part of the full arena. The long wall here is equal in absolute size to the short wall in the training arena. Pigeons responded according to the shape. In this example, they preferred to search at a corner with a shorter wall to the right and a longer wall to the left, even though in the test space, the absolute lengths of walls did not match those in the training space.

Figure 20. Kelly & Spetch (2001) apparatus (small version).

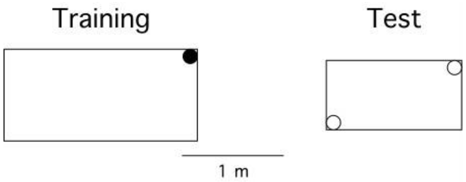


Figure 21. Kelly et al. size transformation experiment.

Touchscreen study on pigeons.

Pigeons have also been tested on a vertically oriented computer monitor (Kelly & Spetch, 2004b). In Figure 22, a bird is shown facing a schematic rectangle on the monitor of a computer. The task is much like the typical arena task; one corner of the schematic rectangle always leads to food when pecked. Pecks on the screen are picked up by a touchscreen device. Food for correct responses is delivered to one of the food magazines on each side of the monitor.

Note that the orientation of the rectangle can change from trial to trial, and that all stimuli are vertically presented. Both facts are important in accounting for the results. In training, six different orientations were used; two other orientations (180 degrees apart) were saved for transfer tests. Figure 23 shows a schematic example of the training situation with both featural and geometric cues. Pigeons learned this task readily. They cope perfectly if the gray shading of the rectangle was removed on the test. But other manipulations led to worse but still above chance performances:

- Removing the color of features by making them all the same color.
- Removing the shape of features by making them all the same shape.
- Moving the configuration on the screen .
- Removing the features at the target and the diagonal opposite, as shown in Figure 24.

Figure 22. Stimulus and subject in Kelly & Spetch's (2004b) experiment.

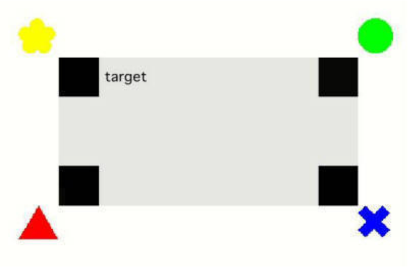


Figure 23. Stimulus properties in Kelly & Spetch's (2004b) experiment.

Figure 24. A test with two of the features removed.

Some manipulations led to the appearance of systematic rotational errors (Table 1). When color information was removed by making all symbols the same color (shape only), when the feature at the target location and its diagonal opposite were removed (distant features), or when only a single feature at an adjacent corner was provided on a test (single feature), the percent of correct choices decreased compared with control tests. The errors, however, tended to be rotational errors. If the errors were distributed evenly, only one third of the errors should have been rotational errors, but the rotational errors in Table 1 exceed this chance value.

Test	% correct	% rot. error	% other errors
shape only	41.6	34.0	24.4
distant features	59.6	24.9	15.5
single feature	54.9	30.4	14.7
(on other side of short wall)			

Table 1. Results from Kelly & Spetch's (2004b) experiment.

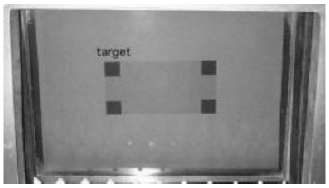


Figure 25. Pigeons were also trained and tested without featural cues; this tests whether they can learn to use geometric cues alone.

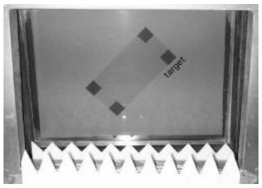


Figure 26. Again, six different orientations were used in training, with two new orientations (180 degrees apart) saved for transfer tests. The birds managed to learn geometry, but a few characteristics of the results are very interesting.

Again, six different orientations were used in training, with two new orientations (180 degrees apart) saved for transfer tests (Figures 25-27). The birds managed to learn geometry, but a few characteristics of the results are very interesting.

Interesting results with geometric cues only.

•When started on this task, learning was slow, significantly slower than learning the featural task shown above.

• Having learned the featural task first sped the learning of this task. Features, far from overshadowing the learning of geometry, may have facilitated the learning of geometry.

• Pigeons did not transfer at all to the new orientations. This suggests that what they learned was orientation specific. A likely explanation is that on a vertical surface, the orientation with respect to gravity (i.e., up-down) defines a axis that is used for orientation.

• Again, removing the gray shading of the rectangle did not affect performance, while translating the rectangle led to a significant drop in performance that was, however, still above chance.

Kelly and Spetch's (2004) data on human adults on the touchscreen task showed many similarities.

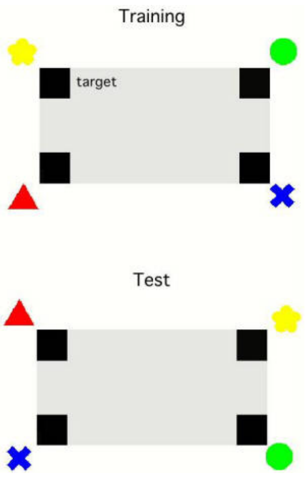


Figure 27. Featural and geometric cues are put in conflict in the test shown in the lower panel. At this stage, the birds had learned both the featural task and the geometric task. The birds' choices indicate the use of both geometric and featural cues. Thus, in this example, they chose the red, green (geometrically correct) and yellow (featurally correct) cues more often than the blue cross (which is the only location that is both geometrically and featurally wrong).

2.4 Fish

Figure 28. Fish (*Xenotoca eiseni*) tested by Sovrano, Bisazza, and Vallortigara (2002, 2003). Left: males; Right: female.

Thanks to Giorgio Vallortigara and Valeria Sovrano for sending us pictures on their work, featured in this section.

The task for the fish (Figure 28) was aversively motivated. They were to swim out of the rectangular arena, through one of the doors in the corners, to join their peers. One of the doors was always the correct one (the others would not open). The arena was rotated from trial to trial. Again, this was a reference memory task. Figure 29A shows a condition in which only geometric cues were available. The fish learned this task, concentrating their search at the correct corner and its diagonal opposite. Fish were also trained and tested in arenas with featural cues, such as a blue wall (Figure 29B) or panels in the corners (Figures 29C). Figure 29D shows closer views of the panels in the corners. Fish learned to use the featural cues, a colored wall or panels. They searched mostly at the correct corners, and did not make systematic rotational errors. In this way, they resemble the birds, except that their performance level was typically worse.

Figure 29A. Apparatus used in Sovrano, Bisazza, and Vallortigara (2002, 2003)

Figure 29B. Apparatus showing featural cue.

Figure 29C. Apparatus showing featural cues in each corner.

Figure 29D. View of featural cues in corner panels.

When trained with features but tested with features removed, the fish still used geometric cues. In the example in Figure 30, they would search mostly at the top left or bottom right. Thus, as with birds and rats, learning to use features did not overshadow the learning of geometry.

The fish were also presented with conflict tests (Figure 31). On these tests (right), the panel at the target was moved to a geometrically different corner, resulting in a conflict between geometric and beacon cues. The fish split their choices between geometry and beacon. In this example, they would search at the top left (geometrically correct), top right (correct beacon), or bottom right (geometrically correct). The results were that the bottom left (geometrically and featurally wrong) was chosen the least.

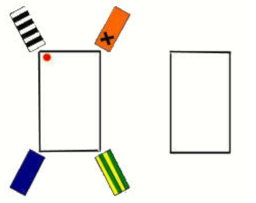


Figure 30. Schematic of geometry-only test following geometry & feature training. Left: trained with features. Right: tested without features.

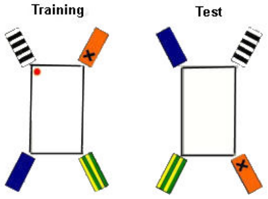


Figure 31. Schematic of conflict test.

Vargas, López, Salas, and Thinus-Blanc (2004) tested goldfish (*Carassius auratus*) in an escape task akin to the task that Sovrano et al. (2002, 2003) used. The goldfish were trained with geometric and featural cues; featural cues were stripes on two adjacent walls (Figure 32). Goldfish proved adept at learning to use both geometric and featural cues. On the test shown in Figure 33, the featural cues had been removed. The fish used the geometric cues, searching mostly at the correct corner or its diagonal opposite. On the test shown in Figure 34, only featural cues were provided; the arena had been transformed into a square. Fish succeeded in the task, choosing mostly the correct corner.

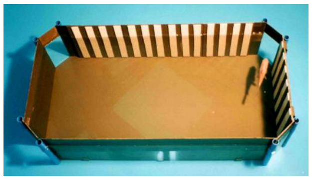


Figure 32. Rectangular apparatus with featural cues. Thanks to Juan Pedro Vargas for the photos of the goldfish and apparatuses.

Figure 33. Rectangular apparatus with featural cues removed.

Figure 34. Square apparatus with featural cues.

Dissociation tests were also conducted (Figure 35). On these tests, the stripes were shifted in the manner shown (training situation on left, test situation on right). On this test, the fish were at chance choosing the four corners. We explain the labels below. The results of a dissociation test depended on the target location. With a target location at an intersection of striped walls, the fish went with the featural cues most (some 60%), chose the geometrically correct corners next most, and chose the fourth corner least (Figure 36).

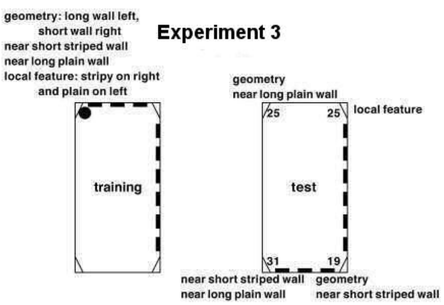


Figure 35. Results (percentages) and alternative explanation of Experiment 3 of Vargas et al. (2004).

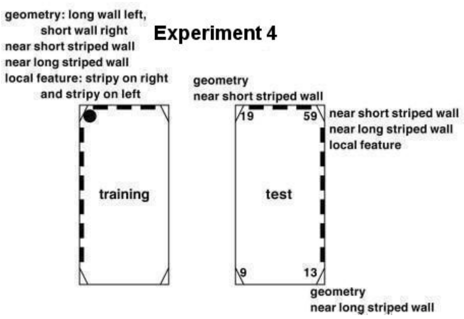


Figure 36. Results (percentages) and alternative explanation of Experiment 4 of Vargas et al. (2004).

Explaining dissociation tests.

Vargas et al. interpreted the results from dissociation tests as showing the fish to use different strategies in the two test situations. In the first situation (their Experiment 3) with the chance results, the fish were said to use a map-like strategy. In the second test situation, in which the fish preferred featural cues, they were said to use a guidance strategy.

It seems problematic to base an interpretation of map-like strategy on chance results. And the guidance strategy also does not explain why geometrically correct corners were chosen more often than the fourth corner in the second test situation.

As an alternative explanation (Cheng, 2005), we tallied up the likely properties that the goldfish might attempt to match on a test (left), and assumed that the fish would try to match as many as possible. Geometry (long wall to the left, short wall to the right) was one property. A local feature to match consisted of having stripy wall on the right and plain wall on the left. (Panels were left out of consideration because they are the same in every corner.) A property of being near a wall of particular length and decoration pattern (stripy or plain), irrespective of which end of the wall was nearest to the corner, was also considered a property to match. The right panel shows that these properties are distributed across the four corners on the test in Experiment 3. One reasonable prediction is that the fish would search about equally at all four corners, a prediction confirmed by the data.

In Experiment 4, however, when the same set of properties tallied on the left panel are distributed among the different corners on the test, we see that the corner with the correct local feature has the most properties, the two geometrically correct corners have the next most properties, while the corner at the bottom left has nothing to recommend it for matching. The results reflect this ordering.

Vargas and López (2005) dispute this, on the basis of other data, and matters remain unclear.

2.5 Rhesus Monkeys

Gouteux, Thinus-Blanc, and Vauclair (2001) tested rhesus monkeys on reference memory tasks in a space (always of one size) filled with different kinds of features across experiments (Figure 37). Features might be a patch on the middle of a wall or panels in the corners. The pattern of results depended on the sizes of the features.

Small features:

With small features, monkeys used the geometric cues, but not the featural cues. Rotational errors were as frequent as correct choices.

Large features:

With large features, monkeys used geometric and featural cues. Rotational errors were systematic, so that on some trials, the monkeys used only geometric cues. Figure 38 shows an example of an experiment on rhesus monkeys from Gouteux et al. (2001). On the left, results from tests with only geometric cues, no featural cues. On the right, performance when a whole short wall was made a different color. Monkeys clearly chose the correct corner more than the diagonal opposite (rotational error). But the majority of errors consisted of rotational errors.

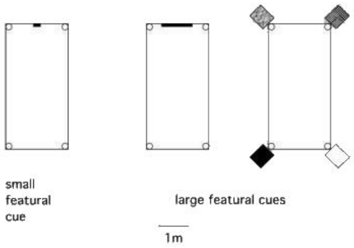


Figure 37. Large and small featural cues.

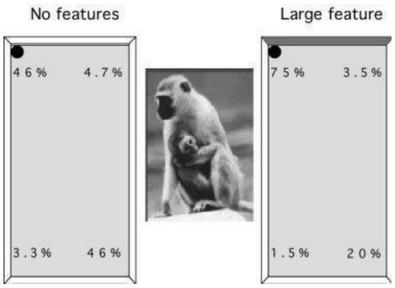


Figure 38. Thanks to Catherine Thinus-Blanc for supplying us the picture.

2.6 Humans

Hermer and Spelke (1994, 1996) tested children of 18-24 months in a reference memory paradigm, albeit one with only 4 trials. In all the experiments, the hidden toy remained in one corner throughout training. The children were disoriented between trials, so that they had to use cues within the arena to orient. They found that the children used geometric properties readily but did not use featural properties. In later work, this lab found that featural cues began to be used at 6 years of age and were virtually always used by adults.

Figure 39 shows a schematic drawing of their 4 by 6 foot rectangular room. Figure 40 shows a photo of a room this size used by the Newcombe lab. Figure 41 shows representative results from one of the Hermer-Spelke experiments with children, followed by a representative result with adults (Figure 42).

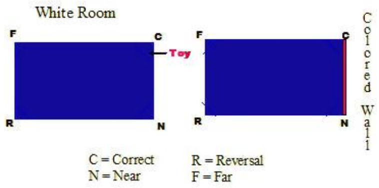


Figure 39. Hermer & Spelke (1994, 1996) experimental conditions.

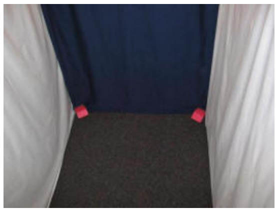
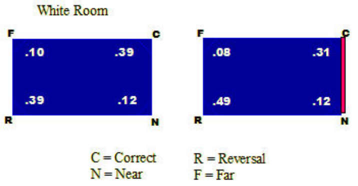


Figure 40. Overhead view of a small rectangular room with identical boxes used to hide small toys.



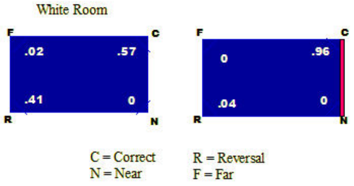


Figure 41. Hermer & Spelke: Search Rates for Toddlers.

Figure 42. Hermer & Spelke: Search Rates for Adults.

This pattern of data led the Spelke group to propose the "Language-as-Bridge" hypothesis. As put by Hermer-Vazquez, Spelke & Katsnelson (1999, p. 34):

> "[A]dults may have a further system of representation that is uniquely human and that emerges over the course of development. This system may connect to many other systems of representation, regardless of their domain-specific content. Its operation may be governed by rules and principles allowing the arbitrary combination of information from distinct, domain-specific sources... The language faculty appears to have all the right properties to serve as this uniquely human combinatorial system of representation."

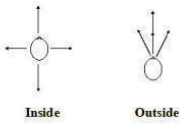


Figure 43. Perspectives inside and outside of a space.

More recent work has followed up both on young children's sensitivity and on whether or not they use features as well as geometry. Taking geometric sensitivity first, Huttenlocher and Vasilyeva (2003) found that children could use geometry to find a hidden object in enclosures of different shapes, triangles as well as rectangles, both when inside and when outside the space. However, they did better when inside the space.

Children rarely surveyed the various locations before going to the corner where they believed the object was hidden, suggesting that they represent the entire space so that, no matter where they face after disorientation, they know their relation to the hiding corner. Using geometric information is easier when an organism is inside a space than outside a space (Huttenlocher & Vasilyeva, 2003). As shown in Figure 43, one likely reason is that the distinctiveness of the space is greater when inside.

Learmonth, Newcombe, & Huttenlocher (2001) found that toddlers CAN use features to reorient, as shown by the data in Figure 44. Searches were much more likely in the correct corner than in the rotational equivalent.

Room size is crucial to whether or not young children use featural cues. Learmonth et al. (2001) used an 8 by 12 foot room, not a 4 by 6 foot room. Learmonth, Nadel & Newcombe (2002, Experiment 1), using a room with moveable walls, found that 4-year-olds did not use the featural cue to reorient in a small room (C 35% vs R 41%) but did use it in a larger room (C 57% vs R 23%).

A small waist-high enclosure (Hermer-Spelke size) centered within "large" room (Learmonth et al. size) gives sense of difference in action possibilities between the two rooms—the larger one is 4x the size of the smaller (Figures 45, 46).

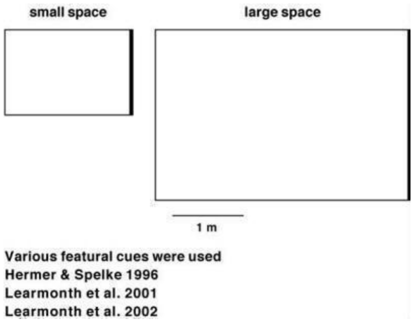


Figure 45. Comparison of spaces used in human experiments.

Figure 46. Child being disoriented in small enclosure situated within larger enclosure.

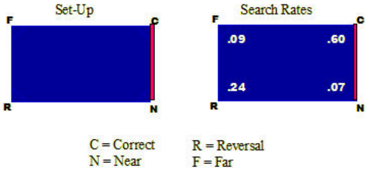


Figure 44. Learmonth, Newcombe, & Huttenlocher (2001) experiment.

Putting together the existing data, Cheng and Newcombe found the developmental pattern shown in Figures 47 and 48:

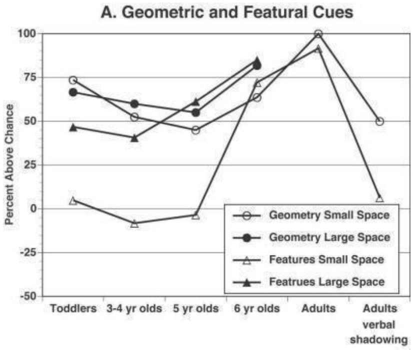


Figure 47. Geometric and Featural Cues.

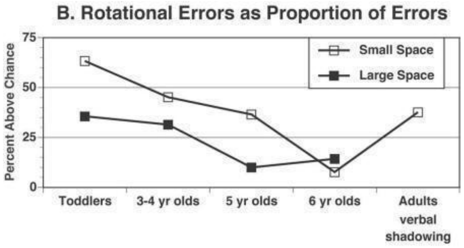


Figure 48. Rotational Errors as Proportion of Errors.

Looking at this developmental pattern undermines the language hypothesis, which cannot explain:

- Why toddlers succeed in the larger room.
- Why there is improvement in rooms of both sizes before and after hypothesized critical language acquisition.
- Why room size makes a difference.

However, the fact that adults doing verbal shadowing tasks do NOT use featural cues (Figure 49) remains to be explained.

One new way to think about the roles of geometric and featural information is that the usage of each kind of information may vary with the situation and with the learning history of the organism (or other variables that determine individual differences). Consider a recent experiment by Hartley, Trinkler, and Burgess (2004). Using virtual reality, people were placed in arenas in which they searched for targets. There were landmarks such as cliffs located in the far distance. Figure 50 gives a sense of the situation.

On some trials, the shape of the arena was changed as shown in Figure 51. People's searches, as also shown in the figure, were guided by a variety of kinds of spatial information, including fixed distance to walls, a ratio of distances, and angles to corners of the arenas. The relative reliance on these types of information varied, with absolute distances more heavily weighted when distances were shorter, and thus likely to be estimated with less uncertainty. In addition, when the shape of the arena was altered, some people seemed to try to continue to use geometry to find the target while others seemed to rely on external features (such as the cliffs) for orientation. How different kinds of information are utilized and combined will likely be understood better in the near future as we analyse these kinds of situational and individual information more closely.

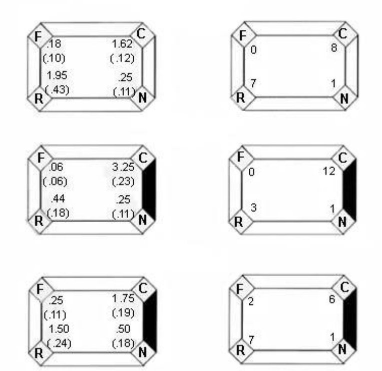


Figure 49. Results from Hermer-Vazquez et al. (1999). Adults performed the task without verbal shadowing (top two rows) or with verbal shadowing (bottom row). Left: average number of each corner chosen out of 4 (SEM). Right: first test only, pooled across subjects.

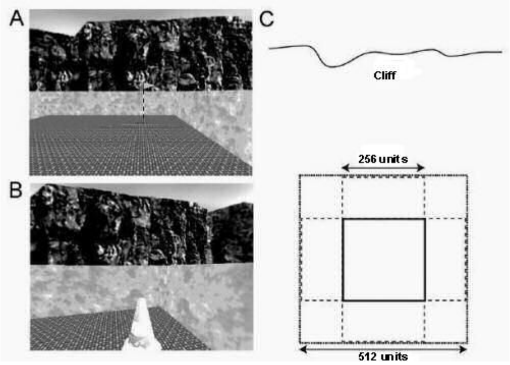


Figure 50. Stimuli (Panels A and B) and Layout (Panel C) used in experiments of Hartley, Trinkler, and Burgess (2004).

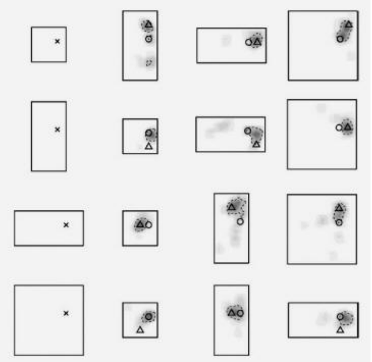


Figure 51. Results from test trials in experiments of Hartley, Trinkler, and Burgess (2004).

III. Cue Competition

In cue competition, the experience of one cue affects the learning of a second cue adversely. In overshadowing, the presence of an additional cue affects learning adversely; thus, A is learned better alone than in AB compound. In blocking, a previously learned cue affects learning adversely. Thus, if B is learned in Phase 1, and AB is presented in Phase 2, A may not be learned well. B is said to block the learning of A.

Cue competition is found in the case of learning to use landmark objects to localize a target. Landmarks overshadow one another, and a previously learned landmark can block the learning of a new landmark (review: Chamizo, 2003). However, the picture is different when it comes to learning to using geometric information.

In chicks (Tommasi & Vallortigara, 2000), pigeons (Kelly et al., 1998) and rats (Hayward et al., 2003; Pearce et al., 2001; Wall et al., 2004), a beacon (landmark right at the target) does not block or overshadow the learning of geometric information.

Tommasi and Vallortigara (2000, Figure 52, top left panel, top part) trained chicks to search in the middle of a square. They either had a prominent beacon at the center or not. The beacon was a potential cue competitor with geometric cues. However, when tested with the geometric cues alone (without the beacon), both groups performed similarly, giving no evidence of the overshadowing of geometric cues by a beacon.

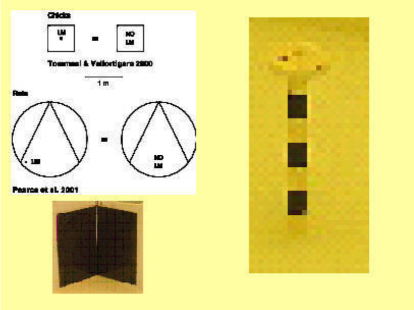


Figure 52. Top-left - The situations used by Tommasi and Vallortigara (2000) and Pearce et al. (2001). Bottom-left and Right - Beacons used for rats (color photos thanks to Anthony McGregor).

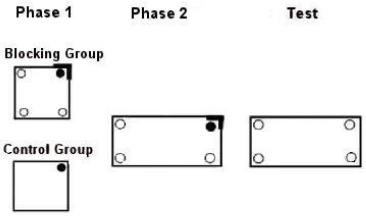


Figure 53. An experiment from Wall et al. (2004).

Pearce et al. (2001) and Hayward et al. (2003) trained rats to find a corner of a swimming pool, where a hidden platform was located for escaping the water. An example is shown in the top left panel, bottom part of Figure 52. They found that having a prominent beacon right at the target corner neither overshadowed nor blocked the learning of geometric cues. The rats in these situations with cue competition still managed to find the target without the beacon present, as well as animals that learned geometric cues without a beacon. A beacon failed to be a cue competitor of geometric cues.

Rats in the blocking group learned to use a beacon to find food in one of four corners in Phase 1 (Figure 53). Control rats had only the food dish, without the beacon, in Phase 1. In Phase 2, geometric cues were introduced in the form of a rectangular arena. Geometric cues were not as good a predictor as the beacon, because it left a two-fold ambiguity. Nevertheless, both groups showed equal evidence of using geometric cues, because they made rotational errors to similar extents. In the test with geometric cues alone, both groups proved to use geometric cues equally well. Thus, a prominent beacon did not block the learning of geometry. Wall et al. concluded that beacons and geometry are learned independently.

Since writing this section, two studies have recently found cue competition with geometric cues, in mountain chickadees (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005) and rats (Pearce, Graham, Good, Jones, & McGregor, 2006). Both provided featural cues not as local beacons, but colors of entire walls.

IV. Artificial Intelligence

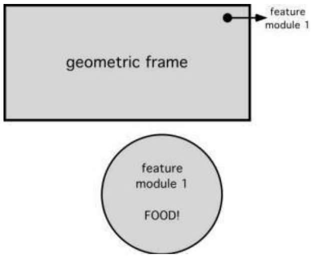


Figure 54. A single feature module for encoding spatial information (Egerton et al., 2000).

A check on recent citations reveals three different sources in the literature on artificial intelligence that have cited Cheng's (1986) paper. Two take the notion of encoding geometry seriously, while one demonstrates how a robot may perform without encoding geometry.

Egerton, Callaghan, & Chernett (2000) took the idea of a geometric module or geometric frame to heart. They suggest a division of labor in encoding spatial information. A geometric frame or module encodes the broad shape of the environment. On it are pointers to feature modules. Feature modules tell about what is to be expected at a particular place or region in space. Figure 54 shows a single feature module, but a functioning system would have a substantial bank of features.

A key point of this separation is to help solve what is called the problem of perceptual aliasing. This refers to the fact that a purely featural description leaves much ambiguity. For example, the description "door" might fit several places in one's space. But a door at a particular region is typically a unique description. Having a global frame makes the use of local information unambiguous. It saves the system from having to encode detailed local information.

Another representation that encodes geometry is the Absolute Space Representation (Yeap & Jefferies, 1999). Yeap and Jefferies were concerned with early cognitive mapping, which has the goal of getting a robot to build up a map of the environment it is navigating through. They suggest the strategy of having the robot build an early map of a local environment specifying where boundaries (such as walls) and exits are. The idea is that the robot should at first 'look past' furniture that clutter a room (indicated in the left panel of Figure 55 by variously shaded rectangles) and figure out where the outer boundaries are. Such a frame with exits allows the robot to navigate through its environment while it builds up more knowledge.

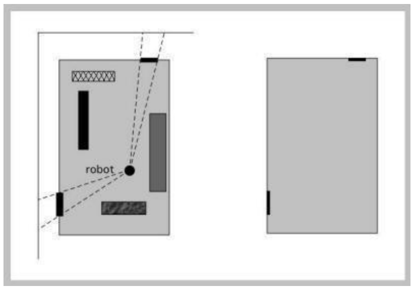


Figure 55. The Absolute Space Representation (Yeap & Jefferies, 1999).

Robotics can benefit the study of animal behavior as well as vice versa (Webb, 2000). The Absolute Space Representation points out the importance of encoding exits. In the animal literature on geometry, the importance of exits has not yet been tested. If exits are important, then they might serve to disambiguate rotational symmetry, whereas other objects of equivalent size might not. Testing this hypothesis is straight forward, and deserves to be done.

Nolfi (2002)'designed' reactive agents for solving Cheng's (1986) task up to rotational ambiguity. A reactive agent has no internal states, and reacts to a stimulus always in the same way. "Design" is in quotes because Nolfi actually let the systems evolve. Better solutions got to 'reproduce,' with some variations, until a system evolved that can readily solve the task. The left panels of Figure 56 illustrate a solution for solving the problem starting from the middle, facing one of the walls. Basically, the robot walks with a veer to the left, until it meets a wall. Then it turns left and hugs the wall until it runs into a corner. If the veer is within a certain range, the robot mostly reaches either the correct corner (filled dot) or its diagonal opposite (open dot). The right panels show a similar solution with the middle of one of the sides (facing center) as starting points. Historically, these were the positions used in Cheng (1986). Nolfi was not concerned to show that animals solve the problem this way. Rather, he was demonstrating the powers of reactive agents.

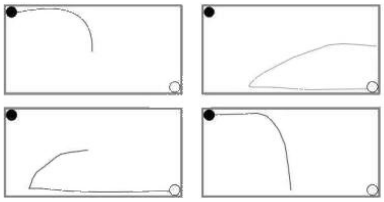


Figure 56. Models of robots problem solving (Nolfi, 2002).

V. Neurophysiology

5.1 Rats

The hippocampus is well known for its role in spatial navigation (O'Keefe & Nadel, 1978). It is beyond the scope of this chapter to review the literature on the hippocampus and space (review: Jeffery, 2003). But we present here some results concerning the encoding of geometric properties.

Hippocampal lesions in rats reduce rats' ability to choose the geometrically correct corners of a rectangular pool (Pearce et al., 2004). The pool (Figure 57) is surrounded by a circle of curtains, and would be filled with water during experimentation.

Figure 57. Pearce et al. (2004) apparatus. Thanks to Anthony McGregor for the photo.

O'Keefe and Burgess (1996) recorded from the rat's hippocampus as the rat wandered in a rectangular space. The rat was oriented and had external cues to direction. It searched in the white rectangle, whose shape can be changed by shifting the walls appropriately (Figure 58). Hippocampal place cells (O'Keefe & Nadel, 1978; Figure 59) are typically found in the hippocampus proper. They fire preferentially when a rat is at a particular place in space.

In Figure 59, the 'training' space was the vertical rectangle on the bottom left of each panel. The rat was then transferred to transformed spaces (the other diagrams) and the firing rate of each cell recorded. What the pattern of results from 28 cells show (see also Hartley, Burgess, Lever, Cacucci, & O'Keefe, 2000) is that these hippocampal cells are sensitive to both absolute distances from walls, and to relative distances, varying according to circumstance. Below in this section, we present the group's model explaining this.

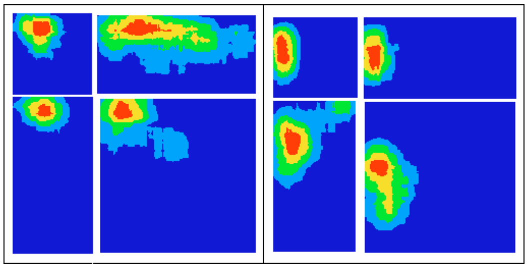


Figure 59. Adapted from Figure 1, O'Keefe & Burgess, 1996. Thanks to Neil Burgess for the picture.

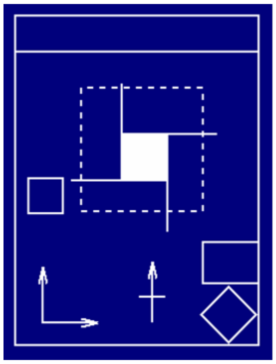


Figure 58: O'Keefe and Burgess (1996) apparatus. Thanks to Neil Burgess for this picture.

The 'performance' of 35 recorded place cells are shown in Figure 60. These firing rates are obtained independent of the direction that the rat is facing.

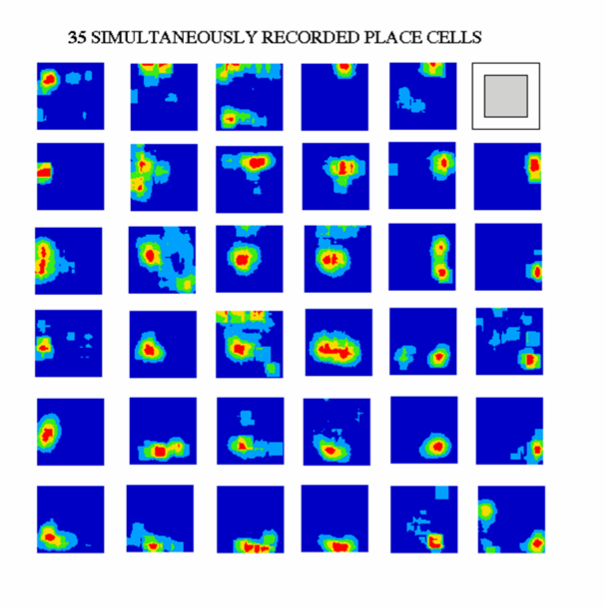


Figure 60. Adapted from Burgess et al. (2000, Figure 1). Thanks to Neil Burgess for the picture.

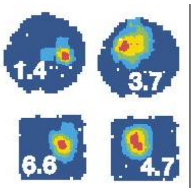


Figure 61. Taken from Lever et al. (2002, Figure 1).

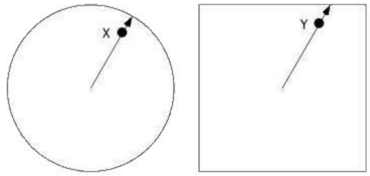


Figure 62. Place cells firing in corresponding locations in different shapes.

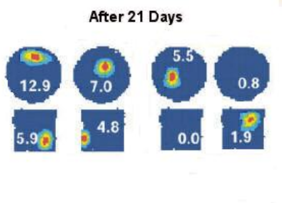


Figure 63. Taken from Figure 3 of Lever et al. (2002).

The shape of the 'training' space can be more radically transformed, and the hippocampal cells will still show systematic firing patterns (Lever, Wills, Cacucci, Burgess, & O'Keefe, 2002; Figure 61). For example, a square may be turned into a circle. Often, cells would fire at corresponding locations in the two spaces (Figure 62). Correspondence is determined as follows. If X is the place of maximal firing in the training space (left), then Y, the place of maximal firing in the transfer space (right) lies in the same direction from the center, at the same proportion of distance from the center to the edge.

Over many days of repeated exposure to both spaces, however, the 'behavior' of the cell in the two spaces may change. After 21 days, a cell might respond in one space but not the other (Figure 63, right), or might respond at different, non-corresponding places in the two spaces (Figure 63, left).

To model the performance of place cells, the existence of boundary vector cells are posited (Burgess et al., 2000; Hartley et al., 2000; Figure 64). These cells, which have not to date been found, respond when the rat is at a particular distance and direction from a surface (the black line), independent of the direction that the rat is facing. The boundary vector cells are upstream from the place cells, and a conjunction of boundary vector cells determine the performance of a place cell. This discussion of place cells in the rat hippocampus suggests that these cells perhaps play a role in encoding local geometry, vectors to surfaces, and not the global orientations that determine which direction is which.

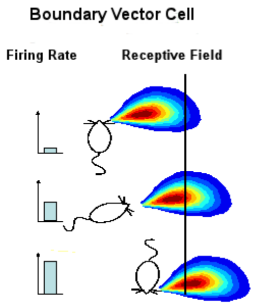


Figure 64. Adapted from Hartley et al. (2000, Figure 1). Thanks to Neil Burgess for the picture.

Other cells in the hippocampal complex, called head direction cells, are sensitive to the direction that the rat's head is facing, irrespective of the place that the rat is currently at (review: Dudchenko, 2003). These cells are typically found outside the hippocampus proper, in diverse areas ranging from the lateral dorsal thalamus to the dorsal tegmental nucleus. As these cells appear to encode direction, we may wonder whether their performance has something to do with encoding geometry and with rotational errors.

Golob, Stackman, Wong, and Taube (2001) probed this question. Head direction cells were recorded while a thirsty rat was in a square arena (Figure 65A). The rat was not disoriented, but circular curtains surrounded the arena. Its home cage might change locations on different trials, as illustrated in Figure 65A. A cue card on one wall provided directional cues. The rat had the behavioral task of finding one constant corner at which water was available; this was thus a reference memory task. The performance of a head direction cell was generally consistent, but on occasional trials, its preferred direction might shift by some multiple of 90º, as the dashed curve in Figure 65 shows.

The question that arises is whether these shifts in the performance of head direction cells predict behavioral errors on the part of the rats. Across a number of experiments, the answer was a clear no. Golob et al. (2001) found no significant relations between the preferred direction of head direction cells and behavior.

5.2 Birds

Many birds show many hemispheric specializations for behavior. Visual input to the bird brain is highly lateralized. By covering one eye, as in Figure 66, information is effectively restricted to half the brain. With the left eye covered, this chick is a left-brained animal visually. Vallortigara, Pagni, and Sovrano (2004) used eye covering to test the role of the hemispheres in encoding geometric and featural cues. In this experiment, chicks were trained with geometric and featural cues, but tested for their use of geometric information. Binocular and left-eyed (right-brained) chicks did fine, while right-eyed (left-brained) chicks failed (Figure 67).

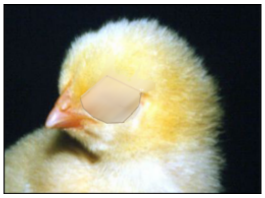


Figure 66. Thanks to Giorgio Vallortigara for the pictures on chicks in this section.

The experiment in Figure 68 tested the use of featural cues. In the tests, geometric cues were removed by making the space square. Both left-eyed and right-eyed chicks did fine, indicating that both hemispheres encode featural cues. In the experiment shown in Figure 69, both the training and test situations had only geometric cues. Left-eyed (right-brained) chicks again did fine. Right-eyed (left-brained) chicks were marginal (did not quite beat chance statistically, at p = 0.06).

The study shows that the left hemisphere encodes only features, while the right hemisphere encodes both features and geometry. Tommasi, Gagliardo, Andrew, and Vallortigara (2003) used lesions of the right or left hippocampus of chicks in the relocation task. They came to similar conclusions. The left hippocampus encodes only featural information, while the right hippocampus encodes geometric and featural information.

The role of the hippocampus in geometric encoding has also been studied in homing pigeons (Vargas et al., 2004). Normal pigeons and birds with their hippocampus lesioned (bilaterally) were trained in a space containing both featural and geometric cues (Figures 70 and 71). Both learned the task, but interestingly, birds without hippocampus reached criterion faster. It seems that learning geometry (in birds with hippocampus) is obligatory, even when it does not help. Even though geometric information is ambiguous and may cause rotational errors, it is nevertheless learned. This point is also clear from the studies on cue competition.

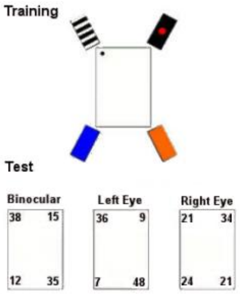


Figure 67. Procedure and results from Vallortigara, Pagni, and Sovrano (2004).

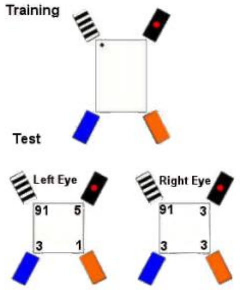


Figure 68. Testing featural cues by removing geometric cues from Vallortigara, Pagni, and Sovrano (2004).

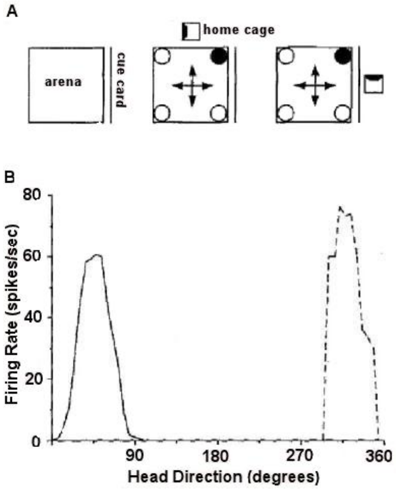


Figure 65. Adapted from Golob et al. (2001), Figures 1 and 2.

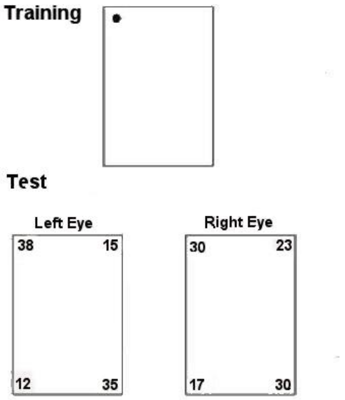


Figure 69. Training and testing with geometric cues only from Vallortigara, Pagni, and Sovrano (2004).

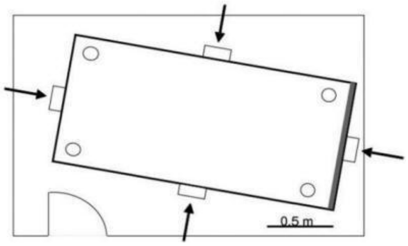


Figure 70. Adapted from Vargas et al. (2004, Figure 1).

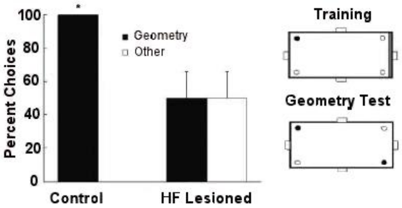


Figure 71. Geometry Test. Adapted from Vargas et al. (2004, Figure 4). Featural cues were removed so only geometric cues remained.

When featural cues (a red wall) were removed on a geometry test, control birds used the geometric cues, whereas birds with their hippocampal formation lesioned failed (Figure 71). When geometric cues were removed by making the search space square on a feature test, both control and lesioned birds succeeded (Figure 72). When geometric cues were put in conflict with featural cues, by making a long wall rather than a short wall red, control birds went with the geometry whereas lesioned birds went with the features (Figure 73).

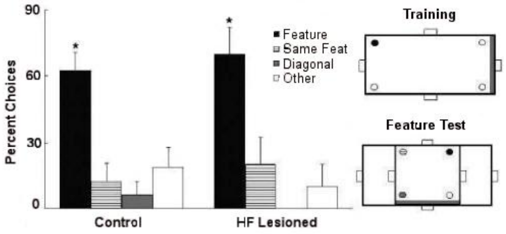


Figure 72. Feature Tests. Adapted from Vargas et al. (2004, Figure 5).

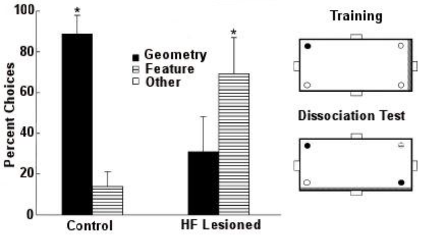


Figure 73. Dissociation Test. Adapted from Vargas et al. (2004, Figure 6).

5.3 Humans

Parahippocampal place area?

It has been proposed that the geometric layout of the environment is constructed in a specific area of the human brain, namely the posterior tip of the parahippocampal gyrus and adjacent regions of the fusiform gyrus (Epstein & Kanwisher, 1998; Epstein, DeYoe, Press, Rosen, & Kanwisher, 2001; Epstein, Graham, & Downing, 2003; Epstein, Harris, Stanley, & Kanwisher, 1999, Figure 74). This area has been termed the Parahippocampal Place Area (PPA).

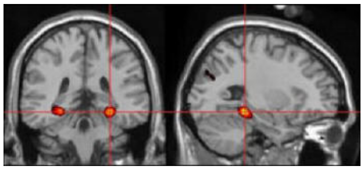


Figure 74. The Parahippocampal Place Area (PPA). This and the next few images come from Russell Epstein.

Human imaging evidence.

Perception of scenes led to differential activation in the PPA, relative to perception of faces, objects, or houses (Epstein & Kanwisher, 1998, Figure 75), even though the subjects were not required to perform any tasks.

More evidence on PPA and geometry.

Coherent geometric structure seemed vital to PPA activation because fractured and rearranged versions of the bare rooms did not elicit a response. Further, activity in the PPA is not further increased when people feel as if they are moving in a scene, suggesting that it is more involved in geometric analysis than in planning routes or monitoring locomotion (Epstein et al., 1999).

PPA seems viewpoint invariant.

Imaging of PPA activity while people looked at scenes such as those in Figure 76 showed that a change in viewpoint (middle row) led to as much activity as a complete change in place (at bottom) with both elevated relative to no-change control (at top).

Figure 75. Scenes used by Epstein & Kanwisher (1998).

Doubts about the PPA as possible substrate for geometric module.

There are alternative interpretations of the role of human parahippocampal cortex (Maguire, Burgess, et al. , 1998; Maguire, Frith, et al., 1998; see also Maguire, Burgess, & O'Keefe, 1999; O'Keefe et al., 1999). They have imaged humans performing a variety of tasks such as navigating around a virtual town (see Figure 77). This group argues that the parahippocampal area is especially involved in locating objects in allocentric space. In fact, Burgess and O'Keefe (2003) suggest that the human parahippocampus is better termed a Spatial Scene Area than a Place Area.

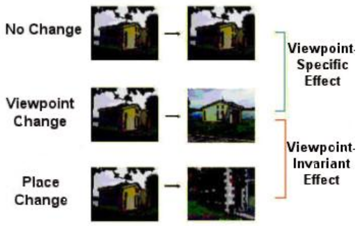


Figure 76. Three Trial Types.

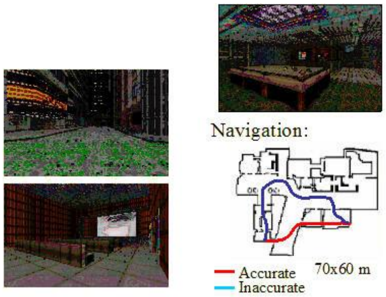


Figure 77. Virtual Reality Town for Testing Spatial and Episodic Memory. Used by Burgess and colleagues. Photo courtesy of Neil Burgess.

Figure 78. Example stimulus (left) and stimulus layout (right) in Ekstrom et al. (2003). Photo coutesy of Michael Kahana.

Place cells in the hippocampus?

Ekstrom et al. (2003) conducted the first single-cell investigation of humans -- 7 patients with pharmacologically intractable epilepsy who were being observed with intra-cranial electrodes participated as taxi drivers in a VR navigation game (Figure 78). They picked up passengers and took them to one of nine distinctive buildings arranged in a grid.

Cells were categorized as place cells if they responded when the patient was in a particular location in the grid, independent of what view was on the screen or what goal was being sought. Similarly cells could be categorized as view cells or as goal cells if they responded to particular views or goals but were not affected by the other two types of information or by interactions. Place cells predominated in the hippocampus (as shown Figure 79, courtesy of Michael Kahana) and view cells in the parahippocampus.

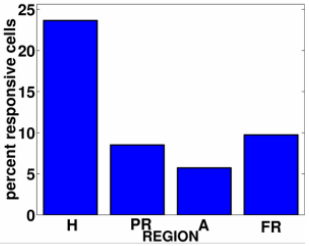


Figure 79. Ekstrom et al. data. Courtesy of Michael Kahana.

VI. Theory of Geometric Encoding

Simpler than shape.

Given the amount of evidence showing that all vertebrate animals tested so far use the geometric properties of space, surprisingly little has addressed how they use geometry or what aspects of geometry play a role. The only prominent theory was formulated by Gallistel (1990, Chapter 6). Gallistel theorized that rats encoded and matched the principal axes of space for determining which direction is which in space. The direction determining is done by matching something far less and far simpler than the entire shape.

The major (long arrow) and minor (short arrow) principal axes of a rectangle are shown in Figure 80. A principal axis goes through the centroid of the space. A centroid is the center of mass. We have assumed in this diagram that the density of 'mass' in the space is uniform, so that the centroid is at the center. But by postulating non-uniform 'subjective density' of space, the centroid might be displaced from the center.

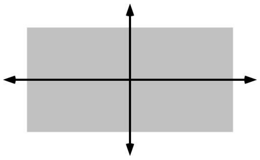


Figure 80. Principal axes of space.

The major (first) principal axis has these properties:

Mechanically, if the space spins around the axis, it would have the minimum angular momentum.
Statistically, the sum of squares of perpendicular distances of points in space to the axis is minimized.

Figure 81 shows that it is the perpendicular distances to the axis that are minimized, not distances to the principal axis along some arbitrary axis (such as the y-axis, as in statistical regression analyses). The minor (second) principal axis is perpendicular to the major axis, but we will not be concerned with it.

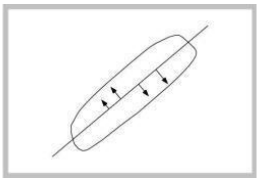


Figure 81. Minimization of distances to the perpendicular axis.

The principal axis is a computationally shorthand way of coding global directions without having to encode all the details of the overall shape. It is simpler than the geometric module in Cheng (1986) and Egerton et al. (2000), or the Absolute Space Representation of Yeap and Jefferies (1999). It is a parameter that can be matched with a deterministic routine, without the use of iterative trial and error. The matching does not 'explode' in complexity as the space becomes more detailed and complicated in shape.

For over a decade, nothing addressed Gallistel's (1990) theory. Then two papers were published in 2004 that claimed to rule out any global geometric representations, including presumably the theory of principal axes. Pearce, Good, Jones, and McGregor (2004) trained and tested rats in a swimming pool task, with the target escape location at a corner (Figures 82, 83, left). The pool was ringed by curtains and rotated from trial to trial. With no featural cues, the rats of course made rotational errors, as often as correct choices. In a crucial test, the shape of the pool was changed to a kite shape (Figures 82, 83, right). This changes Euclidean properties, so that the global shapes of the training and test spaces could not be matched.

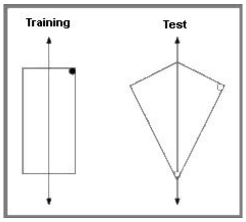
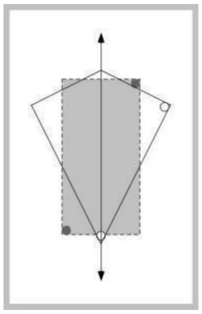


Figure 82. Pearce, Good, Jones, and McGregor (2004) experiment.

Figure 83. The rectangle (left) and kite (right) pools used in the Pearce, et al. (2004) experiments. Both pools would be filled with water during experimentation. Thanks to Anthony McGregor for these photos.

Can a formulation in terms of the principal axis of space explain this behavior?

The answer is a definite yes (Cheng & Gallistel, 2005). In Figure 84, the first principal axis of the test space is shown. In dotted lines, the training situation is superimposed, lined up at middle of the principal axis, and in the direction of the principal axis. Instantly, we see that the rats' chosen corners are near the ones defined in the training space. One needs to define distance (nearness) properly to favor the top right corner of the kite over the obtuse angle at the top. This is readily done by assuming that the rat is looking for something like: the end of the principal axis and as far to the right as possible. In the scheme shown in Figure 85, searching at the apex is akin to a rotational error. When the rat heads down toward the apex end of the kite, it has only one corner to go to.



Another study on chicks in an appetitive food finding task had the birds searching for food in one of four containers placed in the corners of a parallelogram. (Tommasi & Polli, 2004). The filled and open dots in Figure 86 show the target locations of two different groups of chicks. It is crucial to show the results of both locations because they produced important differences.

Figure 85. Thanks to Anthony McGregor for this photo.

In the training situation, the chicks, without any featural cues, of course made rotational errors and chose the diagonal opposite to the target as often as the target. In the figures here, this fact is not shown. Figure 87 shows where the chicks searched in transformed spaces. Again, the chicks make rotational errors (not illustrated). They searched at levels as high as in the training space. The rectangle (left) preserved the lengths of walls, but altered the angles of corners. The authors' interpretation is that the chicks encoded the relative lengths of walls. The rhombus (middle) preserved the angles at the corners, but altered the lengths of walls and their ratios to one another. The authors' interpretation is that the chicks encoded the corner angle.

A reflection of the training space (right) produced the most interesting results. In this space, corner angle and relative lengths of walls were put in conflict. Where the corner angle matched the training situation, the relative lengths were incorrect. For example, for the black-dot group, trained at an acute angle, the long wall was to the right of the short wall in the test space, but to the left of the short wall in the training space. Thus, the acute-angle group (black dots) matched corner angle. The obtuse-angle group (open circle), who chose the same acute-angled corners, matched the relative lengths of walls rather than corner angle. The authors' interpretation is that an acute angle was more salient than an obtuse angle. The chicks were basically matching on the most salient cue.

Figure 84.

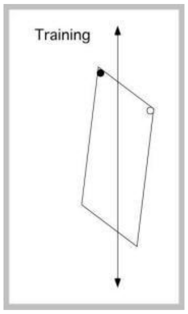


Figure 86. Tommasi and Polli (2004) experiment - Training.

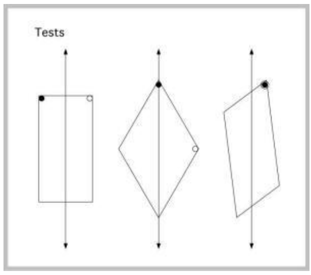


Figure 87. Tommasi and Polli (2004) experiment - Tests.

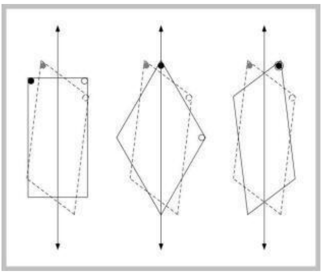


Figure 88. Superimposition of training and testing apparatus with principal axis shown.

Again, can the pattern of results be explained by reference to the principal axis of space, something that the authors rejected? Again, the answer is a definite yes (Cheng & Gallistel, in press). In Figure 88, the ghost of the training space (in dashed lines) is again superimposed on each of the test spaces, with the target locations shown in gray for the acute-angle group (black dots in the test spaces), and in open circles for the obtuse angle group (open circles in the test spaces). Again, test spaces and training space are lined up at the principal axis. If the chicks extracted the principal axis of space, and searched at the nearest location according to the training situation, the figure shows that they would search at the observed places that they chose in the test situations. In this case, other than going to a food bowl, there is no need to encode any other local features, such as the angle of a corner.

Cheng (2005) suggests that principal axes may not be the best scheme for capturing global shape information. The trouble is that a principal axis is always a straight line, no matter what the shape; it really does not tell us anything about the shape. The M-shape in Figure 89 has a roughly horizontal straight line as a principal axis, just as a horizontally oriented rectangle would.

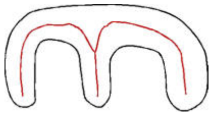


Figure 89. An M-shape, with some axes of symmetry drawn through it in red by free hand.

In Figure 89, we have also drawn in red, by free hand and approximately, a set of axes of symmetry. These bend with the curvature of the shape and capture regional symmetries, roughly bisecting the nearest walls. A glance at the red axes shows that they capture the M of the shape. Such axes of symmetry, a variety of them, can be formally defined (see Leyton, 1992, ch. 6).

Another shape-capturing scheme is the medial axis scheme (Fritsch, Pizer, Morse, Eberly, & Liu, 1994; Pizer, Fritsch, Yushkevich, Johnson, & Chaney, 1999), designed for the purpose of medical imaging. In brief this kind of scheme draws a stick-figure trunk and branch structure to capture the gist of the shape. The trunk goes through the middle of the space, and the branches indicate distances to the boundary. Substructures, such as the middle finger of the M in Figure 89 would have their own skeletons, and be linked to the 'parent' shape. The scheme thus also captures something of the structure of the shape.

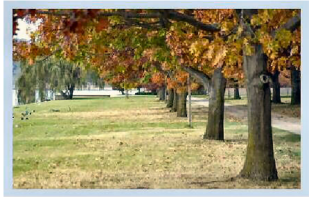


Figure 90. Axes in a natural scene?

A priori, it is likely that some kind of global representation of space is used for navigation. The global representation helps the animal to use the right local cues. The problem with local cues is that there are too many of them (the problem of perceptual aliasing, see section on artificial intelligence). The world has too many trees and stones.

Having a sketchy global representation (such as representing key axes) helps the animal limit the amount of local information that has to be encoded. As an example, imagine encoding enough information about a tree shown in Figure 90 to distinguish it from every other tree in this part of a park. The problem taxes the best 'featural' systems, and explodes in complexity with the number of trees. If, however, a global representation limits the search to a small region, then the number of trees are limited, and the problem does not explode in complexity. Judiciously combining global and local information might make the task tractable at many scales.

These studies are important in forging ahead with methods for testing theories; they provide good methodological models. Since we wrote this, recent work from Pearce's lab have continued the discussion about the nature of geometric encoding (Graham, Good, McGregor, & Pearce, 2006; McGregor, Jones, Good, & Pearce, 2006; Pearce et al., 2006). Far more research using many transformations is needed to constrain theories of geometric encoding.

VII. Modularity

7.1 Three Views of Central Modularity

Figures 91, 92, and 93 (adapted from Figure 3 of Cheng and Newcombe, 2005), show 3 views of modularity that we can identify. Doubtless there are other versions. These views concern modularity in the central system(s) that represent information. We consider below a notion of modularity at output.

In all three views, we have characterized the input processes as modular. Thus, we assume that different visual channels handle and compute geometric and featural properties, a view consistent with Fodor (1983). In fact, visual systems are far more modular than the two boxes shown in the following three pictures (Marr, 1982).

In a strong view of modularity (Wang & Spelke, 2002, 2003), geometric information goes through an impenetrable module that handles only geometric information. "Impenetrable" means that the module does not admit any other kind of information. Featural information, if it is used, is handled by other modular systems. We have listed a view-based module as one example. Thus, the systems run parallel through central processing to action.

Some processes use only the geometric route. In Wang and Spelke (2002), it was the process of determining direction after disorientation. In Wang and Spelke (2003), it was either the process of determining direction or the process of locating a point in space after determining direction. We found the writing ambiguous (see Cheng & Newcombe, 2005, for a fuller discussion).

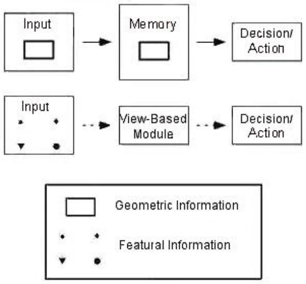


Figure 91. Impenetrable Module. Strong Modularity.

A view of modular subcomponents in the central system characterizes Cheng's (1986) discussion. Note that we have drawn one memory box, in which both geometric and featural information are contained. Hence, this view differs from Wang and Spelke's (2002, 2003) views. But there is some modularity in the central system, in that the geometric information is one submodule, the primary one. Cheng (1986) called it a geometric frame. It encodes the broad shape of the environment. (In the theory section, we report evidence indicating that animals may encode far less than the shape.) On this frame, crucial featural information may be pasted. Rotational errors ensue when featural information fails to be entered at all (learning failure), or fails to be pasted on the geometric frame.

In a completely integrated view (Newcombe, 2002), featural and geometric information are encoded together in the central system. Their use may be weighted by many factors, including reliability of information, stability of landmarks, etc. Rotational errors ensue when featural information is either not entered at all into the central system (learning failure), or if they are weighted very little (e.g., because they are thought to be unreliable).

One of us (Cheng, 2005) has recently put forth another view of modularity that takes on elements of all the views in Figures 91 to 93 (Figure 94). In this view, all spatial information, geometric and featural, is stored together in one representation, in this respect resembling Figure 93 and Newcombe's (2002, 2005) views. But at least one process that operates on the stored information is modular, the heading-by-axes process. This is a global direction-determining process that uses global shape parameters derived solely from geometric properties based on the entire shape of the space. This process is consistent with Wang and Spelke's (2002) views. Other processes are not modular in this fashion. In particular, the process of determining an exact location of a target is based on both featural and geometric information. This process, however, weights preferentially cues near the target location. Such a view is foreshadowed in Cheng (1986, p. 172)

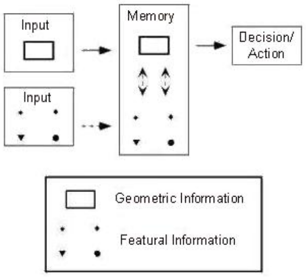


Figure 92. Modular Memorial Subsystems. Modular Subcomponents.

7.2 Modularity at Output

A different kind of modularity concerns the use of information in guiding action, modularity at output. According to the view shown in Figure 95 (Panel A), different kinds of information guide action separately. They do not interact. In contrast, the theory shown in Figure 95 (Panel B) proposes that different kinds of information guide action together. The information is integrated at output. We have shown geometric and featural information in this picture, but the same notion applies to other kinds of information as well. Here, we are not concerned with how information is centrally organized (the ? in A reflects this uncertainty), but with whether different kinds of information are integrated at output.

This idea of modularity at output is best explained with concrete experimental examples. In the training set up in Figure 96 (left) the search space is the gray ring. The searcher has the problem of determining direction: at which direction from the center of the ring to search at. Around the ring are distant cues for direction determination. We assume that the animal is disoriented, but it has unambiguous geometric cues (the trapezoidal arena) and a featural cue at the top left corner.

After sufficient training, the cues are put in conflict (Figure 96, right panel). The featural cue is moved to the top right corner. Arrows indicate interesting theoretical possibilities. The animal might rely completely on geometric information (left arrow). It might rely completely on the featural cue (right arrow). It might vacillate between the locations dictated by the geometric and the featural cues. Or, it might average the dictates of geometric and featural cues, and search somewhere between the right and left arrows.

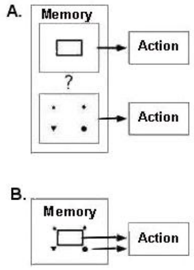
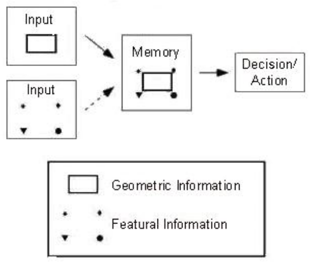


Figure 95. Modulartity at Output: A. Modular Systems. B. Unified System.

This last outcome indicates integration of geometric and featural information at output. The vacillation outcome is ambiguous. It might result from the existence of competing modules, or it might occur with integrated representations if the animal computes degree of match between competing locations and finds two imperfect matches.

This conceptual paradigm is not limited to geometric and featural cues. Consider for example an oriented animal trained in the training set up on the left in Figure 97. Its inertial sense of direction and the geometric cues of the trapezoidal arena both give directional cues. The two kinds of cues are put in conflict on the right, when the trapezoidal space is rotated in Earth-based coordinates. This puts geometric and inertial cues in conflict. Thus, many kinds of cues can be tested in this fashion. One recent theory of the evolution of spatial cognition (Jacobs & Schenk, 2003) suggests that a part of the hippocampus is devoted to determining bearing or direction. If we read these authors right, this bearing system would use all available directional cues in an integrated fashion.



ure 93. Modular Input Systems Only. Integrated.

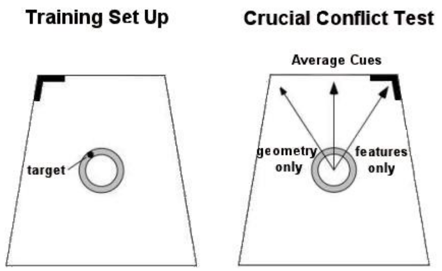


Fig 96. Dissociation of Feature and Geometric Cues.

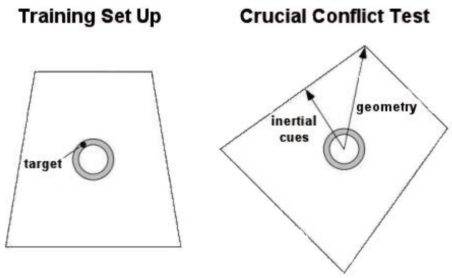


Figure 97. Dissociation of Geometric and Inertial Cues.

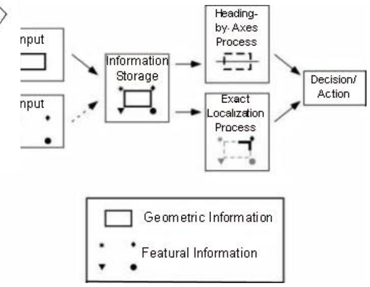


Figure 94. Theory proposed by Cheng (2005) incorporating elements of all three versions of central modularity.

VIII. Conclusions

Currently, debate concerning 1) the nature of geometric cues encoded, and 2) the modularity of geometric encoding form current topics of research. The work reviewed all use domesticated species or at least animals living most of their lives in rectilinear indoor spaces. This applies to the humans, monkeys, rats, pigeons, chicks (although they had few days of life before being tested), and even the fish in aquaria. Cheng and Newcombe (2005) wondered what this experience with rectilinear spaces in development might contribute to the encoding of geometric and featural cues. Recent research has also spread to wild-caught birds who have had at least substantial experience outdoors in natural settings. Some interesting differences have already been found (Gray et al., 2005), and perhaps more will be found (e.g., Kelly's program of testing Clark's nutcrackers in 'geometry' paradigms).

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