THEORETICAL AND REVIEW ARTICLES

Is there a geometric module for spatial orientation? Squaring theory and evidence

KEN CHENG
Macquarie University, Sydney, New South Wales, Australia

and

NORA S. NEWCOMBE
Temple University, Philadelphia, Pennsylvania

There is evidence, beginning with Cheng (1986), that mobile animals may use the geometry of surrounding areas to reorient following disorientation. Gallistel (1990) proposed that geometry is used to compute the major or minor axes of space and suggested that such information might form an encapsulated cognitive module. Research reviewed here, conducted on a wide variety of species since the initial discovery of the use of geometry and the formulation of the modularity claim, has supported some aspects of the approach, while casting doubt on others. Three possible processing models are presented that vary in the way in which (and the extent to which) they instantiate the modularity claim. The extant data do not permit us to discriminate among them. We propose a modified concept of modularity for which an empirical program of research is more tractable.

To navigate in the world, an animal usually needs to figure out which direction is which, a problem also known as *determining the heading* (Gallistel, 1990). That is, it needs to establish which way it is facing with respect to some frame that specifies directions. Such a frame may be given by cues external to the animal, such as the pattern formed by the sun and polarized light in the sky or the pattern formed by distant landmarks. But the "frame" may also be given by internal cues—for instance, when nothing external to the animal is available. An animal may compare its current heading with the direction in which it started its journey. In some cases of navigation, the heading needs to be continuously computed. Path integration is such a mechanism (for reviews, see Biegler, 2000, Collett & Collett, 2000, 2002, Etienne, Berlie, Georgakopoulos, & Maurer, 1998, Gallistel, 1990, Newcombe & Huttenlocher, 2000, Wehner, Michel, & Antonsen, 1996, and Wehner & Srinivasan, 2003). In path integration, an animal keeps track of the straight-line distance and direction to its starting point as it travels. In

outdoor environments, many animals, especially insects and birds, use a sun compass (e.g., Wehner & Wehner, 1990; Wiltschko & Balda, 1989) and large-scale landmarks (Dyer & Gould, 1983; Gagliardo, Ioalé, & Bingman, 1999; von Frisch & Lindauer, 1954) to establish heading. Vertebrates tested in indoor environments, however, do not have cues from the sky. They typically use the surrounding landmark cues to tell which direction is which. One kind of cue that has received marked attention over the past 2 decades is the overall geometric shape of the environment, called *geometric information* or *geometric cues*. Evidence that we will review below shows that geometric information is frequently used in relocating desired targets in a range of vertebrate species.

The idea that vertebrate animals use the geometry of the surrounding environment to locate places started with the work of Cheng (1986). Since then, similar paradigms of research have been conducted on a range of species, including human children and adults, monkeys, birds, and fish. Gallistel (1990) formulated a theoretical mechanism by which environmental geometry is extracted by computing the major and minor axes of a space and proposed that a geometric module is responsible for these computations. The idea of a geometric module forms a cornerstone of a recent proposal that human spatial representation is typically limited in nature—momentary, egocentric, and limited in informational content (Wang & Spelke, 2002, 2003)—as well as of proposals that initial modularity in human infants is overcome in adults through the acquisition of spatial language (Hermer &

Spelke, 1996; Hermer-Vazquez, Moffet, & Munkholm, 2001). In terms of underlying neural mechanisms, Epstein and Kanwisher (1998) have proposed that a part of the human brain, in the parahippocampal area, is dedicated to parsing and encoding the geometry of the environment, although others have disagreed (e.g., Maguire, Burgess, et al., 1998; Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998), and there is evidence that a major function of the rat hippocampus is the encoding of environmental geometry (Lever, Wills, Cacucci, Burgess, & O'Keefe, 2002; O'Keefe & Burgess, 1996). The idea of a geometric frame has also influenced some work in artificial intelligence on designing navigating robots (Egerton, Callaghan, & Chernett, 2000; Yeap & Jefferies, 1999), although we will not review this topic.

The aim of this review is twofold: first, to bring together the extant data, and second, to discuss a number of issues surrounding this burgeoning empirical literature. We will discuss Gallistel's theory for the use of geometry and will sketch some possible lines of research. We will discuss the nativist–empiricist controversy in development (Newcombe, 2002), a topic closely related to modularity of mind. Modularity is typically associated with nativist views, although this relation is by no means forced by logic (Fodor, 2001). We will consider the kinds of experience that might contribute to the reliance on geometric cues. We also will discuss a number of other topics that could form the agenda for further research.

But the central issue for discussion is modularity. A module of the mind uses only a subset of the potentially available information for a task. It is *encapsulated* from some kinds of information (Fodor, 1983, 2001). We will outline the position of Wang and Spelke (2002, 2003) and contrast it with Cheng's (1986) original writing, as well as with another recent view (Newcombe, 2002). From the discussion, we will formulate new ideas about modularity and the integration of information and will suggest programs of empirical research.

REVIEW

Basic Phenomenon

In most of the studies that we will review, subjects had the task of relocating a place within a rectangular enclosure (we will note exceptions along the way)—typically, one corner of the arena. Subjects typically have been disoriented before the relocation task, so that internal inertial cues for keeping track of which direction was which were eliminated. The search space was often rotated as well, making inertial cues irrelevant for relocation. The available views may be divided conceptually into two kinds. The rectangular shape of the arena provides one source of information: the geometric cues. Other, nongeometric cues, which we will call *featural cues*, may also be available. These vary across studies and species, but they are such cues as the colors of the walls of the arena, panels with different characteristics at the corners, or discrete landmark objects within the arena. Defining a location with respect to these distinct featural cues de-

A. Performance on task
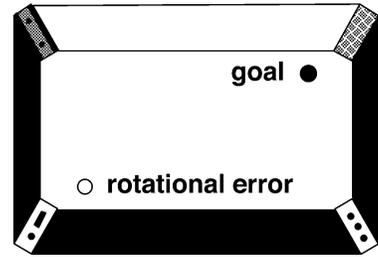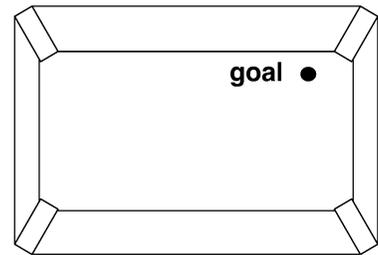

B. Geometric information

Figure 1. Geometric and featural (nongeometric) information in the relocation task. (A) The task in a rectangular arena as seen from above. In attempting to relocate the goal after disorientation, the rotational error is frequently committed. This is the location at 180º rotation through the center from the correct location. (B) The geometric information is contained in the broad shape of the arena. The featural information is what is not shown: patterns on the panels, different brightnesses of walls, smells in the corner, and the like. In using a "map" containing only geometric information, the goal and the rotational error cannot be distinguished. From "Mechanisms of Landmark Use in Mammals and Birds," by K. Cheng and M. L. Spetch, in *Spatial Representation in Animals* (p. 4), S. Healy (Ed.), 1998, Oxford: Oxford University Press. Copyright 1998 by Oxford University Press. Adapted with permission.

livers a single unambiguous location as the target. Defining a location solely with respect to geometric cues, however, leads to an ambiguity in defining the target location (as is shown in Figure 1). Both the correct location and a rotational error fit the definition. The rotational error is located at 180º rotation through the center from the correct location. It is produced when the "map" is matched to the world in the "wrong" way, rotated 180º from what it "should be."

It is pertinent to indicate the geometric properties needed to solve the problem up to the point of geometric ambiguity (Cheng & Gallistel, 1984). The subject needs to use metric properties (distances and angles), to distinguish the long walls from the short walls, and also needs to encode sense, or the distinction between left and right. Thus, when the subject faces the target corner in Figure 1, the long wall is to the left of the short wall. Without sense, this location is equivalent to the mirror-reflected corners, at the bottom right and top left.

We have listed in the data tables (Tables 1 and 2) the evidence regarding choices in various studies with various species, including the percentage of correct choices

(labeled %C), the percentage of rotational errors (labeled %R), and the percentages of other responses (labeled %O). In all but one study, *other* errors were nonsystematic: As a proportion of the errors, they did not occur at levels higher than that expected by chance. In the columns on the right of Tables 1 and 2, we have recalculated the data with chance level subtracted out; the numbers thus represent percentage above chance. The *geometry* column estimates the extent to which geometric information is used. These figures are derived from comparing geometrically correct choices (correct choice and rotational error) and geometrically incorrect choices. The *feature* column shows the extent to which correct relocations exceed rotational errors. These numbers are negative if choice levels are below chance. The *rotational error* column (rightmost) represents the proportion of errors that are rotational errors. Again, the chance level (typically one third) has been subtracted out, so that positive numbers mean that rotational errors are a higher proportion of errors than would be expected by a model of equal errors at all locations. To the extent that rotational errors were systematic, the subjects relied solely on geometric cues for relocation on some trials. Where possible, we have indicated whether the results in the geometry, feature, and rotational error columns are significantly above chance (bold) or not (normal font). Italics indicate that we were unable to determine statistical significance. Statistical tests were either reported in the original papers or calculated on the basis of published data or data supplied by the authors.

Rats

Rotational errors were first reported in rats (Cheng, 1986). The rats were tested in both working memory and reference memory paradigms. The rectangular arena was completely enclosed; no cues outside of it were visible. The rats were familiarized with the space. During familiarization and throughout testing, the arena was rotated from trial to trial. In the working memory paradigm, the correct location could be anywhere in the arena, and a different correct location was shown to the rats on each trial. The rats were shown a rectangular dish of sweet cereal. They got to eat three pellets before they were taken out for 90 sec. Aside from being carried outside the test room, no effort was made to further disorient the animals. They were then put back in an exact replica of the arena, with the food buried at the same location in the arena as during exposure. Multimodal featural cues (including olfactory, visual, and tactile characteristics) were offered in panels in the corners. In one experiment, one long wall was white, whereas three other walls were black. The results were similar across experiments and are displayed in Table 1, line 1. Rotational errors were systematic, and the rats did not reliably choose the correct location over the rotational error. The nonsignificant tendency for correct choices to exceed rotational errors was attributed to the fact that the rats were not completely disoriented. Margules and Gallistel (1988) repeated the working memory paradigm with complete

disorientation of the rats. The results (Table 1, line 2) again showed systematic rotational errors and, this time, no tendency for correct choices to exceed rotational errors. Worth noting is the point that the rats in Cheng's (1986) working memory experiments had 2 min to recover food in the relocation (postdelay) part of a trial. Those that committed a rotational error thus had plenty of time to correct themselves. None ever did so.

In the reference memory paradigm of Cheng (1986), the possible locations to choose from were the corners, and the correct location remained the same from trial to trial. At first, the rats were proffered only one bottle full of sweet cereal at the correct corner. When they had become proficient at knocking over the bottle and taking the food (5 consecutive trials), bottles of food were placed in all four corners. The food, however, would spill out of the bottle only at the target corner. The arena was again rotated from trial to trial. The rats chose the correct location far more often than they made the rotational error, but they made systematic rotational errors in learning the task (Table 1, line 3). The rats were trained until they made a streak of 9 correct out of 10 trials. In the majority of cases, these 9/10 streaks were reached in fewer than 30 trials (measuring to the start of the streak). Thus, it does not take rats long to learn to use featural information. When the featural information (the panel) at the target location was removed, however, the use of the remaining, more distant features fell to chance levels (Table 1, line 4), although the rats continued to use geometric cues. In a follow-up experiment with the same animals (Cheng, 1986, Experiment 3, data not shown here), all the animals continued to be perfect in using geometric cues. Errors were exclusively rotational errors, a small amount (9%) in 3 rats and a large and systematic amount (43%) in a 4th rat.

In a more recent study on rats, using quite a different paradigm, Benhamou and Poucet (1998) tested rats in a circular swimming pool. Cues were provided only within the pool, in the form of distinct landmarks sticking above the water. When the cues were arranged in an equilateral triangle, the configuration of landmarks (disregarding their identity) left a threefold geometric ambiguity. Orientation with respect to the identity of the landmarks, however, left no ambiguity about target location. The rats were at chance at disambiguating the geometry after 75 training trials (Table 1, line 5). In a second condition, the rats were provided with three distinct landmarks arranged in an isosceles triangle. The geometric configuration of objects unambiguously specified the target location for this group. They solved the task after 75 training trials (Table 1, line 6). This experiment suggests that rats can utilize a geometry inferred from separated objects that define the vertices of a geometric figure. It also suggests that, as in the experiments in the rectangular arena, featural information either is not used or is used less easily than geometric information.

Commenting on this experiment, Poucet, Lenck-Santini, and Save (2003) noted that the task is more difficult for rats to learn than the typical swimming pool task in which

Table 1
Data on Nonhuman Animals

	Species	Study	Task and Cues	%C	%R	%O	Geom.	Feat.	Rot.
1	Rats	Cheng, 1986	working memory, geometric and featural cues	44.0	25.0	31.0	**38.0**	*27.5*	**37.7**
2	Rats	Margules & Gallistel, 1988	working memory, geometric and featural cues	35.0	31.0	33.0	**32.0**	*6.1*	**42.0**
3	Rats	Cheng, 1986	reference memory, geometric and featural cues	73.5	21.5	5.0	**90.0**	**54.7**	**71.7**
4	Rats	Cheng, 1986	reference memory, geometric and nonlocal featural cues	47.0	53.0	0.0	**100.0**	*–6.0*	**100.0**
5	Rats	Benhamou & Poucet, 1998	reference memory, featural landmark identity	–	–	–	–	*–3.5*	–
6	Rats	Benhamou & Poucet, 1998	reference memory, geometric configuration of landmarks	–	–	–	**47.5**	*5.9*	–
7	Chicks	Vallortigara, Zanforlin, & Pasti, 1990	reference memory, geometric cues only	45.0	40.0	15.0	**70.0**		*59.1*
8	Chicks	Vallortigara et al., 1990	reference memory, geometric and featural cues	99.0	1.0	0.0	**100.0**	**98.0**	–
9	Chicks	Vallortigara et al., 1990	reference memory, geometric and nonlocal featural cues	54.0	46.0	0.0	**100.0**	*8.0*	*100.0*
10	Chicks	Vallortigara, Pagni, & Sovrano, 2004	training: geometry and features, test: geometry only	38.0	35.0	27.0	**46.0**	*4.1*	*34.7*
11	Chicks	Vallortigara et al., 2004	training and test same as line 10, test: left eye only	36.0	48.0	16.0	**68.0**	*–14.3*	*62.5*
12	Chicks	Vallortigara et al., 2004	training and test same as line 10, test: right eye only	21.0	21.0	58.0	*–16.0*	*0.0*	*–10.1*
13	Chicks	Vallortigara et al., 2004	features only on test, left eye only	91.0	1.0	8.0	–	**88.0**	–
14	Chicks	Vallortigara et al., 2004	features only on test, right eye only	91.0	3.0	6.0	–	**88.0**	–
15	Chicks	Vallortigara et al., 2004	geometry only on training and test, left eye only	38.0	35.0	27.0	**46.0**	*4.1*	*34.7*
16	Chicks	Vallortigara et al., 2004	geometry only on training and test, right eye only	30.0	30.0	40.0	*20.0*	*0.0*	*14.3*
17	Pigeons	Kelly, Spetch, & Heth, 1998	reference memory, geometric cues only	49.0	42.0	9.0	**82.0**	*7.7*	**73.5**
18	Pigeons	Kelly et al., 1998	reference memory, geometric and featural cues	99.3	0.7	0.0	**100.0**	**98.7**	–
19	Pigeons	Kelly et al., 1998	reference memory, geometric and nonlocal featural cues	76.0	22.0	1.0	**96.0**	**55.1**	**93.5**
20	Pigeons	Kelly et al., 1998	reference memory, geometric cues and color only	81.0	15.0	3.0	**92.0**	**68.8**	**75.0**
21	Pigeons	Kelly et al., 1998	reference memory, geometric cues and shape only	64.0	33.0	3.0	**94.0**	**32.0**	**87.5**
22	Fish (*Xenotoca*)	Sovrano, Bisazza, & Vallortigara, 2002	reference memory, geometric cues only	39.7	35.5	24.8	**50.4**	*5.5*	*38.4*
23	Fish (*Xenotoca*)	Sovrano et al., 2002	reference memory, geometric and featural cues	55.5	9.5	35.0	**30.1**	**70.8**	*–18.0*
24	Fish (*Xenotoca*)	Sovrano, Bisazza, & Vallortigara, 2003	reference memory, geometric cues and panels	26.0	36.0	38.0	**24.0**	*–16.1*	*23.0*
25	Fish (*Xenotoca*)	Sovrano et al., 2003	geometric cues, training panels removed	46.0	46.0	8.0	**84.0**	*0.0*	**77.8**
26	Rhesus monkeys	Gouteux, Thinus-Blanc, & Vauclair, 2001	reference memory, geometric cues only	46.0	46.0	8.0	**84.0**	*0.0*	**77.8**
27	Rhesus monkeys	Gouteux et al., 2001	reference memory, geometric and small featural cues	47.7	38.3	14.0	**72.0**	*10.9*	**59.9**
28	Rhesus monkeys	Gouteux et al., 2001	reference memory, geometric and large featural cues	76.8	18.3	5.0	**90.0**	**61.6**	**67.7**

Note—%C indicates correct choices, %R indicates rotational errors, and %O indicates other choices, each in percentages. Geom., percentage correct above chance in distinguishing geometrically correct (correct corner and rotational error) and incorrect corners; Feat., percentage correct above chance in distinguishing the correct corner from the rotational error; Rot., percentage of errors that are rotational errors, above chance levels. Negative numbers in the rightmost three columns indicate levels below chance. If the chance level, in proportion, is C and the observed proportion is D, the formula for subtracting chance is $(D - C) / (1 - C)$. Bold font indicates significantly above chance ($p < .05$); normal font indicates not significantly above chance; italics indicate that we were unable to determine whether the reported datum was above chance.

cues surrounding the pool are available (more than 60 trials to asymptote in the former, as compared with fewer than 30 trials in the latter). Under some circumstances, human children and adults also find it more difficult to learn or remember the geometric configuration made up by individual objects, rather than by continuous surfaces (reviewed below).

Birds

Of avian species, chicks and pigeons have been tested in these paradigms. Vallortigara, Zanforlin, and Pasti (1990) first tested chicks in a rectangular arena in a reference memory paradigm. Without any featural cues, the chicks solved the problem up to geometric ambiguity: They chose mostly either the correct location or the rotational error (Table 1, line 7). When visually distinct panels in the corners provided featural cues, they were almost perfect (Table 1, line 8). In case of conflict between featural and geometric cues, the chicks' behavior was controlled mostly by the featural cues. Thus, chicks can use both geometric and featural cues for relocation. As with rats, featural cues near the target played a major role. When these were removed, the use of nonlocal features fell to chance levels (Table 1, line 9).

Vallortigara, Pagni, and Sovrano (2004) used a similar paradigm in a rectangular arena on chicks restricted to one eye. In birds, the eyes deliver information mostly to the contralateral hemisphere, so that left-eyed birds are effectively right-brained birds and right-eyed birds are effectively left-brained birds. When chicks were trained with geometric and featural cues but tested with geometric cues only, both chicks viewing the world binocularly (Table 1, line 10) and left-eyed birds (Table 1, line 11) used the geometric cues for relocation, whereas right-eyed chicks (Table 1, line 12) failed. When trained with geometric and featural cues but tested with featural cues only (in a square arena with panels), both left-eyed and right-eyed chicks succeeded (Table 1, lines 13 and 14). When trained and tested with geometric cues only, left-eyed chicks again succeeded (Table 1, line 15), whereas right-eyed chicks showed a trend for using geometry that just failed to reach statistical significance (Table 1, line 16). Finally, chicks were trained with both geometric and featural cues and tested with the cues in conflict (results not tabulated). Left-eyed chicks "went with" the local (target) featural cue 54% of the time, while "going with" geometric cues 41% of the time. Right-eyed chicks went with featural cues 85% of the time, showing no tendency to use geometric cues for relocation. These experiments show that the left hemisphere seems to process mainly featural information, whereas the right hemisphere processes both geometric and featural information. A study in which the technique of hippocampal lesions was used came to similar conclusions (Tommasi, Gagliardo, Andrew, & Vallortigara, 2003).

Tommasi and Polli (2004) recently tested the encoding of geometric cues in chicks. No featural cues were available to the chicks, who were trained in a rhombus-shaped arena. The rhombus had walls that were 35 and 70 cm in length and had corner angles of 60° and 120°. One group found the reward at a 60° corner, whereas another group found the reward at a 120° corner. The chicks were then tested with various transformations of the space. In the control test in an unmodified arena, both groups succeeded (60° group, 81% geometrically correct; 120° group, 77%). In one transformational test, corner angle information was removed by testing the chicks in a rectangular arena. The lengths of the long and short walls were preserved. Both groups chose the geometrically (approximately) correct locations (60° group, 78%; 120° group, 73%). In a second transformation, the corner angles were preserved, whereas the length differences of the walls were removed. The arena was still rhombus shaped, with the same corner angles, but all the walls were 52 cm long. In this transformation, the angle formed by the axes of space through the centers of opposing walls was also preserved. The results showed both groups using the corner angle cues or geometric relation according to the axes of space (60° group, 72%; 120° group, 71%). In the final transformation, the space was mirror reflected. Now the axes of space through the middle of opposing walls could not be matched to those of the training space. When only the long axis was used, however, the correct corner angle was now on the opposite side of the major axis. Interestingly, the results differed for the two groups. The 60° group went with the corner angle, searching most (82%) at a location that was on the wrong side of the major axis. The 120° group, however, abandoned the corner angle and went with an approximately geometrically correct location, at one of the corners with a 60° angle (72%). A control experiment with untrained chicks showed no preference for the 60° corner when all four corners offered rewards. The authors' interpretation was that the corner angle constituted a local geometric cue and that a 60° corner was more salient than a 120° corner. A salient local geometric cue is chosen over global geometric cues (e.g., according to the major principal axis), whereas a less salient local geometric cue is subordinated to the global geometric cues. The interpretation for these results remains open, but the transformational approach (Cheng & Spetch, 1998) promises to reveal more on the basis of geometric encoding. In this approach, animals are trained with one setup or arrangement and then are tested with various transformed arrangements, typically on unrewarded and occasional, infrequent tests. We will expand on this in the Discussion section.

Pigeons were also tested in reference memory paradigms (Kelly, Spetch, & Heth, 1998). Without any featural cues, the pigeons also solved the problem up to geometric ambiguity, choosing mostly either the correct corner or the rotational error (Table 1, line 17). With featural cues, in the form of either two-dimensional panels or three-dimensional objects in the corners, the birds were almost perfect (Table 1, line 18). Thus, the pigeons also could use both geometric and featural cues to relocate a target. In case of a conflict between geometric and featural cues, the results depended on the birds' prior experience. Those birds biased initially to use only geo-

metric cues showed mixed results, sometimes going with the geometric cues, sometimes with the featural cues. Those trained initially with featural cues, like the chicks, relied mostly on the featural cues. Even when the featural cue near the target was removed, the birds were still above chance at using the distant features (Table 1, line 19), although systematic rotational errors appeared. Kelly et al. also tested the birds with degraded featural cues, stripping away either the shape information or the color information. In each case (Table 1, lines 20 and 21), rotational errors appeared.

Both species of birds have also been tested with size transformations of the arena. In pigeons (Kelly & Spetch, 2001), when the arena was made slightly smaller, the trained birds relied on the shape of the arena, thus showing the use of relative distances or relative lengths of walls. Tommasi and colleagues (Tommasi & Vallortigara, 2000, 2001; Tommasi, Vallortigara, & Zanforlin, 1997) trained chicks to search in the middle of a square arena and then expanded the size of the arena. The chicks showed significant tendencies to search both at the center (thus preserving relative distances or going with the shape) and at the correct absolute distance from a wall. This pattern of results has recently been found in pigeons as well (Gray, Spetch, Kelly, & Nguyen, 2004).

Birds, especially pigeons, have also been tested with configurations defined by discrete landmarks. Although pigeons used global cues in a lab room to define a position (Spetch & Edwards, 1988), they also used nearby experimentally provided landmarks (Cheng, 1988, 1989; Spetch & Edwards, 1988). Pigeons learned to search in the center of a square array of four discrete landmarks, presented on a computer monitor (Spetch, Cheng, & MacDonald, 1996) or on the floor of an arena (Spetch et al., 1997). When the array was expanded, however, the birds no longer searched in the center but, typically, maintained the correct vector to a single landmark. Adult humans tested in the same situations continued to search at the center of expanded arrays (reviewed below).

The basis for the different responses of pigeons to arenas versus discrete landmarks remains to be fully investigated. One likely factor is that surfaces form a continuous surround, whereas discrete landmarks do not. This factor plays a role in the responses of children (reviewed below). Another factor that plays a role is the number of configurations used in training. Kamil and Jones (1997) trained Clark's nutcrackers to search in the middle of two landmarks. Across trials, the landmarks were set at a number of different distances. The nutcrackers solved the task and also generalized to new interlandmark distances. These results were replicated by Jones, Antoniadis, Shettleworth, and Kamil (2002), who, in addition, found that pigeons and jackdaws also could learn the task, although they performed less well. Nutcrackers (Kamil & Jones, 2000) and pigeons (Spetch, Rust, Kamil, & Jones, 2003) can also learn more complex geometric rules, such as maintaining constant bearings to two landmarks set at different interlandmark distances across trials or maintaining a constant distance to two landmarks.

Fish

Recently, one fish species (*Xenotoca eiseni*) was tested in a reference memory escape paradigm in a rectangular enclosure located within a bigger tank (Sovrano, Bisazza, & Vallortigara, 2002). Without featural cues, the fish solved the problem up to the point of geometric ambiguity, picking mostly either the correct corner or the rotational error (Table 1, line 22). When featural cues in the form of a colored wall were provided, the fish solved the geometric ambiguity as well, showing no systematic rotational errors (Table 1, line 23).

The authors replicated these experiments, finding similar results (Sovrano, Bisazza, & Vallortigara, 2003). In addition, they trained and tested fish with panels in the corners as featural cues. The fish learned to use panels as well (first choices on tests; Table 1, line 24). When the panels were removed, the fish continued to use the geometric cues (first choices on tests; Table 1, line 25). Thus, having featural cues present in training does not hinder or interfere with the learning of geometry, a theme we will review more fully in a later section. When the panel at the target and its diagonal opposite were removed, however, the fish failed to use the remaining, distant features to disambiguate geometry (data not tabulated). In another experiment, the authors put the target feature and the geometric cues in conflict by moving the target panel to a geometrically different corner. The fish showed conflicting response tendencies (data not tabulated), sometimes searching at a geometrically correct corner (but one with the wrong features), sometimes searching at the correct panel (but one at a geometrically wrong location). The result was that the sole corner that was both geometrically and featurally wrong was chosen the least.

Monkeys

Rhesus monkeys were recently tested in reference memory paradigms (Gouteux, Thinus-Blanc, & Vauclair, 2001). Many experiments were run, and the pattern of results depended mostly on the size of the featural cues provided in the corners or at the middle of a side of the arena (whose size remained constant throughout). We have thus summarized the results by dividing the experiments according to size of featural cues. With only geometric cues, the animals solved the task up to the point of geometric ambiguity (Table 1, line 26). With small featural cues, the monkeys used the geometric cues, but not the featural cues, in the relocation task (Table 1, line 27). With large featural cues, they chose the correct corner significantly more often than they made the rotational error (Table 1, line 28), but they continued to exhibit systematic rotational errors. Thus, with large enough featural cues, monkeys use both geometric and featural cues in the relocation task.

Human Adults

As would be expected, disoriented adults use the geometry of a rectangular room to divide their searches for objects between the geometrically correct and the incorrect

Table 2
Data on Humans

	Age	Study	Task and Cues	%C	%R	%O	Geom.	Feat.	Rot.
1	Adult	Hermer & Spelke, 1996	small space, geometric cues only	54.2	43.8	2.1	95.8	10.6	93.2
2	Adult	Hermer & Spelke, 1996	small space, geometric cues and blue wall (1.2 m)	95.8	4.2	0.0	100.0	91.7	—
3	Adult	Hermer-Vazquez, Spelke, & Katsnelson, 1999	geometric cues only	40.5	48.8	10.8	78.5	-9.2	72.9
4	Adult	Hermer-Vazquez et al., 1999	geometric cues and blue wall, no shadowing	86.9	5.2	7.8	84.3	88.6	10.2
5	Adult	Hermer-Vazquez et al., 1999	geometric cues and blue wall, rhythmic shadowing	73.5	11.0	15.5	69.0	74.0	12.3
6	Adult	Hermer-Vazquez et al., 1999	geometric cues and blue wall, verbal shadowing	39.9	35.1	25.0	50.0	6.3	37.6
7	Adult	Gouteux & Spelke, 2001	geometric cues from three objects	—	—	—	84.9	—	—
8	Adult	Gouteux & Spelke, 2001	geometric cues from four objects	54.0	42.9	3.2	93.7	11.5	86.2
9	Adult	Gouteux, Vauclair, & Thinus-Blanc, 2001	geometric cues only	43.0	52.0	5.0	90.0	-9.5	86.8
10	Adult	Gouteux, Vauclair, & Thinus-Blanc, 2001	tabletop, geometric cues and yellow wall	100.0	0.0	0.0	100.0	100.0	—
11	18–24 months	Hermer & Spelke, 1996	small space, geometric cues only	39.6	39.6	20.8	58.3	0.0	48.3
12	18–24 months	Hermer & Spelke, 1996	small space, geometric cues, and blue wall (1.2 m)	40.0	46.3	13.7	72.6	-7.3	65.8
13	18–24 months	Hermer & Spelke, 1996	small space, geometric cues, and objects	51.1	36.2	12.8	74.5	17.1	60.9
14	18–24 months	Hermer & Spelke, 1996	small space, oriented, featural cues only	81.3	18.8	—	—	62.5	—
15	18–24 months	Hermer & Spelke, 1996	small space, disoriented, featural cues only	62.5	37.5	—	—	25.0	—
16	18–24 months	Hermer & Spelke, 1996	small space, disoriented, object memory	75.0	25.0	—	—	50.0	—
17	18–24 months	Learmonth, Newcombe, & Huttenlocher, 2001	large space, geometric cues only	42.0	34.5	23.5	53.0	9.8	39.2
18	18–24 months	Learmonth et al., 2001	large space, geometric cues, and blue wall (2.4 m)	60.0	24.0	16.0	68.0	42.9	40.0
19	18–24 months	Learmonth et al., 2001	large space, geometric cues, and objects	61.4	21.7	16.9	66.2	47.9	34.3
20	20–24 months	Huttenlocher & Vasilyeva, 2003	reference memory, triangular space	—	—	—	55.0	—	—
21	20–24 months	Huttenlocher & Vasilyeva, 2003	working memory, triangular space	—	—	—	37.0	—	—
22	20–24 months	Huttenlocher & Vasilyeva, 2003	reference memory, outside of triangular space	—	—	—	34.0	—	—
23	20–24 months	Huttenlocher & Vasilyeva, 2003	reference memory, outside of rectangular space	—	—	—	38.0	—	—
24	18–25 months	Wang, Hermer, & Spelke, 1999	no geometric or featural cues (square space)	—	—	—	1.3	—	—
25	18–25 months	Wang et al., 1999	featural red wall cue (2 m) only (square space)	—	—	—	—	0.7	—
26	18–25 months	Wang et al., 1999	featural red wall cue (2 m) only, oriented	—	—	—	—	78.7	—
27	18–25 months	Wang et al., 1999	geometric cue only, bump in wall	—	—	—	44.0	—	—
28	18–24 months	Garrad-Cole, Lew, Bremner, & Whitaker, 2001	geometric cues from four objects	32.0	36.0	32.0	36.0	-5.9	29.4
29	18–24 months	Garrad-Cole et al., 2001	geometric and featural cues from four objects	49.0	19.0	32.0	36.0	44.1	5.9
30	3–4 years	Learmonth, Nadel, & Newcombe, 2002	small space, geometric cues only	39.5	40.7	19.8	60.5	-1.5	51.0
31	3–4 years	Learmonth et al., 2002	large space, geometric cues only	45.0	36.3	18.8	62.5	10.8	48.9
32	3–4 years	Learmonth et al., 2002	small space, geometric cues, and blue wall (1.2 m)	35.0	41.3	23.8	52.5	-8.2	45.2
33	3–4 years	Learmonth et al., 2002	large space, geometric cues, and blue wall (2.4 m)	56.3	23.8	20.0	60.0	40.6	31.4
34	3–4 years	Hermer-Vazquez, Moffet, & Munkholm, 2001	small space, blue wall, target at blue wall (1.2 m)	82.2	8.0	9.8	80.4	82.3	17.4
35	3–4 years	Hermer-Vazquez et al., 2001	small space, blue wall, target at corner (1.2 m)	41.7	33.4	24.9	50.3	11.0	36.0
36	3–4 years	Gouteux & Spelke, 2001	geometric cues from three objects	—	—	—	6.8	—	—
37	3–4 years	Gouteux & Spelke, 2001	geometric cues from four objects	30.9	24.2	44.9	10.2	12.3	2.5
38	3–4 years	Gouteux & Spelke, 2001	geometric and featural cues from three objects	—	—	—	—	73.6	—
39	3–4 years	Gouteux & Spelke, 2001	geometric cues from four surfaces	46.6	38.1	15.3	69.5	10.0	57.1
40	3 years	Gouteux, Vauclair, & Thinus-Blanc, 2001	tabletop, geometric cues only	23.0	30.0	47.0	6.0	-13.2	8.4
41	3 years	Gouteux, Vauclair, & Thinus-Blanc, 2001	tabletop, geometric cues, and yellow wall	18.0	34.0	48.0	4.0	-30.8	12.2
42	4 years	Gouteux, Vauclair, & Thinus-Blanc, 2001	tabletop, geometric cues only	32.0	40.0	28.0	44.0	-11.1	38.2
43	4 years	Gouteux, Vauclair, & Thinus-Blanc, 2001	tabletop, geometric cues, and yellow wall	42.0	13.0	45.0	10.0	52.7	-16.4
44	5 years	Gouteux, Vauclair, & Thinus-Blanc, 2001	tabletop, geometric cues only	35.0	40.0	25.0	50.0	-6.7	42.3
45	5 years	Gouteux, Vauclair, & Thinus-Blanc, 2001	tabletop, geometric cues, and yellow wall	63.0	7.0	30.0	40.0	80.0	-21.6
46	5–6 years	Hermer-Vazquez, Moffet, & Munkholm, 2001	small space, blue wall, target at blue wall (1.2 m)	92.0	6.5	1.6	96.9	86.9	71.0
47	5–6 years	Hermer-Vazquez et al., 2001	small space, blue wall, target at corner (1.2 m)	65.0	23.9	11.2	77.7	46.3	52.2
48	5–6 years	Hermer-Vazquez et al., 2001	no geometric or featural cues (square space)	—	—	—	5.5	—	—

Table 2 (Continued)

	Age	Study	Task and Cues	%C	%R	%O	Geom.	Feat.	Rot.
49	5–6 years	Hermer-Vazquez et al., 2001	featural red wall cue (2 m) only (square space)	–	–	–	–	**34.3**	–
50	5 years	Learmonth et al., 2002	small space, geometric cues, and blue wall (1.2 m)	35.0	37.5	27.5	**45.0**	–3.4	**36.5**
51	6 years	Learmonth et al., 2002	small space, geometric cues, and blue wall (1.2 m)	70.5	11.4	18.2	**63.6**	**72.2**	7.7
52	5 years	Learmonth et al., 2002	large space, geometric cues, and blue wall (2.4 m)	62.5	15.0	22.5	**55.0**	**61.3**	10.0
53	6 years	Learmonth et al., 2002	large space, geometric cues, and blue wall (2.4 m)	84.1	6.8	9.1	**81.8**	**85.0**	14.3

Note—%C indicates correct choices, %R indicates rotational errors, and %O indicates other choices, each in percentages. Geom., percentage correct above chance in distinguishing geometrically correct (correct corner and rotational error) and incorrect corners; Feat., percentage above chance in distinguishing the correct corner from the rotational error; Rot., the percentage of errors that are rotational errors, above chance levels. Negative numbers in the rightmost three columns indicate levels below chance. If the chance level, in proportion, is C and the observed proportion is D, the formula for subtracting chance is $(D − C)/(1 − C)$. Bold font indicates significantly above chance ($p < .05$); normal font indicates not significantly above chance; italics indicate that we were unable to determine whether the reported datum was above chance.

corners. They show this behavior both in a reference memory paradigm (Hermer & Spelke, 1994, 1996; Table 2, line 1) and in a working memory paradigm (Hermer-Vazquez, Spelke, & Katsnelson, 1999; Table 2, line 3). They also use the geometric configuration even when it is suggested only by the presence of three or four identical objects arranged in a triangular or rectangular shape, with no extended surfaces (walls) joining the "corners" (Gouteux & Spelke, 2001; Table 2, lines 7 and 8). In addition, they use the geometric cues provided by a tabletop arena, which they view from outside the arena (Gouteux, Vauclair, & Thinus-Blanc, 2001; Table 2, line 9).

Wang and Spelke (2000), however, found that after disorientation, adults remembered the configuration made up by individual objects less well than the configuration made up by continuous surfaces. In these experiments, the subjects, while oriented, first learned to point to a number of objects in the room, as well as to the corners of the room. In different experiments, the configuration (of corners and objects) might be regular (rectangular) or irregular. After learning, the subjects were disoriented and were asked to point to the corners and the objects again, without vision. A crucial measure was the configurational error. This dependent measure subtracts out the average signed error and measures how accurate the direction of pointing to each corner or object was, relative to one another. Basically, the "shape" made up by the directions pointed to was compared with the correct "shape." After disorientation, configurational errors increased for pointing to objects, but not for pointing to corners. In this way, then, the shape of the room seems more durable than the shape made up by individual objects. Wang and Spelke (2000, 2002, 2003) suggested that a human's spatial relations to individual objects are coded independently, on an egocentric basis. This independent, egocentric coding means that as the person becomes more disoriented, the error with respect to each object increases in an independent fashion. This causes an increase in configurational error. In contrast, a representation, or *map*, containing all the objects together should not increase in configurational error with disorientation.

With the addition of featural information (a colored wall) in the standard rectangular arena with continuous surfaces, adults are successful in focusing on the correct corner, again both in a reference memory paradigm (Hermer & Spelke, 1994, 1996; Table 2, line 2) and in a working memory paradigm in a room (Hermer-Vazquez et al., 1999; Table 2, line 4) or on a table (Gouteux, Vauclair, & Thinus-Blanc, 2001; Table 2, line 10). However, the addition of a verbal shadowing task reduces their performance, so that they seem unable to use the blue wall to differentiate the corners. It also reduces the ability to encode and use geometric information (Hermer-Vazquez et al., 1999; Table 2, line 6). Hermer-Vazquez et al. (1999) argued that this reduction in the ability to combine featural and geometric information occurs because human adults rely on language to conjoin these cues. Their comparison case was a nonverbal, rhythmic shadowing task,

which did not eliminate the ability to combine featural and geometric information (Table 2, line 5). However, the case for the linguistic thesis is weakened by the fact that although both shadowing tasks reduced the ability to use geometric information, the verbal shadowing task led to a greater reduction. Thus, the relocation task is harder with verbal shadowing as a dual task. The linguistic thesis is also at odds with findings, already reviewed, that nonlinguistic animals can conjoin these sources of information in some cases. An alternative interpretation of this data set is that the verbal shadowing task interfered with an information integration process (as shown in the theoretical models in Figure 5B and 5C) that could also possibly be affected by a nonverbal, but spatial, shadowing task. The rhythmic shadowing task may engage different neural structures than those required for spatial functioning, or may simply not be as hard as verbal shadowing.

Adults have also been tested recently on the geometry task presented on a vertically oriented computer monitor (Kelly & Spetch, 2004). A rectangular *arena* was marked by gray shading on the monitor. In addition, different colored shapes served as landmarks in the corners. The numerous results (not tabulated) showed that the subjects learned to use both features and geometry. In this case, the geometry was harder to learn, and some subjects never reached criterion. Even features "distant" from the target were used to disambiguate the geometry. The most interesting results concern geometric transformations in the geometry-only (no-features) conditions. Subjects were trained with six of eight orientations of the stimulus array placed at the center of the monitor. The subjects performed well when the array was translated to a new location but retained a familiar (training) orientation. With an unfamiliar orientation, however, performance fell to chance levels. One interpretation of this pattern of results is that the geometric cues used were orientation specific. The vertical orientation of the space meant that gravity defined a salient and privileged axis; on a horizontal plane indoors, on the other hand, one compass direction is just like another. This interpretation suggests that in the geometry-only conditions, the subjects learned a number of different configurations at different orientations, which made it harder to learn to use geometric cues. A new orientation would present a new problem to the subjects, and little transfer should take place, which is what the results indicated. Of course, the differences in performance on monitors and in rooms need further investigation.

As with birds, human adults have been tested with geometric transformations of spatial cues. Spetch et al. (1996; Spetch et al., 1997) presented subjects with arrays of landmarks made up of individual objects, on a computer monitor, on a table, or on the ground. The target was at the center. The pattern of responding to expansions of the array was similar in all cases: The subjects continue to search mostly at the middle. Hartley, Trinkler, and Burgess (2004) presented arenas of continuous rectilinear surfaces, using virtual reality in the form of a video game on a monitor. The subjects were to note the location of a target in the arena. The arena was surrounded at a virtual distance by far landmarks (e.g., cliffs). The shapes of the arenas were then transformed (while the subjects were virtually away from the arena), and the subjects were returned to the arena and were asked to indicate the location of an object that they had seen earlier. In this paradigm, the subjects used both the fixed absolute distances of targets from walls and the fixed ratio of distances. On the whole, the responses reflected a weighted average of these two kinds of dictates, with weighting depending on distance from the walls and, hence, on the relative uncertainty of the two types of information. Angles to the corners of the arena probably played a role as well. As will be reviewed below, certain hippocampal place cells in rats "behave" in a similar manner (O'Keefe & Burgess, 1996). In addition, when rectangles were rotated 90° (or equivalently, squashed in their long dimension and stretched in their short dimension), some subjects searched at locations defined by the geometry of the rectangle, whereas others relied on cues external to the arena (such as cliffs) for orientation. Thus, there were individual differences in the use of geometric versus featural cues to establish orientation in this ambiguous task.

Children

Like human adults and nonhuman animals, very young children (from 18 to 24 months of age) use the geometry of an unmarked rectangular room to concentrate their searches for a hidden object in the correct corner and the diagonally opposite corner (Hermer & Spelke, 1994, 1996; Learmonth, Newcombe, & Huttenlocher, 2001; Table 2, lines 11 and 17). This fact adds to the evidence that children have an early ability to code distance (Huttenlocher, Newcombe, & Sandberg, 1994), a point that had, historically, been controversial in the field of cognitive development. Recently, Huttenlocher and Vasilyeva (2003; Table 2, lines 20–23) have added to our knowledge of the processing of geometric information in young children in three ways. First, they have shown that geometric information is used when children of 20–24 months are outside, as well as inside, enclosed spaces. This finding suggests, contrary to Wang and Spelke's (2002) hypothesis, that geometric sensitivity is not specifically a sensitivity to surrounding surfaces. Second, they showed that children, like rats, can use the geometry of isosceles triangles, as well as that of rectangles, extending the generality of the findings. Third, their data on children's search behavior indicated that children represent the entire set of internal geometric relations of the enclosed spaces, not just the appearance of particular corners.

There have, however, been inconsistent findings with regard to whether very young children can use landmarks to distinguish the correct corner from the diagonally opposite corner (rotational error) in a rectangular room. Several experiments have shown that children do not use a colored wall to concentrate searches on the correct corner, nor do they use discrete landmarks, such as a toy bear (Hermer & Spelke, 1994, 1996; Table 2, lines 12, 13, and 15). Oriented children distinguished between the correct corner and the rotational error (Table 2, line 14),

and children remembered features in a recognition memory test (Table 2, line 16), findings that suggest that the lack of a use of features is specific to coping with disorientation. However, other experiments have shown children succeeding in tasks very similar to those in Hermer and Spelke, both with discrete landmarks and with a colored wall (Learmonth et al., 2001; Table 2, lines 18 and 19). Success with the presence of discrete landmarks is less interesting, because it could be considered as based on their providing geometric information. Indeed, Wang, Hermer, and Spelke (1999) found that 18- to 24-month-olds could use a projecting bump in a square room to find a hidden object after disorientation (Table 2, line 27), even though they could not use a colored wall to succeed (Table 2, line 25). Again, oriented children succeeded (Table 2, line 26), and not surprisingly, disoriented children provided with no cues failed (Table 2, line 24). However, Wang et al.'s findings do not explain reports of early success with a flat colored wall, shown in Learmonth et al. (2001).

The conflicting results on toddlers' use of a colored wall are crucial for the hypothesis of an impenetrable geometric module. An important factor leading to contrasting results seems to be the size of the rectangular room and, possibly, the correlated scaling of the size of the featural information. Hermer and Spelke (1994, 1996) used a very small room, 1.2×1.8 m, whereas Learmonth et al. (2001) used a larger room of 2.4×3.6 m. Children 3, 4, and 5 years of age do not use a colored wall to disambiguate geometrically identical corners in a small room, although children 6 years of age do (Learmonth, Nadel, & Newcombe, 2002; Table 2, lines 32, 50, and 51). Hermer-Vazquez et al. (2001) found a similar developmental pattern when testing children in a small room (Table 2, lines 35, 47, and 49). In contrast, Learmonth et al. (2002) found that children at all the ages tested could use the colored wall to succeed in a larger room (Table 2, lines 33, 52, and 53). Hermer-Vazquez et al. (2001) found that children of all ages could relocate a target at a feature (middle of a blue wall) in a small room (Table 2, lines 34 and 46), and not surprisingly, disoriented children given neither geometric nor featural cues failed (Table 2, line 48). In both of these studies, children used geometric information to relocate a target when it was available (Table 2, lines 30–35, 46, 47, and 50–53).

Gouteux, Vauclair, and Thinus-Blanc (2001) tested children 3 to 5 years of age with a tabletop rectangular arena, in a working memory task. Unlike Huttenlocher and Vasilyeva's (2003) study of toddlers located outside a geometric space, the children were not disoriented before the relocation task; rather, the array was rotated by 90°. This manipulation might have been important in producing their pattern of results. When the children tested with only geometric cues, Gouteux, Vauclair, and Thinus-Blanc found that 3-year-olds failed (Table 2, line 40), although 4- and 5-year-olds succeeded (Table 2, lines 42 and 44). When a differently colored (yellow) wall was added as a featural cue, 3-year-olds still failed (Table 2, line 41). The older children showed evidence of using

the featural information (Table 2, lines 43 and 45) but made systematic reflection errors. Thus, if the target was at a corner with the yellow wall extending to its right, they might sometimes choose the corner with the yellow wall extending to the left, a geometrically wrong corner. Such a reflection error has not been found in any other study. We suspect that the manipulation of rotating the tabletop arena (and not the children) caused this pattern of results, but only more research can sort this issue out.

Another possible contrast between the performance of human children and that of adults concerns the ability to take advantage of a geometry that is only suggested by the presence of separated landmarks marking the vertices of a geometric figure. Whereas adults use geometric information in this situation, children of 3 and 4 years of age apparently do not (Gouteux & Spelke, 2001; Table 2, lines 36 and 37). They need at least a set of partial extended surfaces, although not necessarily a closed figure, to use geometric information (Table 2, line 39). They can also use the features of objects (Table 2, line 38). Garrad-Cole, Lew, Bremner, and Whitaker (2001), however, found results very different from those in Gouteux and Spelke. In their work, even younger children (18–24 months) succeeded in using the geometry of four separated objects to define search (Table 2, line 28). In addition, Garrad-Cole et al. found that featural information, when available, was used as well by these very young children (Table 2, line 29), even though the rectangle defined by the four separated objects was a small one, of the same size as that used by Hermer and Spelke (1996).

There are several points of contrast between the two articles on separated objects. One difference is the use of a reference memory task (Garrad-Cole et al., 2001) versus a working memory task (Gouteux & Spelke, 2001). A second difference is that parents conducted experimental procedures with children in Garrad-Cole et al.'s study, and they were asked to judge whether or not the children "peeked" during the disorientation procedure. Although many of the Hermer-Spelke studies also used parents as experimenters, such a practice is potentially of concern in cases in which data show unexpected success, because parents generally try to help their kids "look smart." Only further research can resolve this discrepancy.

In order to better visualize developmental trends, we have plotted a number of studies conducted in rectangular rooms (Figure 2). The graphs summarize some of the information shown in the three rightmost columns of Table 2. As in the table, chance levels have been subtracted out. Inferential statistics across diverse studies are clearly inappropriate, but visual inspection shows some notable trends. Although the use of geometric cues fluctuates across studies, the use of featural cues increases with age, with both small and large spaces (Figure 2A). As has already been noted, even toddlers use features at above-chance levels in the large space. Rotational errors decrease with age (Figure 2B), in both large and small spaces. Adults performing the relocation task while verbally shadowing (in a small space) resemble 5-year-olds performing in a small space.
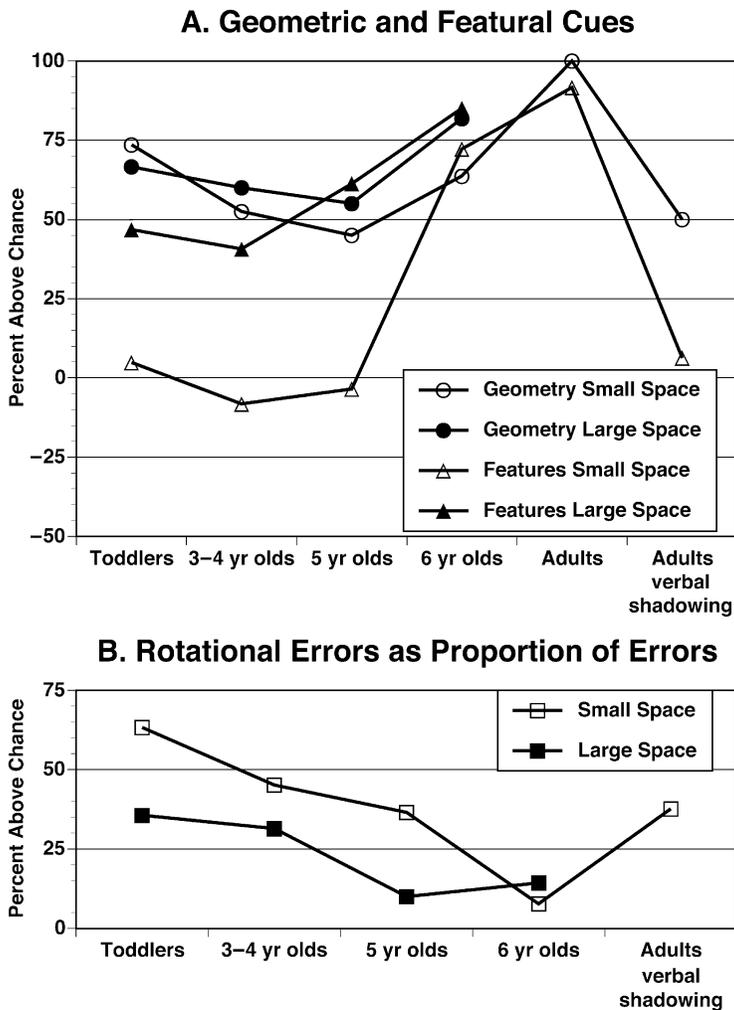
A. Geometric and Featural Cues

B. Rotational Errors as Proportion of Errors

Figure 2. Summary data from various studies on humans. (A) Percentage above chance on the use of geometric and featural cues in small (1.2 × 1.8 m) and large (2.4 × 3.6 m) rectangular arenas. (B) Percentage of rotational errors as a proportion of all errors, with chance level (one third) subtracted out. Toddlers' data are from Hermer and Spelke (1996; small space) and Learmonth, Newcombe, and Huttenlocher (2001; large space); 3- to 6-year-olds' data are from Learmonth, Nadel, and Newcombe (2002); adults' (no-shadowing) data are from Hermer and Spelke (1996); adults' verbal-shadowing data are from Hermer-Vazquez, Spelke, and Katsnelson (1999). Where applicable, data have been averaged across multiple relevant conditions in each study, weighted by number of subjects in each condition.

Sex Differences?

There is evidence that males and females differ on spatial navigation tasks, both in a general way (Isgor & Sengelaub, 1998; Moffat, Hampson, & Hatzipantelis, 1998) and in a fashion that may specifically affect issues relating to the geometric module (Sandstrom, Kaufman, & Huettel, 1998; Williams, Barnett, & Meck, 1990). Williams et al. worked with rats and showed that alteration of the geometry of the testing room affected spatial memory in normal males, as well as in females who had been treated neonatally with estradiol benzoate. However, such geometric changes did not affect normal females or neonatally castrated males. Sandstrom et al.

worked with humans in a computer-generated virtual environment, finding that females relied primarily on landmark information, whereas males used both landmarks and geometric information to guide spatial search. On the basis of these findings, Jacobs and Schenk (2003) have suggested that the general reliance in some studies in the literature on studying male animals may bias results. Specifically, they argued that the findings of Benhamou and Poucet (1998), showing primacy of relocation when the geometry of landmarks, rather than their identity, was used may be limited by their exclusive use of male rats. We note that male rats were also used in Cheng (1986) and Margules and Gallistel (1988). This

issue clearly needs further study. In studies on human children large enough to compare boys and girls on the relocation task, no sex differences in the use of geometry or landmarks have been found (Learmonth, personal communication, October 2002), although that work did not entail pitting one type of cue against another.

Geometric Information Withstands Cue Competition

Cue competition is often found in associative learning, including the spatial domain (for reviews, see Cheng & Spetch, 1998, and Shettleworth, 1998). In overshadowing, for example, the subject is presented with two cues, both of which predict a target, whether temporally, as in classical conditioning, or spatially, as in landmark learning. The subject may learn one or both of the predictor cues less well because it has been presented in the presence of the other predictor cue. Learning would have been better had either cue been presented alone. In blocking, a cue that is learned first adversely affects the learning of cues that are presented subsequently, together with the already learned cue.

Overshadowing has been amply demonstrated in the spatial domain, with landmarks or beacons (landmarks right at the target location) overshadowing other landmarks. For example, Spetch (1995) found that a landmark on a computer monitor near the target overshadowed a landmark that was farther from the target, in both pigeons and adult humans. Overshadowing has been found in rats as well (e.g., Diez-Chamizo, Sterio, & Mackintosh, 1985). Blocking in learning to use landmarks has also been found in rats (Biegler & Morris, 1999; Roberts & Pearce, 1999; Rodrigo, Chamizo, McLaren, & Mackintosh, 1997).

In the case of relocating the target with respect to the geometry of surfaces, however, overshadowing by beacons has so far not been found. Kelly et al. (1998) had one group of birds first learning a target corner location with both featural and geometric cues present. One of the corner featural cues was a beacon. When the birds were later tested without featural cues, they still showed excellent use of geometric information. As has already been mentioned, a similar test was done on fish (Table 1, line 25; Sovrano et al., 2003), and the fish, too, used geometry after the removal of features usually present during training. Tommasi and Vallortigara (2000) trained chicks to search in the center of a square arena. In one experiment, a beacon was provided. When the chicks were later tested in the absence of the beacon, they still searched predominantly at the center. In a series of well-controlled experiments on rats tested in a swimming pool, Pearce, Ward-Robinson, Good, Fussell, and Aydin (2001) placed a target platform in a geometrically unambiguous pool. Some rats were trained with a beacon at the target. When the rats were later tested without the beacon, they searched equally well for the target on the whole, whether they had experienced a beacon at the target or not. This pattern of results has been replicated, in the same lab, with various shapes of swimming pools (Hayward, McGregor, Good, & Pearce, 2003). Indepen-

dence of learning featural and geometric information has also been demonstrated for rats searching for food in rectilinear arenas (Wall, Botly, Black, & Shettleworth, 2004). Thus, in one experiment, a blocking group first learned to use a black panel in a corner to find food in a square arena. The control group had only one container (which contained food), but no panel in any corner. Thus, these animals did not have to learn geometry or features but could simply run to the food. The groups were then transferred to a rectangular arena, with the panel and the food at the corner with the panel. Both groups learned to use the geometry of the rectangle readily, and to a similar extent. The obligatory nature of using geometric information is shown by the performance of the blocking group. Despite having learned to use the black panel in the first, blocking phase, the animals started making rotational errors when transferred to the rectangular arena. They made rotational errors to a slightly greater extent than the control group, despite the fact that the feature, which they had already learned to use, was a better predictor of reward location than the geometry was.

If this pattern proves consistent in further studies, then, as Pearce et al. (2001) point out, "it will suggest strongly that the *principles* that govern spatial learning based on the shape of a test environment are different to those that apply to learning based on individual landmarks" (p. 343, our emphasis). The finding that the geometry of the test environment is not subject to cue competition constitutes an interesting difference in principles of learning depending on the type of cue. However, the difference does not further imply that environmental geometry and individual landmarks are learned by different modules. In classical conditioning, evidence shows that biologically salient stimuli are not subject to cue competition, whereas less salient stimuli are (Denniston, Miller, & Matute, 1996; Miller & Matute, 1996). Thus, we would not want to use this pattern of data to argue that more and less salient conditioned stimuli are learned by different modules. We will return to a consideration of the modularity of spatial learning in the Discussion section.

Is There Neurological Evidence for Specialization for Geometric Processing?

The hippocampal area has long been known to play a role in spatial cognition in rats, with evidence of *place cells* that respond selectively when animals are in specific areas of an environment, independently of their orientation (O'Keefe & Burgess, 1996; O'Keefe, Burgess, Donnett, Jeffery, & Maguire, 1999; O'Keefe & Nadel, 1978; for a review, see Jeffery, 2003). Some of these cells may be sensitive to place information on the basis of the processing of geometric cues. Single-cell recording from the hippocampus of freely moving rats, placed in a square arena without featural cues, showed that some cells exhibit sensitivity (by way of increased firing rate) to particular locations (O'Keefe & Burgess, 1996). When transformations involving stretches along one dimension or increases in size (stretches along both dimensions)

were performed, hippocampal cells showed sensitivities to both absolute distances from walls and relative distances from walls, with differences across individual cells. In recent work from the same lab (Lever et al., 2002), the time course of hippocampal cells "learning" to differentiate between environments of different shapes was examined. Untrained rats were placed in two unfamiliar environments, a circular and a square arena of the same diameter with 50-cm-high walls. The two environments coincided at the center. The rats were oriented in direction. They were placed in the arena from the same direction, and one stripe on a curtain provided an extra-arena directional cue. On Day 1, the cells in general reacted the most to a similar location in both environments. Thus, if the circle were *reshaped* into a square, the cells would be firing the most at about the same place in both environments. In reshaping, a point in the circle was mapped to a corresponding point in the square that was (1) in the same direction from the center of space and (2) the same proportion of distance between the center and the perimeter. Over days of (unreinforced) exposure to the two environments, the responses to the two environments were subject to differentiation. In some cases, the response to one of the environments dropped in rate. In other cases, the places of peak responding drifted apart in the two environments. Interestingly, the responses seemed to be tuned particularly to geometry. Most cells generalized across a transformation of the material that composed the walls of the arena. Removing the walls that composed the arena, however, led to significantly different responses from the cells. Thus, it is possible that there are place cells in the rat hippocampus that are specifically attuned to geometry.

Nevertheless, hippocampal cells are sensitive to far more than the geometry of surfaces (e.g., Jeffery & Anderson, 2003; for a review, see Jeffery, 2003). Thus, a purely featural change, such as a change in the color of walls, can drastically affect the firing pattern of hippocampal cells. One model, however, posits the existence of cells, called *boundary* cells, that are sensitive to metric properties (Anderson, Hayman, Chakraborty, & Jeffery, 2003; Jeffery & Anderson, 2003). These are not place cells but are, purportedly, upstream from place cells. The operation of boundary cells is thought to determine when and at which place cells fire. In Anderson et al.'s (2003) words, "these cells are partly driven by sensory information about the distance of the animal from the walls of the environment" (p. 284). The qualifier "partly" is used because the operation of boundary cells is, in turn, modulated by contextual cues. Although boundary cells might form a geometric module, it must be noted that their existence is still entirely theoretical. None has been identified to date.

There has been debate with respect to the role of the hippocampus in spatial cognition in humans. Recently, Epstein and Kanwisher (1998; Epstein, DeYoe, Press, Rosen, & Kanwisher, 2001; Epstein, Graham, & Downing, 2003; Epstein, Harris, Stanley, & Kanwisher, 1999) proposed that the geometric layout of the environment is constructed in an area of the human brain they call the *parahippocampal place area* (PPA), which comprises the posterior tip of the parahippocampal gyrus and adjacent regions of the fusiform gyrus. They based their conclusions in part on brain-imaging results. Perception of scenes led to differential activation in the PPA, relative to perception of faces, objects, or houses (Epstein & Kanwisher, 1998), even though the subjects were not required to perform any tasks. The PPA also responded to empty rooms and to outdoor landscapes more strongly than to faces, objects, or strikingly, to randomly arranged objects that had been removed from the indoor scenes. Coherent geometric structure seemed vital to PPA activation, because fractured and rearranged versions of the bare rooms did not elicit a response. In subsequent work, Epstein et al. (1999) found that activity in the PPA is not further increased when people feel as if they are moving in the scene, suggesting that it is more involved in geometric analysis than in planning routes or monitoring locomotion. Epstein et al. (2003) also found that geometric representations in the PPA appear to be viewpoint specific. Epstein et al. (2001) studied two patients with damage to the PPA and found various deficits, including problems in remembering scenelike stimuli made of Lego blocks. Memory for objects, on the other hand, even objects built using the same Lego blocks as those used in the scenes, was not impaired. This body of work strongly suggests that, in humans, the PPA plays a role in encoding geometric information about the environment into memory.

Other studies support the general idea that the human parahippocampal gyri are involved in spatial tasks, although few have focused specifically on the geometric encoding hypothesis or on the PPA. For example, the parahippocampus shows activation in a variety of work on navigation (Aguirre, Detre, Alsop, & D'Esposito, 1996; Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000; Maguire, Frackowiak, & Frith, 1997; Pine et al., 2002), as well as in other spatial paradigms that may involve the processing of geometry (e.g., Johnsrude, Owen, Crane, Milner, & Evans, 1999). In addition, patients with lesions to the parahippocampal areas show deficits in route learning (Barrash, Damasio, Adolphs, & Tranel, 2000; Habib & Sirigu, 1987; Luzzi, Pucci, Di Bella, & Piccirilli, 2000).

Aguirre and D'Esposito (1999) have emphasized the role of the parahippocampus in spatial orientation and have suggested that the hippocampus proper may play less of a part in human spatial learning than it does in rats. Supporting this perspective, Bohbot et al. (1998) found that only damage to the right parahippocampus, but not damage to the hippocampus proper, led to deficits on an analogue of the Morris swimming pool test. However, many other studies have shown that the human hippocampus is also involved in spatial orientation tasks, using both imaging techniques (e.g., Grön et al., 2000; Hartley, Maguire, Spiers, & Burgess, 2003) and people suffering from damage to the hippocampus (Barrash et al., 2000; King, Burgess, Hartley, Vargha-Khadem, &

O'Keefe, 2002; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001; Spiers, Burgess, Maguire, et al., 2001; see the review by Kessels, de Haan, Kappelle, & Postma, 2001).

Broadly speaking, the work reviewed so far does not contradict Epstein and associates' hypothesis that the human PPA codes geometric information, although the hypothesis has not been tested directly. However, some investigators have found data that conflict with those in Epstein and Kanwisher (1998) and have advanced different interpretations regarding the role of the human parahippocampal cortex. Maguire, Burgess, et al. (1998) and Maguire, Frith, et al. (1998; see also Maguire, Burgess, & O'Keefe, 1999; O'Keefe et al., 1999) have reported imaging work on humans given tasks in virtual reality. Using positron emission tomography (PET), they found that a network of areas in the occipital, parietal, and occipitotemporal regions were active in humans navigating either through virtual space filled with objects or through empty virtual space. The right parahippocampal area, however, was active only on the task in the object-filled space, but not when the space was empty and featureless (Maguire, Frith, et al., 1998), a finding that appears to be at direct odds with the findings of Epstein and Kanwisher. Summarizing a number of imaging studies using different scanning techniques, Maguire et al. (1999) concluded that the parahippocampal area is especially involved in locating objects in allocentric space.

The Maguire et al. hypothesis is consistent with findings in studies in which patterns of brain activation when people learned or visualized spaces from either a route or a survey perspective have been examined (Mellet et al., 2000; Shelton & Gabrieli, 2002). Both Mellet et al. and Shelton and Gabrieli found that the parahippocampus was activated only with routes, but not when people were dealing with survey maps. Because survey maps incorporate geometric information, a lack of activation in survey tasks seems inconsistent with the idea that the PPA is focused on geometric information. By contrast, dealing with routes involves relating objects to each other in a spatial framework, as emphasized by Maguire et al. (1999).

Even more strikingly, the Maguire et al. hypothesis is consistent with data obtained by Ekstrom et al. (2003), who conducted the first single-cell investigation of human spatial functioning. Seven patients with pharmacologically intractable epilepsy, who were being observed with intracranial electrodes, were asked to participate in a virtual reality navigation game. They participated as taxi drivers who 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, independently 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 and view cells in the parahippocampus. Commenting on Ekstrom et al.'s re-search, Burgess and O'Keefe (2003) suggested that the human parahippocampus is better termed a *spatial scene area* than a *place area*.

In summary, there is only sparse evidence for the modularity of geometric processing on the basis of neurological evidence. In rats, there may be hippocampal place cells tuned to geometric information, but these appear to be interspersed with place cells tuned to information dependent on features. Anderson et al. (2003; Jeffery & Anderson, 2003) hypothesize the existence of boundary cells tuned to metric information (distances from walls) but admit that such cells have not been found to date. In humans, although the parahippocampal area seems likely to play a role in the processing of topographical information, very likely including geometric information, the area probably plays other roles in spatial cognition as well. In fact, it may be specialized for recognition of specific views on the basis of either featural or geometric information. Thus, it does not seem to constitute a unique neuropsychological substrate for a geometric module.

DISCUSSION

In this section, we will focus primarily on the issue of modularity of mind in light of the extant behavioral data on the relocation task. We would also like to suggest some issues, in addition to modularity, that are worthy of further research. These issues include what aspects of geometric properties are represented and used for relocation, the role of experience, and the comparison of species. We will begin with a summary of the data.

Key Behavioral Data

Only vertebrate species have been tested on the relocation task inside an arena or a group of landmarks in an indoor setting. The species have included fish, birds, rats, monkeys, and humans of various ages, ranging from 18-month-olds to adults. When continuous surfaces form the geometric properties, all the species tested use geometric properties in relocation. With a group of objects whose configuration defines the geometric properties, 3- to 4-year-old children failed to use geometry (Gouteux & Spelke, 2001), but oddly, 1.5- to 2-year-old children succeeded (Garrad-Cole et al., 2001), as did adults (Gouteux & Spelke, 2001) and rats (Benhamou & Poucet, 1998). All the species tested, of all ages, also used featural properties under some circumstances. This is shown by the data in which correct corners were chosen significantly more often than rotational errors. For human children, the size of the space in which they were tested was a key determinant of whether they used the featural properties (Learmonth et al., 2002; Learmonth et al., 2001). We noted that the featural cues also get bigger in a bigger space. For monkeys, the size of the features was a key determinant of the use of featural properties (Gouteux, Thinus-Blanc, & Vauclair, 2001). Rats used featural properties in a reference memory paradigm, with the reward being given by the same panel trial after trial (Cheng, 1986, Experiment 2). Birds and fish have not

been reported to make systematic rotational errors, at least when featural properties were not degraded in any way on a test. All the mammals, however, made systematic rotational errors under some circumstances. Even human adults made systematic rotational errors while performing a verbal shadowing task (Hermer-Vazquez et al., 1999). Cue competition has been examined in fish, rats, and pigeons. The evidence is that having features, even a beacon at the target location, does not interfere with, overshadow, or block the learning of geometry.

How Is Geometric Information Used?

Gallistel (1990) has provided the only extant theory to date that addresses how geometry is encoded and used. As we read it, the theory concerns how geometry is used to establish which direction is which. It is not concerned with the exact localization of a target. The subject in the typical relocation task has to do both: first reorient herself or himself in the arena, and then head to a particular location to dig, peck, or search. Gallistel (1990) claimed that a particular *organ* (module) of the brain has the job of matching the remembered shape of an environment to the currently perceived environment. This modular matching process excludes featural information, taking "no account of the smells emanating from surfaces, their reflectance or luminance characteristics, their texture, and so on" (Gallistel, 1990, p. 208). In fact, the geometric characteristics used for matching are further simplified: Matching is done by aligning the principal axes of space encoded in memory with the perceived principal axes of space. This is a form of global matching, in which a small number of parameters are extracted for matching. The theory implies that details about the geometric shape of space are not part of the package of geometric information for establishing which direction is which, although they may be encoded as features. Global matching of this kind reduces both what has to be stored in memory and the computations involved in matching. The computational processes involved in finding principal axes are direct calculations, not iterative trial-and-error processes. They do not "explode" (become intract-ably large).

There is little information addressing this issue of what aspects of geometry are matched. The only relevant data are some pilot data on rats (Cheng, 1984, unpublished data). In these experiments, the rectangular arena contained two corner panels at one short wall. The fine-scale geometry is thus rotationally slightly asymmetric, although the principal axes still carve up the space similarly. Consistent with Gallistel's global-matching strategy, the rats still made rotational errors. But clearly, more research is needed to investigate which aspects of geometric information are encoded, as well as how geometry is used. The experimental paradigms will have to rely on geometric transformations of space, to see how animals transfer across different shapes of space. The paradigms should also disentangle two possible uses of geometric information: (1) to tell broadly which direction is which, and (2) to pinpoint a target location exactly. We will suggest paradigms below that unconfound these two uses.

Central Modularity?

In various ways, modularity has been claimed with regard to the relocation task (e.g., Cheng, 1986; Wang & Spelke, 2002, 2003). The systematic rotational errors made under a range of conditions by mammals fuel these views. The modularity concerns not (just) peripheral input systems, but the central organization of information. We have organized various views of central modularity for explaining the behavioral data in mammals in Figure 3. To be explained are the following data: (1) Geometric information is used in all or almost all circumstances when it is instantiated by enclosed and connected surfaces (but only variably when organisms must construct geometry from separated objects). (2) Featural information is used under some circumstances. (3) Featural information sometimes fails to be used (a deduction from systematic rotational errors).

In Figure 3, we have depicted input systems as modular in nature in each of the three panels. Input systems include perception and learning. It is not controversial that the visual system is modular in nature (Marr, 1982). In fact, the modularity is far more extensive than the two boxes that are depicted. The input boxes are meant to depict this peripheral modularity.

Beyond that, things become uncertain. The learning process extracts relevant information from visual (or other) input to be laid down in memory for future use. To Gallistel (2000, 2003b), learning is modularized to a great extent. A main basis for this view is that the rules for extracting useful information depend on the domain of learning. For example, useful rules for extracting regularities in temporal relations between events (as in classical conditioning) differ from those for extracting spatial relations (as in matching principal axes of space). In Gallistel's (1990, 2000, 2003a, 2003b; Gallistel & Gibbon, 2000, 2002) work, these intuitions are backed by theories that are clearly tailored to different domains of learning.

Whether there is modularity in learning geometric and featural cues is unclear. Feature learning might take place via a different module, a position espoused by Wang and Spelke (2002, 2003), which we will discuss below. Or it may be that features and geometry take the same route in learning and end up in the same module but some animals sometimes learn geometry more easily than features. Evidence for a unified system of learning comes from the fact that all the animals tested used features in the relocation task under some circumstances. Another intuitive argument for a unified system of learning is that some overlapping information needs to be learned about geometric and featural cues. Geometric relations and directions figure in both cases. For instance, in exact localization, vectors from various cues, geometric and featural, are likely to play a role (Cheng, 1988, 1989, 1994).

What about central modularity? We have depicted the central system relevant to the relocation task as a box labeled "memory" in Figure 3. This question is of interest because an influential view of the mind argues for modularity at the input end but for an encompassing web (no modularity) in the center (Fodor, 1983, 2001). A metaphor

A. Impenetrable module
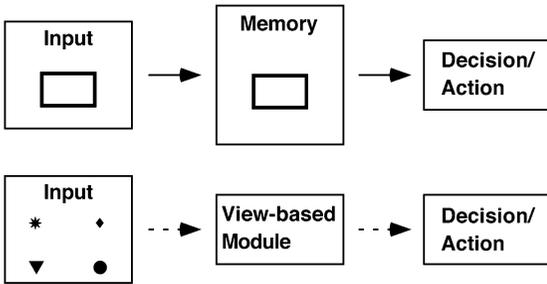
B. Modular memorial subsystems
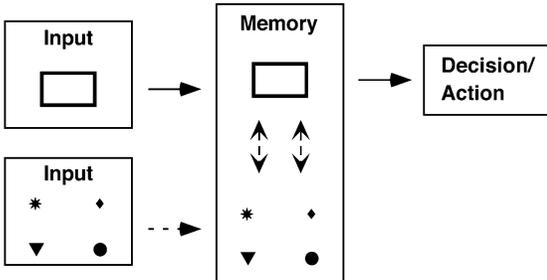
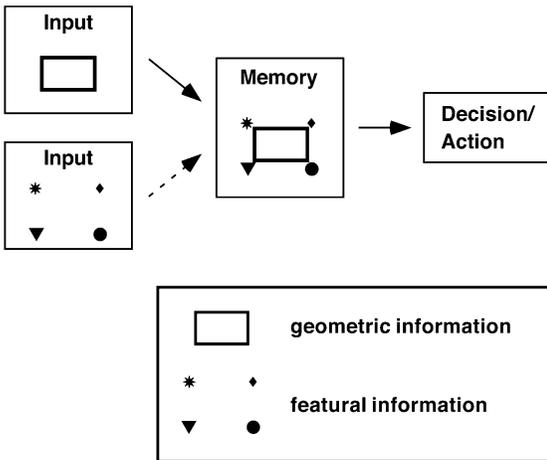## C. Modular input systems only

Figure 3. Views of modularity in reorientation. The input systems consist of perceptual and learning processes. Some modularity in processing geometric and featural information is assumed. (A) In the impenetrable module, featural information does not enter into the memorial system used for reorientation. If featural information is used at all, it goes through other central modules, one of which does view-based matching. (B) In a system with modular components, a metric frame (box inside the memory box) contains only geometric information. Featural information may be pasted onto the frame in addition (represented by arrows inside the memory box). (C) An integrated system in which featural and geometric information are put together for reorientation. In both panels B and C, featural information may fail to be input into memory. This failure can cause systematic rotational errors. See the text for further details.

for this view of the center is a *web of belief* (Quine & Ullian, 1970). Like a spider web, every strand represented in the center is connected with every other strand, if sometimes distantly. Potentially anything on the web (all

information) may be brought to bear on any course of action. A modular central reorientation system would provide a counterexample to this claim. On this question, various views have been expressed: a completely modular system (Figure 3A), a system with modular components (Figure 3B), and a system that integrates geometric and featural information (Figure 3C).

We take the modular reorientation system (Figure 3A) to be the view of Wang and Spelke (2002, 2003), who claimed that reorientation is done "by means of an encapsulated system operating on a geometric description of the surface layout" (Wang & Spelke, 2002, p. 377). The term *encapsulated* means that no other kinds of information get into the system (Fodor, 1983), even though some of the information (features) might be available in other modules for other tasks, and might help the animal in reorientation. The reorientation system is impenetrable to information other than geometry. It is also task specific and applies only to problems of relocation of a target after disorientation. Such a system clearly violates Fodor's (1983) claim about central systems.

Wang and Spelke (2002, 2003) did not simply ignore data showing that featural information is used under some circumstances. Their explanation for these data is that featural information enters other modules, not the reorientation module. One such module, for view-based scene matching (Wang & Spelke, 2002, 2003), is shown in Figure 3A. Thus, "children form local, view-specific representations of significant locations" (Wang & Spelke, 2003, p. 134), but "these view-specific representations do not serve as a cue to a global reorientation process" (pp. 134–135). One might suppose from these words that the reorientation process refers to establishing heading. Geometry would seem to constitute a directional cue. But then Wang and Spelke (2003) claimed otherwise only a little later. Another possible module for featural information to go into is a direction-determining module. A distinctive feature, such as a colored wall, is used "as a directional cue rather than as a landmark for reorientation" (Wang & Spelke, 2003, p. 135). Children have "direction-sensitive mechanisms that are distinct from their representations of environmental locations" (p. 135). Since geometric cues can be used to specify direction, as well as to pinpoint an exact location, the notion that a direction-determining module is distinct from the geometric module seems unclear. It seems just as plausible that geometric information forms part of a system for determining which direction is which. This idea was clearly expressed in Margules and Gallistel (1988), in which the idea of geometry being used to determine heading appeared in the title. The unique, modular role of geometry, then, would seem to consist of specifying an exact position. But then, as far as we can determine, the local view-specific information helps the animal to do this as well. We admit to being not entirely clear about what exactly is claimed to be modular. Nevertheless, key to this view is to have featural information go into different modules and systems rather than the encapsulated reorientation system, which uses only geometric information.

The typical relocation task mixes the determination or the establishment of heading with exact localization. We suggest that, in future research, it would be beneficial to separate these aspects of the task. We will suggest methods for doing so. We can then test how cues, including geometry, but also including features, sky compass, inertial, and other cues, are or are not integrated in determining direction for guiding action.

A central system with modular components for geometric and featural information (Figure 3B) is a depiction of the view in Cheng's (1986) article. Thus, rats are said to possess "a modular organization in their spatial representation" (Cheng, 1986, p. 172). A geometric frame codes the metric properties of space and sense (distinction of right/left or mirror images). Features are linked to the metric frame by address labels. These address labels on the metric frame permit the "look up" of features at particular locations. Rotational errors are said to result from "the failure to use featural information from other modules" (Cheng, 1986, p. 172). When features are used, the target place "is still specified as an address on the metric frame. But in addition, some requisite features near the target are 'glued' on" (Cheng, 1986, p. 173). A system containing modular components with crosstalk captures the view well (Figure 3B). The dashed arrows in the memory box indicate that the pasting of features is sometimes not done. The decision and action are based on the metric frame (rectangle in the memory box), which sometimes may contain added featural information.

In Cheng's (1986) view, then, features do not go into separate systems from the geometric information. The opposite is the case: The use of features is tightly linked with the use of geometry. This is expressed in the idea of *gluing* features near a target onto a metric frame. The gluing idea was motivated by the data in the article. Rats failed to use features distant from the target even with repeated training. And rearranging the distant features did not disrupt performance, as long as the feature near a target remained the same. Thus, geometry plus feature near target equals good performance. A metric frame and featural subsystems (both terms from Cheng, 1986) form part of the same system for reorientation, although Cheng (1986) suggested that they form separate subsystems. Featural and geometric properties are thus represented separately. Geometry is preferentially used for orientation, but some features (those near the target) may be integrated.

The idea of impenetrability does not appear in the Discussion section of Cheng's (1986) article. If it is implied, it applies to a part of the system, the geometric frame, not to the whole reorientation process. Gallistel (1990) clearly invokes impenetrability, but again, the writing suggests application to a particular process: "Cheng's data provide a clear example of impenetrability. The organ that computes congruence between perceived shape and remembered shape appears to be impenetrable to information about aspects of surfaces other than their relative positions" (p. 208).

A view that geometric and featural information are combined (Figure 3C) has been expressed by Newcombe (2002, in press). Although geometric information is clearly encoded and used by children, Newcombe (2002) claims that "there is no reason to believe that information is encapsulated. It is indeed integrated with other relevant information about the spatial world" (p. 398). We have represented this position, using a memory box in which featural information is found together with the geometric information (Figure 3C). In this view, although initial input may be through modular processing mechanisms, there is a central integration system that combines input from these various mechanisms in a variable, weighted fashion that reflects characteristics of the input (e.g., the size of features or their apparent moveability) and characteristics of the organism's learning history. Details aside, geometric and featural information, once processed at input, are always put together in the same representation, to be used for reorientation and, quite probably, other spatial tasks as well.

All three views can account for the major patterns of data to be explained. Thus, all the views place emphasis on the use of geometric information in reorientation. For Wang and Spelke (2002, 2003), the "re" in reorientation is emphasized. For the other views, geometry is salient in any kind of orientation. Failure of input can explain why featural information fails to be used in some cases. But in all cases, the featural information may, in addition, fail to be used even when it is in memory. How featural information is used differs in the different accounts. In the modular reorientation system (Figure 3A), the use of featural information is by a module other than the geometric module, either one that does view-based matching or one that determines direction. In the system with modular components (Figure 3B), featural information is used if there is sufficient crosstalk between the geometric module and featural subsystems. In the integrated system (Figure 3C), featural information may fail to be used, even though it forms part of the *map* for reorientation, if there is reason to think that it is less reliable than geometric information. A geometrically correct but featurally wrong match may pass a threshold criterion for matching and be accepted as a locally maximal match. In this fashion, a rotational error may be akin to a cognitive illusion.

Modular or Unified System at Output: A Program of Research

We would like to suggest that at the current state of the science, sorting out the issue of central modularity is not possible. However, further research can be imagined that might result in more diagnostic outcomes. We will illustrate a possible strategy with the example of geometric and featural information, although the concept has wider application than this example. We will assume, supported by the data just reviewed, that both kinds of information are encoded and may be used, at least under some circumstances. The criterion that governs output modularity concerns whether the two kinds of information can interact, or be integrated, in guiding an action. If the animal always relies on one or the other kind of information, but never both together, we have modular out-

put systems (Figure 4A). If the two kinds of information can be integrated, if they guide action together, we have a unified system (Figure 4B). In Figure 4, we have drawn central systems to go with the output modularity or lack thereof. But strictly speaking, this link between output modularity and central modularity is not necessary.

We can illustrate this approach with one kind of experimental data that could be used to make the important distinctions (Figure 5). The paradigm raises the question of whether different cues are integrated in determining direction. It specifically isolates the problem of directional determination and separates it from the exact localization of a position. The basic idea is to train an animal with two redundant cues and then test with the two cues in conflict. The conflict test should allow for the possibility of integrating the two cues. We refer to Figure 5 as a concrete example. We assume that both the geometric and the featural cues provided are readily learned by the animal. In an experimental program, of course, these points need to be empirically demonstrated. We also assume that other potential cues are eliminated. Thus, the animal would be deprived of sky compass, inertial, magnetic, and other cues by appropriate manipulations, such as rotation of the animal, blocking out the sky, and so forth. In the experiment illustrated, the geometry (trapezoidal shape) has no ambiguity. For the purposes of testing output modularity, this property is desirable. The featural cue is indicated by the thick bars in the top left corner of Figure 5A. It could be any kind of feature, but let us suppose that it is a patch of distinct color on the wall of the arena.
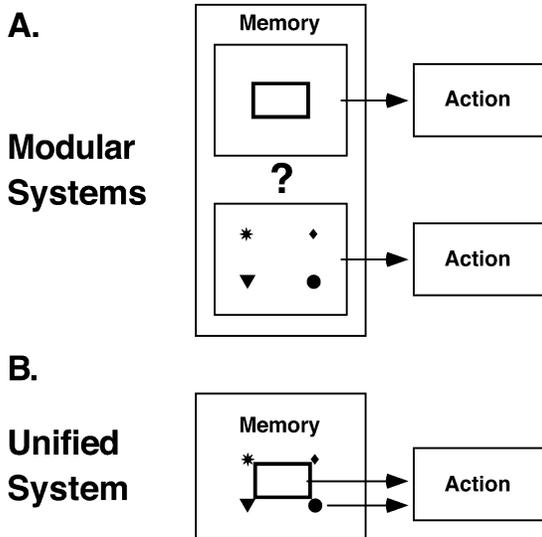

Figure 4. Modular or unified system at output. (A) Modular systems. Action is based solely on one kind of information or another. The figure shows geometric and featural information, but the concept applies to other kinds of information as well. The two kinds of information are not integrated in any way. (B) Unified system. Different kinds of information are integrated in guiding action. The different kinds of information may be together, as shown, or in separate *central modules*. See the text for further details.

Another modification from the typical experimental paradigm of a *geometry* experiment is needed. That is, we need to move the target location away from the corners, to put the target far from the walls and far from the features and geometry that can be used to determine direction. This tactic disentangles two confounded uses of both geometry and features. In the typical experiment with a corner target, features and geometry are used both for determining direction (heading) and for exact localization of the target. In Figure 5A, the search space is thus a ring. The ring serves as the cue for exact localization, whereas the surrounding cues (features and geometry) are necessary for determining where around the ring to search. The search space does not have to be a ring. Equally good is a target at a constant direction and (small) distance from a cylindrical landmark somewhere in the middle of the space, a paradigm that has been used with pigeons (Cheng, 1994) and honeybees (Cartwright & Collett, 1983; Cheng, 1998). From this standpoint, it is desirable that the surrounding geometric and featural cues be large, salient, and reasonably far from the target. Central to the training situation is that both geometric and featural cues specify the target direction (around the ring) in redundant fashion.

Central to the crucial test (Figure 5B) is to set the two cues in conflict. We have shown one example of this in which the featural cue has been displaced to another corner. As is typical of such transformational experiments, we assume that the test is unrewarded (so that there is no right answer) and given only occasionally (so that responding does not extinguish). Figure 5B also indicates possible interesting outcomes with arrows. The animal might follow the geometric cues completely and search mostly at the direction indicated by the left arrow. Or the animal might follow the featural cues completely and search mostly in the direction indicated by the right arrow. Clear demonstration of the integration of the two kinds of cues would come from responses in the area shown by the third (middle) arrow. If the animal searches mostly at a direction intermediate between what geometric and featural cues would dictate, the two kinds of cues must have been integrated (averaged) in determining a course of action. This constitutes evidence for a unified system. Another possible outcome is vacillation: An animal might search equally often at the geometric and the featural locations or search mostly at one and then switch to trying the other. Such behavior is ambiguous. It might derive either from switching between modules or from changing the weight attached to various types of cues in an integrated system.

The evidence for or against a unified system is akin to an existence proof. The system is unified at output if, and only if, under some set of parameters, this kind of averaging behavior is clearly demonstrated. The system has modular output systems if, and only if, under all parameters, the animals rely solely on one kind of cue or the other. If we see vacillation, we have an ambiguous outcome and must think of further tests. Another am-

A. Training setup
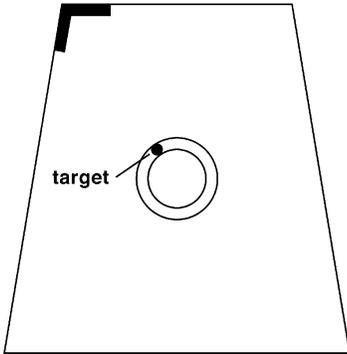
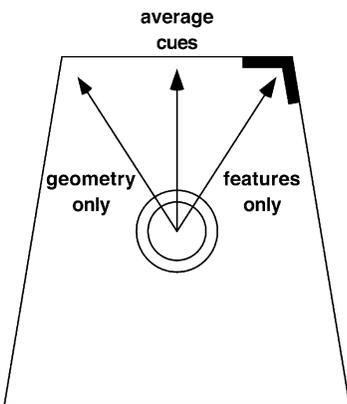## B. Crucial conflict test

Figure 5. Experimental paradigm for testing the integration of information at output. (A) Example of a training setup. The search space is a ring roughly in the middle of a large space. The target is hidden during training. The shape of the space gives unambiguous geometric cues, whereas a feature in the corner (e.g., a panel of a different color) provides featural cues. The two kinds of cues are redundant in specifying the direction around the ring in which to search for the target. (B) Conflict test. In the most important test, the two kinds of cues (geometric and featural) are in conflict with one another. Arrows indicate theoretically interesting directions in which a subject may search. It is assumed that the test is without reward. The same kind of logic can apply to other kinds of cues. See the text for further details.

biguous outcome would be a set of findings under which featural cues are followed in certain situations and geometric cues in other ones.

We have described only one experimental paradigm. Many more paradigms pitting various kinds of featural and geometric cues may be imagined. Importantly, other possible direction-giving cues may also be tested in this fashion. Thus, sky-compass cues and large-scale landmarks (shore of a lake or a long line of trees) have been put into conflict for honeybees (von Frisch & Lindauer, 1954). This was done by training the bees in one location in one afternoon and then moving the hive of bees to a different location overnight. The difference between the two locations was that a salient extended large-scale landmark (e.g., shore along a lake) ran in different directions from the hive. In such cases, bees from hives

near a salient large-scale landmark mostly followed the landmark. The discrepancies between the cues were large, and the possibility of averaging cues was not investigated.

Without launching into a full review, a number of systems have been shown to be unified at output in this sense. Closest to the topic of this article is landmark use by pigeons (Cheng, 1988, 1989). Pigeons were trained to locate a goal indicated by multiple and redundant landmarks. The birds were oriented, and the point of the research was to investigate processes underlying exact localization. When a key landmark was then shifted on a crucial test, the birds often struck an average between the dictates of the shifted landmark and those of the unshifted landmarks. In one case (Cheng, 1988), the shifted landmark was clearly featural (a strip of cardboard on the arena wall), whereas the unshifted landmarks included geometric cues (the shape of an arena). The averaging behavior of the birds suggests a system that unifies geometric and featural cues in exact localization. But the data are far from clean for this purpose. By adapting suitable modifications to this kind of paradigm of redundant training with conflict tests, however, such questions may be further pursued.

Cues originating from different sensory systems may be integrated into a unified output system. Gepshtein and Banks (2003) gave humans conflicting haptic and visual information for size judgments. The judgments reflected a compromise (average) of the dictates of the two kinds of cues. Cues from different domains of experience may also be unified at output. Cheng, Spetch, and Miceli (1996) trained humans and pigeons in the same experimental paradigm with redundant spatial and temporal cues. On each training trial, a square moved horizontally across the computer screen at a constant rate. At a particular point in time, redundant with a particular position on the screen, a reward became available. The subjects could thus use spatial or temporal cues to determine when to respond. On crucial tests, the stimulus moved at a different speed than normal. This put the dictates of spatial and temporal cues in conflict. The behavior of both species reflected a compromise between the spatial and the temporal cues. Humans and pigeons average space and time.

Returning to the use of geometric and featural cues in determining direction, it is germane to test more than these cues on the issue of output modularity. Other direction-determining cues may be pitted against either geometric or featural cues as well. For example, inertial cues may be included by having oriented animals that always enter an arena from one direction. Geometry can be pitted against inertial cues by rotating the surrounding arena by a certain amount, while the animal stays oriented. Sky-compass cues may be included by appropriate tests outdoors.

A variety of this paradigm can also be used to research how one particular kind of cue is used to determine direction. Gallistel's (1990) theory of matching principal axes, for example, can be tested. In this case, one would restrict the animal to geometric cues only. After suitable training, one can transform the surrounding cues for

tests. A strong prediction is that, so long as the principal axes that the animal can extract from the test space are similar to those found in the training space, the animal will make the predicted response according to these axes, details of geometric shapes aside.

On the issue of integration, the integration of geometric and featural information may not go far enough. Perhaps more kinds of cues than those two types are integrated in determining direction for action. One recent theoretical view along these lines is Jacobs and Schenk's (2003; Jacobs, 2003) parallel hippocampal systems. One of the systems is a bearing map, one of whose jobs is to tell which direction is which. The bearing map is instantiated in an evolutionarily older part of the hippocampus in vertebrate animals. It "is constructed from the integration of self-movement cues and directional cues" (Jacobs & Schenk, 2003, p. 291). If we read these authors correctly, this means a unified system that integrates all possible bearing (directional) cues. Strong unification at output is predicted. Experimental paradigms along the lines of Figure 5 can address some of the major behavioral predictions of this recent theory.

To make some sense of the issue of modularity, we would like to reformulate a version of Fodor's (1983) position: We embrace both modularity and integration, but in different contexts. At input, modularity makes sense. Information needs to be processed by different specialized modules. Modularity is perhaps the only manageable way to do multiple jobs at the input end. Some processes of matching, such as Gallistel's (1990) proposal for matching principal axes of space, may also be best served by a modular unit. Nevertheless, at output, in guiding action, it makes sense to integrate available information. Using multiple, redundant sources increases accuracy. For the spatial domain, this theme has been echoed in various contexts (Huttenlocher, Hedges, & Vevea, 2000; Kamil & Cheng, 2001). Between input and output, we have a great gulf, in which we need to work out how information is organized.

Other Topics for Further Research

Another topic of interest is the role of general experience in the use of geometry and features in relocation. In human spatial cognition, Newcombe and Huttenlocher (2000) have identified general and almost universal experience (e.g., having a floor beneath) as an important contributor to development. Intriguing in this regard are data showing that the geometry defined by separated objects, as opposed to continuous or nearly continuous surfaces, sometimes fails to be used in relocation (Gouteux & Spelke, 2001). Objects in the natural world, from rocks to trees to hills, often stand out as landmarks. If geometry is to be used in orientation, it would seem pertinent to encode and use the geometry of the arrangement of objects. We note that all the animals tested so far have been raised largely in indoor, mostly rectangular environments filled with continuous surfaces. Lab-reared birds, rats, and monkeys, fish in aquaria, and humans from the civilized world, who spend large amounts of time indoors, all fill this bill. Perhaps exposure to solid surfaces, or at least to stable environments, is a necessary precursor to geometric sensitivity. Rearing lab animals in different controlled environments (e.g., circular ones), testing the few nomadic humans who do not live indoors, and experimenting on animals caught in the wild are all relevant in this regard. Prior researchers have not examined these specific hypotheses, but the importance of such investigation is demonstrated by the fact that experience affects spatial learning in a more general way; for example, rats reared in the dark perform less well than light-reared animals in the Morris swimming pool (Tees, Buhrmann, & Hanley, 1990).

A scattered array of vertebrate species have been tested so far. These species are convenient ones to test in lab setups, but the array does not amount to a comparative approach (Shettleworth, 1998). The role of phylogeny has not been taken into account. It is inappropriate to compare differences, but perhaps the diverse range of species indicates that the use of geometric cues is widespread among vertebrates.

In a similar vein, what about invertebrates? Arthropod navigation has been much studied (for reviews, see Cheng, 2000, Collett & Collett, 2002, Gallistel, 1990, and Wehner, 1992), but we do not know whether and how arthropods use the geometric arrangement of surfaces and large-scale objects. Honeybees can tell which direction is which inside a lab room; this is demonstrated by the fact that they can be trained to find a target that stands in a constant spatial relation to a single cylindrical landmark (Cartwright & Collett, 1983). Insects are known to use the sun compass and large-scale landmarks outdoors to determine which direction is which (Dyer & Gould, 1983; von Frisch & Lindauer, 1954; Wehner, 1994), but we do not know much about the cues they use to tell direction indoors. Fry and Wehner (2002) found evidence for an egocentric framework, but it is possible that other cues for direction are also used. We are also unclear about how they use large-scale landmarks.

CONCLUSIONS

In sum, a number of vertebrate species have been tested in relocation tasks in indoor settings. In most of the studies, continuous surfaces of the test arena provide geometric information in the broad shape of the arena. All the species tested use this geometric information. The arenas typically contained geometric ambiguities, so that according to the geometry, more than one location was correct. Other, featural cues disambiguated the geometry. These featural cues were also used, at least under some circumstances, by all the species tested. We have presented various schematic pictures of central cognitive architectures to account for the key behavioral data (Figure 3). Our conclusion is that the extant data are at present insufficient to settle the issue of central modularity. We suggest approaching the issue of modularity at output as a more empirically tractable program of research (Figures 4 and 5).

The notion that the geometry of space is a key element in spatial behavior has proved to be important in the literature on a variety of species and has influenced research on the neuropsychology and neuroscience of spatial cognition as well. However, this review shows that more research is needed to unravel how animals use geometric information in spatial tasks.

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