

# Whither geometry? Troubles of the geometric module

Ken Cheng

Centre for the Integrative Study of Animal Behaviour, Macquarie University, Sydney, NSW 2109, Australia

**In rectangular arenas, rats often confuse diagonally opposite corners, even when distinctive cues differentiate them. This led to the postulation that rats rely preferentially on the geometry of space, encoded in a dedicated geometric module. Recent research casts doubt on this idea. Distinctive featural cues such as entire walls of a distinct color can hinder or aid the learning of geometry. In one situation in which using geometry would help greatly, rats had trouble learning the task. An associative model has been developed to capture these different learning processes, and view-based matching has been proposed as an alternative to the explicit coding of geometric cues. Considerations about how cues interact in learning are crucial in a recent theory of human spatial cognition.**

## Modularity of geometry in doubt

In the 1980s, modularity of mind was an influential proposal [1,2]. Fodor [2] proposed that peripheral perceptual processes are largely modular, but that central cognitive processes are largely nonmodular. Out of the flourishing study of spatial cognition in rats at the time [3–6], a case of central modularity was proposed with the discovery of rotational errors in rats [7,8]. In these errors, rats confused diagonally opposite locations in a rectangular arena (Box 1). The phenomenon suggested that the rat had encoded only the geometric properties of space in making these rotational errors, and led to the postulate of a geometric module in the rat's brain [7]; a central module that encodes and deals only with geometric information.

Subsequently, a substantial corpus of 'geometry' studies tested various vertebrate species, including fish [9,10], birds [11,12] and monkeys [13] (see review in Ref. [14]). Systematic rotational errors are made by human children and even adults under some circumstances [15–19]. Research on the topic continues to burgeon (Table 1). This article focuses on 'geometry' work with rats, reviewing several important developments since Cheng and Newcombe's review [14]. Cheng and Newcombe [14] wrote of the 'obligatory nature of using geometric information' (p. 12), but this claim has since been eroded. Sometimes, salient non-geometric cues, called featural cues, can hinder the learning of geometric cues [20,21]. Furthermore, in one task that cried out for the use of geometric information, rats proved poor at learning the target location [22]. These developments have led to an associative learning theory modeling how featural cues can sometimes help and some-

times hinder the learning of geometric cues [23]. And they have led to an approach of view-based matching, in which geometric properties are not explicitly encoded [24,25]. Finally, the article discusses a new formulation of geometry and features in human spatial cognition linked intimately with research on rats [26,27].

## Cue competition

Cue competition is a key concept in animal learning [28]. When multiple cues can be learned, one cue might interfere with the learning of another. When both Cue A and Cue B presented together predict an outcome, A might be less well learned than if it had been presented alone as the predictor. This phenomenon is called overshadowing [29]. Alternatively, a prior history of learning Cue B as a predictor might result in slower learning of Cue A when Cue A and Cue B are subsequently presented together; the phenomenon of blocking [30]. Cheng and Newcombe's review [14] suggested that 'geometric information withstands cue competition' (pp. 12), a claim that crumbled soon after its publication.

In the cue competition studies reviewed in Ref. [14], the competing featural cues were individual objects, small in size compared with the overall arena. For example, in one study, rats had to swim to a hidden platform in a geometrically unambiguous swimming pool to escape from water [31]. Some rats learned the task with an object at the target location; the object provided a beacon for navigation. Others learned the task without the beacon. When tested with the beacon and platform absent, rats in the two groups searched equally at the location of the (now absent) platform. This indicates a lack of overshadowing of geometric cues by the beacon.

After initial evidence in wild-caught mountain chickadees [20], evidence of overshadowing of geometric cues was found in rats when featural cues spanning entire walls competed with geometric cues [21]. For example, an overshadowing group searched in a rectangular pool with two black walls and two white walls, whereas the control group searched in an all white pool (Figure 1a). Neither group has sufficient information to distinguish the correct corner from the diagonally opposite corner, but information is available to both groups for distinguishing these two geometrically correct corners from the other two corners. The overshadowing group can do so on the basis of the arrangement of colors (features) as well as geometry, whereas the control group must use only geometric cues. After suitable training, the rats were tested in an all white rectangle; this test forced them to use geometric cues. The control

Corresponding author: Cheng, K. (ken@galliform.bhs.mq.edu.au).

**Box 1. Geometric and featural cues explained**

Geometry is the branch of mathematics usually used to characterize spatial relations. Geometric properties can be defined as the relations between points *qua* points, that is, without considering nonspatial properties of points such as the amount of light reflected at the point [6]. Schematically, geometric properties can be represented by stripping away such nonspatial properties from a drawing. At the top right of Figure 1 is a drawing of an arena as seen from above with the ceiling removed. One long wall is black and the other three are white. At one corner is accessible food (goal); food is inaccessible at the other corners. The geometric representations show the geometric properties of this space; basically, the contour edges are shown. The two representations are geometrically indistinguishable, as one is simply a rotation of the other. If one slides the top left representation across, it shows one match between the representation and the world. This match would lead to searching at the goal. Sliding the middle right representation up onto the physical world, however, indicates another equally good match, in this case indicating a goal at the bottom left of the physical world. Searching at this location, diagonally opposite from the actual goal, is known as a rotational error. Visual representations that encode the shape of the space, or a subset of shape properties (e.g. long wall to the left of a short wall), or abstract descriptions of shape properties (e.g. to the left of the long axis of space), or representations that highlight edges and contours, can all produce rotational errors.

At the bottom of Figure 1 is a representation of the model proposed by Cheng [7]. On a 'geometric frame' of space are attached 'address labels' that permit the rat to 'look up' important featural properties found at various locations. Using the geometric frame without consulting features other than the food location would lead to rotational errors. The rat data (middle left) are from Ref. [7], Experiment 2.

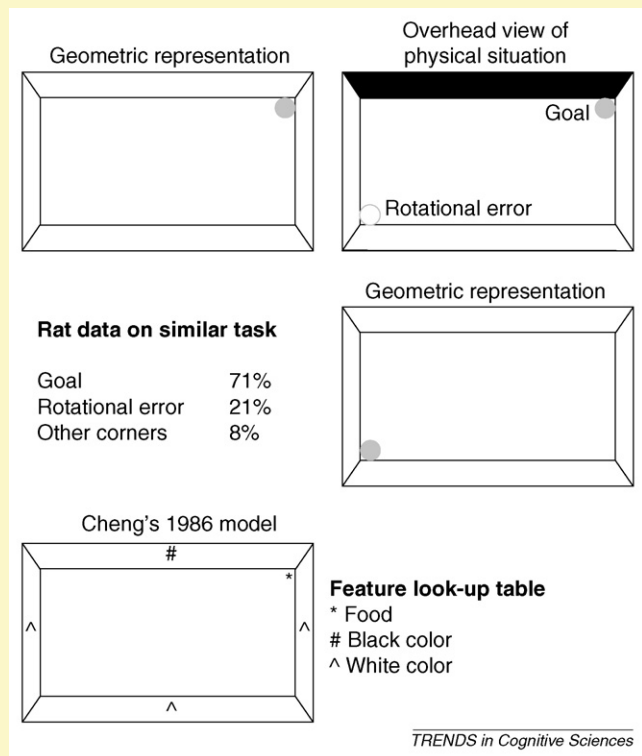


Figure 1. Geometric cues, featural cues and rotational errors.

group searched more at geometrically correct quadrants than at geometrically incorrect quadrants, but not the overshadowing group, which searched about equally in all quadrants.

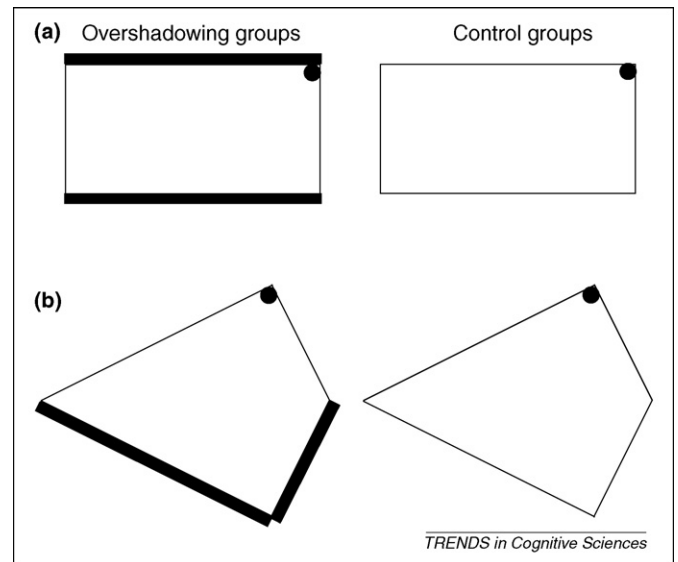


Figure 1. Overshadowing experiments with features and geometry. These experiments compared how animals learned to use geometric cues when a featural cue, the color of entire walls in a swimming pool (thick lines, black; thin lines, white), was available (left) or not (right). After suitable training with the goal (hidden platform) in the location of the black dot, rats were given unrewarded tests with all walls having the same color, that is, under conditions in which control groups were trained. These tests examined how well the animals used geometric cues. In (a), no unique solution is possible; at best an animal can choose one of the two geometrically correct corners (the target corner or its diagonal opposite) over the geometrically incorrect corners. Rats who were trained with a potentially overshadowing feature in a rectangular pool also performed more poorly on the geometry test [21], showing overshadowing of geometry by features. But in (b), rats trained with a potentially overshadowing feature in a kite-shaped pool performed better on the geometry test than controls, showing a case of potentiation [21].

The same study [21] showed wall colors blocking geometric cues. A blocking group learned (in phase 1) to find a hidden platform in a square pool with two adjacent black walls and two adjacent white walls; the target was at the all white corner. The square pool had no geometric cues distinguishing the four corners, so that the rats had to rely on featural cues (wall colors). In phase 2, these rats were trained to swim to the white corner in a rectangle with two adjacent black walls and two adjacent white walls. This pool had useful geometric cues, but the rats failed to use them. When tested in an all white pool, they searched equally in all quadrants. Suitable control groups without the blocking manipulation learned to use geometric cues. Thus, large wall-spanning featural cues can overshadow or block geometric cues.

The opposite of overshadowing can also be found, a phenomenon called facilitation or potentiation [32]. Sometimes, rats learn geometry better when both features and geometry can be used to locate a target, compared with a situation in which geometry alone must be used to locate the target [21,31]. An example is finding a target corner in a kite-shaped pool. Rats in a potentiation group were trained to go to the white corner in a black-and-white kite-shaped pool, whereas a control group was trained in an all white kite-shaped pool [21] (Figure 1b). During training, the potentiation group learned slightly (and significantly) better than the control group, although, after 13 training days with four trials per day, both groups mostly chose the correct corner before its mirror opposite. The rats

**Table 1. A selective sample of work since 2005 on the use of geometry and features**

Species	Topic	Refs
Convict cichlid fishes	How the shape of the environment in which the fish was raised affects the use of geometric and featural information	[61]
Redtail splitfin fishes	How the size of the arena affects the use of geometric and featural information	[62]
Chicks	How the size of the arena affects the use of geometric and featural information	[63,64]
Rats	How rats use the geometric arrangement of discrete landmarks	[65]
Human toddlers	A demonstration that toddlers can use some featural cues better than others, leading to a recasting of what geometry is about	[66]
Human children	How the size of the arena affects the use of geometric and featural information	[67]
Human children	An argument for modularity in coding geometry and features	[57]
Human children	An argument against modularity in coding geometry and features	[68]
Human adults	How adults use geometry and features in a virtual environment depicted on computer	[69]
Human adults	New data on dual-task performance in geometry tasks	[59]

were then tested in an all white pool, which required them to use geometric cues. The potentiation group visited the correct corner more than its mirror opposite, but control rats did not.

### If only they learned geometric cues: obligatory learning in doubt

In an important finding, rats had trouble learning to use geometric cues in a task in which it would have helped greatly to do so. Let us call this the color flip-flop task because the colors of walls changed frequently in the kite-shaped pool during training [22]. One side of the kite had a long black wall adjacent to a short black wall, the other side had a long white wall adjacent to a short white wall. But which color was on which side (top or bottom walls in Figure 1b) changed at random from trial to trial. Even after 20 training sessions, rats in this color flip-flop task chose the correct corner before its mirror opposite only ~65% of the time. The rats would have obtained ~50% had they been only choosing corners at random. Rats that could use featural as well as geometric cues were virtually perfect after six sessions at choosing the black target corner. In a test with all black walls, rats in the color flip-flop task failed to discriminate the correct corner from its mirror opposite. This result casts doubt on the claim that the learning of geometric cues is obligatory [14]. In the color flip-flop task, features are confusingly unreliable, whereas geometry predicts the goal perfectly; this is surely a task in which one should focus on geometry. Equally, a purely geometric module seems doubtful. If a module encoding only geometric properties can be used, one that ignores features by not encoding them, surely it should be used in this situation. Failure in this task provides evidence against the representation of pure geometry devoid of features.

### Associative model of geometry and feature learning

How can features sometimes help the learning of geometry and sometimes hinder it? A recent associative model adapted the famous Rescorla-Wagner model [33] for geometry studies [23] (Box 2). The Rescorla-Wagner model was designed to account for cue competition in experiments on classical conditioning, in which all important events are determined by the experimenter. Events include one unconditioned stimulus of biological significance such as the presentation of food or electric shock and conditioned stimuli; initially neutral stimuli that can help predict the

occurrence of the unconditioned stimulus. Learning a conditioned stimulus is characterized as gaining associative strength. Cue competition arises because the total pool (asymptotic level) of associative strength for conditioned stimuli to acquire is limited. Different conditioned stimuli are treated as separate elements playing a zero-sum game. What one element gains in associative strength is not available to others. In blocking, for example, the blocking stimulus gains much of the associative strength in the first phase of training, before the blocked stimulus has ever appeared. The blocked stimulus is ‘fighting for’ a small piece of the pie.

Miller and Shettleworth’s model [23] chooses a corner with a probability proportional to the total associative strength found at the corner. Geometric and featural cues are separate elements, but each corner has its own combination of the two kinds of cues. This separation of geometric and featural elements preserves a sense of modularity, with interacting effects such as cue competition and potentiation arising out of learning principles instantiated in the model. If the target is found at the chosen corner, the associative strengths of all cues at the corner (geometric and featural) increase. If the target is not found, the associative strengths of all cues at the corner decrease towards zero. Choosing the featurally correct corner also increases the associative strength of geometric cues at that corner, a process called feature enhancement. Feature enhancement can counter or even reverse blocking and overshadowing.

The associative model can predict rotational errors, cue competition in a rectangular pool, potentiation in a kite-shaped pool and diverse other recent findings in rats. One finding that the model fails to account for is the color flip-flop task [22]. When tested in an all black kite, the rats failed to discriminate the correct corner from its mirror opposite. But the associative model sensibly piled most associative strength onto geometric cues, and thus succeeded.

### View-based matching

A different attempt to deal with the troubles of the geometric module is view-based matching, a scheme that requires neither explicit extraction of geometric properties nor, *a fortiori*, a geometric module. The idea is not new at all; it has had a long tradition in insect navigation [34–38]. The basic idea is to take a ‘snapshot’ of the scene surrounding the goal. The snapshot becomes the target view to

### Box 2. Associative model of learning about geometry

Miller and Shettleworth's model [23] is based on the Rescorla-Wagner model of classical conditioning [33]. Learning about a conditioned stimulus is a matter of gaining associative strength, called  $V$ . The gain of  $V$  on a trial is governed by:

$$\Delta V = \alpha\beta(\lambda - V) \quad (\text{Equation 1})$$

In Equation 1,  $\Delta V$ , the change in associative strength, increases from  $V$ , the current total associative strength for all stimuli combined, towards asymptote,  $\lambda$ . With more than one stimulus at hand, appropriate subscripts might be added. The proportion of  $V$  gained is governed by free parameters  $\alpha$  and  $\beta$ , representing the saliency of the stimulus and the learning rate, respectively.

Importantly, the  $V$  for a stimulus can only change when that stimulus is encountered on a trial. For 'geometry' experiments, a trial is defined as a visit to one of the potential target positions (corners in the illustration). A positive outcome usually drives towards a  $\lambda$  of 1, whereas not finding the target drives the  $V$  towards 0.

Figure 1 shows an example of a blocking paradigm [70]. Cues are notated left to right, with black-black standing for black on the left of the corner and on the right. The blocking group would learn in Phase 1 to go to the top right corner in the figure. Black-black would gain associative strength in Phase 1. In Phase 2, the same features appear again, but the geometric cues are all different because two of the walls have changed lengths. The new target thus has the geometric property of a long wall to the left and a short wall to the right.

If  $V_{\text{black-black}}$  has become close to maximum ( $\lambda$ ) in Phase 1, say, 0.95, then too little room is left between 0.95 and 1 for  $V_{\text{long-short}}$  to increase in Phase 2. This is classic blocking. But if  $V_{\text{black-black}}$  is, say, 0.3 at the end of Phase 1, an assumption made in the model [23], that makes the agent in Phase 2 more likely to visit the black-black, long-short corner at the start of Phase 2, a prediction that is empirically borne out [70]. When a reward is found at the black-black, long-short corner, both the featural property black-black and the geometric property long-short increase their  $V$ . In this fashion, featural learning might enhance or hinder geometric learning.

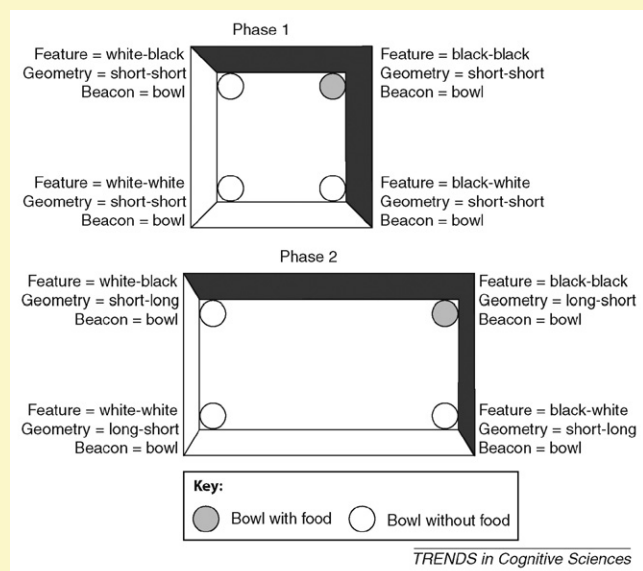


Figure 1. Geometric and featural elements in a blocking experiment.

recover, and the animal moves so as to reduce the discrepancy between the current view and the target view. At its simplest, the representation can be an unprocessed pixel-by-pixel record of the surrounding view [39].

Simulations from Zeil's laboratory (Box 3) showed that with minimal visual processing limited to edge extraction, rotational errors in rectangular spaces can result from view-based matching, even in a rectangle with one white

wall and three black walls [24]. Intuitively, this is because the edges between walls and ceiling look similar at diagonally opposite corners, both dominated by the contours between the bright 'sky' and the walls. Although experimentalists focus on the cues supplied on the walls, the space and the view it engenders encompass more.

View-based matching can account for some of the recent results in a kite shape as well [25]. One particular achievement was explaining the difficulty that rats encountered in the color flip-flop task. This task also proved very difficult for a view-based algorithm. As noted, view-based matching is thought to be common in navigating insects. Recent discoveries of stereotypical paths in pigeons homing over natural terrain [40,41] hint that they too might employ view-based matching to some extent. View-based matching has also been suggested in humans [42]. A serious current deficiency is specifying how views are learned. The modeling in Ref. [25] starts with an acquired view, ignoring the learning process. But learning processes must be addressed to account for blocking. In blocking, how an animal behaves in phase 2 depends on prior history (phase 1). If a view-based approach simply takes some acquired view in phase 2 as a start, the models have no way of letting prior history play a part and, thus, no way of explaining blocking.

### Whither geometry? Some speculations

Research on rats has a large influence on the study of human spatial cognition. In an exciting recent reformulation of geometry and features, phenomena of cue competition play a crucial part in delineating systems of spatial representation [26,27]. In virtual search tasks on a computer monitor, cue competition was found when humans located objects on the basis of nearby individual landmarks. By contrast, cue competition was absent when humans located objects with reference to the boundaries of the space. The boundaries in the studies did not have features, but directional cues were provided by the virtual landscape beyond the boundaries. This formulation delineates a 'map-like' system dealing with measurements with respect to boundaries, a system based on incidental learning, not subject to cue competition and instantiated in the hippocampal formation. A separate associative system localizes targets based on landmarks, a system based on Rescorla-Wagner style reinforcement learning, subject to cue competition and instantiated in the striatum.

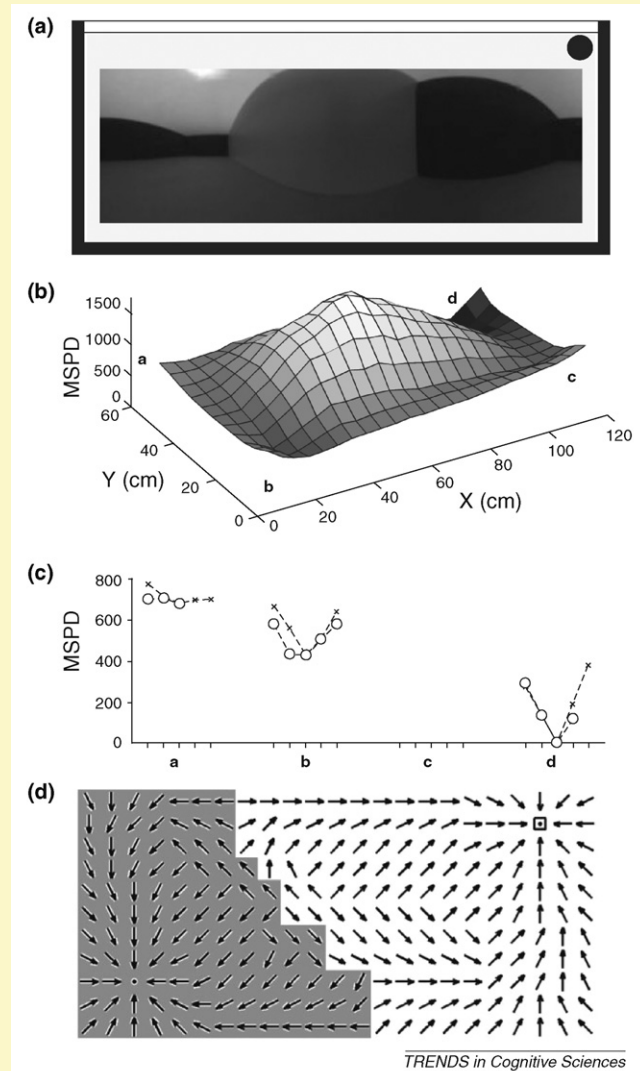
Research shows that, in addition to humans [43], rats [44–46] and pigeons [47–50] also use the distance to a boundary in spatial search. The role of views in measuring distances to boundaries deserves empirical investigation. Hamilton and colleagues [45,46] found that rats persisted in matching target locations relative to the pool when the pool was shifted in the room. This amounts to matching the distance to boundaries, with directions defined by cues external to the pool. Might the task be accomplished by matching the large chunk of view that a boundary provides? Interestingly, in one experiment in which the boundary was deliberately made low and far less salient, rats no longer preferred to match the target location relative to the pool when the pool was shifted [45]. These recent results could well have a view-based explanation,

### Box 3. View-based image matching in a rectangular box

In view-based matching, a view of the visual scene surrounding a target location is used for navigation [24,25,36,37]. The animal moves in order to recover the target view. A panoramic snapshot is taken at the target corner by a camera (Figure 1a), controlled by a robotic arm, looking down on a parabolic reflecting surface [24]. In this example, the goal has a long white wall to the left and a short black wall to the right. Similar photos are taken at a regular grid over the arena, and the pixel-by-pixel mismatch between these photos and the target view is calculated (Figure 1b). Each view is rotated to minimize mismatch, measured as the mean square of pixel differences. Three local minima are found, whose mismatch values across the x-axis transects (crosses) and y-axis transects (circles) are shown in Figure 1c. One of the local minima is found at the rotational error 'b'. If a model agent follows a gradient descent algorithm, it is most likely to end up at either the target corner or its diagonal opposite. At each point in Figure 1d, the agent looks over a grid of 25 neighboring cells, and the arrow indicates the direction of steepest descent in the image mismatch function shown in Figure 1b. If the agent starts in the white 'catchment' area, it would end up at the correct corner; if it starts in the gray area, it would end up at the diagonally opposite corner, making a rotational error.

A simple performance model of view-based navigation can be specified [25], but to make a more realistic model requires more detailed paths of travel by rats than are currently available, better specification of the visual characteristics of the spaces used in experimentation and more information on visual acuity in rats. The performance model created by Cheung *et al.* [25] contains three components guiding movement: (i) a view-based matching procedure driving the agent to find lower mismatches with the target view, (ii) an inertial component driving the agent to keep moving in a similar direction (a free parameter), and (iii) a random error component (another free parameter). Both an error component and a tendency to keep going in the same direction seem biologically realistic for swimming rats. The model accounts for many results, but performs worse than rats in some cases.

**Figure 1.** Modeling view-based matching in a rectangular arena. (a) Panoramic view at the target corner. (b) Mismatches (mean squared pixel differences) between the views taken at points in the arena and the view at the target location. (c) Mismatches along the x-axis transects (crosses) and y-axis transects (circles) at the local minima. (d) Directions of steepest descent in mismatch. Adapted, with permission, from Figure 3 in Ref. [24].



but proper simulations need to be done to ascertain or refute the claim. Animals with excellent visual systems probably extract the approximate distance to the boundary, so that a view-based scheme might need to include this information. A substantial body of evidence indicates that pigeons measure distances to surfaces [50], and rats might do so as well.

Given that rats seem to have trouble extracting feature-less geometry in the color flip-flop task, the notion of a 'pure' geometric module should be abandoned. The rats' problems with this task could also lead to the downfall of an associative model that treats geometry and features as separate elements. A system that separates out geometry as an element should be able to solve this task readily, as Miller and Shettleworth's model [23] does. Any geometry represented is likely to be bundled together with features [51]. In this light, an associative model based on a configurational view that puts geometric and featural cues together is worth exploring. Such a model might be based on Pearce's pioneering work [52].

Finally, rats in their natural habitats, along with insects, fish, birds and humans, navigate over scales larger

than those provided by typical experimental arenas (Box 4). In Calhoun's classic study [53], rats mostly followed routes at night with poor views. It is important to expand the study of spatial cognition, literally and figuratively, to include larger scales, more species and more naturalistic conditions. Insects, well known for view matching, would be interesting to investigate in 'geometry' studies. Over larger spatial scales, multiple views are likely to be encoded and used for navigation. In addition to matching a target view, encoded views might also be sources of procedural instructions (e.g. turn left at the tree), which move the navigator one segment along a route. Such a process has been proposed for humans [42] as well as insects [54,55]. How geometry, features, and associative and nonassociative learning figure in these instructions requires far more investigation.

#### Concluding remarks

Several claims about geometry and features in Cheng and Newcombe's review [14] have been overturned by recent evidence in rats. Recent work shows that geometry and features are not always learned independently. Inter-

#### Box 4. Questions for future research

- Miller and Shettleworth's model [23] specifies a learning process, whereas the performance model of Cheung *et al.* [25] specifies some cues and performance processes used in navigation. Can learning and performance be put together into the same model?
- The view-based model uses a static target view. Moving animals also have dynamic visual cues for possible use. What roles do these dynamic cues have in navigation?
- If view-based matching is a component of rat navigation, what else has a role? Rats follow routes, and sensori-motor routines come to mind, but how do these routines interact with view-based navigation? How do kinesthetic cues provided by sloping terrain, characteristic of natural spaces, interact with visual cues?
- Rats move over much larger scales than the arenas used in the vast majority of experiments, with many changes of views. How do they navigate while traveling natural distances over their natural terrain?
- How do insects (well known for their view-based matching) perform in 'geometry' tasks?
- How much do the current ideas for 'rat geometry' apply to humans, who also show phenomena of cue competition, associative learning and view-based learning?

actions in the form of cue competition and potentiation are rife, with large features hindering or sometimes helping the learning of geometric cues. Specifying the conditions favoring cue competition, independent learning or potentiation is an important empirical problem on which theoretical developments depend. Importantly, the failure of rats in the color flip-flop task indicates that a pure geometric representation devoid of featural cues seems unlikely. A Rescorla-Wagner style model is innovative, but should be compared to other, later-developed learning models, including configural models and nonassociative models. These wait to be developed for spatial cognition. Views probably play an important part in spatial cognition in rats and humans. Views are likely to be more than a pixel-by-pixel record, and include some distance information. Developing realistic view-based representations in rats requires better characterization of the visual system of the animal. Finally, the 'geometric module' in humans is debated [26,27,56–60], and this review can hopefully help inform that lively line of research as well.

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