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Learning About Environmental Geometry: An Associative Model

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K. Cheng (1986) suggested that learning the geometry of enclosing surfaces takes place in a geometric module blind to other spatial information. Failures to find blocking or overshadowing of geometry learning by features near a goal seem consistent with this view. The authors present an operant model in which learning spatial features competes with geometry learning, as in the Rescorla–Wagner model. Relative total associative strength of cues at a location determines choice of that location and thus the frequencies of reward paired with each cue. The model shows how competitive learning of local features and geometry can appear to result in potentiation, blocking, or independence, depending on enclosure shape and kind of features. The model reproduces numerous findings from dry arenas and water mazes.

Keywords: spatial learning, geometric module, Rescorla–Wagner model, associative learning, water maze

Cheng (1986) was the first to show that animals can use the geometry of an enclosure to locate a hidden goal. In a working memory task, he found that distinctive corner panels did not prevent rats from learning about the shape of a rectangular enclosure and that rats sometimes ignored the panels and searched for a hidden reward at the diagonally opposite, geometrically identical, corner of the enclosure, dubbed the *rotational corner* (see Figure 1). Cheng concluded that shape parameters of the enclosure are learned separately from featural information in a specialized *geometric module*. Later studies have shown that, in a reference memory version of Cheng's task, features are also eventually learned (e.g., Cheng, 1986, Experiments 2 and 3; Wall, Botly, Black, & Shettleworth, 2004). Many other species, including fish, birds, monkeys, and human children, learn geometry in a similar way (see review in Cheng & Newcombe, 2005).

Studies of geometry learning raise two essentially separate issues. One is, what is encoded in geometry learning? This debate has centered on whether animals extract some global parameter of a space, such as its principal axis, or use local geometric features, such as sizes of angles and sides (see Cheng & Gallistel, 2005). Here we focus on the other fundamental issue in the area: How does learning based on the hypothesized geometric module interact with learning based on other spatial cues? In the most recent version of the geometric module hypothesis, Cheng and Newcombe (2005; see also Cheng, 2005b) suggested several interpretations for the modularity of geometric information. Rather than being entirely separate from processing of features, geometry could combine with featural information in memory or in determining performance. Pearce, Ward-Robinson, Good, Fussell, and Aydin (2001) were apparently the first to point out that reliance on geometric cues for learning the location of a goal, even in the presence of more informative features, implies that geometry and features are learned independently rather than competing for learning as do conventional conditioned stimuli (CSs). The signature phenomena of cue competition in conditioning are overshadowing and blocking. In overshadowing (Pavlov, 1927), when two cues are redundant predictors of the same outcome, less is learned about either than when it is the sole predictor of the outcome. In blocking (Kamin, 1969), training with a single cue reduces (blocks) learning about a second, redundant cue added later.

Several studies have looked for blocking or overshadowing of geometric information by features (for a review, see Cheng & Newcombe, 2005). Most studies have concluded that a predictive feature near a goal does not block learning about the shape of an enclosure (e.g., Hayward, Good, & Pearce, 2004; Pearce et al., 2001; Wall et al., 2004). Moreover, in contrast with the expected competition between cues, geometry is sometimes learned better in the presence than in the absence of informative features. Pearce et al. (2001), for example, found that a beacon improved learning about the geometry of a triangular water tank. Other researchers have come across hints of this same phenomenon (e.g., Hayward et al., 2004; Hayward, McGregor, Good, & Pearce, 2003). Using a geometrically unambiguous kite-shaped water tank, Graham, Good, McGregor, and Pearce (2006) demonstrated in rats substantial potentiation of geometry learning by a feature. Kelly and Spetch (2004a, 2004b) also found clear evidence of potentiation of geometry learning by a feature in an operant task in which people and pigeons were reinforced for choosing a particular corner of a rectangle on a touch screen. In contrast with these results, a few studies have claimed to show overshadowing or blocking of geometry learning by features (e.g., Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005; Pearce, Graham, Good, Jones, & McGregor, 2006).

Here we present a model of geometry learning that offers what is, to the best of our knowledge, the first suggested explanation for

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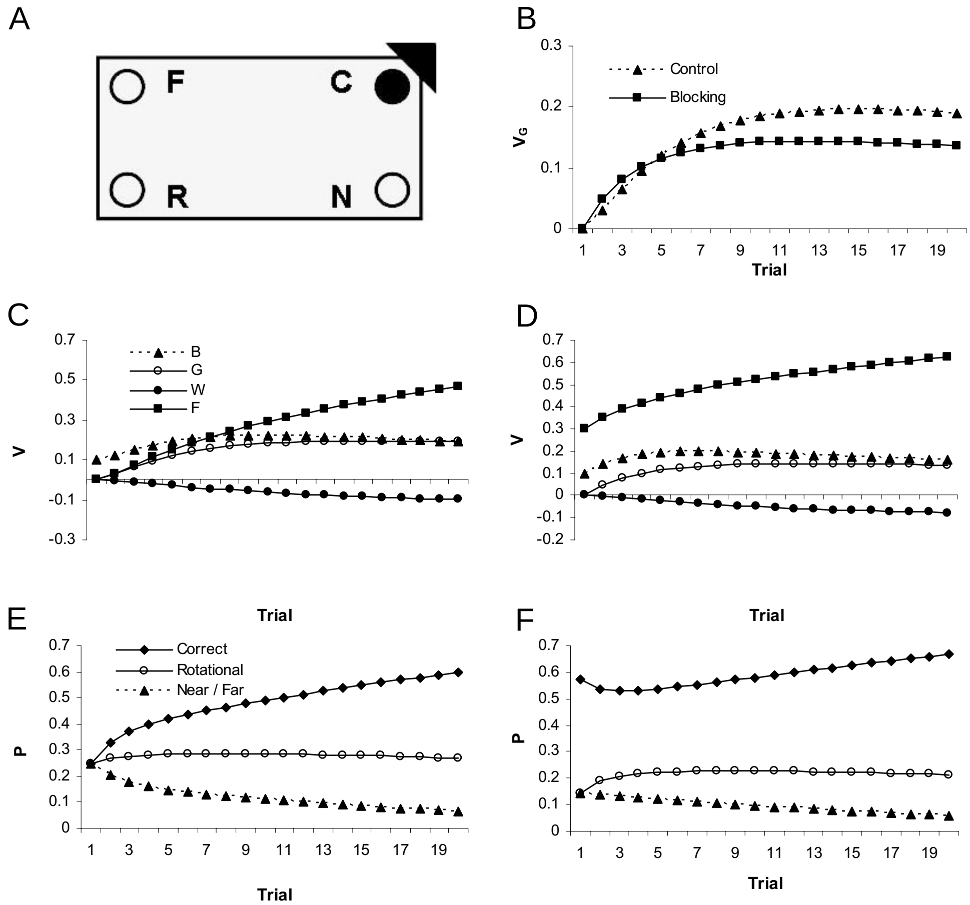

Figure 1. The model of Wall et al. (2004, Experiment 3). Panel A shows the enclosure used in the example. The filled circle indicates the rewarded corner, marked C. The black triangle indicates a feature. Panel B shows a comparison of the associative strength of the correct geometry (V_G) across trials between the control and blocking groups. Panel C shows associative strengths of all model elements for the control group. Panel D shows associative strengths of all model elements for the blocking group. Panel E shows first choice probabilities for each of the four corners for the control group. Panel F shows first choice probabilities for each of the four corners for the blocking group. F (in Panel A) = far corner; C = correct corner; R = rotational corner; N = near corner; B = bowl; G = geometry of the correct corners; W = geometry of the incorrect corners; F (in Panel C) = feature; V = associative strength; P = probability.

these conflicting results. We present an associative model of geometry learning that can account for potentiation, blocking, or independence between geometry and features without the need to invoke a special status for geometric cues during learning. The model is based on the Rescorla–Wagner model of classical conditioning (Rescorla & Wagner, 1972). Geometry learning is considered as a form of conditioning in which cues at the correct location become associated with the reward found there (i.e., they become CS+s). Similarly, cues at incorrect locations become associated with the lack of a reward (CS–). However, geometry learning tasks are operant conditioning tasks because the subject chooses which location to search. Therefore, the subject's behavior determines the proportion of the different possible types of trials. The model assumes that the distribution of a subject's choices among different locations is determined by the relative total associative strengths of the cues (both geometric and featural) at those locations. We show that such a model predicts the potentiation effects seen in the studies discussed earlier and that these effects can explain the lack of cue competition seen in many geometry-learning experiments. Because the mechanism that we suggest may underlie the apparent lack of cue competition is conceptually different from the mechanisms assumed to underlie potentiation (e.g., in taste aversion conditioning; for a review, see Graham et al., 2006, pp. 57–58), we propose a different term, *feature enhancement,* to describe it. The model also shows how training with different kinds of features and shapes of enclosures sometimes leads to blocking and overshadowing, as in recent studies by Pearce, Graham, Good, Jones, and McGregor (2006).

This article has two main parts, corresponding to two kinds of training procedures used in geometry-learning studies. In food-rewarded tasks, such as the one used by Wall et al. (2004), animals typically choose only one location per trial, for example, searching in a single corner before being removed from the enclosure. The model is introduced with tasks of this kind. When rats are trained in a water tank, however, they are typically allowed to find the reward (the dry platform) on every trial, perhaps visiting many other parts of the experimental enclosure along the way. Such tasks require a more complex version of the model in which animals make multiple choices per trial and every trial ends in a reward. This is presented in the second part of the article. Applying the model to a series of studies by Pearce and colleagues with several different shapes of enclosures and kinds of features (e.g., Graham et al., 2006; Pearce et al., 2001, 2006) shows how these variables influence whether animals' choices appear to reflect cue competition, potentiation, or independence.

Single-Choice Model

Model Structure

The Rescorla–Wagner model states that the associative strength (V) gained by any CS is a function of its inherent salience (α) and the learning rate (β) related to the unconditioned stimulus (US) and is asymptotic to a level determined by the magnitude of the US (λ). Thus, the gain in associative strength (ΔV) on a given trial is as follows:

$$\Delta V = \alpha\beta(\lambda - V). \tag{1}$$

Different CSs presented together compete for a limited amount of associative strength. This leads to predictions of blocking and overshadowing (Rescorla & Wagner, 1972). The associative strength of different CSs is marked with subscripts: V_A, V_B, and so forth.

Because US-mediated effects have not generally been tested in geometry-learning experiments, we set β to equal 1 and ignored its effect. Rescorla (2002) suggested that β, the learning rate, is greater on reinforced trials than on nonreinforced trials. Although we do not present the data here, incorporating this assumption into our single-choice model does not alter the direction of the results. We also set λ, the asymptotic associative strength, to 1 when the US was present. On trials where the US was not present, extinction trials, λ was 0 (for details, see Rescorla & Wagner, 1972). For simplicity, in all of the examples given here, we set all α values to 0.15 (this value was selected to make the term $\alpha \times \beta = 0.15$, as in all the examples in Rescorla & Wagner, 1972).

Obviously, the behavior of the model is partially dependent on the value chosen for α. However, the relationship between the saliences of each of the CSs and their effect on the results depends on the particulars of the experiment. It is not possible to formulate a rule for the effect of increasing or decreasing α on the final results of the model. For this reason, for the experiments discussed under each version of the model, the same value of α is used for all CSs, except where stated otherwise.

We use the name *elements* for all the different cues that the subject could encode—corresponding to the CSs in a classical conditioning experiment. A corner of a rectangle in a typical geometry experiment may contain many elements, such as a black stripe, a long wall on the left, and a 90° angle. Each element is either present or absent at each possible location that the subject can choose. At each time step (loosely corresponding to a trial), we calculate a separate ΔV_E for each element (E). We assume, for the moment, that the associative strengths for all elements start at 0 (see Rescorla & Wagner, 1972). Apart from the associative strengths of each of the elements (V_E), we can also define V_L, the associative strength of a particular location (L), as the sum of the associative strengths of the elements present at that location.

To make our version of the Rescorla–Wagner model work with geometry-learning tasks, which are operant tasks, the model requires some measure of the probability, P, of a subject choosing a particular location, L. We assume that at the beginning of training, all choices are equally probable. We require the probability of choosing a particular location (P_L) to be proportionate to the associative strengths of all the elements present at that location (V_L). Another way of putting this is that the subject's choice of a location is guided by what the subject has learned about the elements present at this location, relative to the total associative strengths of elements present at the other locations:

$$P_L = V_L/\Sigma V_L, \tag{2}$$

where V_L is the associative strength of location L, and ΣV_L is the sum of the Vs for all the locations. Note that ΣV_L is not simply the sum of the Vs for all elements, because certain elements may be present at more than one location but rather is the sum of all the V_Ls. Note also that although we model choice, choices per se are not reinforced. Rather, the subject's choices reflect the relative attractiveness of cues or sets of cues that have gained or lost value by being experienced in close spatial proximity to reward or nonreward, respectively, much as in studies of conditioned place preference.

We assume, following the Rescorla–Wagner model, that the associative strength of an element changes only on trials when it is presented, but in an operant situation like geometry learning, the probability of choosing each location determines how often any element in it is presented. We model this by multiplying the change in associative strength of an element (ΔV_E) by the probability of making each choice at which that element is present (P_L). Thus, in our model, all the associative strengths change on every "trial," but the rate of change (ΔV) is modulated by the frequency with which the various elements are experienced (which is the probability of visiting any corner containing that element). Thus, our formula for ΔV_E becomes as follows:

$$\Delta V_E = \alpha(\lambda - V_L)P_L. \tag{3}$$

We need to add a term to this equation for each location at which the element is present. Where the location is rewarded, λ is 1, and where it is unrewarded, λ is 0. A detailed example is given in the *Results* section. For simple cases where each element is present at only one location, the elements do not influence each other's associative strengths, and the current model reduces to the Rescorla–Wagner model.

Elements that are present at more than one location may be compared with predictors with a contingency of less than 1. In a rectangular enclosure, the geometry has a contingency of 0.5 because following the geometry leads to a reward half of the time. When low-contingency elements are present at the same locations as higher contingency elements, the elements interact (i.e., they influence each other's associative strengths). The higher contingency elements increase the probability of that location being chosen, thus increasing the associative strengths of other elements present at the same location. These interactions are the cause of what we term *feature enhancement*, in which low-contingency elements gain more associative strength than expected because of learning that is based on higher contingency elements increasing the frequency with which they are paired with reward.

The lack of cue competition displayed by the model is driven by feature enhancement. Feature enhancement may be simply understood thus: In a rectangular enclosure, such as that shown in Figure 1A, a feature at a correct corner is learned faster than the geometry because of its higher predictive value. The quick learning about the feature leads the subject to be more often exposed to the correct corner than the rotational corner, and this causes the associative strength of the geometry to increase faster than it would have if the subject had relied only on geometry. The subject may be said to have misjudged the reward contingency of the geometry, assuming it to be higher than 0.5, because the subject is rewarded on more than half of the visits to a geometrically correct corner. As the associative strength of the geometry increases, subjects make more rotational choices, and the perceived contingency of the geometry begins to decrease toward its true value. When subjects are tested in the absence of the feature, usually after a relatively small amount of training, they display more control by the geometry than expected. Thus, feature enhancement can account for the lack of overshadowing observed in many studies. This same result is obtained if the feature, rather than being a better predictor of the reward than geometry, is assumed to have a higher salience than the geometry, as in the studies of Graham et al. (2006) discussed later.

Lack of blocking is mediated by essentially the same process. Early exposure to featural information alone in the initial phase of any blocking study causes the associative strength of the feature to increase. In this phase, the feature is the only consistently rewarded element, so the location with the feature soon comes to be chosen on a high proportion of trials, and the feature appears to be well learned long before its associative strength is near asymptote. Thus, feature enhancement can still occur in the second phase of the experiment, when the feature element is paired with the geometry element. An example of such a scenario is explained later.

Results

In this section, we model several key geometry-learning studies in single-choice paradigms and show that our model generates similar results. All calculations were performed with an implementation of the model in Visual Basic. Application files and source code are available from Noam Y. Miller. All values of α were set at 0.15. All examples were run for 20 trials of training before the tests were modeled. Because all the associative strengths change on each trial of the model, this does not correspond exactly to 20 trials of a real experiment. However, it could correspond to the mean performance of a large group of animals.

Wall et al.'s (2004) Experiment 3. Failures of a feature near or at a goal to block geometry learning are most striking when the geometry predicts the location of the goal less well than does the feature, as in the rectangular enclosure with one rewarded location depicted in Figure 1A. We take Experiment 3 of Wall et al. (2004), in which rats searched for buried food, to illustrate how the model applies to such experiments. This first example is worked through in some detail to demonstrate the steps involved in the calculation.

One group of rats, the blocking group, was first trained to find food buried in a bowl in a corner of a square enclosure. The correct corner was marked by a feature. Another group, the control group, was trained in a square enclosure with no feature that contained just one bowl, which contained a reward. After training to criterion, both groups were retrained in a rectangular enclosure with the same feature indicating the correct corner (as shown in Figure 1A), and then both groups were tested in the rectangular enclosure in the absence of the feature. Previous exposure to the feature when there was no geometric information available would be expected to block learning about the geometry in the blocking group as compared with the controls. However, in the test with no feature, both groups of rats showed a clear and statistically indistinguishable preference for both the correct and rotational corners.

In the second phase of this experiment, when both groups are trained in a rectangular enclosure, there are four locations (the four corners) that the subjects can choose to search: The correct, rotational, near, and far corners. Each location contains certain elements, cues that the subject can associate with the locations and later use to orient itself. The only cues available are those within the enclosure. This reflects the fact that in most geometry-learning studies, subjects are disoriented prior to each trial and isolated from extraenclosure cues (for the importance of disorientation, see, e.g., Margules & Gallistel, 1988).

Several cues exist at all the corners, such as a 90° angle, a bowl, or a certain pattern of light and shadow. We include in the model only one of these cues, because the cues are always present together. Let us assume that what we are coding is the presence of the bowl, although the precise identity of the element is not important, and call this element B.

The correct corner also contains the feature (shown as a black triangle in Figure 1A) that is unique and is therefore a second element in the model (element F). The correct and rotational corners also have the same geometry, which we call element G. Note that the model does not specify which aspects of the geometry are encoded (e.g., whether these are the principal axes of the shape or the lengths of the walls and their sense). The near and far corners also have the same geometry, opposite to that of the correct and rotational corners, and this is element W (for wrong). Thus, our model for this example has four elements: B, F, G, and W. Element B is present at all corners, element F is present at the correct corner only, element G is present at the correct and rotational corners, and element W is present at the near and far corners.

We now calculate the choice probabilities for each of the four locations. By Equation 2, the probability of the subject searching at the correct corner (P_{Corr}) is given by $P_{\mathrm{Corr}} = V_{\mathrm{Corr}}/\Sigma V$. Here, V_{Corr} is the sum of the associative strengths of the elements present at the correct corner: $V_{\mathrm{B}} + V_{\mathrm{F}} + V_{\mathrm{G}}$. ΣV is the sum of the associative strengths of the elements present at all corners and is given by the following:

$$\Sigma V = V_{\mathrm{Corr}} + V_{\mathrm{Rot}} + V_{\mathrm{Near}} + V_{\mathrm{Far}} = 4 \times V_{\mathrm{B}} + 2 \times V_{\mathrm{G}} + 2 \times V_{\mathrm{W}} + V_{\mathrm{F}}, \quad (4)$$

where Rot stands for rotational corner, and Corr stands for correct corner. Similar calculations give us the initial probabilities for the other corners as well.

Our definition of *P* creates a problem during the first trial: When all the *V*s are initially set to 0, we attempt to divide by 0 when calculating the choice probabilities. The simplest solution to this problem is to make the initial value of one of the elements greater than 0. For simplicity, we set the initial V_B, the associative strength of the bowl element, to 0.1. Assuming a nonzero initial associative strength for the bowl is comparable with giving subjects a brief period of pretraining with the bowl, a procedure often followed in geometry-learning experiments (e.g., Kelly, Spetch, & Heth, 1998; Wall et al., 2004) or, as in this case, an initial phase with training in a different enclosure.

Setting the initial V_B at 0.1 and all the other Vs at 0 gives, by Equation 4, $\Sigma V = 0.4$. Thus, $P_{Corr} = 0.25$, which is what we expected. Because there has not yet been any learning, we expect all the choice probabilities to be equal (i.e., for the subject to choose at random).

We now calculate the ΔVs for the first trial, for each element. We start with the feature at the correct corner:

$$\Delta V_F = \alpha(1 - V_{BFG})P_{Corr}. \tag{5}$$

V_{BFG} is the sum of V_B, V_F, and V_G, the associative strengths of the elements present at the correct corner. P_{Corr} is the probability of choosing the correct corner, currently at 0.25. Because V_B is 0.1, and V_F and V_G are 0, we have $\Delta V_F = 0.034$.

For the geometry element, which is present at two corners, we need a two-term equation:

$$\Delta V_G = \alpha(1 - V_{BFG})P_{Corr} + \alpha(0 - V_{BG})P_{Rot}. \tag{6}$$

The first term in this equation is the same as the previous equation and represents the change in the associative strength of the geometry that results from visits to the correct corner. However, the geometry element is also presented on visits to the rotational (unrewarded) corner. The second term of the equation gives the change to V_G resulting from rotational choices. λ is 0 in this term as this is an unrewarded location. Solving the equation gives $\Delta V_G = 0.03$.

Note that in Equation 6 the associative strength of the geometry both increases and decreases. This may be thought of as corresponding to the results of a large group of animals, a certain proportion of which visit either the correct or rotational corner, as determined by the relative values of P_{Corr} and P_{Rot}.

Element W, the geometry of the incorrect corners, is also present at two corners, both of which are unrewarded. Thus, it also has a two-term equation:

$$\Delta V_W = \alpha(0 - V_{BW})P_{Near} + \alpha(0 - V_{BW})P_{Far}. \tag{7}$$

Because both terms of this equation are always negative, the associative strength of this element only decreases and is always negative (i.e., element W, the geometry of the wrong corners, becomes a conditioned inhibitor). Solving the equation gives $\Delta V_W = -0.0075$.

Finally, ΔV_B, the change in the associative strength of the bowl, which is present at all four locations, is given by the following:

$$\Delta V_B = \alpha(1 - V_{BFG})P_{Corr} + \alpha(0 - V_{BG})P_{Rot} + \alpha(0 - V_{BW})P_{Near} + \alpha(0 - V_{BW})P_{Far} = 0.023. \tag{8}$$

This equation has one term for each location at which the bowl is presented. Because the initial value of V_B was 0.1, we now have $V_B = 0.123$. The other Vs, because their initial values were 0, are now $V_F = 0.034$, $V_G = 0.03$, and $V_W = -0.0075$. Note that the associative strength of the feature grows fastest, followed by the geometry.

After this first trial, by Equation 2, we have $P_{Corr} = 0.327$, $P_{Rot} = 0.268$, $P_{Near} = P_{Far} = 0.202$. Thus, the probability of choosing the correct corner grows faster than the probability of choosing the rotational corner, and the probability of choosing the near and far corners decreases. The associative strength of the geometry (V_G) eventually begins to decrease, when the second term of Equation 6 becomes larger than the first (as a result of the inexorable increase in V_F). The associative strength of the feature continues to increase indefinitely and asymptote at λ (i.e., the feature eventually usurps control of the behavior).

The example above shows the process of feature enhancement in action. The associative strength of the feature (V_F) grows faster than that of the geometry (V_G), because the feature is present only at the correct corner (Equation 5 does not have a negative term, but Equation 6 does). The increase in V_F increases the probability of choosing the correct corner (P_{Corr}), because the feature is present only at that corner. The increase in P_{Corr}, in turn, increases the associative strength of the geometry (V_G), by increasing the positive term of Equation 6. If there were no feature, P_{Corr} would increase more slowly, as would V_G. Thus, the presence of the feature early on in training, rather than competing with the geometry, enhances learning about the geometry.

Feature enhancement is a transitory phenomenon and operates only when all the associative strengths are relatively small. When the associative strength of the feature becomes large enough, overshadowing does occur. Thus, if there were no feature in our earlier example, Equation 6 would become as follows:

$$\Delta V_G = \alpha(1 - V_{BG})P_{Corr} + \alpha(0 - V_{BG})P_{Rot}. \tag{9}$$

The second term of the equation, representing the change in associative strength due to visits to the rotational corner, has not changed, because nothing has changed in that corner. The first term of the equation has changed in two ways: First, $(1 - V_{BGF})$ has become $(1 - V_{BG})$, which is a larger number (because $V_F > 0$), thus increasing the overall associative strength of the geometry. Second, P_{Corr} has become smaller, because it is now proportional to V_{BG} rather than to V_{BGF} (the correct corner is less likely to be chosen in the absence of the feature). Thus, the addition of the feature pushes V_G in opposite directions, leading to an increased associative strength of geometry early on (when V_F is small) corresponding to feature enhancement and to a lowered rate of associative strength increase later (when V_F is large), corresponding to overshadowing.

Next, we model the blocking group in the same experiment. The difference in the past experience of the two groups is represented by giving the blocking group a high initial associative strength for the feature (V_F). All other values are as described earlier, and all the same equations are used. From these initial settings, an important difference between the two groups emerges: Because the blocking group has had previous experience with the feature and associates it strongly with the reward, members of this group tend to make fewer errors at the beginning of the second phase (this may be seen in Wall et al.'s, 2004, Figure 4); thus, they have a high initial value for P_{Corr}, the probability of making a correct choice.

During the first stage of the experiment, when the blocking group is exposed to the feature in the absence of geometric information, there is nothing to compete with the feature. Thus, V_F

does not need to get very large before choice of the corner with the feature reaches a high level. We arbitrarily assume an initial V_F of 0.3 for the blocking group for the purposes of this example and in all further examples of a blocking paradigm. If V_F is assumed to be much larger (around 0.6 for this example), corresponding to a large amount of training in the initial phase of a blocking experiment, cue competition effects swamp the feature enhancement effect.

In the second phase of the experiment, both groups (blocking and control) are given both types of cues: featural and geometric. There is more feature enhancement in the blocking group than in the controls, because of the high initial associative strength of the feature for that group. Thus, the blocking group learns about the geometry faster than the controls. In fact, there is a dip in the blocking group's P_{Corr} early on as members of this group make more geometric errors (cf. our Figure 1F with Figure 4 of Wall et al., 2004). No such dip is seen in the controls, obviously. It is important that choice of the rotational corner (i.e., a geometric error) is more common than choice of the other unrewarded corners in both groups, as it was in the real experiment.

Figure 1 shows the associative strengths and choice probabilities for this example, for the first 20 trials of training, and for the control and blocking groups. The figure directly compares the associative strengths of the geometry (the V_Gs) for the two groups. The blocking group initially learns about the geometry faster than the controls as a result of feature enhancement. Note also that element W, the geometry of the wrong corners, gains some inhibitory strength (V_W is negative). This is explored in more detail in the following example.

Finally, to model Wall et al.'s (2004) probe tests on the control group, with the feature removed, we simply remove the feature element from all equations (or set V_F to equal 0). All other associative strengths retain the values they held at the end of training ($V_B = 0.192$, $V_G = 0.19$, $V_W = -0.1$). We then calculate the choice probabilities with Equation 2. The results are as follows: $P_{Corr} = P_{Rot} = 0.4$, $P_{Near} = P_{Far} = 0.1$. Without the feature to disambiguate the geometry, the equations and results for P_{Corr} and P_{Rot} become identical. In this test, the model for the control group predicts 80% geometrically correct choices on the test. The associative strengths for the blocking group at the end of training are as follows: $V_B = 0.16$, $V_G = 0.14$, $V_W = -0.08$. The same calculation we used earlier gives us the following: $P_{Corr} = P_{Rot} = 0.39$, $P_{Near} = P_{Far} = 0.11$. Thus, the model predicts 78% correct responses from the blocking group on the test, a score almost identical to that of the controls. These predictions are very close to the actual results obtained by Wall et al. (2004; blocking group, 83%; control group, 75%).

Cheng's (1986) Experiments 2 and 3. Cheng (1986, Experiment 1) first trained rats in a working memory paradigm to find buried food in one corner of a rectangular enclosure with distinctive panels at all four corners. The location of the reward changed randomly from trial to trial. Rats given extensive exposure to the task eventually learned to relocate the place where they had just sampled food, but they searched just as often in the rotationally equivalent corner, showing that they retained geometric but not featural information from a single trial. The current model cannot account for the results of this experiment. Because it is essentially a successive reversal procedure in which the rats must learn to ignore all but the most recent location of the reward, we assume factors not captured by the model come into play.

In his Experiments 2 and 3, Cheng (1986) trained rats in a reference memory version of Experiment 1, in which the rewarded corner was stable across training (Figure 2A). When the rats were consistently searching in the correct corner, they were given several tests. First, Cheng (Experiment 2) removed the features at the correct and rotational corners (Figure 2B). Then (in Experiment 3) he rotated all the features one corner clockwise, essentially performing an affine transformation of the enclosure (Figure 2C). Thus, the feature that had previously been at the correct corner (and thus a good predictor of the reward) was now at the near corner. The feature that had been at the near corner was at the rotational corner and so on.

In the first test, Cheng (1986) found that rats searched primarily at the correct and rotational corners but did not use the cues provided by the remaining features (at the near and far corners) to distinguish between them. In the second test, rats searched almost equally at the correct, rotational, and near corners and almost never searched at the far corner.

The model of this experiment requires, in addition to elements B, G, and W introduced earlier, four more elements (F1, F2, F3, and F4) representing the four panels placed at the corners. The first column of Table 1 shows which elements are present at each corner for this example. We set, as before, the initial V_B to 0.1 and set all other initial *V*s to 0. Figure 2 shows the associative strengths and choice probabilities for the first 20 trials of this example.

As Figure 2 shows, four of the elements gain inhibitory (negative) strength: W (as in the previous example), F2 and F4, the features at the incorrect corners, and F3, the feature at the rotational corner. F3 gains the strongest inhibitory value. During training, element F3 is always presented together with element G, the geometry of the correct and rotational corners, but is never rewarded. Element G is also presented with F1, the feature at the correct corner, when it is rewarded. This is very similar to the $AX+$, $BX-$ discrimination task discussed by Rescorla and Wagner (1972, p. 82). Eventually the element that is always unrewarded, in this case F3, gains a strong inhibitory value (cf. our Figure 2 with Rescorla & Wagner's, 1972, Figure 6).

To model the tests performed by Cheng (1986), we apply the test manipulations to the associative strengths and calculate the choice probabilities. The columns labeled *Test 1* and *Test 2* in Table 1 (corresponding to Figure 2B and 2C) show which elements are present at which corners for both tests. For the first test, in which the panels at the correct and rotational corners were removed, we set V_{F1} and V_{F3} to 0. All other associative strengths retain their values from the end of training. The calculation (by Equation 2) gives the following: $P_{Corr} = P_{Rot} = 0.4$, $P_{Near} = P_{Far} = 0.1$, consistent with the finding that the correct and rotational corners were chosen equally often.

Kelly et al. (1998), in testing pigeons also trained in a rectangular enclosure with a distinctive feature at each corner, found that the pigeons still searched primarily at the correct corner when the features at the correct and rotational corners were removed (see Kelly et al.'s, 1998, Figure 3). This result conflicts with the results obtained by Cheng (1986, Experiment 2). In this case, the pigeons must have been using the remaining two features (at the near and far corners) to disambiguate the correct corner from the rotational corner. This is a mechanism not captured by the current model, although it could be (several additional elements representing, e.g., the corner along a short wall from the blue feature would be

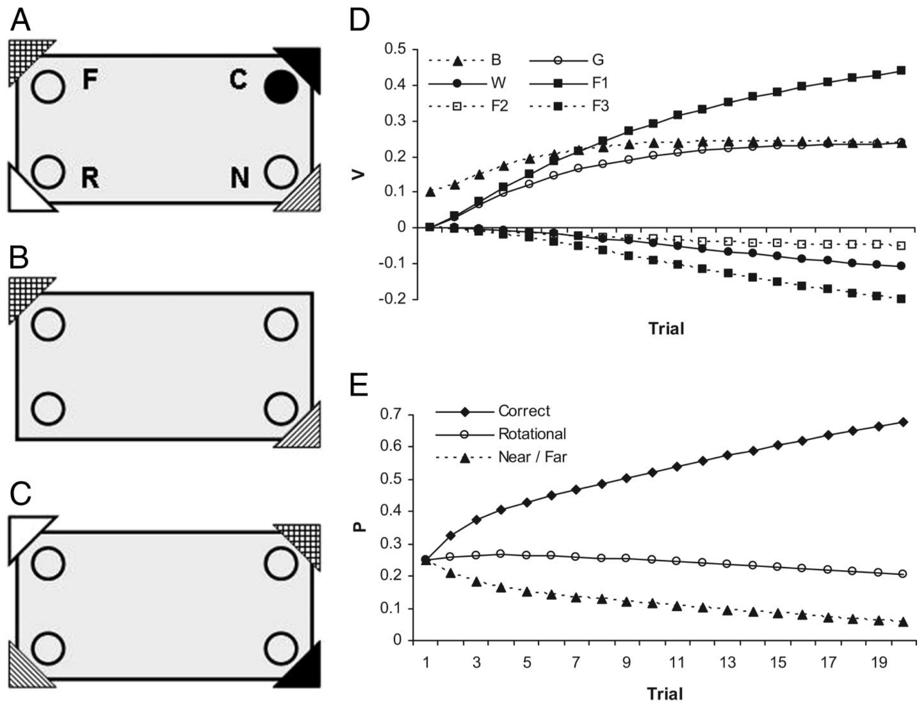

Figure 2. Model of Cheng (1986, Experiments 2 and 3). Panel A shows the training enclosure. The filled circle represents the rewarded corner. The triangles at each corner represent the distinctive panels used by Cheng. Panel B shows the test manipulation (Cheng, 1986, Experiment 2), whereby the panels at the correct and rotational corners were removed. Panel C shows the affine transform test (Cheng, 1986, Experiment 3), whereby all the panels are rotated by one corner. Panel D shows associative strengths for the model, and Panel E shows choice probabilities for the model. F (in Panel A) = far corner; C = correct corner; R = rotational corner; N = near corner; B = bowl; G = geometry of the correct corner; W = geometry of the incorrect corners; F1 = feature at the correct corner; F2 = feature at the near corner; F3 = feature at the rotational corner. F4 is not shown because it is identical to F2.

required). These conflicting results demonstrate that there may be species-specific differences in the types of elements and the relative salience of different elements encoded during learning. This would be a fruitful area for future research.

The manipulation for Cheng's (1986) second test is more complex: Elements B, G, and W remain present at the same corners as during training, because the geometry of the enclosure does not change. However, element F1 is now moved, together with its associative strength, from the correct to the near corner; F2 is moved from the near to the rotational corner, and so on (Table 1, column labeled *Test 2*; Figure 2C). The results predicted by the model depend on the amount of training given. If the rats were trained for a very long time, they would eventually search exclusively at the corner containing F1 in the test. Calculating the choice probabilities after 20 trials of training gives the following: $P_{\mathrm{Corr}} = P_{\mathrm{Rot}} = 0.32$, $P_{\mathrm{Near}} = 0.42$, $P_{\mathrm{Far}} = -0.05$. Obviously, the negative result cannot be interpreted at face value (there is simply no check in the model to avoid negative probabilities), but it emphasizes an important point. The strong inhibitory value acquired by F3, which was at the rotational corner during training, now causes subjects to avoid the far corner, to which F3 is moved by the test manipulation. This explains why Cheng's rats spent the least amount of time at the far corner during the affine transform test. A similar result for an affine transform of features was reported for pigeons by Kelly et al. (1998), in an operant version of the same task (Kelly & Spetch, 2004b), and for fish (Sovrano, Bisazza, & Vallortigara, 2003). However, another explanation is also possible (Cheng, 2005a): The correct and rotational corners still have the same geometry (they still contain element G), which was rewarded during training; the near corner contains F1, the feature that was rewarded during training; the far corner, in contrast, contains no elements that were rewarded during training. Thus, without further

Table 1
Elements Present at Each Corner During Training and Testing in the Model of Cheng (1986, Experiments 2 and 3)

Corner	Training	Test 1	Test 2
Correct	B, G, F1	B, G	B, G, F4
Rotational	B, G, F3	B, G	B, G, F2
Near	B, W, F2	B, W, F2	B, W, F1
Far	B, W, F4	B, W, F4	B, W, F3

Note. B = bowl; G = geometry of the correct and rotational corners; W = geometry of the incorrect corners; F1 = feature at the correct corner; F2 = feature at the near corner; F3 = feature at the rotational corner; F4 = feature at the far corner.

tests, such as those suggested at the end of this article, it also remains possible that the corner containing F3 is visited least because it is the only corner that does not contain a formerly rewarded geometric or featural cue (Cheng, 2005a).

Disorientation. In most studies of geometry learning, subjects are thoroughly disoriented before the start of each trial, by rotating the enclosure and/or the subjects themselves, so that only cues within the enclosure are available (including its geometry). Wang and Spelke (2002) described use of geometry as a mechanism for reorientation. Similarly, Cheng (2005b) suggested that the geometry of an enclosure is used as a cue only after disorientation. These accounts imply that geometry is simply not processed if subjects are well oriented or otherwise exposed to stable cues outside the enclosure. However, the current model shows that even if we assume oriented subjects do learn about geometry in the same way as disoriented subjects, they learn less about it.

A nondisoriented subject may be assumed to have some cue to the orientation of the enclosure relative to the outside world. This is comparable with having a distinct feature at each wall or corner indicating an absolute direction in the world. If the enclosure is rotated between sessions, these cues do not accurately predict the location of the food and merely serve to slow geometry learning by causing the subject to make more errors during training by following irrelevant cues. To our knowledge, such a direct comparison of geometry learning between disoriented and nondisoriented subjects has not been reported, although there has been one report of overshadowing of geometry learning by features in nondisoriented chickadees (Gray et al., 2005).

Other examples. The current model can be used to explain several other results from the geometry-learning literature, particularly if we allow the values taken by α to vary, reflecting the varying salience of different elements. It is likely that featural information has a different salience than geometric information, although the experimental data so far are unclear as to which is greater (see, e.g., Kelly et al., 1998; Pearce et al., 2001), and it is also likely that the relative saliences are species specific and specific to the feature used, as well as specific to the shape of the enclosure. For instance, Goutex, Thinus-Blanc, and Vauclair (2001) found that rhesus monkeys learned about both features and geometry as cues to a reward only when the features were large and not when they were small (compare their Experiment 5 with their Experiment 8 or their Experiment 6 with their Experiment 7). The current model predicts similar results if we assume that large, prominent features located in close proximity to the reward have a higher salience than smaller, more distant features, making them better able to enhance learning about geometry.

We can also model the different effects of features relative to geometry in enclosures of different sizes. When young children are tested in working memory tasks, geometry has greater influence in small than in large enclosures (see Cheng & Newcombe's, 2005, Figure 2). A greater influence of geometric cues and a smaller influence of features in smaller enclosures has been found in fish (Sovrano, Bisazza, & Vallortigara, 2005) and chicks (Sovrano & Vallortigara, 2006; Vallortigara, Feruglio, & Sovrano, 2005), and a comparison across studies suggests that pigeons also show the effect (see Bingman, Erichsen, Anderson, Good, & Pearce, 2006). In the studies with fish and chicks, relative control by geometry versus features was tested by transferring the animal from one rectangular enclosure to one of a different size and/or by changing the position of the features within the enclosure. If we allow the salience of the geometry and features to vary in our model—with geometry more salient in small enclosures than large ones and with features less salient in small enclosures (see Vallortigara et al., 2005, p. 399)—the current model matches the results of tests in these studies.

A fuller understanding of the interactions between enclosure size and feature salience must await experiments that directly examine effects on geometry and feature learning of both feature size and enclosure size by themselves. Such studies should also control for the potentially confounding factor of feature size relative to enclosure size. Progress might also be made by distinguishing between a whole colored wall and a corner panel as a feature in such studies. A colored wall changes the feature present in two corners of a four-sided arena and leaves the two empty corners the same on a featural level, whereas a single corner panel changes only one corner and leaves three the same. A setup with four distinct corner panels, as in Cheng's (1986) experiment modeled earlier, is different again. The model indicates that these kinds of arrangements may have different effects on behavior in later tests with geometry alone.

Vargas, Lopez, Salas, and Thinus-Blanc (2004) trained goldfish to locate a goal in one corner of a rectangular enclosure. The corners could be disambiguated by a black feature that spanned two adjacent walls of the tank, effectively creating a unique feature at each corner. In Vargas et al.'s Experiment 3, the rewarded corner was at one end of the feature (i.e., between a black wall and a white wall). In Experiment 4, however, the rewarded corner was in the middle of the feature, between two black walls. In the tests of both experiments, the feature was rotated by 90°, thus placing featural and geometric information in conflict, as in Cheng's (1986) affine transform test discussed earlier. Goldfish tended to search at random in the test when the reward had been at one end of the feature but followed the movement of the feature if the reward had been in the middle of the feature (i.e., they continued to search at the all-black corner). These results can be explained by assuming that the all-black corner, in the middle of the feature, was more salient than the black-and-white corner, adjacent to only one feature wall (see our later discussion of Graham et al., 2006, for a similar example involving rats). When the two-wall feature was rotated by 90° for the test, fish searched least at the corner that was between two blank walls (Vargas et al.'s, 2004, Figure 4). During training, it was the rotational (geometrically correct) corner that was between two blank walls. Thus, by the current model, the blankness of the walls became a conditioned inhibitor, much like the feature at the rotational corner in Cheng's experiments, causing the fish to shun it during the test. In a recent comment on this article, Cheng (2005a) offered an explanation of these results that was similar in spirit to the present account, in that he suggested geometry is used along with other informative cues.

In an intriguing article, Tommasi and Polli (2004) trained chicks to find food hidden in one corner of a parallelogram. When later tested in a rectangle (in which the wall lengths and sense, but not the corner angles, were preserved) or in a rhombus (in which corner angles, but not wall lengths, were preserved), chicks were able to use either type of cue to locate the correct corner. However, when tested in a reversed parallelogram, in which wall lengths and sense and corner angle were in conflict, chicks trained with the reward at an acute angled corner followed the corner cues, whereas chicks trained with the reward at an obtuse angled corner followed wall lengths and sense. In an additional control experiment, Tommasi and Polli found that untrained chicks have no innate preference for approaching acute angled corners over obtuse angled corners and suggested that a difference in the perceptual salience of the two corner angles must have driven the results. Assuming that perceptual salience translates into higher α for the acute angled corner, the current model predicts the pattern of results observed by Tommasi and Polli.

Multiple-Choice Model

Several important studies on geometry learning have been performed on rats in water tanks of various shapes (e.g., Graham et al., 2006; Pearce et al., 2001, 2006; Pearce, Good, Jones, & McGregor, 2004). Some of the experiments in these studies show overshadowing or blocking of geometry learning by features, whereas others seem to show feature enhancement. For this reason, they are well worth modeling. In a water tank, however, the animal is usually allowed to swim on each trial until it locates the platform. Thus, the probability of visiting the correct corner (the platform) is always 1, but unless the subject is at asymptote, there is also some nonzero probability of visiting each of the other corners along the way. Therefore, the model presented in the first half of this article needs to be modified to take multiple choices into account. A detailed description of the calculation steps involved is given in the Appendix. Here we give an informal description.

We assume that the learning that occurs as a result of visits to the various corners remains the same as in the original model. Thus, the change in associative strength of an element E on a trial where it is presented is given by Equation 3: $\Delta V_E = \alpha(\lambda - V_L)P_L$. Here, as before, V_L is the sum of the associative strengths of the elements at corner L. P_L stands for the overall probability of corner L being visited on a given trial. When L is an incorrect corner, the value of P_L is based on the fact that the subject may take various paths that include this corner. For example, it may swim to corner L and then to another unrewarded corner before finding the platform in the correct corner. Or it may swim to two incorrect corners, then corner L, then finally find the platform. We assume that after visiting a particular corner, the subject will avoid that corner for the remainder of that trial, which is the same as saying that even if the subject revisits that corner on the same trial it does not learn any more about the elements there. The probability of taking a particular path to the correct corner is the product of the probabilities of visiting each of the corners involved in that path (see the Appendix and Table A1 for details). The overall probability of visiting a particular corner on a given trial (P_L) is equal to the summed probabilities of all the paths that include that corner. Because all paths conclude at the correct corner, the overall probability of visiting the correct corner is 1.

On a given trial of the model, we first calculate the overall probability of visiting each corner and then calculate the changes in the associative strengths of each of the elements. The initial probability of visiting each corner is calculated in the same way as before (by Equation 2). For the correct corner, this is the probability of finding the platform (and terminating the trial) on the first choice. Suppose, however, that the rat goes first to an incorrect corner. We assume it makes its next choice among only those corners yet unvisited, as determined by the relative total associative strengths of just those corners. That is to say, we use the same calculation as before, but we take into account only the corners not yet visited on that trial. Thus, there is a series of conditional probabilities for each of the paths the subject can take. The overall probability of visiting a particular corner on a given trial is the sum of these probabilities, and this determines the changes in associative strength of the elements located at those corners (see the Appendix for details).

Because all trials in the current model conclude with a visit to the correct corner, what we have termed *feature enhancement* cannot occur as readily as in the examples above. The greater associative strength of the correct corner as a result of a distinctive feature there cannot increase the probability of visiting that corner, because it is already 1. However, the feature can still affect the choice probabilities by means of two related mechanisms. Note first that it is only the overall probability of visiting the correct corner, that is, the probability that this corner will be visited at some point in the trial (P_C), that is equal to 1; the probability of visiting the correct corner first, notated $P_{C|}$ (see the Appendix) is still subject to the same influences as in the examples given earlier. It is this probability that most affects the likelihood of visiting the other, unrewarded corners because a visit to the correct corner terminates the trial. Thus, by increasing the probability of visiting the correct corner first ($P_{C|}$), a feature at the correct corner can still lower the overall probability of visiting an incorrect corner and by so doing decrease the amount learned about other stimuli. Whether this influence makes itself felt in a test depends on the details of the procedure, because in a test with the feature removed, the model predicts choices based on the relative associative strengths of the remaining stimuli. Because all the associative strengths are decreased by the addition of the feature, the relative amount by which each decreases is important, and the feature may yet serve to increase performance on the test (see, e.g., the example described later from Pearce et al.'s, 2006, Experiment 1).

A feature can also affect the amount of learning about other stimuli when it is in an incorrect corner. An inherently attractive feature, such as that in the example from Graham et al. (2006) described later, or a feature present at both correct and incorrect corners (Pearce et al.'s, 2001, Experiment 4) may increase the attractiveness of an incorrect corner. This increases the probability of visits to the incorrect corner, and the feature serves to make other stimuli, such as the geometry of that corner, more inhibitory. This, in turn, improves performance in tests in the absence of the feature by decreasing choices of the incorrect corners.

Once the additional experience with the incorrect corners is taken into account, the model still predicts the probabilities of choosing each of the corners first on each trial of an experiment. However, choice is not a popular measure of learning for experiments conducted in a water tank. Often latency to arrive at the platform is the measure of acquisition, and results of test trials with the platform absent are reported as a proportion of some fixed time, usually a minute or so, in the quadrant of the tank where the platform should be found. In some of the experiments by Pearce and his colleagues (e.g., Pearce et al, 2006) discussed later, performance is presented as the proportion of trials in which the rats entered the correct corner of the tank before entering some other corner, such as the rotational corner. This measure does not necessarily correlate well with first choices given by the model (cf., e.g., Pearce et al.'s, 2004, Figure 2 panels that show first choice and correct choice for the same rats). We have avoided, in most cases, modeling those experiments for which only this type of data is available. In some cases, we have modeled experiments where test results are given as a proportion of time spent in a particular quadrant; where we have done so, we have assumed that this measure correlates with choice. This may not be entirely correct, as quadrant preference might be expected to attenuate over a minute of unreinforced swimming, an effect that the model does not capture.

Results

We focus on three articles that have provided important data on cue competition (Graham et al., 2006; Pearce et al., 2001, 2006) and on experiments in those articles in which the data are largely presented in a manner consistent with the output of the model. In some of these experiments, a rectangular tank was used, and in others, two novel unambiguous shapes—an isosceles triangle (Figure 3, inset) and a kite shape (an irregular quadrilateral; Figure 4, inset). In addition, the features added to the differently shaped enclosures indicated the goal unambiguously in some experiments, whereas in others the same feature was shared by the goal and one other location. Furthermore, in some cases, unrewarded locations all shared the same feature, and in others each unrewarded location had a different feature. It is not surprising, given these variations in the potential informativeness of both the geometric and the featural cues, that as a group these studies contain evidence for every possible kind of cue interaction in the control of choice. Pearce et al. (2001) and Graham et al. (2006) presented results consistent with a lack of cue competition or with potentiation (feature enhancement), whereas Pearce et al. (2006) found some evidence for overshadowing and blocking. Nevertheless, most of the results can be modeled on our assumption of underlying competition for associative strength between geometric and featural cues.

All models were run for 20 trials before testing. In the experiments modeled, rats were trained for between 9 and 17 sessions of 4 trials each. As with the single-choice model, a trial of the model does not necessarily correspond to a trial or session in the experiment. Because, in the multiple-choice version of the model, the choice probabilities are summed over all possible paths to the goal, it was found that using a value of 0.15 for α, as earlier, caused the model to reach asymptote within a very few trials, and transient differences between groups (such as feature enhancement, usually observed only early in training) were lost. Therefore, in the next examples, all values of α were set at 0.04, unless stated otherwise. All other details are as described earlier. As a result of the lower α value, the changes in the choice probabilities and associative strengths in this version of the model are more gradual than those of the single-choice version. To demonstrate the calculation steps involved in the multiple-choice version of the model, in the Appendix we model the same example as for the single-choice version as if it had been run in a water tank.

Pearce et al.'s (2001) Experiments 3, 4, and 5. Pearce et al. (2001, Experiment 3) trained three groups of rats to find a submerged platform in one of the two corners at the base of a triangular water tank with a curved base (see Figure 3). Unlike the case in any of the experiments modeled in the first part of this article, the geometry of this enclosure was unambiguous (i.e., each corner had a unique combination of angle, wall lengths, and sense as well as a unique relationship to the principal axis of the enclosure). Therefore, our model of the experiment assigns a different geometric element to each corner. During training, the beacon group additionally had a distinctive beacon attached to the platform, which was always in the same corner. There was also a no-beacon group. Finally, the random group had a beacon attached

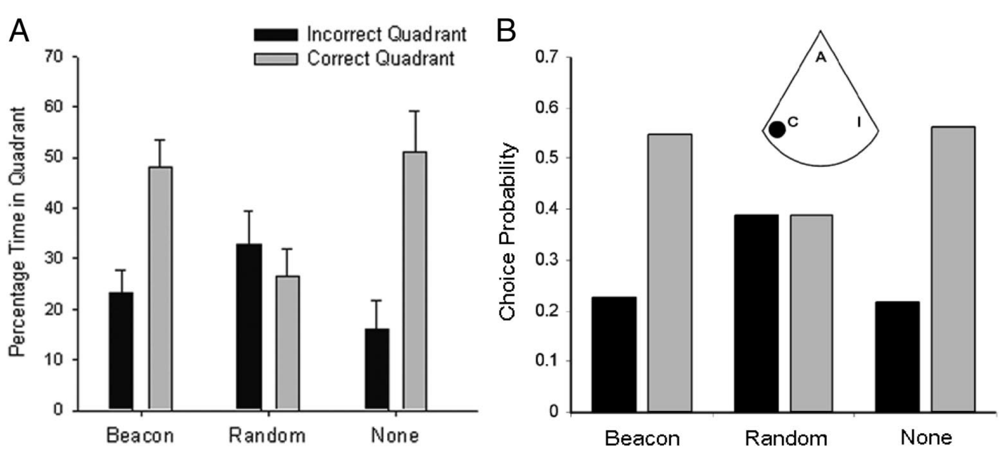

Figure 3. Model test results and corresponding data for Pearce et al. (2001, Experiment 3). Panel A shows the percentage of time spent in the correct and incorrect quadrants by the three groups during the first 15 s of an unrewarded test trial. Panel B shows model choice probabilities for the correct and incorrect corners after 20 trials of training for the three groups. The inset shows the triangular water maze used for the experiment. The black circle represents the platform. A = apex; C = correct corner; I = incorrect corner. Panel A is from "Influence of a Beacon on Spatial Learning Based on the Shape of the Test Environment," by J. M. Pearce, J. Ward-Robinson, M. Good, C. Fussell, & A. Aydin, 2001, *Journal of Experimental Psychology: Animal Behavior Processes, 27,* p. 336.

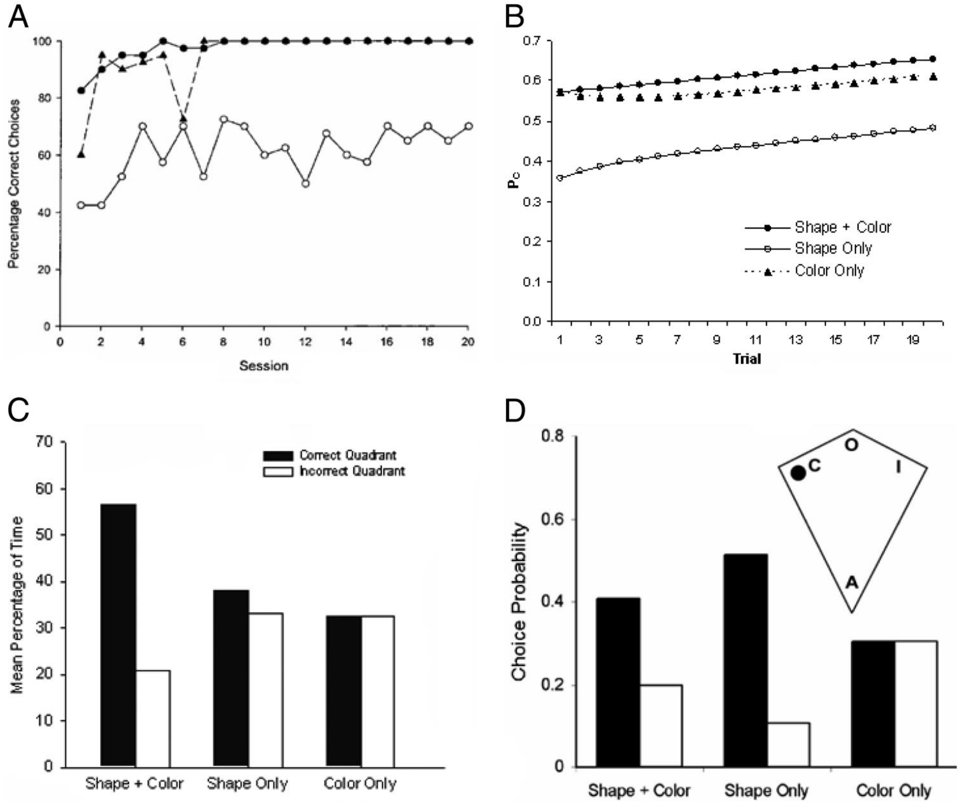

Figure 4. Model results and corresponding data for Graham et al. (2006, Experiment 1). Panel A shows acquisition data for the three groups of the experiment. Panel B shows the model's correct first choice probabilities (P_C) for 20 trials of training. Panel C shows overall percentage of time spent in the correct and incorrect quadrants by the three groups during the 1-min test trial. Panel D shows model choice probabilities for the correct and incorrect corners after 20 trials of training for the three groups. The inset shows the kite-shaped water maze used for the experiment. The black circle represents the platform. O = obtuse corner; C = correct corner; I = incorrect corner; A = apex. Panels A and C are from "Spatial Learning Based on the Shape of the Environment Is Influenced by Properties of the Objects Forming the Shape," by M. Graham, M. A. Good, A. McGregor, & J. M. Pearce, 2006, *Journal of Experimental Psychology: Animal Behavior Processes, 32,* p. 47.

to the platform, but the location of the platform (with the beacon) varied randomly between the two corners at the base of the triangle. When all three groups were given a probe test in an enclosure with no beacon or platform, only the beacon and no-beacon groups spent significantly more time in the correct than in the incorrect quadrant of the pool (see Figure 3A). Thus, Pearce et al. concluded that the beacon did not overshadow learning about the shape of the enclosure, consistent with claims that geometry is learned in an independent module.

In the model of this experiment, there are three locations where the rats can search, labeled *correct, incorrect,* and *apex* (see Figure 3, inset). The model has five elements: Element B, as in the single-choice examples, represents contextual features present at all three corners; element F represents the beacon attached to the platform for the beacon and random groups, which is present only at the rewarded corner; element G represents the geometry of the correct corner; element I represents the geometry of the incorrect corner at the base of the triangle; and element A represents the geometry of the apex. The initial associative strength for element B, as earlier, is set to 0.1. All other elements start with a V of 0.

The equations for V can be derived from Equation 3. The equations for the random group have two terms, each multiplied by 0.5, reflecting the fact that the platform is sometimes at the geometrically correct corner and sometimes at the geometrically incorrect corner. For the no-beacon and the beacon groups, for which geometry is a good predictor of the platform, the geometry of the correct corner (G) acquires more associative strength than it does for the random group, for which the geometry is ambiguous. This is reflected in the results of the tests, in which the geometry of the enclosure is the only available cue.

Figure 3B shows the results of the modeled test, with the beacon removed ($V_F = 0$). Figure 3A shows the experimental results, reproduced from Pearce et al.'s (2001) Figure 5. The results of the model match the experimental results well. The presence of the beacon at the correct corner during training causes the beacon group to learn less about the correct geometry than the no-beacon group (at the end of training, the model gives the following: the beacon group, $V_G = 0.29$; the no-beacon group, $V_G = 0.41$); that is, there is some overshadowing as predicted by standard associative models, but this difference is not apparent in the test with the beacon absent. In the test, the choices made by the subjects do not depend solely on the value of V_G but also depend on the associative strengths of elements at the other corners. Recall that the probability of a particular corner being chosen is proportional to the associative strengths of elements present at that corner divided by the associative strengths of all the elements. Thus, for example, the no-beacon group in the current example also learns to avoid the geometric cue at the incorrect corner more than the beacon group (the no-beacon group, $V_I = -0.065$; the beacon group, $V_I = -0.05$). This serves to decrease the difference between the groups as it decreases the relative weight of the correct geometry (element G) in the choice probability calculation (Equation 2) for the no-beacon group relative to the beacon group. Only the random group, for whom both the correct and incorrect corners were rewarded equally often (i.e., $V_I = V_G$), visit the incorrect corner just as often as the correct corner at test in the absence of the beacon.

In Pearce et al.'s (2001) Experiment 4 an additional control group, trained with two identical beacons at the correct and incorrect corners, was used to support the conclusions of the first experiment. Finally, in Experiment 5, Pearce et al. investigated whether the apparent lack of cue competition would extend to a blocking paradigm. The training for all three groups in this experiment was similar to the training for the groups in the previous experiments, except that the blocking and random groups were given prior experience with the beacon alone in the absence of geometric cues. This was modeled by giving the beacon element (F) a higher initial associative strength ($V_F = 0.3$) for these groups in the second phase of training when geometric cues were introduced. In the test, the blocking group preferred the geometrically correct corner (i.e., this group's choices showed no evidence of blocking), whereas the random group, for which geometry had not predicted the location of the platform, did not prefer the geometrically correct corner. The model matches these results well (not shown). These groups are modeled in the same way as the corresponding groups in Experiment 3, except that the initial value of V_F is higher. Again, the expected cue competition effect is seen in the blocking group if one looks only at the associative strength of the geometrically correct corner at the time of test ($V_G = 0.15$ for the blocking group vs. 0.22 for the control group), but this is counteracted by the other terms in Equation 2. However, the model cannot explain why the control group, trained from the outset with the beacon and platform in a consistent location, failed to discriminate between the correct and incorrect quadrants in the test. The control group was trained in the same way as the beacon groups in the previous experiments but for fewer trials. Pearce et al. suggested that the small number of training sessions led to the control group not learning the task.

In summary, Pearce et al. (2001) used an unambiguous triangular water maze and found—as did Wall et al. (2004) and others who have used food rewards in geometrically ambiguous enclosures—no overshadowing or blocking of geometry learning by a beacon. Our competitive learning model with multiple choices per trial explains these findings well, contrary to Pearce et al.'s conclusion that "spatial learning based on the shape of a test environment may not take place in the same way as that based on more discrete landmarks" (p. 329).

Graham et al. (2006). Graham et al. (2006), using a geometrically unambiguous kite-shaped water tank (Figure 4, inset), also found no evidence for cue competition. Indeed, under some conditions, they found clear evidence of potentiation of geometry learning by a feature. An important way in which their experiments differ from those of Pearce et al. (2001) is in the feature at the correct corner. When used, this consisted of two whole adjacent walls of the enclosure being black. This feature actually makes every corner different: One is all black, one is all white, one is black on the left and white on the right, and one is black on the right and white on the left. The model treats this as four separate features, one at each corner. Note that we do not model possible generalization effects from one feature or corner to another, although these may play a part in the rats' choices.

Graham et al. (2006) used several similar groups in all three of their experiments. Some rats were trained with the escape platform always in the same 90° corner and always in an all-black (or all-white corner). For these groups, both the geometry and the color were good predictors of the platform. We call these the SC groups (in Graham et al.'s, 2006, notation, shape + color). Other groups were trained with the platform always in the same corner, but the color of the corner (all black or all white) varied randomly from trial to trial, thus making color a bad predictor of the platform. We call these the S groups (shape only). Some groups were trained with the platform always surrounded by the same color walls, but the location of the platform and the black walls varied randomly between the rewarded and the opposite 90° corner, making only color a good predictor of the platform's location. We call these the C groups (color only). In Experiments 2 and 3, two groups also had a beacon at the platform during training. We call these the SCB groups (shape + color + beacon) and the SB groups (shape + beacon). Finally, in Experiment 3, one group was trained in an enclosure with all four walls the same color and the platform always in the same location. We call this group the SNC group (shape + no color).

In Experiment 1, three groups of rats were trained: SC, S, and C. The SC and C groups always had the platform at an all-black corner (never all white). Throughout training, the S group performed significantly worse than the other two groups (see Figure 4A). After 20 sessions of training, all three groups were tested in an enclosure that had four black walls, thus eliminating wall color as a discriminative cue. Only the SC group spent more time in the correct than in the incorrect quadrant in the test (Figure 4C).

Throughout this experiment and the experiments that followed, Graham et al. (2006) found that rats were attracted to the corner surrounded by two black walls, whether or not this corner contained the platform (see pp. 50–52). Rats consistently approached this corner first significantly more often than other corners, even on the first trial of training. This implies that the black walls had a high salience and also that the rats had an innate preference for the black corner. This preference is reflected in the model by assuming that the element representing wall color at the all-black corner has an initial associative strength that is higher than 0 and an α value that is higher than that of the other elements. It is possible, alternatively, that the black corner is only innately attractive and does not have a higher salience (see Graham et al., 2006, p. 48). A version of the model incorporating only this assumption gave the same pattern of results, but it did not match the data as well as the model that also assumed a higher α. The model with both an innate attraction and an increased salience of the all-black corner is presented.

Rats may encode the geometry of the kite-shaped enclosure in several different ways. For instance, if they encode the size of the corner angle our model should contain an element representing the fact that the correct corner and the one opposite to it are both 90° corners. Each corner of the kite-shaped enclosure is geometrically unique, and this too could be represented by additional elements in the model, one for the geometry of each corner. Models of the experiment were constructed both with and without all these elements, and the effect of the added elements on the results was negligible. For simplicity, they are not included in the model as presented. Thus, the elements of our model are as follows: B, contextual features common to all corners; G, the geometry of the correct corner; and F1–F4, the colors of the walls at the various corners. For the SC group, for which the wall colors and the location of the platform are stable, F1 is always at the correct corner, F2 is always at the opposite 90° corner, and F3 and F4 are always at the obtuse and apical corners, respectively.

We set the initial associative strength of element B to 0.1, as in all other examples. The initial associative strength of the black wall element (F1) is set to 0.3, and its α value is set to 0.08, to reflect the rats' preference. All other α values are set at 0.04, and the remaining initial associative strengths are set at 0. As might be expected, the model predicts that the two groups for which the salient black corner predicts the location of the platform (the C and SC groups) learn faster than the S group, as reported by Graham et al. (2006; see our Figure 4A). Figure 4B shows the model of this experiment, which matches the pattern of Graham et al.'s data, except for the obvious ceiling effect in their data. Note also that Figure 4A shows the percentage of trials on which the rats chose the correct corner without first choosing the opposite 90° corner, whereas the model predictions in Figure 4B represent the probability of visiting the correct corner on the first choice.

Figure 4C and Figure 4D present the experimental and model test results. Note the model does not predict the main finding of this experiment, a greater preference for the correct location by the SC group than by the S group. It should be kept in mind that the model predicts first choices, which may not correlate exactly with quadrant preference in the experimental test.

Experiment 2 of the same article was designed to address whether the wall-color cues in Experiment 1 had given an advantage to the SC and C groups over the S group by adding a beacon to the platform to aid the groups for which color was not a good predictor of the platform. Thus, this experiment consisted of the S, SC, SB, and SCB groups. Half of the rats in each of the four groups were trained with the platform in an all-white corner, and the other half were trained with the platform in an all-black corner. Each group was then tested in a kite-shaped enclosure in which all four walls were the same color as the walls around the rewarded corner during training for that group (so rats trained with the platform in an all-black corner were tested in an all-black enclosure, etc.). The platform and beacon were removed during the test.

During training, the SC and SCB groups performed consistently better than the other two groups (see Figure 5A). During the test, consistent with the acquisition results, the same two groups showed a stronger preference for the correct quadrant over the incorrect quadrant than did the corresponding groups for which color was not a good predictor of the platform.

In modeling this experiment, groups trained with the platform in an all-black corner must be modeled separately from groups trained with the platform in an all-white corner, as the increased salience and attractiveness of the all-black wall-color element causes the two halves of each group to behave differently. Thus, there are actually six groups in the current model: SCB (black), SCB (white), SC (black), SC (white), SB, and S. The SC (black) and S groups are identical to the corresponding groups in the previous experiment. In displaying the results, the data from the two halves of each group are averaged, as they are in Graham et al.'s (2006) presentation (see Graham et al.'s, 2006, Figures 4, 5, and 6).

The elements of this model are identical to those of the model for the previous experiment, with the exception of one additional element, N, representing the beacon attached to the platform for the SCB and SB groups.

Figure 5B shows the probability of a correct first choice for the first 20 trials of the model. Figure 5A shows first corner choices reproduced from Graham et al.'s (2006) Figure 4. The model

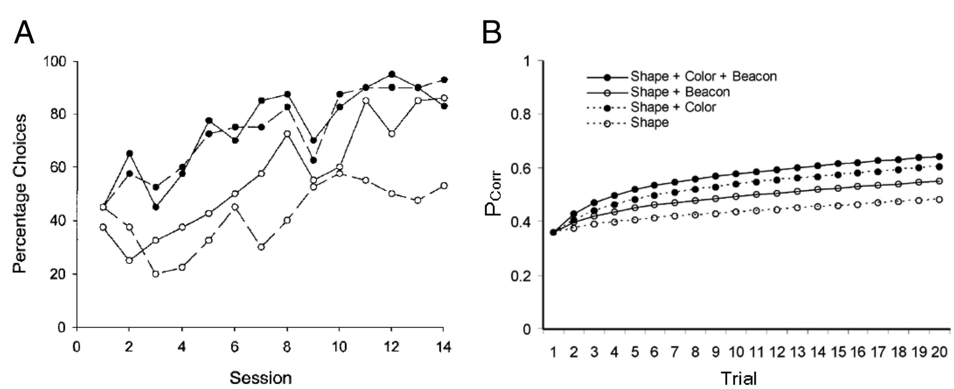

Figure 5. Model of Graham et al. (2006, Experiment 2). Panel A shows the percentage of times subjects chose the correct corner on their first choice over the course of training for the four groups. Panel B shows the model's probabilities of first choice of the correct corner for the first 20 trials of training. Panel A is from "Spatial Learning Based on the Shape of the Environment Is Influenced by Properties of the Objects Forming the Shape," by M. Graham, M. A. Good, A. McGregor, & J. M. Pearce, 2006, *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, p. 50.

correctly predicts the relative success of the various groups in locating the platform on the first choice, except that a minor difference between the SCB and SC groups, present in the model, is not seen in the experimental results. This may be a result of a ceiling effect, because the experimental rats were close to asymptotic at the end of training, and the model is not.

The model does not correctly predict the results of the unrewarded test for this experiment. Although, at the end of acquisition, the two groups for which color is relevant are performing better than the other two groups, the model predicts that the two groups for which color is not relevant have learned more about the geometry (i.e., have a higher V_G) and should thus do better in the test. The model here predicts quite different results for the groups trained with the reward in the all-black corner than for the groups trained with the reward in the all-white corner. This difference is not observed in the data (kindly provided to us by John Pearce, personal communication, January 31, 2007). The experiments by Pearce et al. (2006) modeled later explore this type of difference in more detail.

The final experiment of Graham et al. (2006) was designed to test the possibility that the groups in the previous experiments for which color was not a good predictor of the reward were adversely affected by the random changes in wall color from trial to trial. Thus, a third group was added, the SNC group, which was tested in an enclosure with 4 walls of the same color. For half of the rats in this group, the walls were black, and for the other half, the walls were white. The remaining groups, SC and S, were trained in the same manner as in the previous experiment. All three groups had a beacon attached to the platform during training. Before testing, Graham et al. gave all three groups an unrewarded probe trial in their training enclosures. This probe trial was repeated after the test.

The results of the two probe trials are presented in Figure 6A and Figure 6B. All three groups spent significantly more time in the correct than in the incorrect quadrants when trained and tested with the platform in an all-black corner (see Figure 6A). However, only the SC group performed better than chance when trained and tested in an all-white corner (see Figure 6B).

The SC and S groups in this experiment are modeled in the same way as the corresponding groups in the previous experiment. The model for the SNC group has elements B, G, and N, as before. In addition, for that half of the group that was trained in an all-black enclosure, given what we know of the attractiveness of all-black corners, an additional element, F, was added, present at all corners

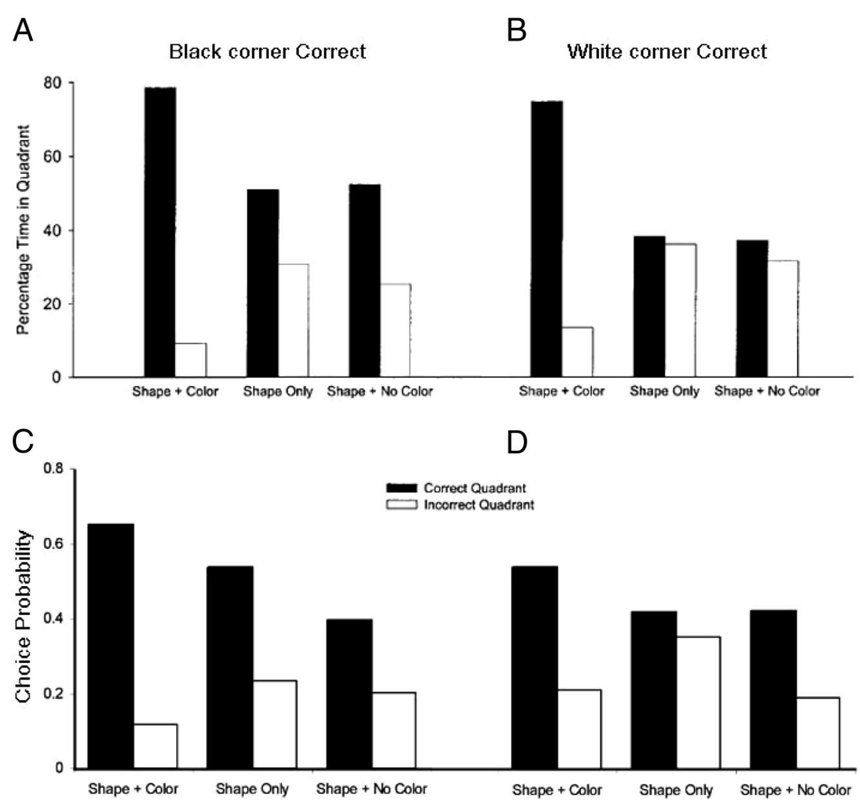

Figure 6. Model probe test results and corresponding data for Graham et al. (2006, Experiment 3). Panels A and B show the overall percentage of time spent in the correct and incorrect quadrants by the three groups during the probe trial. Panel A shows rats trained and tested with the platform in an all-black corner. Panel B shows rats trained and tested with the platform in an all-white corner. Panels C and D show the model's first choice probabilities for the correct and incorrect corners after 20 trials of training for the three groups in each training condition. Panels A and B are from "Spatial Learning Based on the Shape of the Environment Is Influenced by Properties of the Objects Forming the Shape," by M. Graham, M. A. Good, A. McGregor, & J. M. Pearce, 2006, *Journal of Experimental Psychology: Animal Behavior Processes, 32*, p. 54.

(because all the corners are all-black for this group), with a high initial associative strength ($V = 0.3$) and increased salience ($\alpha = .08$).

Figure 6C and Figure 6D show the model's results for the unrewarded probe trials. Figure 6A and Figure 6B show the experimental results, reproduced from Graham et al.'s (2006) Figure 8. The model correctly predicts that the SC group performs well whether the rewarded corner is black or white, whereas the S group performs better when the rewarded corner is black than when it is white. This is an effect of the innate attractiveness of the all-black corner, which leads to it being visited often whether it is rewarded or not. In Graham et al.'s data, the SNC group trained and tested in an all-white kite shape had a smaller preference for the correct corner than the comparable group trained and tested in the black kite shape. The latter group's preference for the correct corner was more robust through several tests. The model does not predict this, although it is possible that being surrounded by all-black versus all-white walls in a water tank has motivational and/or behavioral effects on the rats that influence amount of learning.

In summary, Graham et al. (2006) used a geometrically unambiguous kite-shaped enclosure to search for overshadowing of geometry learning by a black feature that spanned two walls of the enclosure. This large feature serves to uniquely identify every corner of the enclosure. In addition, Graham et al. observed that the all-black corner was more attractive than the other corners, whether or not it was paired with a reward. We modeled this innate attractiveness by assuming a high initial associative strength and a higher salience for this corner than for the remaining corners. The model correctly predicts the patterns of acquisition of all three experiments but fails to explain the potentiation of geometry learning by the feature seen in the tests of Experiments 1 and 2.

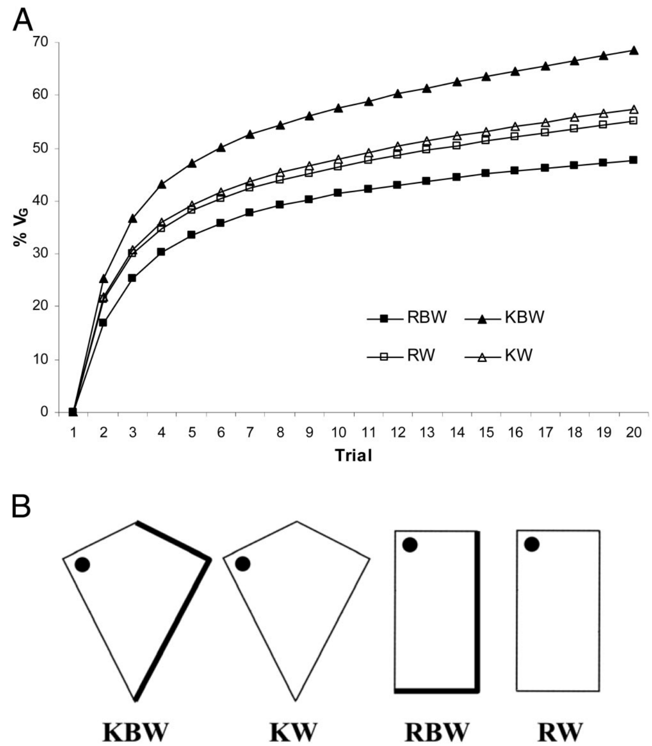

Figure 7. Comparison of the percentage of associative strength captured by V_G for the four groups in the model of Pearce et al. (2006, Experiment 1) for the first 20 trials of training. Panel A shows % $V_G = [V_G/(V_B + V_G + V_W)] \times 100$. Panel B shows the training enclosures used for the experiment for each group. The black circle represents the rewarded corner. The heavier lines represent the walls that were black. RBW = rectangle black-and-white group; KBW = kite black-and-white group; RW = rectangle white group; KW = kite white group.

Pearce et al. (2006). Pearce et al. (2006) used both rectangular and kite-shaped enclosures that also had black features spanning two walls. In contrast to the experiments of Graham et al. (2006) and Pearce et al. (2001), they demonstrated both overshadowing (Experiment 2) and blocking (Experiments 3 and 4) of geometric cues by such features. Most intriguingly, in Experiment 1, Pearce et al. (2006) found overshadowing in a rectangular enclosure and potentiation in a kite-shaped enclosure. In that experiment, they trained two groups of rats in a kite-shaped enclosure (K groups) and another two in a rectangular enclosure (R groups). Note that the kite-shaped enclosure was geometrically unambiguous (like the triangular enclosure used by Pearce et al., 2001), whereas the rectangular enclosure was ambiguous. In each shape, one group was trained in an all-white enclosure (the KW and RW groups), and another group was trained in an enclosure with two white and two black walls (the KBW and RBW groups). The correct corner, in all cases, was flanked by two white walls, as illustrated in Figure 7B. A beacon was attached to the platform for all groups. After training, all groups were tested in an all-white enclosure that matched the shape in which they were trained. Because only geometric information was available in the test, only geometrically correct or incorrect choices were measured. Thus, for the R groups, chance performance was 50%, and for the K groups it was 25%. The KBW group performed better on the test than the KW group, implying that geometry learning was potentiated by the wall-color cues in the kite, whereas the RW group performed better on the test than the RBW group, implying that the wall-color cues had overshadowed geometry learning in the rectangle. These results are consistent with the results of Pearce et al. (2001), who found a lack of overshadowing in an unambiguous triangular enclosure. In the 2001 experiment, the no-beacon group learned more about the geometry of the triangle than the beacon group, just as the KW group in the present experiment learned more than the KBW group. There are, however, differences in the performance of the models of the two experiments, which result from differences in the experimental paradigm. The beacon group in Pearce et al. (2001), for example, had an attractive feature at the correct corner to follow, whereas the KBW group in the present study had an attractive feature in an incorrect corner. These differences affected the number of errors (visits to unrewarded corners) that the subjects made during acquisition, and these in turn affected how much they learned about the various cues in the enclosure. We explain this in detail for the KW and KBW groups later.

The model of this experiment has eight elements, the distribution of which varies from group to group. For the R groups, we have the following: B, contextual elements present at all corners; G, the geometry of the correct and rotational corners; W, the incorrect geometry (of the near and far corners); and N, the beacon attached to the platform. For the RBW group, we add elements F1–F4, the features (distinct wall colors) at each corner, as earlier.

The K groups have the same elements, with two important differences: G, the geometry of the correct corner, is present only at the correct corner in the kite, because the geometry of the kite is unambiguous, and, W, the geometry of the incorrect corner, is present only at the opposite 90° corner in the kite. In modeling previous experiments in kite-shaped enclosures (e.g., Graham et al., 2006), we do not include an element for the incorrect geometry when this is also disambiguated by the features, but in this case an element was added to facilitate comparisons of the K groups with the R groups. Omitting element W was found to have only a negligible effect on the results. In this experiment, the highly attractive all-black corner is always the rotational or opposite corner, not the correct corner. Thus, this element, F2, has a high initial associative strength ($V = 0.3$) and a high salience ($\alpha = .08$) for the RBW and KBW groups.

When modeling any test, the associative strengths of the various elements present at the time of the test are taken from the end of training, and a single trial of the model is calculated to give the test choice probabilities. Thus, the distribution of choices follows the relative associative strengths of the elements. In the present experiment, the only elements present in the test, in an all-white enclosure with no beacon, are B, G, and W. Of these, only G is a predictor of the rewarded location. Thus, the percentage of choices of a geometrically correct corner depends on the relative weight of V_G in the sum $V_B + V_G + V_W$. Figure 7 shows the percentage of this sum accounted for by V_G as a function of trial for all four groups. It can be seen that the RW group does better than the RBW group and that this is reversed for the K groups (KBW does better than KW). Because the test results are directly proportional to the value plotted here, this model predicts the pattern of results observed by Pearce et al. (2006). In addition, because the lines do not cross each other (i.e., the relative positions of the groups do not change over the course of training), the model predicts that the same result is obtained regardless of the stage of training at which the animals are tested. As the next example shows, this is not always the case.

Why does the relative associative strength of element G vary as it does between the different groups? Indirectly, this reflects the difference between geometrically ambiguous enclosures, such as the rectangle, and enclosures that are unambiguous, such as the kite. The geometric ambiguity gives rise to several differences between the two groups. For example, the R groups make many more rotational errors than the K groups, primarily because the probability of such errors (P_R) in the R groups is partially dependent on element G, which is also present at the correct corner. This, in turn, gives rise to a first important difference between the effects of features in the two groups: The all-black feature (F2) in the RBW group has the effect of increasing the number of rotational errors early on (because it is innately attractive) and decreasing them later on as this feature becomes a powerful conditioned inhibitor. Thus, in later trials, the RW group makes more rotational errors than the RBW group. The situation is reversed in the K groups. Here, there are fewer errors to the opposite 90° corner early on in the KW group, because this corner is not more attractive than the correct corner and quickly becomes less attractive and because the opposite corner is sufficiently disambiguated from the correct corner by the geometry itself. Members of the KBW group, on the other hand, are attracted to the opposite 90° corner by the feature there, but they visit it less often than members of the RBW group, because the geometry of the enclosure disambiguates the opposite corner from the correct corner. As a result, the all-black wall-color element (F2) becomes a weaker conditioned inhibitor in the KBW group than it is in the RBW group, and the KBW group continues to make more rotational errors than the KW group. The model does, however, predict that the KBW and RBW groups make more correct choices than the KW and RW groups, respectively, soon after the start of training, as found by Pearce et al. (2006, Figure 1). This is due to the W groups making more visits to geometrically incorrect corners (i.e., near and far corners in the rectangle and apex and obtuse corners in the kite) than the BW groups, most of whose errors are visits to the attractive black corner opposite the corner with the platform.

A second effect of the geometric ambiguity is apparent in the course of the changes in the associative strength of the incorrect geometry, element W. The equations for this element for all four groups are as follows:

$$\text{RBW group, } \Delta V_W = \alpha(0 - V_{BWF3})P_N + \alpha(0 - V_{BWF4})P_F; \quad (10)$$

$$\text{RW group, } \Delta V_W = \alpha(0 - V_{BW})P_N + \alpha(0 - V_{BW})P_F; \quad (11)$$

$$\text{KBW group, } \Delta V_W = \alpha(0 - V_{BWF2})P_R; \quad (12)$$

$$\text{KW group, } \Delta V_W = \alpha(0 - V_{BW})P_R. \quad (13)$$

Comparing first the two equations, for the R groups, it can be seen that the RW group learns more about element W than the RBW group (i.e., V_W is more negative). This is because V_{F3} is negative (element F3, the wall color at the near corner, is also a conditioned inhibitor) and because the RW group makes, over the course of training, more visits to the incorrect corners than the RBW group (as explained earlier). Among the K groups, however (Equations 12 and 13), the KBW group learns more than the KW group about element W, both because of its higher prevalence of rotational errors and because of the large initial associative strength of the all-black wall-color element (F2). Thus, the distribution of V_W among the groups mirrors the test results.

In Experiment 2, to further examine the interactions between large black wall-color features and the geometry of a rectangular enclosure, Pearce et al. (2006) placed the black walls opposite each other, so that either the two long walls or the two short walls of the enclosure were black. Of importance, the color of the walls here does not provide any additional information beyond that provided by the geometry of the rectangle.

Three groups of rats were trained in the rectangular enclosure. For the experimental group, the two long walls of the enclosure were black, and the two short walls were white. The control–W group was trained in an all-white enclosure, and the control–BW group was trained in an enclosure in which either the long or short walls were black, and this varied randomly from trial to trial. Thus, for this group, the color of the walls (or, equivalently, the left–right arrangement of black and white walls at the corners) was not a good predictor of the location of the platform. None of the groups had a beacon attached to the platform. All three groups were later tested in an all-white enclosure.

During training, the experimental group, which could use both wall color and geometry, consistently performed better than the other two groups (Figure 8A). However, in the test, the experimental group performed significantly worse than the other two

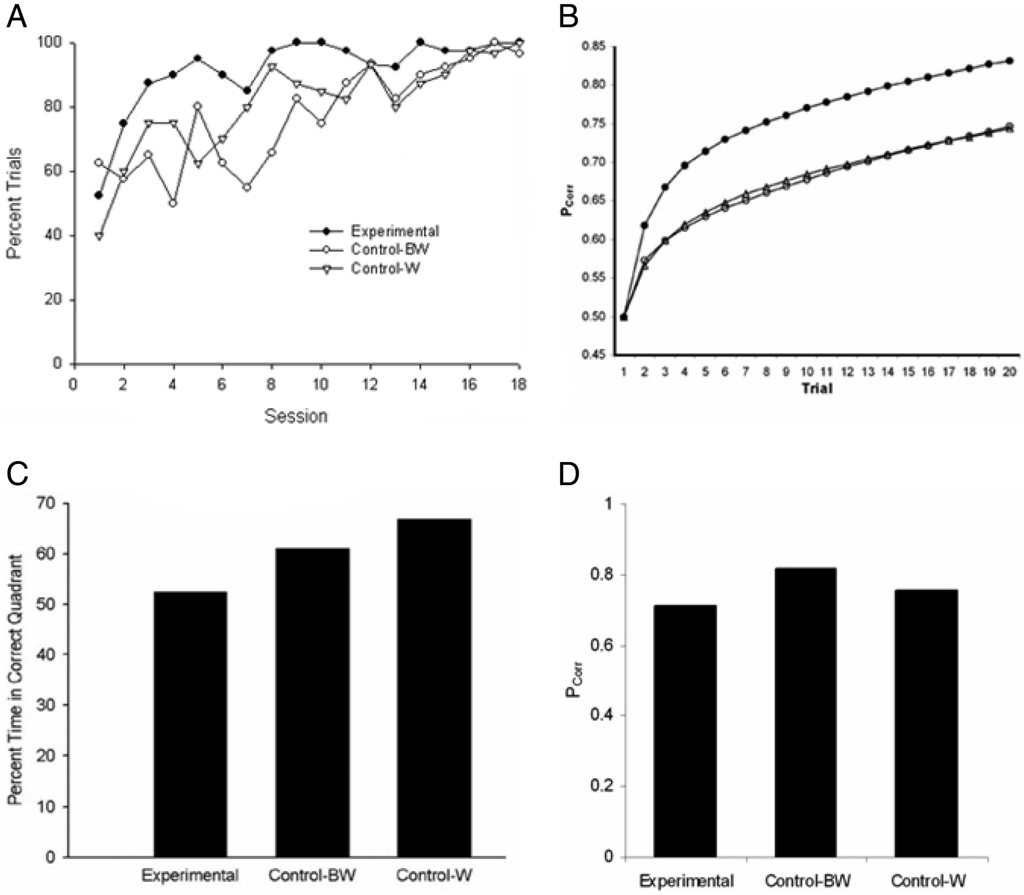

Figure 8. Model results and corresponding data from Pearce et al. (2006, Experiment 2). Panel A shows the percentage of times subjects chose the correct corner over the course of training for the three groups of the experiment. Panel B shows the model choice probabilities for the correct corner for the three groups over the first 20 trials of training. Panel C shows the percentage of time spent in the correct quadrant by the three groups during the test trial. Panel D shows the model's test choice probabilities for the correct and incorrect corners after 20 trials of training for the three groups. B = black; W = white; P_{Corr} = probability of searching the correct corner. Panels A and C are from "Potentiation, Overshadowing, and Blocking of Spatial Learning Based on the Shape of the Environment," by J. M. Pearce, M. Graham, M. Good, P. M. Jones, & A. McGregor, 2006, *Journal of Experimental Psychology: Animal Behavior Processes, 32,* pp. 206 and 207, respectively.

groups (Figure 8C). Pearce et al. (2006) concluded that the presence of the black walls overshadowed learning about the geometry in this group, consistent with the findings of overshadowing in the rectangle in the previous experiment.

To model this experiment, we use the three elements familiar from previous models of rectangular enclosures: B, G, and W. In addition, for the experimental and control–BW groups, we add two elements (F1 and F2) representing the color of the walls. For the experimental group, F1 is present at the correct and rotational corners, and F2 is present at the near and far corners. For the control–BW group, these two elements vary between the geometrically correct and incorrect corners from trial to trial. Note that because elements F1 and F2 are present at the same corners as elements G and W, they do not provide any additional information. Additionally, the arrangement of the black walls in this experiment causes each corner of the enclosure to be between a black and a white wall. Thus, in this experiment, there is no feature with a higher salience or innate attractiveness than the others. Finally, because there is no way to distinguish geometrically identical corners in any of the three groups (i.e., correct from rotational or near from far), all choices to geometrically identical corners are summed for both training and test as they are in Pearce et al.'s (2006) presentation.

Because, for the control–BW group, the incorrect geometry (W) is sometimes paired with the color of the walls associated with the correct corners (F1), this group visits the incorrect corners more often, and the incorrect geometry acquires more inhibitory value in this group than in the experimental group. The presence of this confusing cue in the control–BW group initially causes this group to perform worse than the control–W group, which is not attracted to the geometrically incorrect corners by a feature; this effect is barely visible in Figure 8B. The experimental group, which has two reliable cues to the location of the platform (the geometry and the wall color), performs best throughout training. Figure 8B shows the probability of a correct choice for the first 20 trials of this model. Figure 8A shows the first choice data reproduced from Pearce et al. (2006, Figure 3). Figure 8 shows the test predictions of the model (Figure 8D) and the experimental data (Figure 8C; reproduced from Pearce et al.'s, 2006, Figure 4). The model correctly predicts that the experimental group performs worst on the test. In neither model nor data are the differences among the groups very large.

In Experiment 3, Pearce et al. (2006) attempted to reproduce the overshadowing results from Experiment 2, using a blocking paradigm. An experimental group and a control group were first trained in a square enclosure that had two adjacent black walls. The platform, for both groups, was in a corner that was between a white wall and a black wall (e.g., black on the left, white on the right). After 14 sessions of training, both groups were given additional training in a rectangular enclosure that also had two adjacent black walls. For the experimental group, the platform was in a corner consistent with the color of the walls during training (e.g., black on the left, white on the right). For the control group, the rewarded corner now had wall colors opposite to those used during training (e.g., white on the left, black on the right). After a further 14 sessions of training, both groups were tested in either an all-black or all-white enclosure, without a platform. This test was repeated after 8 further sessions of training.

In the first test, neither group spent significantly more time in the correct than in the incorrect quadrant. However, in the second test, the control group performed significantly better than chance. Pearce et al. (2006) concluded that, with sufficient training, previous experience with the black walls blocked learning about the geometry in the experimental group.

Because the first phase of the experiment already contains a distinctive cue at each corner (provided by the two black walls), we begin by modeling this phase. All elements carry the associative strength they have at the end of this phase to the next phase of training (in the rectangle). Both groups have the same elements: B, present at all corners, and F1–F4, representing the distinctive wall color at each corner. There are no geometric cues in this phase of the experiment. It is possible to assume, as we did earlier, that the all-black corner has a higher salience and innate attractiveness than the other corners. A version of the model incorporating this assumption was constructed, and it was found that the difference it made to the results was negligible (because the all-black corner is never rewarded). For the second phase of the experiment, when both groups were trained in a rectangular enclosure, two more elements were added to the model: G, the rewarded geometry, and, W, the incorrect geometry.

In the second phase of training, the experimental group is rewarded in a corner consistent with the wall color of the first phase, whereas the control group is rewarded in the diagonally opposite corner. The initial values for elements F1–F4 in the second phase were taken from their value after the 20th trial of the first phase. The associative strength of element B was reset to 0.1 for the second phase, and elements G and W began with a value of 0 because there were no geometric cues in the first phase.

Here, as in the model of Experiment 1 of this article, what determines the outcome of the tests is the relative weight of V_G in the sum $V_B + V_G + V_W$, because elements B, G, and W are the only cues available at test time. The percentage of this sum captured by V_G is always greater in the control group than in the experimental group, and this difference increases with continued training. Thus, we expect that after sufficient training, the control group would be significantly better than the experimental group, precisely as observed by Pearce et al.'s (2006) Figure 4.

Experiment 4 of Pearce et al. (2006) expands and confirms the results of Experiment 3 by showing that they hold even when the rewarded corner is at an all-white or all-black corner. A model of this experiment is not presented.

Summary

As the examples given earlier show, the current model is capable of generating both cue competition and potentiation of geometry by featural information. The model makes clear that even when cue competition always occurs, choice in instrumental spatial learning does not always directly reveal it. Instead, results resembling potentiation or independent learning of cues may be found. In some cases, what we have termed *feature enhancement* may dampen the effects of overshadowing or blocking because of the way in which the course of learning is determined by prior learning and the animals' choices. The key, however, to the different results seen is in the differential effect of cue competition on the different elements, particularly in ambiguous enclosures. In such cases, where geometric cues interact by being present at some of the same corners as featural cues, the choices made by the subject can result in nondiscriminative elements, such as contextual elements or the incorrect geometry, being affected by cue competition more than the geometry. At test, it is the relative associative strengths of the remaining elements that determine whether overshadowing or potentiation is seen, despite the underlying cue competition in all situations.

Thus, we can state a few general rules concerning when cue competition is seen in geometry studies, according to our model. Cues (elements) that occur at the same locations influence each other's associative strengths. In the Rescorla–Wagner model, this influence is purely competitive, but in our model, which models operant tasks, cues that co-occur can also increase (or decrease) the probability of visiting the locations in which they occur, thus enhancing (or interfering with) learning about other cues at the same location. When this occurs at rewarded locations, it leads to feature enhancement (such as in Wall et al., 2004, in which an unambiguous cue at the rewarded location enhanced learning about the geometry of that location). Additionally, when cues that are innately attractive or highly salient (such as the all-black corner in Graham et al., 2006, and Pearce et al., 2006) co-occur with other cues, they also enhance learning about these other cues, whether or not they are at a rewarded location. When an attractive cue is at an unrewarded location, it may hasten the development of inhibition to the geometric cues at that location.

The model also emphasizes the important difference between geometrically ambiguous and unambiguous enclosures. In the model's terms, a geometrically ambiguous enclosure is one at which the correct geometry (element G in the examples given earlier) occurs at more than one location. In the absence of additional cues (such as corner panels or colored walls), the model predicts that subjects do better in the unambiguous enclosures (e.g., the KW group does better than the KBW group in Pearce et al.'s, 2006, Experiment 1). This difference, however, is usually swamped by the interactions between features at rewarded and unrewarded locations with geometric cues. The model also makes clear that although various kinds of features—one or more colored walls, a single beacon—may serve to disambiguate geometric cues, the nature and arrangement of such cues should be taken into account in geometry-learning studies.

The current model does not accurately predict all the results in the literature (e.g., group shape only in Graham et al.'s, 2006, Experiment 1 and group shape + no color in Experiment 3 of the same article). The model as presented here also does not capture generalization between similar cues, such as angles of the same size at different locations (e.g., the two right angles in a kite-shaped enclosure) because it treats each geometric cue as a unique combination of angle and left–right wall lengths. Decomposing the geometric cues into additional elements in the model would be straightforward and might be useful for some purposes.

Numerous studies of spatial learning in water tanks, radial mazes, and other laboratory environments have firmly established overshadowing and blocking as phenomena of spatial learning when geometric cues are not involved (Chamizo, 2003). For example, training with a beacon at the platform in a water tank blocks learning about landmarks later introduced around the tank (Roberts & Pearce, 1999). Our model makes clear, however, that it is not the nature of the spatial cues but rather the way in which they are arranged that leads to different results with geometry. Unlike the unambiguous arrays of unique objects typical of laboratory tests of landmark learning, the enclosures used in some of the studies modeled in this article render geometric cues ambiguous. In addition, in demonstrations of cue competition between landmarks and beacons, differences in salience among different classes of cues may favor some classes of cues overshadowing others. Landmarks are by definition further away from a goal than a beacon, and thus they are likely less salient. This could make them easily blocked in a situation like that used by Roberts and Pearce (1999).

Predictions of the Model

Apart from explaining the results of past studies, the current model makes several predictions that have not yet been tested. The feature enhancement effect, for example, is transient and operates only when the associative strengths are relatively small. When the associative strengths of the geometry and features are close to asymptote, the effects of cue competition become apparent in the animal's choices. The associative strength of the geometry begins to decrease, and tests in the absence of features should show overshadowing or blocking of the geometry. This requires that subjects be trained for a long time in, for instance, the initial phase of a blocking experiment, so that the blocking cue gains high associative strength as well as a high probability of being chosen.

Additionally, the model predicts that a feature at the rotational corner of a rectangular enclosure—as in the example of Cheng (1986), discussed in the Single-Choice Model section of this article, and Kelly and Spetch, (2004b)—becomes a conditioned inhibitor. If this is true, and the feature may be assumed to retain its associative strength when tested in a different context, it should be possible to test subjects' responses to the features in the absence of geometric cues. For instance, in the model of Cheng, F3, the feature at the rotational corner, and F2, the feature at the near corner, both become conditioned inhibitors. However, the associative strength of F3 is more negative that that of F2. If we test similarly trained subjects in a square enclosure (in which there are no geometric cues) in which two of the corners contain F3 and the other two contain F2, the model predicts that subjects prefer the corners that contain F2 over those containing F3, even though neither feature is ever paired with a reward during training, and F3 was paired with the correct geometry during training.

Finally, the assertion that geometry learning and feature learning interact associatively raises the possibility of designing traditional operant conditioning experiments that imitate geometry-learning experiments. If the results of these experiments are consistent with the results of geometry-learning experiments (as, e.g., the results of Cheng, 1986, are consistent with the results of $AX+$, $BX-$ discrimination studies), this would constitute further support for the current model. Kelly and Spetch (2004a, 2004b) have trained pigeons and people in a two-dimensional operant version of the task studied by Cheng (1986). The results for both species were similar to those reported by Cheng for rats, in that although features provided better information for solving the task, geometry was still learned, and in fact learning of geometry was enhanced by the availability of featural information. Kelly and Spetch (2004a) discussed their findings in terms of the correspondence between encoding processes in two-dimensional and three-dimensional spatial tasks, but the similarities between their results and those obtained in three-dimensional environments could as well result from the common underlying learning process depicted by our model and could have little to do with the fact that the tasks are both spatial.

Conclusion

The model presented here is an adaptation of the Rescorla–Wagner model of classical conditioning (Rescorla & Wagner, 1972) for geometry learning and indeed for instrumental choice more generally. It is a purely associative learning model that preserves the competition for associative strength inherent in the Rescorla–Wagner model and is shown to be capable of explaining several of the basic features of geometry learning, such as high levels of rotational errors during training, potentiation of geometry learning by features (feature enhancement), and an apparent lack of cue competition in some situations and not others. Of importance, it is precisely these features and their apparent incompatibility with associative learning processes that have been taken (e.g., by Pearce et al., 2001; Wall et al., 2004) to support suggestions (Cheng, 1986; Cheng & Gallistel, 2005; Gallistel, 1990) that geometry learning functions by means of a privileged process. Because spatial learning tasks are operant tasks, the model predicts that the choices made by subjects, which determine which stimuli they are exposed to, also determine the course of learning. The model does not, however, attempt to explain how geometry is encoded or what aspects of the geometry are encoded. It remains true that animals are somehow capable of extracting some aspect of the shape of an enclosure and encoding it in memory (see Cheng & Newcombe, 2005). It is likely that there is a perceptual or other low-level module that accomplishes this. However, as the present model shows, once geometric information has been encoded, there is no need to assume that it then enters into learning in any special way.

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Appendix

Multiple-Choice Version Example

This appendix presents a detailed example of how the multiple-choice version of the model is calculated. We model a water-maze analogue of Wall et al.'s (2004) Experiment 3, which served as an example for the single-choice version of the model. To the best of our knowledge, precisely this experiment has not been performed, although Hayward et al. (2003, 2004) reported several somewhat similar studies in which rats were trained in rectangular water tanks with a beacon at the goal (the platform). The current model correctly predicts Hayward et al.'s results (compare Panel A of Figure A1 in this article with the top panel of Hayward et al.'s, 2004, Figure 2), although we do not present a model of the control groups they used. Aside from illustrating the working of the model with a comparatively simple and (by now) familiar example, modeling this hypothetical experiment demonstrates that the multiple-choice version predicts the same pattern of results as the single-choice model. Because the only difference between the two versions of the model is the way in which choice probabilities are calculated, we expect the two versions to generally give similar, if not identical, results.

We assume that a group of rats is trained in a rectangular water tank to locate a submerged platform in one corner, as in Figure 1. The platform is marked by a distinctive beacon. Platform and beacon are always in the same corner of the enclosure. The model for this experiment has four elements: B, representing the elements present at all corners; G, the geometry of the correct and rotational corners; W, the geometry of the incorrect corners; and F, the beacon attached to the platform. We assume, as we did earlier, that the associative strength of B starts at 0.1, and that the associative strengths of all the other elements start at 0. All α values are set at 0.04.

In a rectangular or any other four-sided enclosure, there are 16 possible paths that a subject can take to the rewarded corner. These are listed in Table A1, along with the probability of occurrence of each path on Trial 1.

In Table A1, C refers to the correct corner, R to the rotational corner, N to the near corner, and F to the far corner (see Figure 1). Thus, for example, the path designated RFC refers to the rat choosing the rotational corner first, followed by the far corner, and then the correct corner.

$P_{R|}$ is the probability of choosing the rotational corner first. $P_{C|R}$ is the probability of choosing the rotational corner first and then the correct corner (i.e., it is the probability of C given that R). $P_{R|NF}$ is the probability of choosing the near corner first and then the far corner and then the rotational corner and so on. Note that choices of the correct corner after all the other corners have been visited (e.g., $P_{C|RNF}$) are not included, because this probability is always 1. In addition, choices of corners after choosing the correct corner are not included, because a visit to the correct corner always terminates the trial.

The initial probability of choosing each corner is calculated as before, by Equation 2: $P_L = V_L/\Sigma V_L$. Thus, the initial probability of first visiting the rotational corner for this example is given by the following:

$$P_{R|} = (V_B + V_G)/(4 \times V_B + 2 \times V_G + 2 \times V_W + V_F). \quad \text{(A1)}$$

Once a particular corner has been visited, the following choice is made from among only the remaining corners. The sum of the associative strengths of the elements at all the corners (ΣV_L), the denominator of the equation for P_L, needs to be modified to reflect the fact that the corner or corners already visited cannot be revisited. Thus, the probability of visiting the correct corner after having visited the rotational corner ($P_{C|R}$) is given by the following:

$$P_{C|R} = (V_B + V_G + V_F)/(3 \times V_B + V_G + 2 \times V_W + V_F). \quad \text{(A2)}$$

Here, the denominator is not the sum of all the associative strengths of the elements at all corners but is the sum of only the

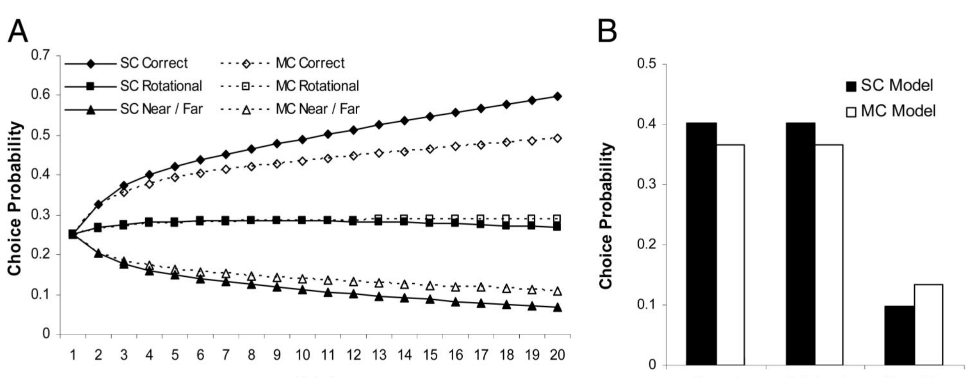

Figure A1. Comparison of acquisition and test results for the worked example of each version of the model. Panel A shows first choice probabilities for the first 20 trials of the example. Panel B shows choice probabilities for the test after 20 trials of training in both versions of the model. SC = single-choice version; MC = multiple-choice version.

(*Appendix continues*)

Table A1
List of Possible Paths and Sample Calculations of the Probability of Occurrence of Each Path for the Demonstration of the Multiple-Choice Model

Path	Probability	Numerical probability
C	$P_{C\|}$	0.25
RC	$P_{R\|} \times P_{C\|R}$	0.0833
NC	$P_{N\|} \times P_{C\|N}$	0.0833
FC	$P_{F\|} \times P_{C\|F}$	0.0833
RNC	$P_{R\|} \times P_{N\|R} \times P_{C\|RN}$	0.0416
RFC	$P_{R\|} \times P_{F\|R} \times P_{C\|RF}$	0.0416
NRC	$P_{N\|} \times P_{R\|N} \times P_{C\|NR}$	0.0416
FRC	$P_{F\|} \times P_{R\|F} \times P_{C\|FR}$	0.0416
NFC	$P_{N\|} \times P_{F\|N} \times P_{C\|NF}$	0.0416
FNC	$P_{F\|} \times P_{N\|F} \times P_{C\|FN}$	0.0416
RNFC	$P_{R\|} \times P_{N\|R} \times P_{C\|RN}$	0.0416
RFNC	$P_{R\|} \times P_{F\|R} \times P_{N\|RF}$	0.0416
NRFC	$P_{N\|} \times P_{R\|N} \times P_{F\|NR}$	0.0416
NFRC	$P_{N\|} \times P_{F\|N} \times P_{R\|NF}$	0.0416
FRNC	$P_{F\|} \times P_{R\|F} \times P_{N\|FR}$	0.0416
FNRC	$P_{F\|} \times P_{N\|F} \times P_{R\|FN}$	0.0416

Note. C = correct corner; R = rotational corner; N = near corner; F = far corner. Thus, for example, RFC represents the path rotational–far–correct. $P_{R|}$ = probability of choosing the rotational corner first; $P_{C|R}$ = probability of choosing the rotational corner first and then the correct corner (i.e., probability of C given that R); $P_{R|NF}$ = probability of choosing the near corner first, then the far corner, then the rotational corner, and so forth.

elements at corners C, N, and F (i.e., those corners from which the subject is making its choice).

Given that we have set all the initial associative strengths for the elements (see our earlier discussion), we can now calculate numerically the probability that each possible path occurs on the first trial. Thus, for example, the probability of the RC path occurring is given by the following:

$$P_{RC} = P_{R|} \times P_{C|R} = 0.25 \times 0.333 = 0.0833. \quad \text{(A3)}$$

The *Numerical Probability* column of Table A1 gives the probability for the occurrence of each possible path. The sum of the probabilities of all the paths is equal to 1.

The overall probability of a particular corner being visited on a given trial is the sum of the probabilities of all the paths that include that corner. Thus, using Table A1, we can calculate that the overall probability of visiting the rotational corner on a given trial is as follows:

$$\begin{aligned} P_R = {} & (P_{R|} \times P_{C|R}) + (P_{R|} \times P_{N|R} \times P_{C|RN}) + \\ & (P_{N|} \times P_{R|N} \times P_{C|NR}) + (P_{R|} \times P_{N|R} \times P_{F|RN}) \\ & + (P_{N|} \times P_{R|N} \times P_{F|RN}) + (P_{N|} \times P_{F|N} \times P_{R|FN}) \\ & + (P_{R|} \times P_{F|R} \times P_{C|RF}) + (P_{F|} \times P_{R|F} \times P_{C|FR}) \\ & + (P_{R|} \times P_{F|R} \times P_{N|RF}) + (P_{F|} \times P_{R|F} \times P_{N|RF}) \\ & + (P_{F|} \times P_{N|F} \times P_{R|NF}). \quad \text{(A4)} \end{aligned}$$

For the first trial of the present example, this comes to 0.5.

We can now calculate the changes in the associative strengths of the elements as a result of visits to the various corners. For example, the change in the associative strength of element G, present at the correct and rotational corners, is given by the following:

$$\begin{aligned} \Delta V_G = {} & \alpha(1 - V_{BFG}) + \alpha(0 - V_{BG})P_R = 0.04(1 - 0.1) \\ & + 0.04(0 - 0.1)0.5 = 0.034. \quad \text{(A5)} \end{aligned}$$

This equation has two terms, similar to Equation 6, one for each corner at which the element is present. Note that the first term, representing the learning resulting from visits to the correct corner, is not multiplied by a choice probability. This reflects the fact that the overall probability of choosing the correct corner on a given trial in the current version of the model is always 1 (i.e., the correct corner is visited on every trial). The changes in associative strengths of the other elements are calculated in a similar manner: $\Delta V_B = 0.03$, $\Delta V_F = 0.036$, $\Delta V_W = -0.004$.

Figure A1 shows a comparison of the results of this experiment, as given by both versions of the model. Panel A shows the choice probabilities for the first 20 trials as predicted by both the single-choice and multiple-choice versions. Panel B displays the predicted test results. The two models give similar, although not identical, results. Part of the difference, no doubt, is due to the different value for α used in the different models. Most importantly, however, both predict that the majority of errors are to the rotational corner and that animals will strongly prefer the geometrically correct location when tested in the absence of the feature.

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