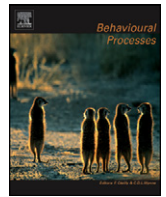




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Review

Modeling the effects of enclosure size on geometry learning

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ABSTRACT

Several recent studies have shown that chickens, fish, and humans trained to find a reward in a corner of a rectangular enclosure with distinctive features rely more on the geometry of the enclosure in small enclosures and rely more on the features in large enclosures. Here, these results are modeled using a recent associative model of geometry learning [Miller, N.Y., Shettleworth, S.J., 2007. Learning about environmental geometry: an associative model. *J. Exp. Psychol. Anim. B* 33, 191–212]. By adjusting the salience of either geometric or featural information or both the model is capable of reproducing much of the data on the effects of enclosure size on geometry learning.

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1. Introduction

Over the past 20 years, a wide range of species has been shown to be capable of using the geometry of an enclosure to locate a hidden target (reviewed in Cheng and Newcombe (2005)). For the most part, such experiments are performed in a rectangular enclosure with a reward hidden in one of its corners. Subjects are disoriented before being placed in the enclosure, to avoid the use of any directional cues external to the enclosure. After training is complete, probe tests in the absence of a reward show that fish, rats, monkeys, chickens, and humans all search for the reward primarily in two corners of the rectangle, namely the correct corner and the geometrically identical corner diagonally opposite to it, implying that the subjects have learned something about the shape of the enclosure. Often, subjects will ignore featural cues that could be used

to disambiguate the two geometrically identical corners, leading to suggestions that geometry is encoded in the brain by a dedicated 'geometric module' (Cheng, 1986; Gallistel, 1990) which is blind to non-geometric, featural, information. In support of the modular view, learning about the geometry of an enclosure appears to not be subject to associative processes of cue competition such as blocking or overshadowing by more informative features (e.g. Pearce et al., 2001; Wall et al., 2004).

Recently, an additional twist has been added to the literature on feature–geometry interactions. As first reported by Learmonth et al. (2002; see also Learmonth et al., 2001), the absolute size of the testing enclosure has an effect on whether features or geometry are used for reorientation. Learmonth et al. (2002) showed that children under the age of 6 years could not combine featural and geometric information (i.e. use features to disambiguate the rotational from the correct corner) in a small room (4 ft × 6 ft) but were able to combine the two kinds of information in a large room (8 ft × 12 ft). Similar results, implying that animals pay relatively more attention to geometric information in small than in

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large spaces, have since been reported for chickens (Vallortigara et al., 2005; Sovrano and Vallortigara, 2006; Chiandetti et al., 2007) and fish (Sovrano et al., 2005, 2007). The current paper attempts an explanation of these results, by fitting them into the framework of an existing model of geometry learning.

Miller and Shettleworth (2007) presented an associative model which is capable of generating many of the characteristics of geometry learning and is particularly successful at explaining the apparent lack of cue competition between geometric and featural information. The model assumes that the learning underlying spatial choice is described by a modified version of the classic Rescorla–Wagner equation in which all cues (elements, E) at a particular location (L) compete for associative strength. An element's success in capturing some of the finite amount of associative strength (λ) available depends on that element's salience (α). The change in associative strength (ΔV) on a given trial for any element is given by

$$\Delta V_E = \alpha P_L (\lambda - V_L). \quad (1)$$

Rescorla and Wagner's (1972) US-dependent learning rate parameter, β , is removed from the equation, for simplicity. The probability of choosing to search at a particular location (P_L) depends on what has been learned about the elements present at that location. The model defines the attractiveness of a location (r_L) as the sum of the associative strengths of the elements there ($\sum V_L$) if that sum is positive, and 0 otherwise (Miller and Shettleworth, 2008). P_L is then a function of the attractiveness of a location relative to the total attractiveness of all locations:

$$P_L = \frac{r_L}{\sum r_L}. \quad (2)$$

The apparent special features of geometry learning arise because the animal's choices determine the contingencies between cues and reward in a dynamic way and because some cues, such as certain shapes of corners, may be shared among locations.

Here, I attempt to apply Miller and Shettleworth's (2007) model to the data on feature–geometry interactions in enclosures of different sizes. I show that the model can explain the results in several different ways, by manipulating the salience values of either geometry or features or both, incidentally exposing a lack of discussion in the existing literature over which of the two types of information is affected by enclosure size. I also suggest several ways in which future research could test this interpretation of the data.

In the simulations they presented, Miller and Shettleworth (2007, 2008) set the salience (α) of all cues in all simulations at the same value, 0.15, with a few exceptions. This was done to show that the model explains key features of geometry learning, such as the apparent lack of cue competition, without resorting to ad hoc manipulations of its one free parameter. Here, the effects of enclosure size on feature–geometry interactions are modeled by allowing α to vary as a function of the size of the enclosure. Thus, the salience of geometry in small enclosures is given a higher value than that for large enclosures and the salience of features in large enclosures a higher value than that for small enclosures. These changes are sufficient to generate similar results to the reported data. In most cases, the experimental data can also be modeled by changing the salience values for features alone or geometry alone.

The model does not address the question why geometry should be more salient in small enclosures and/or features more salient in large enclosures. Several answers to this question have been suggested (see Section 4; reviewed in Chiandetti and Vallortigara (2008)) but none of them has yet been rigorously tested. In addition, no experimental data exist that attempt to separate the effects of enclosure size on learning of geometry from its effects on learning of features. The model only suggests a mechanism by which the preference for one kind of information over another might mani-

fest, that of adjusting the salience of different cues in differently sized enclosures.

2. Methods

All the simulations presented below were performed as previously described (Miller and Shettleworth, 2007, 2008). Simulations were all run using the Single Choice version of the model, which assumes that the subject makes one choice per trial and that not all trials end in reward, as all of the data to be modeled came from discrete choice experiments. Simulations were run for different numbers of trials, depending on the experiment being modeled: in all the animal studies modeled subjects were trained to a performance criterion and the simulation was trained to the same criterion; in the human studies modeled subjects were trained for a small number of trials and, as the model learns at a slower rate, simulations were trained for 30 trials before testing, which brought the model to a reasonable level of responding.

In all the experiments being modeled, rectangular or square enclosures were used and the reward was located at one of the corners of the enclosure. In a rectangular enclosure there are four corners the subject can search for the reward: the correct corner (C), the geometrically equivalent rotational corner (R), the corner along a short wall from the correct corner (the near corner, N), and the corner along a long wall from the correct corner (the far corner, F). In addition, in all of the simulations below, there are three categories of cues subjects can learn about: geometric cues, which consist of the correct geometry (represented in the simulations by element G, present at the correct and rotational corners) and the incorrect geometry (element W, present at the near and far corners); contextual cues that are present at all corners (element B); and featural cues such as colored walls or corner panels, the locations of which change by experiment. These designations are summarized in Fig. 1.

In the studies modeled here, two different kinds of featural cues were used. In some cases there were distinctive panels at each corner of the enclosure (Chiandetti et al., 2007; Vallortigara et al., 2005, Experiment 2). These are modeled by assigning a separate element to each panel (Fig. 1, right panel). In other cases, researchers used

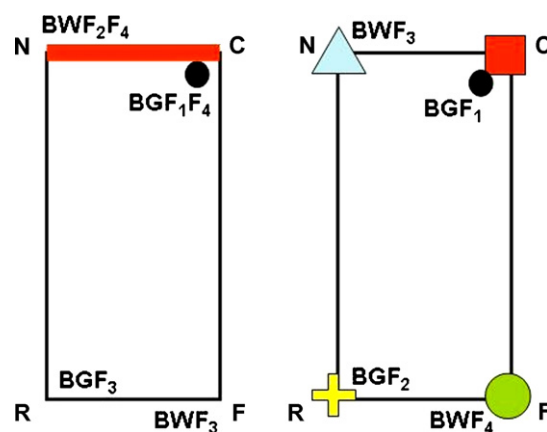


Fig. 1. Demonstration of model terms. The black circle indicates the rewarded location. Single letters indicate the corners: C, correct corner; R, rotational corner; N, near corner; F, far corner. Strings of letters indicate model elements present at each corner: B, context; G, correct geometry; W, incorrect geometry. Left panel: model construction for blue-wall experiments. The colored wall represents the blue-wall feature. F1, element representing the correct color pattern; F2, incorrect color pattern; F3, element representing all-white corners; F4, element representing corners with a colored wall on one side. Right panel: model construction for corner panel experiments. The colored shapes represent the distinctive corner panels. F1, element representing the feature at the correct corner; F2, feature at the rotational corner; F3, feature at the near corner; F4, feature at the far corner. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 1
Locations and salience values for the elements presented in Fig. 1.

E	Name	@Wall	@Panels	α_{Small}	α_{Large}
B	Context	All	All	0.15	0.15
G	Correct geometry	C, R	C, R	0.2	0.1
W	Incorrect geometry	N, F	N, F	0.2	0.1
F1	Feature 1	C	C	0.1	0.2
F2	Feature 2	N	R	0.1	0.2
F3	Feature 3	R, F	N	0.1	0.2
F4	Feature 4	C, N	F	0.1	0.2

Note: E: element symbol; name: description of the element; @wall: locations that each element is present at in blue-wall experiments, such as the left panel of Fig. 1; @panels: locations that each element is present at in corner panel experiments, such as the right panel of Fig. 1; α_{Small} : salience value for each element in the small enclosure; α_{Large} : salience value for each element in the large enclosure. Locations are C (correct), R (rotational), N (near), and F (far).

the blue-wall task, in which one entire wall of the enclosure is a different color to the other three (Vallortigara et al., 2005, Experiment 1; Sovrano et al., 2005, 2007; Sovrano and Vallortigara, 2006; Learmonth et al., 2002). Such experiments are also modeled using four different feature elements: one for the pattern of color at one end of the colored wall (e.g. blue on the left, white on the right), one for the pattern of color at the other end (blue on the right, white on the left), a third for any corner that has one colored and one non-colored wall (i.e. both of the above corners), and a fourth for all-white corners (Fig. 1, left panel).

The associative strength of each element in the model only changes when corners containing that element are visited on a training trial. For each simulation a table is given summarizing which corners each element is present at. Table 1 displays the element summary for the two examples shown in Fig. 1.

In all of the simulations presented, the salience values (α) of the different categories of elements were set as follows (Table 1): contextual cues (element B) were always assigned a salience value of 0.15 (as in Miller and Shettleworth (2007)); geometric cues (elements G and W) were assigned a value of 0.2 in small enclosures and 0.1 in large enclosures; and featural cues, whether they represented a colored wall or a corner panel, were assigned a value of 0.1 in small enclosures and 0.2 in large enclosures. These values reflect the findings cited above that imply that geometry is more salient in smaller than larger enclosures and that features are more salient in larger than smaller enclosures. However, it is also true that similar results may be obtained by modifying the salience of only one type of information (geometric or featural). This was tested for each simulation, with the salience values for the unmodified type of information set at 0.15. Results of these tests are presented in detail only for the first simulation.

Element B always had an initial associative strength of 0.1, so that the overall associative strength of all corners did not begin at 0 (see Miller and Shettleworth (2007)). All other elements began with an associative strength of 0. All other details of the simulations are as in Miller and Shettleworth (2007, 2008). Results for acquisition trials are not presented here as they were not presented in the studies being modeled.

3. Results

In Miller and Shettleworth's model, the available cues in each experiment are represented by elements in the model. A simple scheme is used to decide which elements to use in constructing each simulation: one element is assigned for every cue that does not exactly co-occur with any other cue. Thus, for instance, if two corners of a rectangular enclosure share a wall color that is different from that of the other two corners, and also have the same geometry (e.g. a long wall on the left and a short wall on the right), only one element is needed to describe both cues. If, however, a third corner

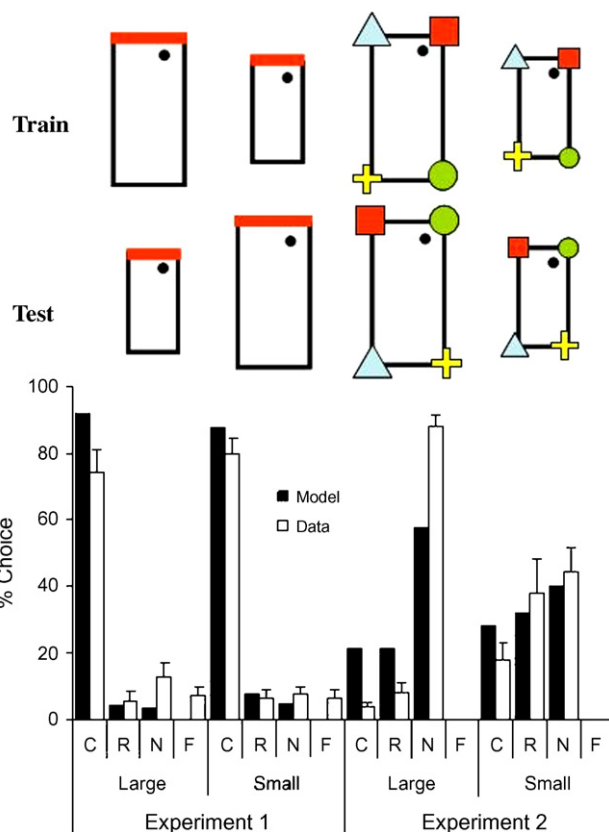


Fig. 2. Results and simulation of Vallortigara et al. (2005). The top part of the figure shows a schematic of the two experiments and the histogram below shows the experimental (white bars) and simulated (black bars) test results. The top row schematic shows the enclosures used during training, the second row those used for testing. Each schematic is above the results for the corresponding experiment. The colored wall in the schematics represents the blue wall used in Experiment 1. The colored shapes at the corners of the enclosures represent the corner panels used during Experiment 2. The small black circle represents the correct (rewarded) corner. Data for the experimental results were extracted from Vallortigara et al. (2005). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

shares the same wall color, an additional element must be added to the simulation to represent the wall color. Descriptions of the elements used are provided for each simulation.

3.1. Vallortigara et al. (2005)

Vallortigara et al. (2005, Experiment 1) trained chicks in either a large or small rectangular enclosure in which one short wall was blue (Fig. 2, top left). Chicks were then tested in an enclosure of the opposite size to their training enclosure with the blue wall still present. Chicks trained in both enclosure sizes searched predominantly in the correct corner at test.

In Experiment 2, chicks were trained in either a large or small enclosure with distinctive panels at each corner (Fig. 2, top right). Chicks were then tested in an enclosure of the same size as their training enclosure in which all the features had been rotated one corner along, placing the geometric and featural information in conflict. This is called an affine transformation of the enclosure. Chicks trained in the large enclosure chose the corner containing the feature that had been correct during training more often than any other corner, and more often than chicks that had been trained in the small enclosure. Chicks trained in the small enclosure chose the two geometrically correct corners more often than chicks trained in the large enclosure. The bottom part of Fig. 2 shows the results of both experiments (white bars). In both experiments, chicks were

Table 2
Model structure for the simulation of Vallortigara et al. (2005).

E	@Exp1	Exp2 train	Exp2 test	α_{Small}	α_{Large}
B	All	All	All	0.15	0.15
G	C, R	C, R	C, R	0.2	0.1
W	N, F	N, F	N, F	0.2	0.1
F1	C	C	N	0.1	0.2
F2	N	R	F	0.1	0.2
F3	R, F	N	R	0.1	0.2
F4	C, N	F	C	0.1	0.2

Note: @Exp1: locations each element is present at in Experiment 1; Exp2 train: locations each element is at during training trials in Experiment 2; Exp2 test: locations each element is at during the test in Experiment 2; all other symbols as in Table 1.

trained to a criterion of 90% correct, and the simulation was trained to the same criterion.

There are 7 elements (cues) in the simulation of Vallortigara et al.'s (2005) Experiment 1 (for detailed explanations of how these simulations are constructed see Miller and Shettleworth (2007)): B, representing contextual features present at all corners; G, the geometry of the correct and rotational corners; W, the geometry of the incorrect corners; and F1–F4, representing the different patterns of color at each corner (see Fig. 1, left panel). There are also 7 elements in the simulation of Experiment 2: B, G, and W, as above; and F1–F4 representing the distinctive panels at each corner (see Fig. 1, right panel). The locations and salience values of all the elements in the simulation are summarized in Table 2. The simulation reached the training criterion after 73 trials, on average (Experiment 1: 85 in the small enclosure, 55 in the large enclosure; Experiment 2: 90 in the small enclosure, 64 in the large enclosure), and was therefore run for 73 trials before testing.

The results of the simulated test are presented in the bottom part of Fig. 2 (black bars), and match the pattern of the experimental data. The simulation predicts that chicks will search in the correct corner in both enclosures in the test of Experiment 1. In Experiment 2, however, the simulation predicts a difference between the two groups in the affine-transformed enclosure.

It is worth explaining why the model predicts the results of these experiments. When the salience of geometry in the simulation is made higher in the small enclosure, the geometry element (G) in that enclosure captures more of the associative strength during training and, when features and geometry are placed in conflict by the affine transformation of the enclosure (in Experiment 2), the simulation predicts that geometry will exert a stronger pull on searching behavior in the small enclosure. In addition, increasing the salience of featural information in the large enclosure causes the feature elements (F1–F4) to capture more of the associative strength in that enclosure, leading the simulation to predict greater reliance on features in the large enclosure.

The above explanation also demonstrates why it is sufficient, in this case, to modify the salience of only one type of information, geometric or featural. The effects described above reinforce each other. Increased salience of geometry in small enclosures leads to greater reliance on geometry in small enclosures which is indistinguishable, in this case, from an increased reliance on features in large enclosures. To demonstrate this, the current simulation was run two more times, each time with only the salience values of one type of information modified by enclosure size. The results of the simulations are presented in Fig. 3, which shows that the differences in test results between the different simulation methods are negligible.

Whilst not modeled here separately, Sovrano et al. (2005) trained fish (*Xenotoca eiseni*) in the same task as Experiment 1 of Vallortigara et al. (2005), with similar results. Ratliff and Newcombe (2007, Experiment 1) performed a similar experiment to Vallortigara et al.'s Experiment 2 using adult human subjects, and also obtained a similar pattern of results.

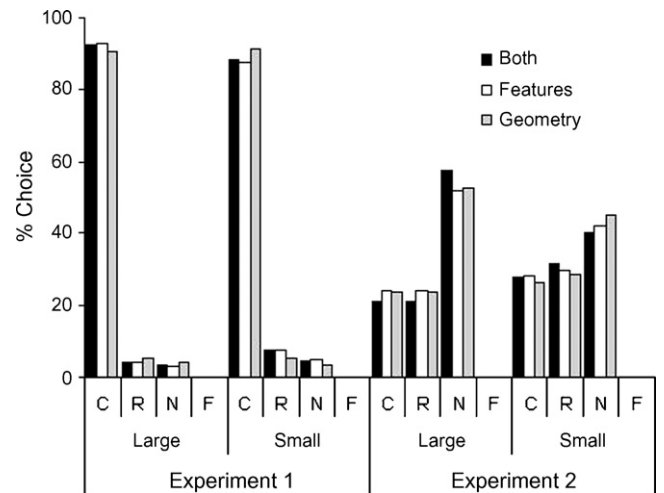


Fig. 3. Effects of changing the salience of features and/or geometry. Results for the simulation of Vallortigara et al. (2005), as in Fig. 2, when either only the salience of features (white bars) or only the salience of geometry (grey bars) or both (black bars) are changed. All unchanged salience values were set at 0.15.

3.2. Chiandetti et al. (2007)

Chiandetti et al. (2007) trained chicks in three experiments to find a food reward in a rectangular enclosure that had a distinctive panel in each corner. Half the chicks were trained in a large enclosure (70 cm × 35 cm), and half in a small enclosure (35 cm × 17.5 cm). The top part of Fig. 4 displays a schematic of the three experiments. In Experiment 1, after reaching the 90% correct training criterion, chicks that had been trained in the large enclosure were tested in the small enclosure and those that had been trained in the small enclosure were tested in the large enclosure. In addition, at testing the enclosure was affine transformed (all the corner panels were rotated one corner along; Fig. 4, top left). In Experiment 2, after an identical training procedure, chicks were tested in rectangular enclosures that were the same size as their training enclosure that had, in addition, all the corner panels removed (Fig. 4, top center). Finally, in Experiment 3, after the same training procedure, chicks were tested in square enclosures. Chicks that had been trained in the large enclosure were tested in a large square and chicks that had been trained in the small enclosure were tested in a small square. The square enclosures contained the same corner panels as during training (Fig. 4, top right).

The bottom part of Fig. 4 shows Chiandetti et al.'s (2007) test results for all three experiments (white bars). In Experiment 1, in both enclosure sizes, chicks chose predominantly the corner containing the panel that had been rewarded during training, despite the fact that it now resided in a geometrically incorrect corner. In Experiment 2 chicks searched primarily in the geometrically correct corners in both enclosure sizes, but chicks that were trained in a small enclosure performed significantly better than chicks trained in a large enclosure. In Experiment 3, chicks in both square enclosure sizes mostly chose the feature that had been paired with reward during training, but chicks trained in the large enclosure performed significantly better than chicks trained in the small enclosure.

In summary, chicks trained in either a large or small rectangular enclosure learned about both features and the geometry of the enclosure, but tended to rely on the features when the two types of information were placed in conflict. In addition, the behavior of chicks trained in a small enclosure was controlled more by geometry than that of chicks trained in a large enclosure, who relied more on features.

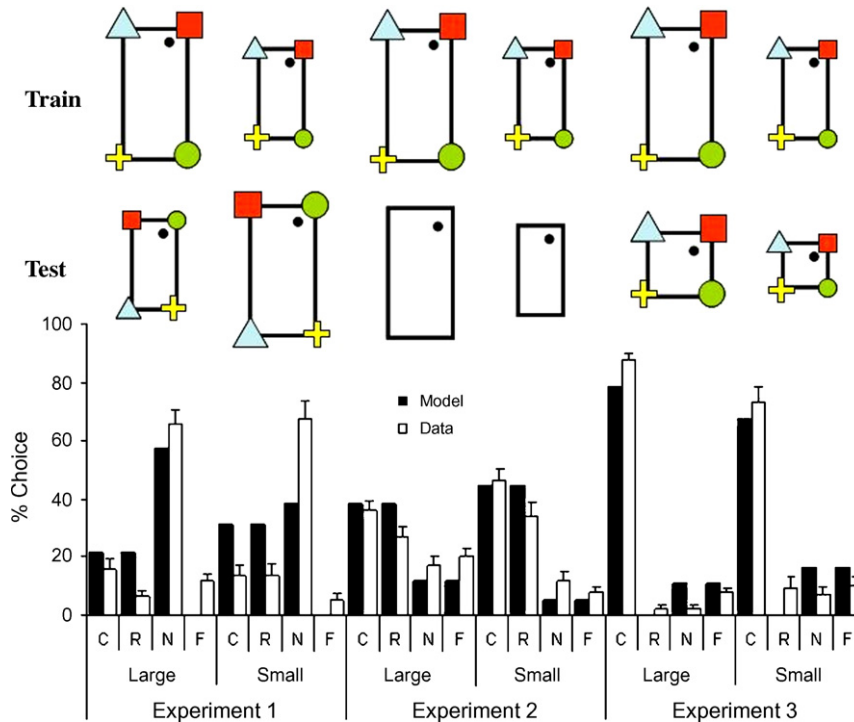


Fig. 4. Results and simulation of Chiandetti et al. (2007). Data for the experimental results and error bars were extracted from Chiandetti et al. (2007).

The simulations of these three experiments are identical to that of Vallortigara et al.'s (2005) Experiment 2, modeled above. The structure of the simulation is presented in Table 3. All three experiments are simulated in the same way, since the experiments differed only in the testing enclosures they used. The simulation reached the training criterion after 73 trials, on average.

The simulation results are presented in the bottom part of Fig. 4 (black bars) and mostly match the pattern of the experimental results. An identical pattern of results is obtained by modifying only the salience of geometry or only the salience of features, for the reasons discussed above.

For Experiment 1, the simulation does not match the experimental data very well. In the experiment, chicks were tested in an affine-transformed enclosure. The simulation predicts that chicks trained in the large enclosure, for whom features have a higher salience, should follow the correct feature (now at the near corner) more than chicks trained in a small enclosure for whom geometry is more salient, a difference not observed in the experimental data (this is also true of the simulation with only featural or only geometric salience values changed). One possible reason for this discrepancy is that the chicks were tested in an enclosure of the opposite size to their training enclosure. As the model assumes that associative strengths do not change between training and testing (i.e. that the test measures prior learning), the size of the enclosure at test has no effect on the results. However, changing the size of the enclosure at test obviously does have an effect

Table 3
Model structure for the simulation of Chiandetti et al. (2007).

E	@Train	Exp1 test	Exp2 test	Exp3 test	α_{Small}	α_{Large}
B	All	All	All	All	0.15	0.15
G	C, R	C, R	C, R	–	0.2	0.1
W	N, F	N, F	N, F	–	0.2	0.1
F1	C	N	–	N	0.1	0.2
F2	R	F	–	F	0.1	0.2
F3	N	R	–	R	0.1	0.2
F4	F	C	–	C	0.1	0.2

Note: All symbols as in Tables 1 and 2.

on the performance of live subjects. Ratliff and Newcombe (2007, Experiment 2) performed a similar experiment to the one under discussion using adult human subjects, in which a single feature was rotated one corner along and the size of the enclosure changed between training and testing. Contrary to Chiandetti et al.'s results, they found greater reliance on features in subjects trained in the large enclosure, although the difference failed to reach significance. In addition, Vallortigara et al. (2005, Experiment 2), in the study modeled above, performed a virtually identical experiment in an affine-transformed enclosure that did not change in size between training and testing. They found a significant difference between chicks trained in large and small enclosures in the direction predicted by the model.

3.3. Sovrano and Vallortigara (2006)

Sovrano and Vallortigara (2006) trained chicks in an identical procedure to Vallortigara et al.'s (2005) Experiment 1, except that the blue wall could be either a long or short wall of the rectangular enclosure. Chicks were tested in an enclosure of the same size as their training enclosure in which the blue wall was shifted one wall along. Thus, chicks trained with a short blue wall were tested with a long blue wall and chicks trained with a long blue wall were tested with a short blue wall (Fig. 5, top).

At test, chicks in all groups chose mostly the two corners that bordered the blue wall. Chicks trained in a large enclosure chose mostly the near corner, which had the same pattern of color as the rewarded corner during training (Fig. 5, top left). Chicks trained in a small enclosure chose mostly a geometrically correct corner that bordered the blue wall (the rotational corner for chicks trained with a short blue wall, the correct corner for those trained with a long blue wall), even though the pattern of color at that corner was opposite to the pattern rewarded during training (Fig. 5, top right). The results of the experiment are shown in the bottom part of Fig. 5 (white bars).

The structure of the simulation of this experiment is identical to that of Vallortigara et al.'s (2005) Experiment 1, above, and is sum-

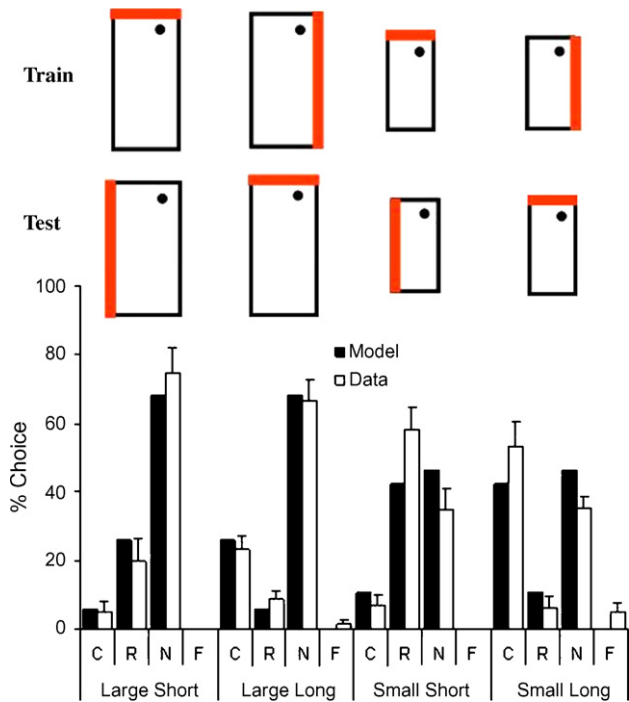


Fig. 5. Results and simulation of Sovrano and Vallortigara (2006). Data for the experimental results were extracted from Sovrano and Vallortigara (2006).

marized in Table 4. The simulation was trained for 67 trials before testing (the average number of trials it took to reach criterion).

The results of the simulation are shown in the bottom part of Fig. 5 (black bars). The simulation matches the results of chicks trained in large enclosures very well. However, the simulation does not predict the pattern of results found for chicks trained in small enclosures. Specifically, chicks trained with a short blue wall chose the rotational corner (which matches the rewarded geometry of training and is adjacent to a blue wall) significantly more than the near corner (which matches the pattern of color that was rewarded during training) and chicks trained with a long blue wall chose the correct corner (which matches geometry and is adjacent to a blue wall) significantly more than the near corner (which matches the pattern of color rewarded during training). The simulation gives opposite results, although it correctly predicts that the differences between the choices in the small enclosure are of a smaller magnitude than in the large enclosure (i.e. the preferences of chicks trained in the large enclosure are more pronounced). Interestingly, with less training (e.g. 30 trials instead of 67), the simulation gives the correct pattern of results. As the number of training trials is increased, the element representing the pattern of color at the correct corner (F1) captures more of the associative strength, as it is the best predictor of reward, and thus dominates the behavior of the simulation at test. The simulation thus predicts that with increased training, chicks trained in the small enclosure would show the same

Table 4
Model structure for the simulation of Sovrano and Vallortigara (2006).

E	Short	Long	α_{Small}	α_{Large}
B	All	All	0.15	0.15
G	C, R	C, R	0.2	0.1
W	N, F	N, F	0.2	0.1
F1	C	C	0.1	0.2
F2	N	F	0.1	0.2
F3	R, F	R, N	0.1	0.2
F4	C, N	C, F	0.1	0.2

Note: All symbols as in Table 1. Short: the enclosure with a short blue wall; long: the enclosure with a long blue wall.

pattern of results as chicks trained in the large enclosure. A similar pattern of results is obtained by changing only the salience of geometry or only that of features.

Sovrano et al. (2007) replicated Sovrano and Vallortigara's (2006) experiment in fish (*X. eiseni*) using the same training and testing paradigm. Fish trained in a large enclosure performed similarly to chicks whereas fish trained in a small enclosure, unlike chicks, distributed their searches almost equally between the geometrically correct corners and the corner that matched the pattern of color that was rewarded during training. This implies that in fish, the primacy of geometric over featural information in small spaces is more pronounced than it is in chicks. Alternatively, the rate at which fish learn about geometry and/or features may be quite different from the learning rate of chicks.

3.4. Learmonth et al. (2002)

Learmonth et al. (2002) allowed children aged between 3 and 6 years to search for a target (a green square) in one corner of a rectangular enclosure that had one short blue wall (Fig. 6, top). Half the children were trained in a small room (4 ft × 6 ft) and half in a large room (8 ft × 12 ft). The results of the experiment are presented in the bottom part of Fig. 6 (white bars). Children aged 3–5 years searched for the target equally at both geometrically correct corners in the small room, failing to use the blue wall to disambiguate the correct from the rotational corner, whereas 3–5-year olds tested in the large room searched primarily in the correct corner (Fig. 6, bottom left). 6-Year-old children searched primarily in the correct corner in both room sizes (Fig. 6, bottom right). Thus, in human children, not only is geometric information more important in small enclosures but the ability to use featural information to distinguish between geometrically identical corners varies with age as well.

The structure of the simulation of this experiment is similar to that of the blue-wall experiments modeled above and is summarized in Table 5. However, there is nothing in the model with which to simulate changes resulting from age differences. Obviously, the pattern of results presented by Learmonth et al. (2002) could be reproduced by altering the relative salience values of geometry and features as a function of age, but there is no theoretical justification for doing so. There is, however, another way to model the results.

In Rescorla and Wagner's (1972) model, in addition to α there is a second parameter, β , that limits the rate at which the associative strengths of cues change. β is a learning rate parameter assumed to be dependent on the unconditioned stimulus. In Miller and Shettleworth's (2007) formulation of the model, β was given a constant value of 1, for simplicity. Assuming that the relevant

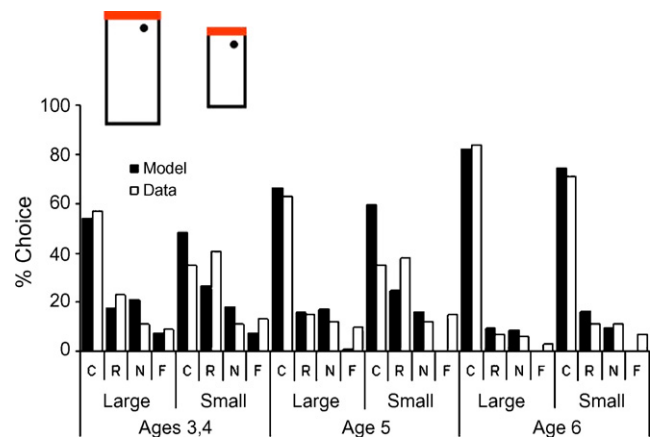


Fig. 6. Results and simulation of Learmonth et al. (2002). The same enclosures were used for all three age groups; only one schematic is shown. Data for the experimental results were extracted from Learmonth et al. (2002).

Table 5
Model structure for the simulation of Learmonth et al. (2002).

E	@Train/test	α_{Small}	α_{Large}
B	All	0.15	0.15
G	C, R	0.2	0.1
W	N, F	0.2	0.1
F1	C	0.1	0.2
F2	N	0.1	0.2
F3	R, F	0.1	0.2
F4	C, N	0.1	0.2

Note: All symbols as in Table 1.

difference for geometry learning tasks between 3- and 6-year-old children is that the latter learn at a greater rate, this difference can be modeled by returning β to the model and assigning a higher β to older children. The equation for change in associative strength on a given trial then becomes:

$$\Delta V_E = \alpha \beta P_L(1 - V_L). \quad (3)$$

Thus, the simulation of Learmonth et al.'s (2002) experiment had the same structure as previous blue-wall simulations, but β increased with age. The value of β was set at 0.2 for 3–4-year-old children, 0.6 for 5-year olds, and 1 for 6-year olds (i.e. 6-year-old children were modeled by the same equation as non-humans). The simulation was trained for 30 trials and the results are presented in the bottom part of Fig. 6 (black bars). The simulation matches the experimental data well for 3–4-year-old children and for 6-year olds. The simulation results for 5-year-old children, whose results are intermediate to those of the other age groups, do not match the data as well. The agreement between the simulation and the data can be improved by setting the β for 5-year-old children closer to the value for 3–4-year olds (0.2). This implies that the increase in learning rate as a function of age is far from linear, and the difference between 6- and 5-year olds much greater than that between 5- and 4-year olds.

Interestingly, a similar pattern of results may be obtained by modifying only the salience values of featural information, but not by modifying only the salience of geometric information. Indeed, making the salience of geometry greater in small enclosures without an accompanying change in featural salience leads to the simulation choosing the correct corner more often in small than large enclosures at all ages, opposite to the experimental results. Adjusting the salience of features alone causes the simulation to choose the correct corner more often in the large enclosure at all ages, as the children did.

If the relevant difference between 6-year olds and younger children is that the former learn at a faster rate, this implies that increased amounts of training should overcome the reported inability of young children to combine geometric and featural information in small spaces. Twyman et al. (2007) have recently reported data that support this view. They have shown that if given either additional training trials or pre-training with the colored wall feature (in a triangular room) children as young as 4 years can use featural and geometric information together even in a small room (4 ft \times 6 ft, the same size as that used by Learmonth et al. (2002)). Studies comparing geometry learning in non-humans at different developmental stages could help determine the role of learning rate in the use of features to inform geometric knowledge.

4. Discussion

As the simulations presented above show, Miller and Shettleworth's (2007) model is capable of explaining most of the reported data on the effects of enclosure size on feature–geometry interactions by allowing the salience of either or both kinds of information to vary with enclosure size. Thus, the model explains

the reported effects as either increased salience of geometric information in small enclosures, increased salience of featural information in large enclosures, or both. The model does not distinguish between these possibilities, nor do the data exist to disambiguate them. As demonstrated in detail for the simulation of Vallortigara et al.'s (2005) study, modifying only the salience of one type of information, featural or geometric, is often sufficient to recreate the experimental results (this is true of all the non-human data modeled here). This is primarily due to the design of current experiments, in which subjects are always trained with both featural and geometric information at the same time. If the suggested changes in the salience of geometric and featural information occur independently of each other, or if only one of them is affected by enclosure size, then the relative contribution of each type of information to the enclosure-size effect could be tested by training subjects with each type of information separately. If subjects trained in a small featureless enclosure were found to be better at learning geometry than subjects trained in a large featureless enclosure, this would imply that the salience of geometric cues is affected by enclosure size, independently of any effect of features. Conversely, if a difference were found between subjects trained to use features in small or large square enclosures, this would imply an effect of enclosure size on the salience of featural information.

Another uncontrolled variable in some of the studies reviewed here (e.g. Sovrano and Vallortigara, 2006) is the size of the features used, especially when the feature is one whole wall of the enclosure. It seems obvious that larger features would have a higher salience, as several authors have suggested (e.g. Cheng and Newcombe, 2005).

Miller and Shettleworth's model does not explain why the relative salience values of geometry and/or features should change as a function of enclosure size. Several other authors have suggested explanations: Cheng and Newcombe (2005) suggested that features are relied upon more in larger enclosures because the features used are themselves larger than those used in small enclosures. Newcombe and Ratliff (2007) suggested that the possibility of moving around within the enclosure, which is greater in larger enclosures, affects the encoding of featural information. They have also suggested an 'adaptive combination' approach to the complexities of feature–geometry interactions, in which the relative weighting of different kinds of information depends on how reliable they are. This differential weighting could be considered an analogue of the changes in salience values proposed here. Sovrano et al. (2005, 2007; see also Vallortigara et al., 2005; Chiandetti et al., 2007; Sovrano and Vallortigara, 2006) suggested that animals are evolutionarily prepared to use only distant cues as landmarks, and that features in small enclosures may be too close to the subject to be used. Sovrano and Vallortigara (2006, Fig. 3) also suggested that animals are able to view two entire walls at once in small enclosures, and thus extract the relevant geometric information, but cannot see two whole walls in large enclosures, where the walls are longer, and thus tend to rely more on featural information in the larger spaces.

The latter two of these explanations may be easily tested against the model presented here by using three (or more) different enclosure sizes. If animals use only cues beyond a certain distance as landmarks, or if being able to view two whole walls is a prerequisite for relying on geometric information, the transition from small-enclosure tactics (relying primarily on geometric information) to large-enclosure tactics (relying primarily on featural information) should be sudden, as it depends on an enclosure size threshold being passed. According to this view, in any enclosure small enough for two entire walls to be seen or in which the walls are 'too close' subjects will rely primarily on geometry. As soon as the enclosure size is increased such that the walls are far enough away or such

that two opposite corners are beyond the limits of the animals' field of view, subjects should switch to relying on featural information. Miller and Shettleworth's (2007) model, on the other hand, suggests that the salience values of geometric and/or featural information vary smoothly as a function of enclosure size, and predicts a linear relationship between enclosure size and reliance on geometric information.

Miller and Shettleworth's model does not explain all of the data reviewed here. In some cases, there are obvious effects that are not captured by the relatively simple associative process of the model. For instance, as associative strengths do not change during testing in the model, changing the size of the enclosure between training and testing has no effect on the simulation results. However, as discussed above, such an effect is clearly visible in the experimental data. One implication of this comparison is that choice in tests of geometry learning is not driven solely by what has been learned during training. Subjects may suffer from a generalization decrement if the testing enclosure is different from that during training (as suggested by e.g. Pearce et al. (2006)), or subjects may be learning about the cues during testing, both effects which are not captured by the model.

Recently, Cheung et al. (2008) have proposed a view-based matching model of geometry learning which is capable of explaining some results that Miller and Shettleworth's (2007) model cannot (reviewed in Cheng (2008)). Although it has not yet been tested on the experimental data reviewed here, the view-based model may also do better at predicting the results of experiments in which the testing enclosure is different to the training enclosure. Miller and Shettleworth's model, unlike the view-based model, requires explicit encoding of any cue that can be learned, as elements in the simulation. In the simulations presented here, the size of the enclosure is not directly encoded by any element, which is why the model fails to predict the effects of changing the size of the enclosure between training and test. The view-based model should not suffer from this problem, although it may have other limitations (Cheng, 2008).

It has also been suggested (Cheng, 2008) that a configural model, such as the one suggested by Pearce (1994), may provide a better match to some of the geometry learning data than Miller and Shettleworth's (2007) model. In a configural model, all the cues presented on a given trial – comparable to all the elements present at a given location – enter into an association with the reward, or lack of reward, as a single unit. On later trials the responses elicited by different combinations of cues are assumed to be the result of differing levels of generalization from previously experienced cue configurations. Such configural models remain to be developed for the geometry learning literature.

Miller and Shettleworth's model retains a key feature of the Rescorla–Wagner model, the competition for associative strength between cues that co-occur. As a result, whenever a particular cue is present that is the best predictor of reward, such as a distinctive panel at the correct corner, that cue will, after sufficient training, usurp control of the simulation's choices and swamp any distinctions due to different salience values in small or large enclosures. Thus, the number of trials for which the model is trained in the above simulations has an effect on the pattern of results. If the simulations are run for a greater number of trials (e.g. 100), the pattern of results becomes identical at all enclosure sizes, with simulations in any enclosure size relying primarily on features. The model therefore predicts that the enclosure-size effects observed in the experiments reviewed here will disappear if subjects are over-trained, with all subjects eventually relying on the features in any size of enclosure. This prediction is demonstrated in the simulation of Learmonth et al.'s (2002) experiments, where the increased rate of learning of older children has the same effect as additional training trials. Importantly, featural information will only come to

be relied upon if features predict reward better than geometry, as they do in all the experiments modeled here, since the model treats all types of information equally. Thus, the reason that featural information dominates in simulations run for many trials is unrelated to any changes in salience that result from the size of the enclosure. If featural information were made as ambiguous as geometric information (e.g. by placing identical features at each pair of geometrically equivalent corners) or completely absented, the differences between small and large enclosures would persist, however much training the simulation were given.

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