The Abdus Salam
International Centre for Theoretical Physics

United Nations
Educational, Scientific and
Cultural Organization

IAEA
International Atomic Energy Agency

1860-17

Borsellino College 2007. Spike Trains to Actions: Brain Basis of Behavior

3 - 14 September 2007

Behavioral Ethology

(Background information: Dissecting the geometric module)

Giorgio VALLORTIGARA
Dept. of Psychology and B.R.A.I.N. Centre for Neuroscience, Univ. of Trieste, Italy

Research Article

Dissecting the Geometric Module

A Sense Linkage for Metric and Landmark Information in Animals' Spatial Reorientation

Valeria Anna Sovrano[1] and Giorgio Vallortigara[2]

[1]*Department of General Psychology, University of Padua, Padua, Italy, and* [2]*Department of Psychology and B.R.A.I.N. Centre for Neuroscience, University of Trieste, Trieste, Italy*

ABSTRACT—*Disoriented children can use geometric information in combination with featural information to reorient themselves in large but not in small spaces; somewhat similar effects have been found in nonhuman animals. These results call for an explanation. We trained young chicks to reorient to find food in a corner of a small or a large rectangular room with a distinctive featural cue (a blue wall)—a task similar to that used with children. Then we tested the chicks after displacement of the feature to an adjacent wall. In the large enclosure, chicks chose the corner that maintained the correct arrangement of the featural cue with respect to sense, whereas in the small enclosure, they chose the corner that maintained the correct metrical arrangement of the walls with respect to sense. On the basis of these findings, we propose a simple model that can explain the effects of room size on spatial reorientation.*

Animals move about in space, and it is crucial for them to be able to retain information about their surroundings. When animals are spatially disoriented in such a way that they cannot keep track of their movements (e.g., when they are moved passively in the absence of visual information), reorientation must be based on spatial features of the environment, which may be geometric or nongeometric. For instance, in the so-called blue-wall task, rats (Cheng, 1986) and human children (Hermer & Spelke, 1994, 1996) who are disoriented in a rectangular room with a single wall of a contrasting color use the shape of the room to reorient themselves, but they fail to use the color of the distinctive wall as landmark information to resolve the 180° ambiguity imposed by the room's symmetry.

Other species have, however, proved able to conjoin geometric (the shape of the room) and nongeometric (the blue wall) information to reorient themselves (see review by Cheng & Newcombe, 2005). This ability has been demonstrated in fish (redtail splitfins: Sovrano, Bisazza, & Vallortigara, 2002, 2003; goldfish: Vargas, Lopez, Salas, & Thinus-Blanc, 2004), birds (domestic chicks: Vallortigara, Zanforlin, & Pasti, 1990; Vallortigara, Pagni, & Sovrano, 2004; pigeons: Kelly, Spetch, & Heth, 1998; Vargas, Petruso, & Bingman, 2004), and mammals (rhesus monkeys: Gouteux, Thinus-Blanc, & Vauclair, 2001; tamarins: Deipolyi, Santos, & Hauser, 2001).

A further complication arises from the fact that the spatial scale of the environment in which the organisms are tested can play a crucial role in their ability to conjoin geometric and landmark information. Learmonth, Newcombe, and Huttenlocher (2001) and Learmonth, Nadel, and Newcombe (2002) replicated the original finding of Hermer and Spelke (1994) with 5-year-old children, concluding that they failed to conjoin geometric and landmark information in a small room (4 ft × 6 ft), using geometric information only, but succeeded in a large room (8 ft × 12 ft).

Work with animals has yielded more complex results, but with a somewhat similar pattern. Fish (redtail splitfins, *Xenotoca eiseni*) tested in the same task used with children proved able to conjoin geometric and nongeometric information to reorient themselves in both large and small experimental spaces. Moreover, the fish were able to reorient immediately when dislocated from a large space to a small space with the same features and geometric relationships, and also when dislocated from the small space to the large space. However, they tended to make more geometric errors (i.e., errors due to using geometric information only) than landmark errors (i.e., errors due to using landmark information only) when transferred from the small to the large space, and to make more landmark errors than geometric errors when transferred from the large to the small space (Sovrano, Bisazza, & Vallortigara, 2005).

Address correspondence to Giorgio Vallortigara, Dipartimento di Psicologia, Università di Trieste, Via S. Anastasio 12, 34134 Trieste, Italy, e-mail: vallorti@univ.trieste.it.

One-week-old domestic chicks were also able to reorient themselves in both a large and a small space (Vallortigara, Feruglio, & Sovrano, 2005). Moreover, the chicks reoriented immediately when displaced from the large to the small experimental space, and vice versa, without showing any difference in the amount of geometric and nongeometric errors. However, when tested with a transformation (affine transformation) that altered the geometric relations between the target and the shape of the environment, chicks tended to make more geometric errors when tested in the small than in the large space.

Overall, these findings suggest that differential reliance on geometric information depending on the spatial scale of the environment is not restricted to the human species. It remains unclear, however, why geometric information should be more important in small-sized environments than in large-sized environments. One possibility suggested by various authors is that organisms are prepared to use only distant featural information as landmarks (Nadel & Hupbach, in press; Spelke, 2003; Wang & Spelke, 2002). However, one problem with this view is that, given the evidence for primacy of geometric information over nongeometric information (see Cheng & Newcombe, 2005, for a review), the basic issue is not why organisms do not use featural information in small spaces (they might not use it simply because of the primacy of geometric information), but rather why they do not continue to use geometric information when tested in large spaces. This question is particularly intriguing, because it is usually maintained that large-scale geometric information provides more stable and reliable cues than local environmental features, such as landmarks (Cheng & Newcombe, 2005).

In the present study, we tried to approach this issue using a different avenue. The solution of the blue-wall task encompasses the combined use of two sources of information, geometric information provided by the shape of the room (i.e., the arrangement of surfaces as surfaces) and nongeometric, landmark information provided by the blue wall (see also Pearce, Good, Jones, & McGregor, 2004). However, geometric information actually comprises two aspects, which have not been considered separately in previous work: metric information and sense. Metric information enables the animal to distinguish between a short and a long wall (irrespective of any other nongeometric property associated with the walls' surfaces, such as color, brightness, and scent). Sense refers, in geometry, to the distinction between left and right.[1] The important point to note is that in certain conditions, animals might use a combination of nongeometric information and sense in order to reorient, without making any use of metric properties of the environment.
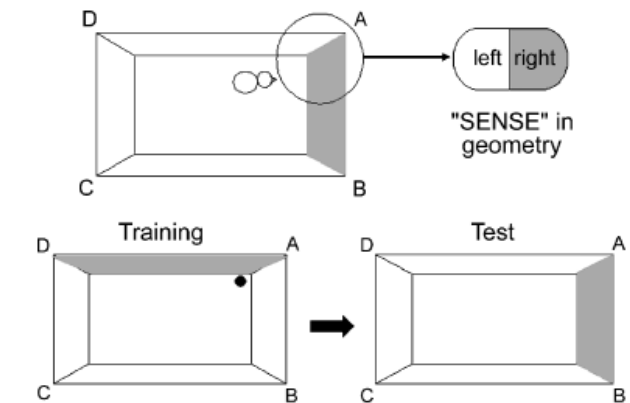

Fig. 1. Combination of sense information with metric and featural information in the blue-wall task. In the situation illustrated at the top, the chick can identify corner A by either an association between metric properties and sense (short wall on the right and long wall on the left) or an association between featural properties and sense (blue, shown in gray, on the right and white on the left). The task used in the experiment is illustrated at the bottom. Chicks were first trained in the rectangular enclosure with the blue wall, and then tested after the displacement of the blue feature to an adjacent wall. The black circle indicates the target (food) position.

Consider the situation depicted in the top illustration of Figure 1. The correct corner (A) can be distinguished from both its geometric equivalent (C) and its featural equivalent (B) without relying on metric information. It suffices that the animal encodes the information that the correct corner is the corner with a white-blue arrangement (featural information) in which the blue is "on the right" (geometric information). This combination of featural information and sense (without any reference to the metric of the environment) would suffice to disambiguate the problem because it allows corner A to be distinguished easily from both corner C (because corner C lacks any blue color) and corner B (because in corner B the blue color, although present, is located in the wrong sense ordering).[2]

We thus devised a test in which such a dissection of sense and metric information is possible. In the training setup, shown at the bottom left of Figure 1, the blue wall is DA. At test, as shown at the bottom right of the figure, the blue wall is moved to AB (of course, the transformation also implies a change in size of the feature, which should be accounted for experimentally by including a counterbalancing condition in which the blue wall is a short wall during training and a long wall at test; see Procedure). As a result of the transformation, it would appear impossible for the animal to find a corner with featural and geometric information (both sense and metric properties) that matches the information experienced during initial training.

---

[1]Even the simple use of purely geometric information requires an ability to combine these two sources of information. In fact, modular hypotheses based on the idea that animals lack a true ability to conjoin different information in the absence of a language medium refer to the lack of ability to conjoin information between different modules (e.g., geometric and landmark information), not within the same module (e.g., metric properties and sense; see Spelke, 2000, 2003, and Spelke & Tsivkin, 2001).

[2]Of course, this is true only when the corner with the featural (blue) information is used as the correct corner; if corner C is used as the correct corner, it would prove impossible to distinguish it from its featural equivalent, corner D, because in this case both corners are completely white colored, and there is no possibility of associating distinctive featural information with sense in order to uniquely identify the correct corner.

Let us consider the possible outcomes of the test. One possibility is that animals simply match metric and sense information, ignoring featural information. If so, choices should be concentrated on corners A and C, and should be equally distributed between these two corners. A second, complementary and opposite, possibility is that animals match featural information, ignoring geometric (metric and sense) information. If so, choices should be concentrated on corners A and B, and should be equally distributed between these two corners. Alternatively, animals may consider both geometric and nongeometric information. If so, choices should again be concentrated along corners of the AB wall, because these are the only locations that possess the correct featural information. However, there are two distinct kinds of geometric information, metric properties and sense. Thus, there are two possibilities (as well as combinations of them). If animals rely mainly on metric properties but tend to ignore sense as it relates to featural information, then corner A should be preferred. This is because corner A possesses the same featural information (the blue color—even though with the wrong sense, because the blue is on the left rather than on the right) and the same metrical arrangement of surfaces as the target corner during training (i.e., long wall on the left and short wall on the right). If, on the contrary, animals rely mainly on the sense of the feature and tend to ignore metric properties of surfaces, then corner B should be preferred. This is because corner B possesses the same featural information (the blue color) with the same sense properties (i.e., blue on the left) as the target corner during training, even though it does not possess the same metrical arrangement of surfaces (i.e., in this case, the long wall is on the right and the short one on the left).

We tested young chicks in this task, using a large and a small environment (the same sizes that in previous work have proved to affect spatial reorientation in this species, as discussed earlier).

METHOD

Subjects

Subjects were 34 male domestic chicks (*Gallus gallus*) of the Hybro strain (a local variety derived from White Leghorn), supplied from a commercial hatchery when they were only a few hours old. The animals were reared singly at a controlled temperature (30 °C), with food and water ad libitum. Rearing cages, 25 cm wide × 30 cm high × 40 cm deep, were illuminated by fluorescent lamps.

Apparatus

The apparatus has been described in detail elsewhere (Vallortigara et al., 2004, 2005). It consisted of two rectangular wooden enclosures (large enclosure: 70 cm deep × 40 cm high × 35 cm wide; small enclosure: 35 cm deep × 40 cm high × 17.5 cm wide) with three uniformly white-colored walls and one blue wall. (At test, the chicks were about 12.5 cm in length, 6.5 cm in

width, and 12 cm in height; their weight was about 98.5 g.) A (cylindrical) transparent, plastic food container (4 cm in diameter and 4 cm in height) that was similar to the food containers in the chicks' home cages was located in each corner. Illumination was provided by a lightbulb placed above the center of each enclosure. The upper part of each enclosure was covered by a one-way screen so that the animals could not use external visual stimuli as directional cues for orientation.

Procedure

The basic procedure has been described in detail elsewhere (Vallortigara et al., 2004, 2005). One group of chicks was trained in the large enclosure, and another group was trained in the small enclosure. Within each group, for some chicks the blue wall was one of the short walls ($n = 9$ for the large enclosure and $n = 10$ for the small enclosure), and for other chicks the blue wall was one of the longer walls ($n = 7$ for the large enclosure and $n = 8$ for the small enclosure; see Fig. 2). This was done to check for any possible difference in results when the blue wall changed from large to small versus small to large from training to test.

In their second day of life, the chicks were accustomed to the experimental environment. During this habituation phase, they
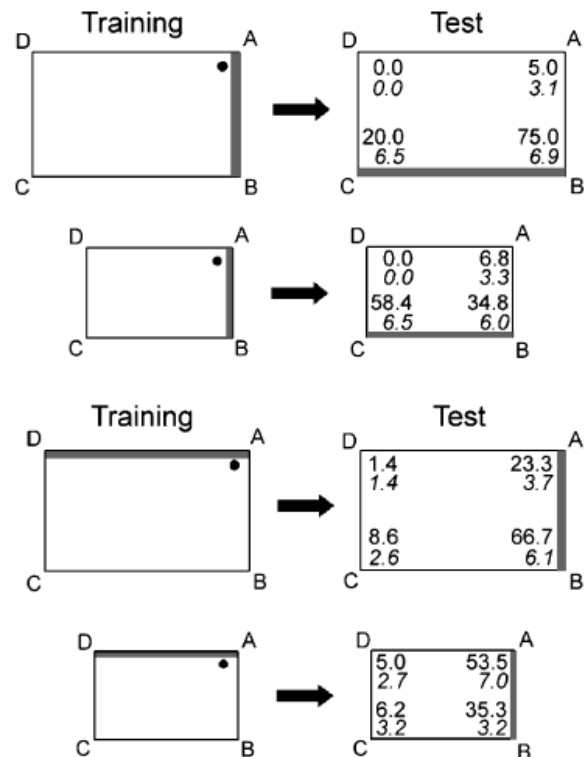

Fig. 2. Illustrations of the four training and test conditions and experimental results. For some chicks, the blue wall (shown here in gray) was a short wall during training and was displaced to a long wall at test (top half of figure); for other chicks, the blue wall was a long wall during training and a short wall at test (bottom half of figure). Both conditions were tested in both a large enclosure and a small enclosure (shown in alternating rows). For each test condition, the mean percentage of choices for each corner is shown (with the standard error of the mean below).

could move freely in the enclosure and peck at food from the feeder placed in the corner that would subsequently be reinforced during training. The procedure was the same as during training (see the next paragraph), except that pecking choices were not recorded. The habituation phase ended when chicks spontaneously searched for food in the feeders placed in the corners.

The next day, the chicks were food deprived to induce the necessary level of motivation. About 8 to 10 hr later, they were placed in the center of the enclosure and were trained to search for the plastic container associated with a particular corner in the enclosure (conventionally referred to as the A corner, as in Fig. 2, although different animals were tested with different corners reinforced). All four containers were filled with food, but in three containers a very fine wire net prevented the chicks from pecking the food. The same wire net was located also in the correct, reinforced container, but a small hole (1 cm in diameter) was cut into it to allow the chicks access to the food.

Training started on the third day of life and consisted of three daily sessions of 10 trials (intertrial interval = 2 min); sessions were separated by 2 hr. In each trial, the chick was placed in the middle of the enclosure and allowed to approach one food container. When the food container in the correct position was chosen, the chick was allowed four or five pecks (reinforcement); after that, the chick was removed and placed in a small, closed cardboard box (20 cm × 20 cm × 30 cm) outside the test enclosure. During the intertrial interval, the small box containing the chick was rotated slowly on a rotating chair to eliminate compass or inertial information (disorientation procedure; see also Vallortigara et al., 1990). The test cage was rotated 90° from trial to trial, as well. When a food container in an incorrect position was chosen, the chick was immediately removed from the test enclosure and, after the disorientation procedure, given another trial. The learning criterion was 90% correct in a single session of 10 trials. One hour after the chick reached the learning criterion, a control session of 10 trials was given; in these trials, all four containers were closed by the wire net (no hole was present in the correct container). This session served as a check that learning was accomplished on the basis of spatial cues and not subtle cues associated with visibility of the hole in the correct container. Three reinforced trials (in which the chick was allowed access to food in the correct container) were intermixed with the control trials, to avoid extinction of the

searching responses (these trials were not considered in the data analysis).

The day after the chicks reached the learning criterion, they were tested with the blue wall displaced. During this test phase, the chicks were given 10 test trials in the absence of food reinforcement (i.e., access to food in all four containers was prevented by the wire net). Choices of the corners were recorded. A choice was considered valid when a chick approached a container and its head entered the arc of a circle 8 cm in diameter and centered on the corner, irrespective of whether the chick made a pecking response. (For scoring, the chicks' behavior was observed on a television monitor with a superimposed transparent grid.) Soon after an approach response, the chick was removed from the test enclosure and, after the disorientation procedure, given another trial. Only first choices were included in the data analysis. (An extinction procedure with recording of only the first responses is usually preferred in these tasks to avoid both learning effects associated with repeated unsuccessful trials and decrease of motivation; see, e.g., Gouteux et al., 2001; Kelly et al., 1998.)

RESULTS

Chicks trained in the small and large enclosures did not differ in the number of errors needed to reach the learning criterion (Table 1; long blue wall: $n_1 = 8$, $n_2 = 7$, $U = 16.5$, $p > .05$, two-tailed Mann-Whitney U test; short blue wall: $n_1 = 10$, $n_2 = 9$, $U = 30$, $p > .05$). The control session confirmed that the chicks' learning was not based on visual characteristics of the food containers and did not reveal any difference associated with the size of the enclosure (Table 1: long blue wall: $U = 17$, $p > .05$; short blue wall: $U = 29.5$, $p > .05$).

Results for the test trials are shown in Figure 2. Frequencies of choice revealed a significant heterogeneity associated with the size of the enclosures, $\chi^2(3, N = 34) = 41.11$, $p = .0001$. The chicks searched mainly along the blue wall in both the small enclosure (long blue wall—BC vs. AD: $T = 0$, $p < .01$, Wilcoxon test; short blue wall—AB vs. DC: $T = 0$, $p < .01$) and the large enclosure (long blue wall—BC vs. AD: $T = 0$, $p < .01$; short blue wall—AB vs. DC: $T = 0$, $p < .02$). However, the distribution of search between the two corners of the blue wall was strikingly different in the large and small enclosures. When tested in the large enclosure, chicks searched mainly in the corner with the

TABLE 1

Mean Number of Errors to Reach Criterion During Training and Percentage of Correct Trials During the Control Session as a Function of Enclosure

	Large enclosure		Small enclosure	
Measure	Short blue wall	Long blue wall	Short blue wall	Long blue wall
Mean errors ± *SEM*	25.1 ± 1.9	28.8 ± 1.9	22.3 ± 1.5	24.8 ± 1.7
Percentage correct ± *SEM*	91.0 ± 2.77	92.8 ± 3.6	86.6 ± 3.37	86.2 ± 3.2

same arrangement of the featural cue (with respect to geometric sense) as during training, irrespective of the sense arrangement of metric information provided by the lengths of the walls (long blue wall—B vs. C: $T = 3, p < .01$; short blue wall—A vs. B: $T = 0, p < .02$). When tested in the small enclosure, chicks searched mainly in the corner with the same metrical arrangement of the walls (with respect to geometric sense) as during training, irrespective of the sense arrangement of the featural cue (long blue wall—B vs. C: $T = 4.5, p < .05$; short blue wall—A vs. B: $T = 2$, $p < .05$).

DISCUSSION

The results of the experiment showed very clearly that chicks made different use of geometric information in the large and small enclosures. In the large enclosure, they chose the corner that maintained the sense relationship of the featural cue with respect to the training conditions (i.e., the corner in which the left-right positioning of the blue cue was the same as in the original training corner). In so doing, they tended to neglect the metrical arrangements of surfaces as surfaces (i.e., irrespective of color), for the corner they chose showed a reversal of the metric properties with respect to sense as learned during training. In the small enclosure, chicks showed the reverse behavior: They chose the corner that maintained the correct metrical arrangements with respect to sense. In so doing, they tended to neglect the sense arrangement of the color cue, for the corner they chose showed a reversal of the left-right positioning of the color cue with respect to training.

How can these results be explained? It has been claimed that use of geometric information for spatial reorientation makes sense ecologically. The large-scale shape of the landscape does not change across seasons, whereas there are important seasonal changes in the nongeometric properties of the landscape (e.g., appearance of grass and vegetation, snowfall and melting; see also Vallortigara, 2004, 2006; Vallortigara & Sovrano, 2002). But of course this is true both in a small environment and in a large environment. However, several authors have suggested a role for animals' well-known preference to use distal rather than proximal cues for orientation. Hebb (1938) noticed this preference originally in rats, O'Keefe and Nadel (1978) reiterated this idea, and Spelke (2003) and Nadel and Hupbach (in press) claimed such a preference explained the room-size effect observed in toddlers. Zugaro et al. (2004) recently obtained some neurobiological evidence favoring this hypothesis. These authors tested rats in an enclosure with proximal and distal cues in either full-light or strobe-light conditions (in the latter condition, animals were deprived of motion parallax and optic flow information and were therefore unable to rely on distal cues). Responses of head-direction cells appeared to be dependent on the information conveyed by distal cues.

Our results with chicks, however, suggest that the issue of spatial reorientation in the blue-wall task could be more com-
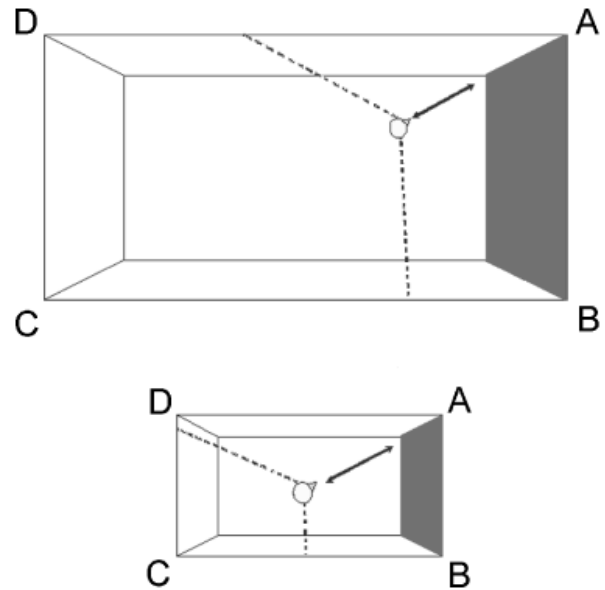

Fig. 3. The information available to a chick looking at a corner from a fixed distance in a small enclosure (bottom) and a large enclosure (top). The dashed lines indicate the angle of visual scanning. In the small enclosure, metric information concerning two of the four surfaces is fully available, but in the large enclosure, metric information is incomplete, and featural information provides more reliable cues for reorientation.

plicated, for it is not simply that animals in the large enclosure tend to use featural information that is neglected in the small enclosure. The key to the puzzle seems to be in the use of different associations with sense information in the two enclosures. In a large enclosure, animals may preferentially associate local featural information with sense information, whereas in a small enclosure, animals may preferentially associate metric properties of the surfaces with sense information. Such different associations could be expected on the basis of the reliability of the information conveyed to the animal in environments of different spatial scale. For example, Figure 3 illustrates that when an animal is a given distance from a corner, visual analysis of the corner (e.g., by head-direction cells) provides different information in small and large spaces. In a small environment (Fig. 3, bottom panel), scanning provides complete information on the length of two surfaces and may therefore be a reliable source of spatial information. In this case, the animal may rely on an association between sense information and the metric properties of the surfaces ("the correct corner has a short wall on the right and a long wall on the left"). In a large environment, however, scanning of the full spatial extent of the surfaces is prevented (Fig. 3, top panel). Thus, the animal must rely on an association between sense information and the featural properties of the surfaces ("the correct corner has a blue feature on the right and a white feature on the left").

This hypothesis is not inconsistent with previous claims of a preference for using distal rather than proximal cues for reorientation, but provides a more precise account of the findings with the blue-wall task in large and small enclosures in a variety

of species (see the introduction). It would be interesting to extend the investigation by using our task to determine whether similar dissociations and associations of metric properties, featural information, and sense can be observed in other species, and in particular with children.

REFERENCES

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23,* 149–178.

Cheng, K., & Newcombe, N.S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review, 12,* 1–23.

Deipolyi, A., Santos, L., & Hauser, M.D. (2001). The role of landmarks in cotton-top tamarin spatial foraging: Evidence for geometric and non-geometric features. *Animal Cognition, 4,* 99–108.

Gouteux, S., Thinus-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal of Experimental Psychology: General, 130,* 505–519.

Hebb, D.O. (1938). Studies of the organization of behaviour: I. Behaviour of the rat in a field orientation. *Journal of Comparative Psychology, 25,* 333–352.

Hermer, L., & Spelke, E.S. (1994). A geometric process for spatial reorientation in young children. *Nature, 370,* 57–59.

Hermer, L., & Spelke, E.S. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61,* 195–232.

Kelly, D.M., Spetch, M.L., & Heth, C.D. (1998). Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *Journal of Comparative Psychology, 112,* 259–269.

Learmonth, A.E., Nadel, L., & Newcombe, N.S. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Science, 13,* 337–341.

Learmonth, A.E., Newcombe, N.S., & Huttenlocher, J. (2001). Toddlers' use of metric information and landmarks to reorient. *Journal of Experimental Child Psychology, 80,* 225–244.

Nadel, L., & Hupbach, A. (in press). Cross-species comparisons in development: The case of the spatial "module." In M.H. Johnson & Y. Munakata (Eds.), *Attention and performance XXI.* Oxford, England: Oxford University Press.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map.* Oxford, England: Clarendon Press.

Pearce, J.M., Good, M.A., Jones, P.M., & McGregor, A. (2004). Transfer of spatial behaviour between different environments: Implications for theories of spatial learning and for the role of the hippocampus in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 30,* 135–147.

Sovrano, V.A., Bisazza, A., & Vallortigara, G. (2002). Modularity and spatial reorientation in a simple mind: Encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition, 85,* B51–B59.

Sovrano, V.A., Bisazza, A., & Vallortigara, G. (2003). Modularity as a fish views it: Conjoining geometric and nongeometric information for spatial reorientation. *Journal of Experimental Psychology: Animal Behavior Processes, 29,* 199–210.

Sovrano, V.A., Bisazza, A., & Vallortigara, G. (2005). Animals' use of landmarks and metric information to reorient: Effects of the size of the experimental space. *Cognition, 97,* 121–133.

Spelke, E.S. (2000). Core knowledge. *American Psychologist, 55,* 1233–1243.

Spelke, E.S. (2003). What makes us smart: Core knowledge and natural language. In D. Gentner & S. Goldin-Meadow (Eds.), *Language in mind: Advances in the study of language and thought* (pp. 277–311). Cambridge, MA: MIT Press.

Spelke, E.S., & Tsivkin, S. (2001). Initial knowledge and conceptual change: Space and number. In M. Bowerman & S. Levinson (Eds.), *Language acquisition and conceptual development* (pp. 70–81). Cambridge, England: Cambridge University Press.

Vallortigara, G. (2004). Visual cognition and representation in birds and primates. In L.J. Rogers & G. Kaplan (Eds.), *Vertebrate comparative cognition: Are primates superior to non-primates?* (pp. 57–94). Amsterdam: Kluwer Academic/Plenum Publishers.

Vallortigara, G. (2006). The cognitive chicken: Visual and spatial cognition in a non-mammalian brain. In E.A. Wasserman & T.R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 41–58). Oxford, England: Oxford University Press.

Vallortigara, G., Feruglio, M., & Sovrano, V.A. (2005). Reorientation by geometric and landmark information in environments of different size. *Developmental Science, 8,* 393–401.

Vallortigara, G., Pagni, P., & Sovrano, V.A. (2004). Separate geometric and non-geometric modules for spatial reorientation: Evidence from a lopsided animal brain. *Journal of Cognitive Neuroscience, 16,* 390–400.

Vallortigara, G., & Sovrano, V.A. (2002). Conjoining information from different modules: A comparative perspective. *Behavioral and Brain Sciences, 25,* 701–702.

Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animals' spatial representation: A test with chicks. *Journal of Comparative Psychology, 104,* 248–254.

Vargas, J.P., Lopez, J.C., Salas, C., & Thinus-Blanc, C. (2004). Encoding of geometric and featural spatial information by goldfish (*Carassius auratus*). *Journal of Comparative Psychology, 118,* 206–216.

Vargas, J.P., Petruso, E.J., & Bingman, V.P. (2004). Hippocampal formation is required for geometric navigation in pigeons. *European Journal of Neuroscience, 20,* 1937–1944.

Wang, R.F., & Spelke, E.S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences, 6,* 376–382.

Zugaro, M.B., Arleo, A., Dejean, C., Burguiere, E., Khamassi, M., & Wiener, S.I. (2004). Rat anterodorsal thalamic head direction neurons depend upon dynamic visual signals to select anchoring landmark cues. *European Journal of Neuroscience, 20,* 530–536.