

Is there an innate geometric module? Effects of experience with angular geometric cues on spatial re-orientation based on the shape of the environment

Cinzia Chiandetti · Giorgio Vallortigara

Received: 2 April 2007 / Revised: 13 June 2007 / Accepted: 23 June 2007 / Published online: 13 July 2007
© Springer-Verlag 2007

Abstract Non-human animals and human children can make use of the geometric shape of an environment for spatial reorientation and in some circumstances reliance on purely geometric information (metric properties of surfaces and sense) can overcome the use of local featural cues. Little is known as to whether the use of geometric information is in some way reliant on past experience or, as would likely be argued by advocates of the notion of a geometric module, it is innate. We tested the navigational abilities of newborn domestic chicks reared in either rectangular or circular cages. Chicks were trained in a rectangular-shaped enclosure with panels placed at the corners to provide salient featural cues. Rectangular-reared and circular-reared chicks proved equally able to learn the task. When tested after removal of the featural cues, both rectangular- and circular-reared chicks showed evidence that they had spontaneously encoded geometric information. Moreover, when trained in a rectangular-shaped enclosure without any featural cues, chicks reared in rectangular-, circular-, or c-shaped cages proved to be equally able to learn and perform the task using geometric information. These results suggest that effective use of geometric information for spatial reorientation does not require experience in environments with right angles and metrically distinct surfaces, thus supporting the hypothesis of a predisposed geometric module in the animal brain.

Keywords Geometric module · Spatial orientation · Modularity · Chicks · Children

Introduction

When disoriented in a rectangular enclosure several vertebrate species (reviews in Cheng and Newcombe 2005; Spelke 2003; Vallortigara 2006) appear to make use of the shape of the enclosure to reorient themselves, relying on metric information (long wall versus short wall) and directional sense (left versus right). Several species have also proved able to conjoin geometric information (the shape of the enclosure) with non-geometric information (e.g. the colour of a wall) in order to reorient themselves [e.g. fish: redbtail splitfins (*Xenotoca eiseni*): Sovrano et al. 2002, 2003; goldfish (*Carassius auratus*): Vargas et al. 2004; birds: chicks (*Gallus gallus*): Vallortigara et al. 1990, 2004; pigeons (*Columba livia*): Kelly et al. 1998; Vargas et al. 2004a; mammals: rhesus monkeys: Gouteux et al. 2001; tamarins: Deipolyi et al. 2001]. Interestingly, however, a “primacy” of geometric information seems to be apparent in spatial reorientation. When animals are trained in the presence of conspicuous local, non-geometric cues, such as panels located at the corners of a rectangular enclosure, and subsequently tested after removal of these featural cues, their behaviour usually reveals that spontaneous encoding of geometric information has occurred, in spite of the fact that featural information alone sufficed for spatial reorientation during training (chicks: Vallortigara et al. 1990; pigeons: Kelly et al. 1998; fish: Sovrano et al. 2003).

The original claims by Cheng (1986) and Hermer and Spelke (1994, 1996) for the existence of an encapsulated geometric module, sensu Fodor (1983), have been tempered in recent years by evidence that conjoining geometric and

C. Chiandetti (✉) · G. Vallortigara
Department of Psychology and B.R.A.I.N. Centre
for Neuroscience, University of Trieste,
Via S. Anastasio 12, 34134 Trieste, Italy
e-mail: cchiandetti@univ.trieste.it
URL: <http://www.psico.univ.trieste.it/labs/acn-lab/>

G. Vallortigara
e-mail: vallorti@univ.trieste.it

non-geometric information is in fact possible in several species, including young human infants under certain testing conditions (e.g. in large rooms, see Learmonth et al. 2002, 2001; Nadel and Hupbach 2006; see also Sovrano et al. 2005, 2007; Vallortigara et al. 2005a; Vallortigara and Sovrano 2002; Sovrano and Vallortigara 2006; Chiandetti et al. 2007 for evidences in other species). Nonetheless, a weak version of modularity has been claimed on the basis of the evidence for a specific neural mechanism (likely located in the hippocampus) dedicated to the treatment of geometric information (Bingman et al. 2006; Vargas et al. 2004b; Vallortigara et al. 2004; Tommasi et al. 2003; Vallortigara in press). Curiously enough, little research has been carried out on the role of experience in the ability to deal with geometric information. Although modules need not be necessarily innate (Karmiloff-Smith 1992), the issue of whether the ability to encode geometric information requires environmental triggering or some sort of experience with angled surfaces of different lengths appears to be unresolved.

A recent result suggests a role of experience in dealing with geometric information. It has been shown that wild-caught mountain chickadees (*Poecile gambeli*), in contrast to the domesticated bird species so far studied (pigeons and domestic chickens; see above) do not spontaneously encode the geometry of an enclosure when salient features are present near the goal; moreover, when trained without salient features they encode geometric information but this encoding is overshadowed by features (Gray et al. 2005). It is unclear, however, the reason why these differences may occur. One explanation could be that wild-caught birds have had little experience of small enclosures with right angles as is typical for birds kept in laboratory cages, thus leading to a reliance on featural over geometric information. However, the possibility of species-specific differences in the dominance of geometric and non-geometric cues cannot be ruled out (and some evidence favouring this view has been reported, e.g. Sovrano et al. 2007).

Here we take advantage of the characteristics of a highly precocial species, the domestic chick, which has been widely used as a model in spatial reorientation studies (reviews in Vallortigara 2004, 2006). In this species precise control on early experience can be combined with the possibility of testing the animal at a young age, because of early motor and behavioural development.

Experiment 1

In the first experiment dark-incubated chicks were placed in rectangular- or circular-shaped rearing cages for a few days, after which they were tested in a rectangular-shaped enclosure with distinctive panels at the corners. After

learning, we removed featural (panels) information and tested chicks for encoding of purely geometric information.

Methods

Subjects

Subjects were 18 males domestic chicks (*G. gallus*) of the Hybro strain (a local variety derived from White-Leghorn), from fertilized eggs supplied from a commercial hatchery (Agricola Berica s.c.r.l., Montegalda, Vicenza, Italy) delivered to our laboratory weekly when the eggs were at day 14 of incubation. Thereafter, and until hatching, the eggs were incubated in complete darkness in an automatically turning incubator FIEM® snc, MG 100/150, under controlled temperature (37.7°C) and humidity (about 50–60%) conditions. Once hatched in the dark, the animals were reared singly at a controlled temperature (30°C), with food and water available ad libitum, in rectangular (22 cm wide × 30 cm high × 40 cm deep; $n = 9$ chicks) or circular-shaped (32 cm wide × 40 cm high; $n = 9$ chicks) cages which were completely closed apart from the top where they were illuminated by light coming from fluorescent lamps.

Apparatus

The experimental apparatus consisted of a uniformly white-coloured rectangular cage (70 × 35 × 40 cm³). Four different cardboard panels (20 × 4.5 cm²) were placed, one for each corner, in the test-cage (see Fig. 1); one panel was yellow with five large vertical purple lines (1.5 cm); the second panel had green and orange vertical stripes (0.5 cm); the third panel had pink and black horizontal stripes (1.5 cm) and the fourth was light-blue with seven horizontal lines (0.5 cm). A different positive panel (i.e. the one that indicated the corner with the food) was used for different chicks. A transparent glass container (4 cm in diameter; 4 cm in height; identical to the food jar present in the chicks' home-cage) was located in each corner.

Procedure

Chicks were trained to search for the reinforced glass container associated with a particular panel and a fixed position in the cage-test. All four containers were filled with food, but covered on top with a wire net in order to prevent the chicks feeding from them. In the "correct", i.e. reinforced container, a small hole (1.5 cm in diameter) was made to allow chicks access to the food while at the same time still making the four containers appear indistinguishable from one another. Training started on day 3 (48–72 h after hatching) of life and consisted of three daily sessions of ten trials (intertrial-interval was 2 min), separated by an interval of 2 h. In each trial,



Fig. 1 The rectangular-shaped enclosure used during training in Experiment 1 (the same enclosure without panels at the corners was used at test)

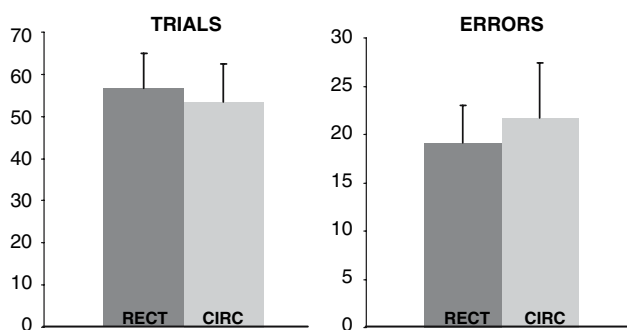
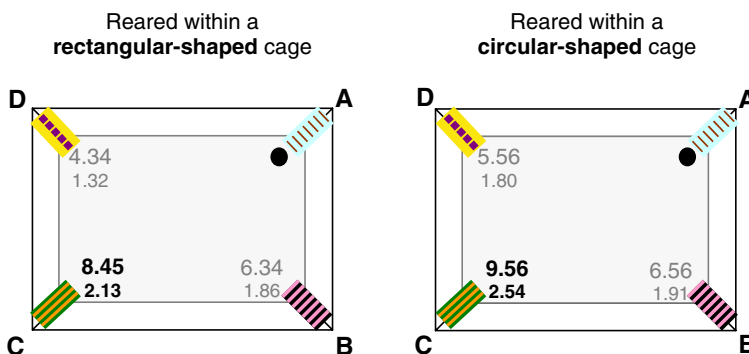


Fig. 2 Mean (with SEM), trials, and errors to criterion during training in chicks reared within a rectangular (*RECT*) or a circular (*CIRC*) cage in Experiment 1

the chick was placed in the middle of the cage 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 at the food (reinforcement); after this, the chick was removed and placed in a small, closed cardboard box (20 × 20 × 30 cm³) outside the test-cage. For the circular-reared chicks, a cylinder (16 × 20 cm²) was inserted in the cardboard box ensuring that chicks were not exposed to geometrical shapes outside the experimental apparatus. During the intertrial interval the small box containing the chick was slowly rotated on a rotating chair to eliminate compass or

Fig. 3 Mean number of errors (with SEM below) during training in the four corners in Experiment 1. “A” indicates the correct (reinforced) corner, and “C” its geometrically equivalent corner



inertial information (disorientation procedure, see also Val-lortigara et al. 1990). When a food container in an incorrect position was chosen, the chick was immediately removed from the test-cage and, following the disorientation procedure, given another trial. Learning criterion was 90% correct in a single session of ten trials.

The day after chicks had reached learning criterion, the four panels were removed. During this test phase the chicks were given ten test trials in the absence of food-reinforcement (i.e. in which access to food was prevented by an occluding wire net on all four containers). Choices for the four corners were recorded. A choice was scored when the chick approached a container to the extent that its head entered an area within 12 cm from a corner, irrespective of pecking responses. Soon after an approach response the chick was removed from the test-cage and, after the disorientation procedure, given another trial. Thus, only the chick’s first choices was considered.

Results

The results for training are shown in Fig. 2. No differences in the number of trials ($U = 37.5, n_1 = 9, n_2 = 9, P = 0.789$, two-tailed Mann–Whitney U -test) and errors ($U = 36, n_1 = 9, n_2 = 9, P = 0.690$, two-tailed Mann–Whitney U -test) to criterion were observed between rectangular- and circular-reared chicks.

In both rectangular- and circular-reared chicks a tendency to make more errors by approaching corner C (the corner geometrically equivalent to the correct corner A, see Fig. 3) than in corners B and D was apparent (Friedman analysis revealed a significant heterogeneity between choices for B, C, and D corners, $\chi^2 = 8.262, n = 9, df = 2, P = 0.016$; choices for corner C were higher than choices for corners B and D, $z = -2.328 P = 0.020$ Wilcoxon test). However, a comparison between the two rearing conditions revealed no differences in the number of geometric errors (choices for corners C) between circular- and rectangular-reared chicks ($U = 37, n_1 = 9, n_2 = 9, P = 0.756$, two-tailed Mann–Whitney U -test).

The results of the test are shown in Fig. 4. Both rectangular-reared and circular-reared chicks showed a preference for the two geometrically correct corners (A, C in Fig. 4) over the geometrically incorrect (B, D in Fig. 4) corners (AC versus BD: rectangular-reared: $z = -2.687$ $P = 0.007$; circular-reared: $z = -2.020$ $P = 0.043$ Wilcoxon test). There were no differences in the preference for the two geometrically correct corners between the two rearing groups (AC rectangular-reared chicks versus AC circular-reared chicks: $U = 26$, $n_1 = 9$, $n_2 = 9$, $P = 0.182$ two-tailed Mann–Whitney U -test).

Experiment 2

The results of training in Experiment 1 showed that there were no differences between rectangular- and circular-reared chicks in their ability to learn to reorient in a rectangular enclosure with features at the corners. Moreover, the results of the test following the removal of the features at the corners showed that both rectangular- and circular-reared chicks had encoded the geometry of the enclosure rather than featural information during training.

Obviously, although the results clearly showed that the two rearing procedures did not produce a difference in the chicks' performance, a major concern in the experimental design used was that the training procedure itself necessarily exposed all animals to a right-angled environment for some periods. This is in some way unavoidable given that animals should learn about these environmental geometric features. Nonetheless, in Experiment 2 we tried to use a procedure that did not involve any training period before testing, i.e. we directly compared the ability of rectangular- and circular-reared chicks to reorient in a featureless rectangular enclosure. This modified procedure minimizes all animals' exposure to a right-angled environment, and makes it possible to test for use of geometry with as little experience of a right-angled testing environment as is possible. We also introduced a third rearing condition: a c-shaped arena, obtained by a transformation of the circular arena (see Fig. 5), in which there were no corners but elongated walls that could provide some metrical information and/

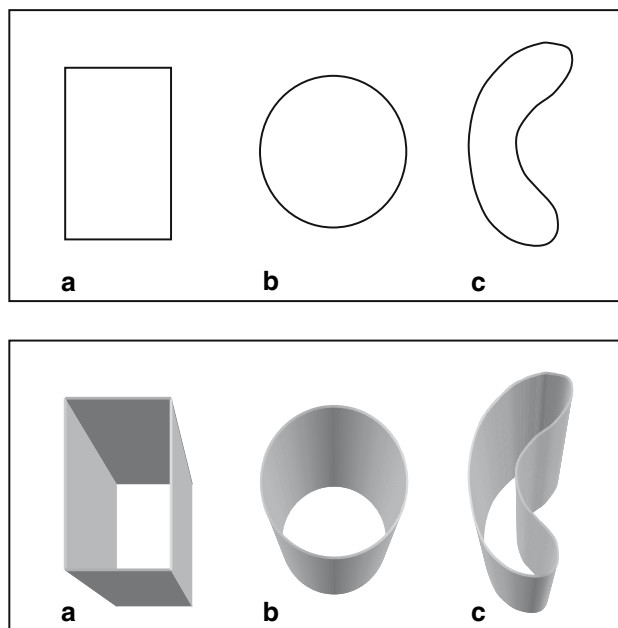


Fig. 5 Two-dimensional (top) and 3D (bottom) schematic representations of the rearing cages used in Experiment 2: rectangular (a), circular (b) and c-shaped (c) cage

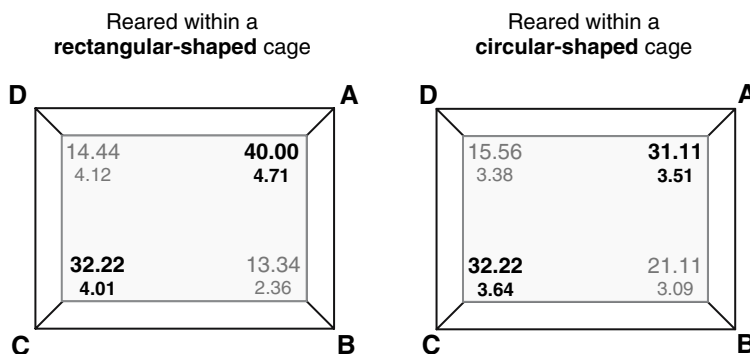
or principal axes and axes of symmetry to encode shape (a circular shape provides multiple axis of symmetry). This was done since, according to some theories, principal axes and/or axes of symmetry maybe used by animals to encode the geometric shape of an environment (see Cheng 2005).

Methods

Subjects

Subjects were 53 males domestic chicks (*G. gallus*) obtained from fertilized eggs and hatched with the same procedure as described in Experiment 1. After hatching in the dark, chicks were immediately taken to their rearing cages: rectangular ($n = 16$ chicks), circular ($n = 17$ chicks), or c-shaped ($n = 20$ chicks) cages which were completely enclosed apart from the top where they were illuminated by

Fig. 4 Experiment 1 test results. Mean percentages of choices for each corner are shown (with SEM below) in chicks reared within a rectangular or a circular enclosure. "A" indicates the corner that was reinforced during training



fluorescent lamps as in Experiment 1 (see for an outline Fig. 5), where they were kept singly at a controlled temperature (30°C), with food and water available ad libitum. The cages were made from fibreglass and coated entirely in white plastic. Rectangular cages measured 22 cm wide × 30 cm high × 40 cm deep; circular cages were 32 cm wide × 40 cm high; c-shaped cages were built up deforming a cylinder 40 cm wide × 40 cm high to obtain an internal corridor about 15 cm wide, thus providing a similar overall surface area for all rearing conditions.

Apparatus and procedure

The apparatus was the same as used in Experiment 1, but this time there were no panels at the corners. Chicks were trained to search for food in a particular corner in a fixed position in the cage-test as in Experiment 1. Different corners were used as “positive” (i.e. reinforced) for different animals. Starting on day 3 of life, chicks were given three daily sessions of ten trials for three consecutive days (inter-trial-interval was 2 min), separated by an interval of 2 h.

Choices for the four corners were recorded as in Experiment 1. Percentages of choices for the two geometrically correct corners were computed. Since the data represented percentages, data were arcsin transformed (Sokal and Rohlf 1969) and then analysed by repeated-measures analysis of variance.

Results

The results of training are shown in Fig. 6. The analysis of variance with sessions as a within-subjects factor and rearing conditions as a between-subjects condition revealed a significant main effect of session [$F(2,100) = 8.057$ and $P = 0.001$]; there were no significant effects associated with rearing conditions [$F(2,50) = 0.686$ and $P = 0.508$] nor was there a significant interaction of rearing conditions by session [$F(4,100) = 1.224$ and $P = 0.305$].

We wondered whether subtle differences associated with the different rearing conditions could have been revealed by an analysis limited to the very early phases of training. In order to check for this we analysed data in the first three blocks of ten trials of the first daily session. The analysis of variance did not reveal any statistical significant effect of rearing conditions [rearing: $F(2,50) = 0.354$ and $P = 0.703$; rearing × block of trials: $F(4,100) = 0.397$ and $P = 0.811$]. We then restricted the analysis to the very first block of ten trials, analysing the data in five mini-blocks of two trials each. As can be seen from Fig. 7, again no difference between the rearing conditions was apparent [rearing: $F(2,50) = 0.549$ and $P = 0.581$; rearing × block of trials: $F(8,200) = 0.707$ and $P = 0.685$].

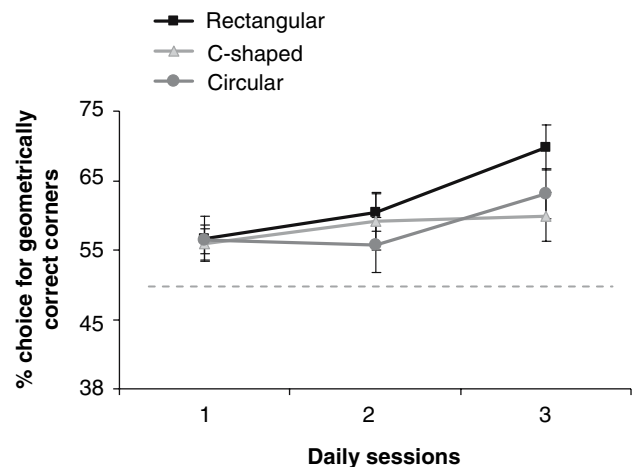


Fig. 6 Experiment 2: training results. Mean percentages of choices (\pm SEM) for the geometrically correct corners in chicks reared in rectangular-shaped, c-shaped, and circular home-cages are shown

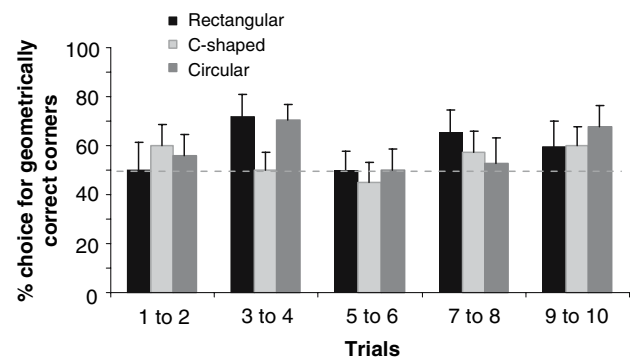


Fig. 7 Experiment 2: early training results. The first session (ten trials) is here divided in five blocks of two trials each. Mean percentages of choices (with SEM) for the geometrically correct corners in chicks reared in rectangular-shaped, c-shaped and circular home-cages are shown

Discussion

In the Experiment 1 results of training showed that there were no differences in the number of trials and errors to criterion in the two rearing groups. Also, no differences in the number of rotational errors (choices for the corner geometrically equivalent to the correct one) were apparent between rectangular-reared and circular-reared chicks during training.

In principle, chicks in Experiment 1 could have limited themselves to the use of featural information provided by the panels to solve the task during the training, without any encoding of geometric information. However, results of the test clearly showed that both rectangular- and circular-reared chicks did not go back to random choices after removal of the panels. On the contrary, they searched

mainly in the two geometrically correct locations, that is, in the two (indistinguishable) corners, A and C, which stand in the same geometric relationships with respect to the shape of the environment. Thus, circular- and rectangular-reared chicks had both (and to the same extent) encoded geometry during training.

These findings were strengthened by the results of Experiment 2. No differences between chicks reared in circular-, rectangular-, or c-shaped cages were apparent in the ability to reorient using purely geometric information (i.e. in the absence of any featural cues). Even in the very first trials of training the reorientation behaviour of chicks reared in the different home-cages appeared to be totally indistinguishable from one another.

It may therefore be concluded that exposure to right angles and surfaces with different metric properties during rearing is not needed for encoding geometric information in spatial reorientation. Reorientation using metric information and using directional sense seems to be possible even in an organism that has not experienced right angles and surfaces with different spatial extent in its environment until testing. The results of Experiment 1 are particularly striking in this regard, since, during training, chicks were not explicitly trained on geometry: to solve the task during training they could have totally ignored the shape of the enclosure. It is therefore particularly remarkable that circular-reared chicks took into account (and conjoined) the metric properties of the environment (long and short walls) with their right–left positions.

Theoretical analyses of how geometry is used in spatial reorientation have suggested alternative strategies to local analysis (i.e. consideration of corners with short/long walls with reference to left/right geometric sense), such as shape parameters of principal axes to determine heading (Gallistel 1990) or, more recently, other kinds of axes, such as symmetry axes and medial axes (Cheng and Gallistel 2005). The results obtained in Experiment 2 with the c-shaped cage suggest that experience is not needed for computation of such global shape parameters either.

A recent paper by Brown et al. (2007), of which we became aware after initial submission of this paper, revealed strikingly similar results with a completely different species. Brown and collaborators reared fish (*Archocentrus nigrofasciatus*) in rectangular or circular tanks and then tested their reorientation abilities in a rectangular tank without any featural cues in a similar vein to that described here in Experiment 2. Results revealed no differences in learning abilities between circular- and rectangular-reared fish. When trained with featural information present, fish proved able to learn both types of information. Interestingly, when cues were in conflict, fish reared in a circular tank showed less use of geometric information than fish reared in a rectangular tank. Thus, early experience during

rearing did not affect the ability of fish to encode geometrical or featural information but, perhaps less surprisingly, it could influence the relative dominance of one or other cue in adulthood. This can probably explain the results obtained by Gray et al. (2005) with wild-caught mountain chickadees mentioned in the Introduction. The issue is certainly of great theoretical relevance since the phrase “innate geometric module” in the developmental science community seems to denote quite different things. On the one hand, it is meant to indicate an innate ability to apprehend extent of surfaces as surfaces together with left–right sense, which is basically what we reported here for chicks [see Newcombe et al. (2005) for studies in human infants]. On the other hand, for some theorists it does not mean simply that there are specific neural mechanisms underlying such apprehension (see Introduction). Spelke’s (2003) proposal is deeply committed to the full Fodorian criterion of impenetrability (see Fodor 1983), and it is the experiments that show failure to use features at all that most favour this idea (e.g. Hermer and Spelke 1996). Clearly the present experiments do not assess the impenetrability versus flexibility issue, but further work on this is in progress in our laboratory.

There are, of course, striking limitations to any experiment that deals with the “innateness” of encoding of certain types of information even when using a precocial species such as the domestic chick as an animal model. How can one determine the “innateness” of anything if assessing that innateness requires prior exposure (before/during test) to the behaviour/stimulus to be learned? (The problem is less acute when using fixed action patterns of response elicited by releasing mechanisms as in classical ethological work, e.g. Tinbergen 1951; and see Vallortigara et al. 2005b; Vallortigara and Regolin 2006 for a more recent demonstration of innate predispositions involving perception of biological motion that makes use of the approach and following response of newly hatched domestic chicks). Unavoidably, once the experimental chicks begin training, they begin to experience geometry, and when the test is performed, the experimental animals have already had some experience with geometry. We addressed this issue in Experiment 2, by looking at learning performance early in training. The results of the very early trials of training were striking in this regard, since no evidence of any difference between circular- and rectangular-reared chicks was apparent.

Thus, overall, the results reported here for chicks and those of Brown et al. (2007) with fish strongly suggest that animals encode geometric information in the absence of (or with minimal) experience of surfaces of different lengths connected together at right angles. This clearly adds to the evidence collected in humans that the foundations of natural geometry are far removed from any strictly linguistic and cultural constraint (Dehaene et al. 2006). Obviously,

the apparent lack of influence associated with experiencing right angles should be not generalized to all experiences: to rule out one specific source of experience does not mean that all sensory or motor experiences are unimportant in the development of natural knowledge of geometry. Nevertheless, the present findings support the idea that biological organisms are endowed with largely predisposed cognitive mechanisms to deal with geometrical information in their natural environment.

Acknowledgements The experiments comply with the European Community and the Italian law on animal experiments. We thank Maddalena Misculin and Anna Grimaldi for help in training the animals, and Jonathan Daisley for revising the English text. The research was supported by grants MIUR Cofin 2004, 2004070353_002 “Intel-lat” and MIPAF “Ben-o-lat” via Dip. Sci. Zootecniche, Univ. di Sassari to G.V. We wish to thank Liz Spelke, Nora Newcombe and three anonymous reviewers for comments on the manuscript.

References

- Bingman VP, Erichsen JT, Anderson JD, Good MA, Pearce JM (2006) Spared feature-structure discrimination but diminished salience of environmental geometry in hippocampal-lesioned homing pigeons (*Columba livia*). *Behav Neurosci* 120:835–841
- Brown AA, Spetch ML, Hurd PL (2007) Growing in circles: rearing environment alter spatial navigation in fish. *Psychol Sci* (in press)
- Cheng K (1986) A purely geometric module in the rat’s spatial representation. *Cognition* 23:149–178
- Cheng K (2005) Reflections on geometry and navigation. *Connect Sci* 17:5–21
- Cheng K, Gallistel CR (2005) Shape parameters explain data from spatial transformation: comment of Pearce et al. (2004) and Tommasi and Polli (2004). *J Exp Psychol: Anim Behav Proc* 31:254–259
- Cheng K, Newcombe NS (2005) Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychon Bull Rev* 12:1–23
- Chiandetti C, Regolin L, Sovrano VA, Vallortigara G (2007) Spatial reorientation: the effects of space size on the encoding of landmark and geometry information. *Anim Cogn* 10:159–168
- Dehaene S, Izard V, Pica P, Spelke ES (2006) Core knowledge of geometry in an Amazonian indigene group. *Science* 311:381–384
- Deipolyi A, Santos L, Hauser MD (2001) The role of landmarks in cotton-top tamarin spatial foraging: evidence for geometric and non-geometric features. *Anim Cogn* 4:99–108
- Fodor JA (1983) *The modularity of mind*. MIT, Cambridge, MA
- Gallistel CR (1990) *The organization of learning*. MIT, Cambridge, MA
- Gouteux S, Thinus-Blanc C, Vauclair J (2001) Rhesus monkeys use geometric and non-geometric information during a reorientation task. *J Exp Psychol Gen* 130:505–519
- Gray ER, Bloomfield LL, Ferrey A, Spetch ML, Sturdy CB (2005) Spatial encoding in mountain chickadees: features overshadow geometry. *Biol Lett* 1:314–317
- Hermer L, Spelke ES (1994) A geometric process for spatial reorientation in young children. *Nature* 370:57–59
- Hermer L, Spelke ES (1996) Modularity and development: the case of spatial reorientation. *Cognition* 61:195–232
- Karmiloff-Smith A (1992) *Beyond modularity: a developmental perspective*. MIT, Cambridge
- Kelly DM, Spetch ML, Heth CD (1998) Pigeons (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *J Comp Psychol* 112:259–269
- Learmonth AE, Nadel L, Newcombe NS (2002) Children’s use of landmarks: implication for modularity theory. *Psychol Sci* 13:337–341
- Learmonth AE, Newcombe NS, Huttenlocher J (2001) Toddlers’ use of metric information and landmarks to reorient. *J Exp Child Psych* 80:225–244
- Nadel L, Hupbach A (2006) Cross-species comparisons in development: the case of the spatial “module”. In: Johnson MH, Munakata Y (eds) *Attention and performance XXI*. Oxford University Press, Oxford
- Newcombe NS, Sluzenski J, Huttenlocher J (2005) Pre-existing knowledge versus on-line learning: what do young infants really know about spatial location? *Psychol Sci* 16:222–227
- Sokal RR, Rohlf FJ (1969) *Biometry. The principles and practice of statistics in biological research*. WH Freeman, San Francisco
- Sovrano VA, Vallortigara G (2006) Dissecting the geometric module: a sense-linkage for metric and landmark information in animals’ spatial reorientation. *Psychol Sci* 17:616–621
- Sovrano VA, Bisazza A, Vallortigara G (2002) Modularity and spatial reorientation in a simple mind: encoding of geometric and non-geometric properties of a spatial environment by fish. *Cognition* 85:B51–B59
- Sovrano VA, Bisazza A, Vallortigara G (2003) Modularity as a fish views it: conjoining geometric and non-geometric information for spatial reorientation. *J Exp Psych: Anim Behav Proc* 29:199–210
- Sovrano VA, 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
- Sovrano VA, Bisazza A, Vallortigara G (2007) How fish do geometry in large and in small spaces. *Anim Cogn* 10:47–54
- Spelke ES (2003) What makes us smart. Core knowledge and natural language. In: Gentler D, Goldin-Meadow S (eds) *Language in mind. Advances in the study of language and thought*. MIT, Cambridge, MA, pp 277–311
- Tinbergen N (1951) *The study of instinct*. Oxford University Press, Oxford, UK
- Tommasi L, Gagliardo A, Andrew RJ, Vallortigara G (2003) Separate processing mechanisms for encoding geometric and landmark information in the avian hippocampus. *Eur J Neurosci* 17:1695–1702
- Vallortigara G (2004) Visual cognition and representation in birds and primates. In: Rogers LJ, Kaplan G (eds) *Vertebrate comparative cognition: are primates superior to non-primates?* Kluwer/Plenum, Dordrecht, pp 57–94
- Vallortigara G (2006) The cognitive chicken: visual and spatial cognition in a non-mammalian brain. In: Wasserman EA, Zentall TR (eds) *Comparative cognition: experimental explorations of animal intelligence*. Oxford University Press, Oxford, UK, pp 41–58
- Vallortigara G (in press) Animals as natural geometers. In: Tommasi L, Peterson M, Nadel L (eds) *Assembling brains: cognition, development and evolution*. MIT, Cambridge, MA
- Vallortigara G, Regolin L (2006) Gravity bias in the interpretation of biological motion by inexperienced chicks. *Curr Biol* 16:279–280
- Vallortigara G, Sovrano VA (2002) Conjoining information from different modules: a comparative perspective. *Behav Brain Sci* 25:701–702
- Vallortigara G, Feruglio M, Sovrano VA (2005a) Reorientation by geometric and landmark information in environments of different size. *Dev Sci* 8:393–401
- Vallortigara G, Zanforlin M, Pasti G (1990) Geometric modules in animal’s spatial representation: a test with chicks. *J Comp Psych* 104:248–254
- Vallortigara G, Pagni P, Sovrano VA (2004) Separate geometric and non-geometric modules for spatial reorientation: evidence from a lopsided animal brain. *J Cogn Neurosci* 16:390–400

- Vallortigara G, Regolin L, Marconato F (2005b) Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns. *PLOS Biol* 3:1312–1316
- Vargas JP, Petruso EJ, Bingman VP (2004a) Hippocampal formation is required for geometric navigation in pigeons. *Eur J Neurosci* 20:1937–1944
- Vargas JP, Lopez JC, Salas C, Thinus-Blanc C (2004b) Encoding of geometric and featural spatial information by Goldfish (*Carassius auratus*). *J Comp Psych* 118:206–216