

Experience and geometry: controlled-rearing studies with chicks

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Abstract Animals can reorient making use of the geometric shape of an environment, i.e., using sense and metric properties of surfaces. Animals reared soon after birth either in circular or in rectangular enclosures (and thus affording different experiences with metric properties of the spatial layout) showed similar abilities when tested for spatial reorientation in a rectangular enclosure. Thus, early experience in environments with different geometric characteristics does not seem to affect animals' ability to reorient using sense and metric information. However, some results seem to suggest that when geometric and non-geometric information are set in conflict, rearing experience could affect the relative dominance of featural (landmark) and geometric information. In three separate experiments, newborn chicks reared either in circular- or in rectangular-shaped home-cages were tested for spatial reorientation in a rectangular enclosure, with featural information provided either by panels at the corners or by a blue-coloured wall. At test, when faced with affine transformations in the arrangement of featural information that contrasted with the geometric information, chicks showed no evidence of any effect of early experience on their relative use of geometric and featural information for spatial reorientation. These findings suggest that, at least for this highly precocial species, the ability to deal with geometry seems to depend more on predisposed mechanisms than on learning and experience after hatching.

Keywords Geometric information · Experience · Innate module · Spatial reorientation · Domestic chicks · *Gallus gallus*

Introduction

Vertebrate species are able to reorient themselves making use of the shape of an environment (see for review Cheng and Newcombe 2005). According to some scientists, this ubiquitous ability of biological organisms would be suggestive of an innately predisposed “geometric module”: i.e., animals would be innately endowed with a cognitive mechanism to apprehend the extent of surfaces as surfaces together with their left–right sense (Cheng 1986; Spelke 2000, 2003; Spelke and Kinzler 2007; Vallortigara 2009).

Geometric information seems to be spontaneously encoded by organisms even when they are trained in the presence of salient visual features that would suffice for successful reorientation (chicks: Vallortigara et al. 1990; pigeons: Kelly et al. 1998; fish: Sovrano et al. 2002, 2003). It has been claimed that this predominance in the coding of geometric arrangement of extended surfaces can be traced back to a natural ability of relying on the large-scale shape of the environment that does not change seasonally and remains stable and unmovable, hence providing a reliable source of information for navigational purposes (Shettleworth 1998 and see for a review Vallortigara 2009).

A remarkable exception to this “primacy” of geometric information was reported recently. In contrast to the domesticated or laboratory species so far studied, wild-caught mountain chickadees (*Poecile gambeli*) did not spontaneously encode the geometry of an enclosure when salient features were present near the goal; moreover, when trained without salient features, the birds encoded geometric

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information, but this encoding was overshadowed by features (Gray et al. 2005). The possibility of species-specific differences in the dominance of geometric and non-geometric cues, possibly associated with ecological differences, cannot of course be ruled out (and some evidence favouring this view has been reported, i.e., Sovrano et al. 2007). However, these findings also suggest a possible role of experience with angular and metric spatial information that is usually available to laboratory animals but not, or to a much smaller extent, to wild animals (Gray et al. 2005; and see also Cheng 2008).

A proper investigation of the role of experience in coding geometric information would require a comparison of the performance of the same species under different and well-controlled-rearing conditions (Vallortigara et al. 2009). Two recent studies have addressed the issue. Brown et al. (2007) reared fish (*Archocentrus nigrofasciatus*) either in circular or in rectangular tanks. Subsequent tests carried out in a rectangular enclosure showed that rearing conditions did not affect the fish reorientation performance. Similarly, domestic chicks (*Gallus gallus*) reared soon after hatching in different home-cages (circular vs. rectangular) and tested on day 3 of life in the same task as the fish, were shown the capability of using geometry for reorientation purposes irrespective of their rearing experience (Chiandetti and Vallortigara 2008a).

Overall, these findings suggest that experience with right angles and metrically distinct surfaces is not needed to encode basic geometrical characteristics such as directional sense and metric relationships. Note, also, that although previous research had shown that wild-caught birds (mountain chickadees) do not spontaneously encode geometric information when a salient feature was located near the goal, more recent work revealed that both hand-reared and wild-caught black-capped chickadees (*Poecile atricapillus*) encoded geometric information even in the presence of a salient landmark (Batty et al. 2009). This would point to species differences rather than to a specific role of learning. Results with fish, however, also highlighted that when geometric and non-geometric information was set in conflict, fish raised in a circular tank showed less use of geometric information than fish reared in a rectangular tank (Brown et al. 2007). Hence, it seems that the rearing environment could affect the relative dominance of non-geometrical (featural) and geometrical information. It should be noted, however, that in the experiment by Brown et al. (2007), fish were reared in groups for quite an extended period (ca. 4 months). Living with companions for so long before testing could therefore have directly exposed the experimental fish to geometric and featural information as that visible on conspecifics' bodies, and in particular it may have favoured use of the location of individual conspecifics as cues for spatial orientation and navigation. Such an imperfect rearing

procedure could have produced the observed difference in performance; hence, a control, with fish totally lacking such an experience, would be important. However, a proper control experiment is difficult to perform in altricial species, such as these cichlid fish, in which an extended period of development is needed before the animal has acquired the necessary level of sensory-motor maturation that would allow it to perform the behavioural task. This is not the case for precocial species, such as the domestic chick, which soon after hatching exhibit sufficiently mature sensory-motor abilities to allow independent locomotion and feeding.

Here, we devised three separate experiments in which we provided chicks (reared singly for 3 days after hatching in different spatial environments similar to those used with fish) with conflicting geometrical and non-geometrical information, in order to determine whether differences in the relative reliance on geometric and non-geometric information could be observed.

Experiment 1: learning with identical panels

In this first experiment, we attempted to replicate the basic finding that rearing in different spatial environments does not affect reorientation abilities in newborn chicks (see Chiandetti and Vallortigara 2008a). The procedure was slightly different than in the original experiments in that we here used identical panels at the corners of the arena in order to perform subsequent experiments dealing with contrast between geometric and non-geometric information. We compared the performance of rectangular- and circular-reared chicks in a rectangular enclosure with discrete panels located at the corners; in this experiment, all the panels were identical so that reorientation would out of necessity have to be based on the geometric layout alone, with the featural information provided by the panels acting only as a distracting cue but not as cue for spatial reorientation.

Methods

Subjects

Subjects were 17 male domestic chicks (*Gallus gallus*) obtained from fertilized eggs supplied from a commercial hatchery (Agricola Berica s.c.r.l., Montegalda, Vicenza, Italy) delivered to our laboratory when the eggs were at day 14 of incubation. Thereafter, and until hatching, the eggs were incubated in complete darkness under controlled temperature (37.7°C) and humidity (about 50–60%) conditions, as described elsewhere (Chiandetti and Vallortigara 2008a). After hatching in the dark, chicks were immediately taken

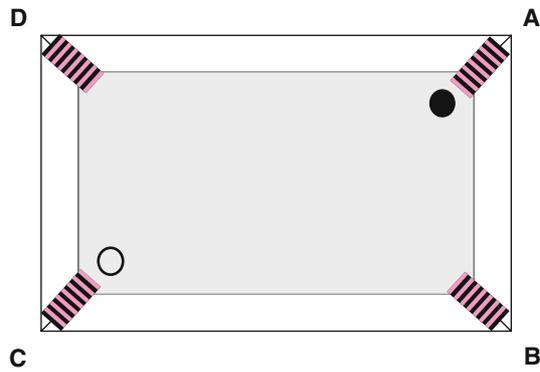


Fig. 1 Exp1—layout of the apparatus used to train rectangular- and circular-reared chicks. Identical panels were provided at the corners. Because of the shape of the enclosure, the reinforced position (*filled dot*) has an indistinguishable geometrical equivalent (*empty dot*)

singly to their rearing cages, either rectangular- (22 cm wide \times 30 cm high \times 40 cm deep; $n = 8$ chicks) or circular-shaped (32 cm wide \times 30 cm high; $n = 9$ chicks) cages that were illuminated from the top by light coming from fluorescent lamps. Temperature was kept constant at 30°C, and food and water were supplied ad libitum.

Apparatus

The experimental apparatus was a uniformly white-coloured large rectangular cage (70 cm deep \times 35 cm wide \times 40 cm high). Four identical cardboard panels (20 \times 4.5 cm) were located at each corner (different features were used for different chicks, but the same panels were maintained throughout the training; an example is visible in Fig. 1). A transparent glass container (4 cm in diameter; 4 cm in height; identical to the food jar present in the chicks' home-cage but completely closed on the top by a wire net) was located beside each panel.

Procedure

Chicks were placed in the centre of the enclosure randomly facing one of the walls and were trained to search for the reinforced glass container associated with a particular corner in the cage-test and to peck at it in order to receive some grains of food, delivered by the experimenter from above the apparatus. The apparatus was free to rotate 360° on its axis, and its position was changed randomly trial by trial; furthermore, the apparatus was covered by a net used to prevent chicks from seeing outer cues. This made sure that chicks were unable to use the presence of the experimenter as a stable cue for reorientation. Training started on day 3 (48–72 h after hatching) of life and consisted of 3 daily sessions of 10 trials (intertrial-interval was 2 min), separated by an interval of two hours. In each trial, the animal was

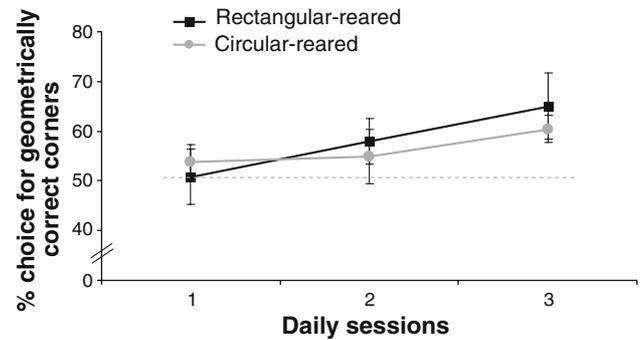


Fig. 2 Exp1—training results. Mean percentages (with SEM) of choices for the geometrically correct corners for chicks reared in rectangular- and circular-shaped cages are shown. Trials are shown in blocks of daily sessions, i.e., 30 trials for each block

left free to approach one food jar: when the correct position was chosen, the chick was given food (reinforcement); when the incorrect one (and the geometrically equivalent corner as well) was chosen, the animal was removed from the cage-test and given the next trial. During the intertrial-interval, the chick was removed and placed in a small, closed cardboard box (20 \times 20 \times 30 cm) outside the cage-test and passively rotated to eliminate inertial information. For the circular-reared chicks, a cylinder (16 \times 20 cm) was placed in the cardboard holding box ensuring that chicks were not exposed to geometrical shapes outside the experimental apparatus. The experimental cage was also randomly rotated 90° from trial to trial. All the chicks underwent 90 trials overall, and none of the animals was discarded.

Percentages of choices for both the rewarded correct corner and the incorrect but geometrically equivalent corner 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. 2. 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 ($F_{2,30} = 3.609$, $P = 0.039$); there were no significant effects associated with rearing conditions ($F_{1,15} = 0.199$, $P = 0.662$) nor was there a significant interaction of rearing conditions \times session ($F_{2,30} = 0.612$, $P = 0.549$).

We then divided the data into five mini-blocks of two trials each and restricted the analysis to the very first block of ten trials. As can be seen from Fig. 3, again no difference

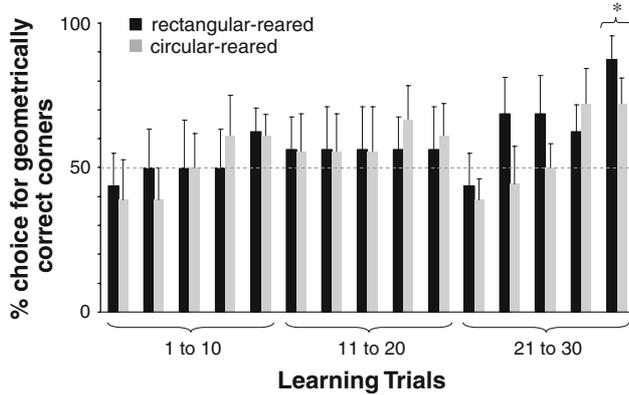


Fig. 3 Exp1—early training results. The first 30 trials were divided into 15 blocks of two trials each. Mean percentages (with SEM) of choices for the two geometrically correct corners for chicks reared in rectangular- and circular-shaped cages are shown. There were no statistically significant differences between the two rearing conditions either at the very beginning of training or when both groups started to show learning [choices above chance level ($*P < 0.05$) are shown: $t_{16} = 2.219$, $P = 0.041$, two-tailed one sample t -Test]

between the rearing conditions was apparent (rearing: $F_{1,15} = 0.009$, $P = 0.925$; rearing \times block of trials: $F_{4,60} = 0.282$, $P = 0.888$).

Both groups of chicks learnt to reach a particular corner (and its geometrical equivalent corner) defined by specific metric features with no differences between rectangular- and circular-reared chicks.

Experiment 2: conflicting information in differently sized enclosures with panels

In the second experiment, we used different panels at the corners, thus providing featural information for individuating the correct position. Chicks were first trained to approach the correct panel to obtain food. Then, at test, panels were displaced according to an affine transformation (see Fig. 4), so that featural and geometric cues provided contradictory information.

Some recent evidence suggests that the size of the experimental space may affect the type of information, geometric and non-geometric, which children (Learmonth et al. 2001, 2008) and animals (Sovrano et al. 2005, 2007; Chiandetti et al. 2007; Vallortigara et al. 2004) preferentially use to reorient. Large environments favour the use of featural information, whereas small environments favour the use of geometric information (see for a review Chiandetti and Vallortigara 2008b). To take this factor into account, we tested circular- and rectangular-reared chicks both in a large and in a small rectangular enclosure.

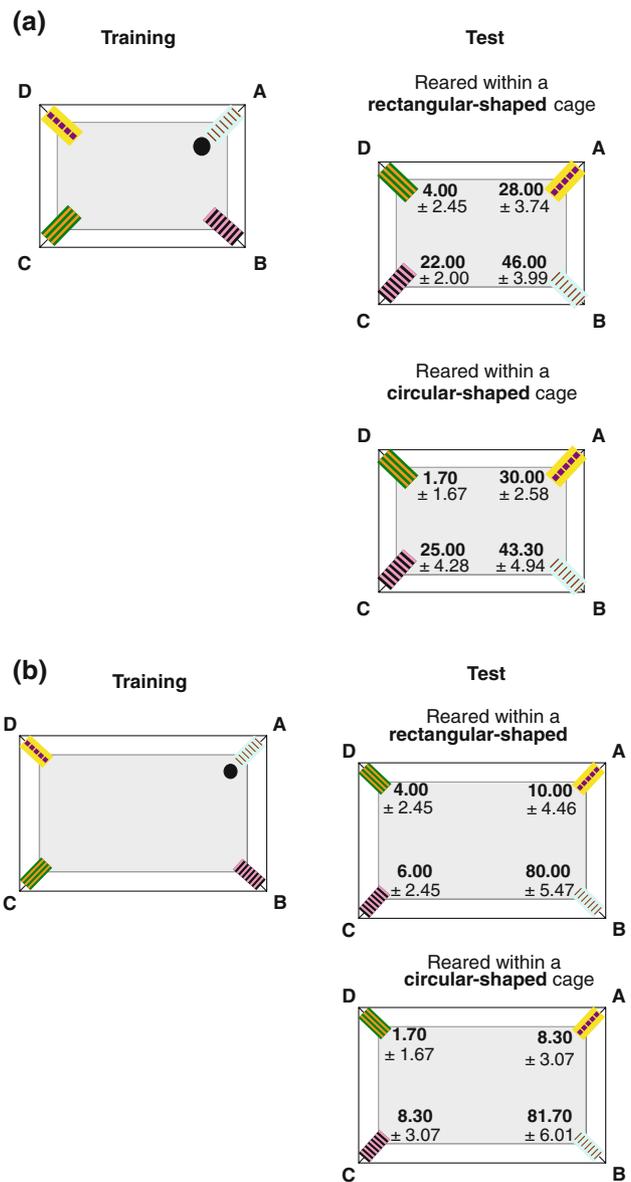


Fig. 4 Exp2—results. Rectangular- and circular-reared chicks were trained in a small (a) or in a large (b) rectangular enclosure with different panels at the corners (leftmost figure) to find food in one particular corner (A) and then tested, after an affine transformation in panel position, so as to provide conflicting geometric and non-geometric (panels) information (rightmost figures). Mean percentages of choices for each corner are shown in bold (with SEM below). The reinforced corner was different for each chick; here, it is shown as corner ‘A’ for illustrative purposes only

Methods

Subjects

Subjects were 22 male domestic chicks (*Gallus 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 ($n = 10$ chicks) and circular ($n = 12$ chicks). All other details were the same as in Experiment 1.

Apparatus and procedure

The experimental apparatus this time consisted of two rectangular white-coloured wooden enclosures (a large enclosure as the one used in Experiment 1: 70 cm deep \times 40 cm high \times 35 cm wide; and a small enclosure: 35 cm deep \times 40 cm high \times 17.5 cm wide) with four different cardboard panels (20 \times 4.5 cm) placed one for each corner (Fig. 4). The panels differed from each other in colour, brightness and texture; one panel was yellow with a central column of violet squares; the second panel had green and orange vertical stripes (0.5 cm large); the third panel had pink and black horizontal stripes (1.5 cm), and the fourth was light-blue with brown horizontal lines (0.5 cm large). The positive panel (i.e., the one that indicated the corner where the food would be delivered) was different for different chicks. All other training details were the same as described for Experiment 1.

Eleven chicks were trained in the small enclosure (rectangular $n = 5$; circular $n = 6$) and 11 chicks in the large enclosure (rectangular $n = 5$; circular $n = 6$). All the chicks underwent 3 sessions of 10 trials each per day until they reached a learning criterion fixed at 9 out of 10 correct choices in a single session. Twenty-four hours after chicks had reached criterion, the chicks were tested, within the same experimental space, after the displacement of all landmarks (Figs. 4, 5) in ten consecutive non-rewarded trials. All other testing procedures were the same as described earlier.

Results

There were no differences either in the number of trials or in the number of errors (choices for corners B, C and D) needed to reach the learning criterion between rectangular- and circular-reared chicks trained in the small (rectangular-reared trials: Mean = 74.00, SEM = 5.99, errors: Mean = 33.00, SEM = 4.61; circular-reared trials: Mean = 76.67, SEM = 6.15, errors: Mean = 34.50, SEM = 3.90, respectively: $U = 13$, $n_1 = 5$, $n_2 = 6$, $P = 0.705$; $U = 15$, $n_1 = 5$, $n_2 = 6$, $P > 0.999$, two-tailed Mann–Whitney U -test) or in the large (rectangular-reared trials: Mean = 76.00, SEM = 7.47, errors: Mean = 32.20, SEM = 3.26; circular-reared trials: Mean = 68.33, SEM = 11.08, errors: Mean = 31.33, SEM = 6.54, respectively: $U = 13.5$, $n_1 = 5$, $n_2 = 6$, $P = 0.773$; $U = 14$, $n_1 = 5$, $n_2 = 6$, $P = 0.855$, two-tailed Mann–Whitney U -test) enclosures.

Mean percentages of choices for the four corners during test (i.e., after rotation of the panels) are shown in

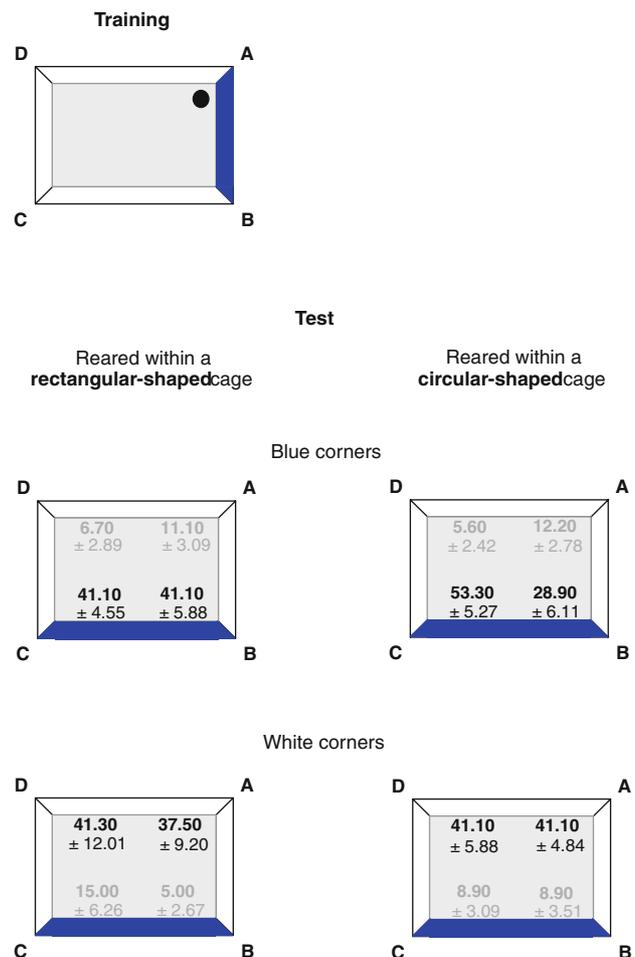


Fig. 5 Exp3—results. Rectangular- and circular-reared chicks were trained in a small rectangular enclosure with one wall painted in blue. For illustrative purposes only, here the shorter wall is coloured blue (top left figure). Chicks had to find food either in the “blue corners” (A or B) or in the “white corners” (C or D) and then were tested, after a displacement of the coloured wall, so as to provide conflicting geometric and non-geometric (blue wall) information (bottom figures). Mean percentages of choices for each corner are shown in bold (with SEM below)

Fig. 4 (a, small enclosure; b, large enclosure). As can be seen, chicks clearly chose the panel on which they had been previously trained, even if located in an incorrect position (i.e., corner B) both in the large and in the small enclosure. No differences in the choices for corner B were apparent between the two rearing conditions (small enclosure: $U = 13$, $n_1 = 5$, $n_2 = 6$, $P = 0.687$; large enclosure: $U = 13.5$, $n_1 = 5$, $n_2 = 6$, $P = 0.779$ two-tailed Mann–Whitney U -test). There was a significant heterogeneity associated with choices for the corners A, C and D in the small cage-test: $\chi^2 = 17.63$, $n = 11$, $df = 2$, $P < 0.001$ Friedman test; however, this was not evident in the large cage-test: $\chi^2 = 4.69$, $n = 11$, $df = 2$, $P = 0.096$ Friedman test. In fact, choices for the geometrically correct corners were more frequent in the

small than in the large enclosure ($U = 000$, $n_1 = 11$, $n_2 = 11$, $P < 0.001$, two-tailed Mann–Whitney U -test).

Rectangular- as well as circular-reared chicks proved equally capable of learning to go for the reinforced panel in both the large and the small enclosures; moreover, at test, they all preferred to choose the correct feature despite it being located in a novel, geometrically incorrect position. As expected on the basis of previous evidence (review in Chiandetti and Vallortigara 2008b), reliance on geometric information was stronger in the small enclosure than in the large enclosure (as shown by the larger number of choices for the AC corners in the former condition), but this effect occurred in both rectangular- and circular-reared chicks.

Experiment 3: conflicting information in a small enclosure with a blue wall

We were concerned with the possibility that the different results were due to the use of panels at the corners rather than a coloured wall as in the Brown et al. (2007) experiments with fish. Panels provided local cues very close to reinforcement, whereas a coloured wall would require also the encoding of a location with respect to more distant cues (e.g., when the correct corner is located between two white walls) and would require the encoding of left/right sense (in the case of coloured/white corners). We thus trained rectangular- and circular-reared chicks in a small rectangular enclosure with one coloured (blue) wall, and then we tested chicks after the displacement of this feature, thus providing conflicting featural and geometric information.

Methods

Subjects

Subjects were 35 male domestic chicks (*Gallus 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 ($n = 17$ chicks) and circular ($n = 18$ chicks). All other details were the same as in Experiment 1.

Apparatus and procedure

The experimental apparatus consisted of a small rectangular wooden enclosure (35 cm deep \times 40 cm high \times 17.5 cm wide) with three uniformly white-coloured walls and one coloured (blue) wall. For 19 chicks (rectangular $n = 9$; circular $n = 10$), the blue wall during training was one of the short walls, and for 16 chicks (rectangular $n = 8$; circular $n = 8$), the blue wall was one of the longer walls.

This was done in order to control for any possible influence of the relative size of the coloured wall. Moreover, within each condition, half of the chicks were trained on the “blue corners” (those corners defined by the joint of the blue wall and a white wall, and for each chick either the corner to the left or the corner to the right of the blue wall was rewarded), the others on the “white corners” (those corners defined by the joint of two white walls, and for each chick either the corner to the left or the corner to the right of the short wall was rewarded). Trials at training, criterion and test were the same as described for the previous experiment. Twenty-four hours after reaching the learning criterion, the chicks were tested, within the same experimental space, after a displacement of the blue-coloured wall (Fig. 5), so that chicks previously trained with the blue wall on the short side were tested with the blue wall on the long side of the enclosure and vice versa. All other testing procedures were the same as described above.

Results

There were no differences in the number of trials or errors needed to reach the learning criterion between rectangular- and circular-reared chicks either in the short blue wall condition (rectangular-reared trials: Mean = 82.22, SEM = 2.22, errors: 38.44, SEM = 1.39; circular-reared trials: Mean = 81.00, SEM = 4.07 errors: 38.20, SEM = 2.34, respectively: $U = 41.5$, $n_1 = 9$, $n_2 = 10$, $P = 0.757$; $U = 41.5$, $n_1 = 9$, $n_2 = 10$, $P = 0.774$ two-tailed Mann–Whitney U -test) or in the long blue wall condition (rectangular-reared trials: Mean = 80.00, SEM = 2.67, errors: 37.38, SEM = 1.29; circular-reared trials: Mean = 75.00, SEM = 4.63, errors 32.88, SEM = 3.54, respectively: $U = 25$, $n_1 = 8$, $n_2 = 8$, $P = 0.440$; $U = 24.5$, $n_1 = 8$, $n_2 = 8$, $P = 0.431$ two-tailed Mann–Whitney U -test).

There were also no differences in the number of trials needed to reach the learning criterion between short-rectangular and long-rectangular trained chicks (trials: $U = 30$, $n_1 = 9$, $n_2 = 8$, $P = 0.525$; errors: $U = 31.5$, $n_1 = 9$, $n_2 = 8$, $P = 0.664$ two-tailed Mann–Whitney U -test) or between short-circular and long-circular trained chicks (trials: $U = 27$, $n_1 = 10$, $n_2 = 8$, $P = 0.226$; errors: $U = 28$, $n_1 = 10$, $n_2 = 8$, $P = 0.285$ two-tailed Mann–Whitney U -test). Since there were no significant effects associated with the location of the blue wall along the shorter or the longer wall, the data related to these two conditions were combined in Fig. 5.

No differences in the number of trials to criterion were found between rectangular- and circular-reared chicks either when trained along the “blue corners” (rectangular-reared trials: Mean = 78.89, SEM = 2.61, errors: Mean = 37.00, SEM = 1.30; circular-reared trials: Mean = 74.44,

SEM = 34.22, errors: Mean = 34.22, SEM = 3.60, respectively: $U = 37$, $n_1 = 9$, $n_2 = 9$, $P = 0.747$; $U = 35$, $n_1 = 9$, $n_2 = 9$, $P = 0.666$ two-tailed Mann–Whitney U -test) or when trained along the “white corners” (rectangular-reared trials: Mean = 83.75, SEM = 1.83, errors: Mean = 39.00, SEM = 1.32; circular-reared trials: Mean = 82.22, SEM = 2.78, errors: Mean = 37.44, SEM = 2.18, respectively: $U = 33.5$, $n_1 = 8$, $n_2 = 9$, $P = 0.791$; $U = 32.5$, $n_1 = 8$, $n_2 = 9$, $P = 0.735$ two-tailed Mann–Whitney U -test).

Results for the test are shown in Fig. 5. Choices of chicks trained on the “blue corners” were transformed so that the two training conditions (along the longer and along the shorter blue wall) were comparable while maintaining the metric and featural distribution; the same was done for chicks’ choices trained on the “white corners”. As can be seen, rectangular- and circular-reared chicks trained on the “blue corners” searched, at test, mainly along the blue wall (rectangular- AD vs. BC: $Z = -2.694$, $P = 0.007$; circular- AD vs. BC: $Z = -2.694$, $P = 0.007$, two-tailed Wilcoxon signed ranks test), and chicks trained on the “white corners” searched mainly along the white wall (rectangular- AD vs. BC: $Z = -2.375$, $P = 0.018$; circular- AD vs. BC: $Z = -2.687$, $P = 0.007$, two-tailed Wilcoxon signed ranks test).

Rectangular- and circular-reared chicks trained either on the “blue corners” or on the “white corners” showed the same pattern of choices at test. Previous exposure to geometry did not significantly affect animals’ choices: rectangular- and circular-reared chicks proved to be equally capable of encoding of geometric information. In fact, although searching close to the two corners with the blue wall occurred as expected, a clear preference for the corner defined by the same characteristic of metric and sense (i.e., geometrical information) as during the training condition was displayed at test by both rectangular-reared and circular-reared chicks.

Discussion

The aim of this study was to test the hypothesis that experience with different geometric characteristics of a spatial layout may affect the encoding and/or the reliance on geometric and non-geometric cues during spatial reorientation. To this aim, we made use of an animal model system in which strict experimental control of early experiences can be combined with testing at an early age because of precocial motor development. Newly hatched domestic chicks were reared in either rectangular or circular cages, in order to provide them with experience of different geometric characteristics in their home-cage environment. In the first experiment, chicks were trained to find a food reward located in one of the four corners of a rectangular enclosure,

all corners being marked by identical landmarks. In such a situation, chicks were forced to rely on geometric information only, because the landmarks did not provide any information to disambiguate the correct corner. Rectangular- and circular-reared chicks showed similar performance. This confirmed previous results with chicks (Chiandetti and Vallortigara 2008a) and fish (Brown et al. 2007) that experience in different spatial environments does not affect the ability to reorient on the basis of geometric information.

In the second experiment, chicks were trained with different landmarks at the corners, so that both geometric and non-geometric information could have been used. At test, after the chicks had reached learning criterion, the landmarks were dislocated according to an affine transformation, so that chicks were faced with contradictory geometric and non-geometric information. Again, no difference between rectangular- and circular-reared chicks was observed even though enclosures of different sizes were used to favour the encoding of either geometric (small-sized enclosure) or non-geometric (large-sized enclosure) information (see Chiandetti et al. 2007; Chiandetti and Vallortigara 2008b; Learmonth et al. 2001, 2008).

In the third experiment, a blue wall, rather than distinct panels at the corners, was used as a landmark (exactly as in the experiments with the chickadees, Gray et al. 2005, and the *Archocentrus nigrofasciatus* fish, Brown et al. 2007). Again, when facing a test in which geometric and non-geometric (blue wall) cues provided contradictory information, rectangular- and circular-reared chicks showed the same pattern of results.

These findings with chicks seem to contrast with those reported for *Archocentrus nigrofasciatus* fish, which suggested that rearing experience, though not affecting the ability to encode geometry per se, did affect the relative dominance of geometric and non-geometric cues when animals were facing conflicting information. The species difference could be accounted for in terms of differences between altricial and precocial species. The species of fish used by Brown et al. (2007) shows biparental, prolonged care (as usually occurs in cichlid fish, see Gagliardi-Seeley and Itzkowitz 2006), whereas domestic chicks are immediately largely independent from parental care following hatching. Altricial species may, therefore, be more sensitive to external stimulation (or to be open to such stimulation for a more extended time period); hence, fish may be affected by rearing experience. Note, also, that the duration of rearing and therefore the amount of exposure was very different in the two experiments. However, for a precocial species such as the domestic chick, it is very unlikely that the duration of exposure used in the present experiment would be insufficient to produce an effect: this animal model shows the very early maturation of both motor

development and visual-cognitive abilities (Rose 2000; Andrew 1991; Regolin and Vallortigara 1995; Vallortigara 2009). Besides this, however, it should be noted that while chicks were reared singly in separate cages, in the experiment by Brown et al. (2007), fish were reared in groups; the fully visible metric and angular colourful features on the body of the social companions could therefore have directly exposed the experimental fish to geometric information. Clearly, there is a need for further experimental research.

Preferential use of the overall metric layout of surfaces as surfaces seems to be a widely used strategy by most vertebrate species when relocating in the environment. Whether experience is needed to trigger these “geometrical abilities” seems debatable. Our findings with animals fit with results coming from traditional populations of humans (hunter-gatherers) who seem to be able to make use of geometry even without any experience of specific geometric conceptualization and/or detailed verbal categorization (Dehaene et al. 2006). From this perspective, it is possible that rudimentary cognitive tools for dealing with elementary geometric problems—such as distances, sense and angles—are shared by vertebrates and are predispositions irrespective of the different ecological niches they inhabit.

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References

- Andrew RJ (1991) Neural and behavioural plasticity: the use of the domestic chick as a model. Oxford University Press, UK
- Batty E, Bloomfield L, Spetch M, Sturdy C (2009) Black-capped (*Poecile atricapillus*) and mountain chickadees' (*Poecile gambeli*) use of geometric and featural information in a spatial orientation task. *Anim Cogn* 12:633–641
- Brown AA, Spetch ML, Hurd PL (2007) Growing in circles: rearing environment alter spatial navigation in fish. *Psychol Sci* 18:569–573
- Cheng K (1986) A purely geometric module in the rat's spatial representation. *Cognition* 23:149–178
- Cheng K (2008) Whither geometry? Troubles of the geometric module. *Trends Cogn Sci* 12:55–361
- Cheng K, Newcombe N (2005) Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychon Bull Rev* 12:1–23
- Chiandetti C, Vallortigara G (2008a) Is there an innate geometric module? Effects of experience with angular geometric cues on spatial re-orientation based on the shape of the environment. *Anim Cogn* 11:139–146
- Chiandetti C, Vallortigara G (2008b) Spatial reorientation in large and small enclosures: comparative and developmental perspectives. *Cogn Proc* 9:229–238
- 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
- Gagliardi-Seeley JL, Itzkowitz M (2006) Male size predicts the ability to defend offspring in the biparental convict cichlid *Archocentrus nigrofasciatus*. *J Fish Biol* 69:1239–1244
- Gray ER, Bloomfield LL, Ferrey A, Spetch ML, Sturdy CB (2005) Spatial encoding in mountain chickadees: features overshadow geometry. *Biol Lett* 1:314–317
- 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, Newcombe NS, Huttenlocher J (2001) Toddlers' use of metric information and landmarks to reorient. *J Exp Child Psychol* 80:225–244
- Learmonth AE, Newcombe NS, Sheridan N, Jones M (2008) Why size counts: children's spatial reorientation in large and small enclosures. *Dev Sci* 11:414–426
- Regolin L, Vallortigara G (1995) Perception of partly occluded objects by young chicks. *Percept Psychophys* 57:971–976
- Rose S (2000) God's organism? The chick as a model system for memory studies. *Learn Mem* 7:1–17
- Shettleworth SJ (1998) Cognition, evolution and behaviour. University Press, New York, Oxford
- Sokal RR, Rohlf FJ (1969) Biometry. The principles and practice of statistics in biological research. WH Freeman, San Francisco
- 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* 85:51–59
- Sovrano VA, Bisazza A, Vallortigara G (2003) Modularity as a fish views it: conjoining geometric and nongeometric information for spatial reorientation. *J Exp Psychol 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 (2000) Core knowledge. *Am Psychol* 55:1233–1243
- Spelke ES (2003) What makes us smart? Core knowledge and natural language. In: Gentner D, Goldin-Meadow S (eds) *Language in mind: advances in the investigation of language and thought*. MIT Press, Cambridge, MA
- Spelke ES, Kinzler KD (2007) Core knowledge. *Dev Sci* 10:89–96
- Vallortigara G (2009) Animals as natural geometers. In: Tommasi L, Peterson M, Nadel L (eds) *The biology of cognition*. MA, MIT Press, pp 83–104
- Vallortigara G, Zanforlin M, Pasti G (1990) Geometric modules in animal's spatial representation: a test with chicks. *J Comp Psychol* 104:248–254
- Vallortigara G, Feruglio M, Sovrano VA (2004) Reorientation by geometric and landmark information in environments of different spatial size. *Dev Sci* 8:393–401
- Vallortigara G, Sovrano VA, Chiandetti C (2009) Doing socrates experiment right: controlled-rearing studies of geometrical knowledge in animals. *Curr Opin Neurobiol* 19:20–26