PAPER

Inexperienced newborn chicks use geometry to spontaneously reorient to an artificial social partner

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Abstract

A fundamental process underlying navigation behaviour, shown to occur in every species tested, uses geometric properties of the environment for location memory and orientation. Here we employ a new method to ask whether this basic geometric orientation ability is innately predisposed in the brain or depends on specific experiences navigating in a geometrically rich environment. Using the newborn domestic chick as a model system, we present a working memory task testing reorientation towards a filial imprinting object under rigorous controlled rearing conditions. In the absence of any previous exposure to a geometrically rich environment, newly hatched chicks spontaneously recovered their bearings by making use of distances and directional relations to reorient themselves to an artificial social partner. These findings provide evidence for an innate capacity to navigate by the geometric structure of the environment.

Research highlights

- Animals reorient in enclosed spaces by relying on surface distances and left–right directional sense.
- Basic geometric orientation ability is innately predisposed in the brain of at least one precocial vertebrate species.
- Chicks undergo a working memory task testing reorientation towards a filial imprinting object.
- Chicks encode geometry without any previous experience of navigating in a geometrically structured environment.

Introduction

Animals can recover their bearings in enclosed spaces by relying on surface distances together with a left–right directional sense (reviewed in Cheng & Newcombe, 2005; Spelke & Lee, 2012; Tommasi, Chiandetti, Pecchia, Sovran & Vallortigara, 2012; Landau & Lakusta, 2009; Vallortigara, 2009). Following passive spatial disorientation in a rectangular enclosure, for example, animals who previously witnessed an object in a corner of the enclosure make equal numbers of visits to the target corner and the diagonally opposite corner with the same arrangement of metric and directional information among surfaces (Cheng, 1986). These findings provide evidence that the animals reorient themselves by the geometry of the surface layout.

Does the ability to reorient by environmental geometry depend on experience navigating in geometrically structured environments, or does it emerge in animals with no such prior experience? Use of geometric information has been documented in young children while reorienting (Hermer & Spelke, 1994; Lee & Spelke, 2011). Also, human infants show sensitivity to a variety of geometric properties, including shape of two- and three-dimensional objects, the physical extent of lines and angles (e.g. Antell & Caron, 1985; Slater, Mattock & Brown, 1990; Schwartz & Day, 1979), and discrimination of corners within a shape (Lourenco & Huttenlocher,

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2008). However, humans cannot be tested in reorientation tasks until they begin to locomote independently in the second year of life, leaving ample opportunity for a role played by learning and experience. Controlled rearing experiments on model animals are thus needed to address this question.

Such experiments have been performed, but their significance is subject to debate. On the one hand, groups of chicks reared either in a geometrically rich environment (with right angles and metrically distinct surfaces) or in a homogeneous, cylindrical environment (uninformative with respect to geometry) showed comparable abilities to reorient by geometry (Chiandetti & Vallortigara, 2008, 2010b). Studies with fish (Brown, Spetch & Hurd, 2007) and mice (Twyman, Newcombe & Gould, 2013) replicated these findings. However, in all the controlled rearing studies performed so far, animals were tested in reference memory tasks with repeated reinforcement training at one target location. The use of a reference memory paradigm has an important drawback for controlled rearing studies because the animals receive repeated training at one specific target location. Thus, the controlled-reared animals received considerable exposure to geometry as provided by the shape of the training enclosure before their sensitivity to geometry was tested.

The use of a reference memory paradigm raises a further problem. Most studies of reorientation in human children, and many studies of reorientation in experienced animals, use a working memory task that requires subjects to return to the same target location at each subsequent trial after a short delay (during which they are rotated and disoriented). The findings of studies using reference memory paradigms may differ from the findings of these studies, because working memory tasks and reference memory tasks are associated with basic differences in information encoding. For example, both human children and non-human animals who are tested in working memory tasks use the relative positions of subtle 3D extended surfaces on the ground to compute their way back to the goal, whereas they do not use such relationships with respect to an array of freestanding objects or high-contrast 2D forms (Cheng, 1986; Gouteux & Spelke, 2001; Lee, Spelke & Vallortigara, 2012; Lee & Spelke, 2011). In contrast, in reference memory tasks animals successfully navigate by such featural cues (Cheng & Newcombe, 2005; Chiandetti & Vallortigara, 2010b; Pecchia & Vallortigara, 2012). Thus, existing experiments using controlled rearing methods do not reveal whether the spontaneous encoding of geometry, observed in human children, arises in the absence of experience navigating in geometrically structured environments.

Here we developed a new method to overcome these limitations. We exploited filial imprinting responses in a working memory version of the reorientation task that controls for previous exposure to geometric information provided by the testing environment.

Filial imprinting in the domestic chick occurs shortly after hatching and both artificial and naturalistic objects can be effective in triggering responses of attachment. Belonging to a precocial species, chicks show immediately after hatching good motor control and early developing perceptual acuity, features that allow them to be tested at a precocial age when experiences are extremely limited. When imprinting objects are made to move and disappear, chicks immediately respond with following behaviour (review in McCabe, 2013). Imprinting proved to be an efficacious phenomenon to investigate several aspects of cognition in the first post-hatching days (i.e. detour and object permanence conception (e.g. Regolin, Vallortigara & Zanforlin, 1995), perception (review in Mascalzoni & Regolin, 2010) and inferences about object physical properties (e.g. Chiandetti & Vallortigara, 2011)). The striking similarity to human perceptual organization and orientation strategies displayed by young chicks leads us to use imprinting, for the first time, as a method to explore spatial reorientation abilities in the absence of previous experience.

In the first experiment, we tested the effects of rearing chicks in environments with different geometries on their spontaneous use of geometry to reorient towards an imprinting object. In the second experiment, we eliminated all previous experience in a geometrically structured environment by allowing chicks to observe (and thus imprint) directly on an object moving in a particular location and then testing them immediately for spatial reorientation.

Experiment 1

In the first experiment, chicks were raised for 3 days with the imprinting object in informative or uninformative rearing cages. Then they were tested in a working memory version of the geometric reorientation task by changing the hiding position on each trial.

Subjects

Twenty-three domestic chicks (*Gallus gallus*) hatched from fertilized eggs supplied from a local commercial hatchery (Agricola Berica s.c.r.l., Montegalda, Vicenza, Italy) were tested. Eggs were incubated in complete darkness and, immediately after hatching, chicks were

reared singly in separate home-cages that were either rectangular ($22 \times 30 \times 40$ cm; $n = 10$ chicks) or circular in shape (32×30 cm; $n = 13$ chicks), as described elsewhere (Chiandetti & Vallortigara, 2008). A red plastic imprinting object (3×5 cm) was suspended by a thin wire in the centre of each cage at about the chicks' head height.

Apparatus

Different enclosures were used for habituating either rectangular- or circular-reared chicks to rejoin the imprinting object. Rectangular-reared chicks were habituated in a white poliplack square-shaped enclosure ($50 \times 50 \times 50$ cm). A cylindrical grid served as the starting place (12×20 cm) and was positioned in the middle of the rear wall; on the other end of the enclosure, and in front of the starting position, there were two identical blue panels (4.5×20 cm) where the imprinting object could be hidden. Illumination was provided by a 25W lamp placed on the centre top of the enclosure; the ceiling was covered by white tulle net to prevent chicks from seeing any cues outside the chamber. Circular-reared chicks were habituated in a fibreglass circular enclosure (55×50 cm); the same cylindrical grid was used to confine chicks on the periphery of the enclosure while the imprinting object was made to disappear behind one or other of the two identical blue panels placed directly in front of the starting position. The light and net were positioned as for the square-shaped enclosure.

The test apparatus was the same for both groups of chicks. It consisted of a rectangular white wooden enclosure ($35 \times 40 \times 70$ cm). The circular grid used during training was positioned in the centre of the enclosure; a circular rotating platform (12 cm in diameter) was suspended 2 mm above the arena floor so that it allowed the enclosure to spin freely on a rotating plate placed beneath it. Four hiding panels (identical to those used for habituation) were positioned at the corners; the light and net were positioned as for training enclosures.

Procedure

Habituation

On day 3, chicks were shown the object disappearing behind one of the panels while they were confined behind the cylindrical grid. Then they were freed to spontaneously rejoin the imprinting object. After five consecutive trials using this procedure, chicks were again shown the object disappearing, but after they were confined under

the cylindrical grid, an opaque cylinder was lowered to prevent them from keeping track of its hiding position. Three seconds later, chicks were freed and allowed to spontaneously rejoin the imprinting object for five more consecutive trials.
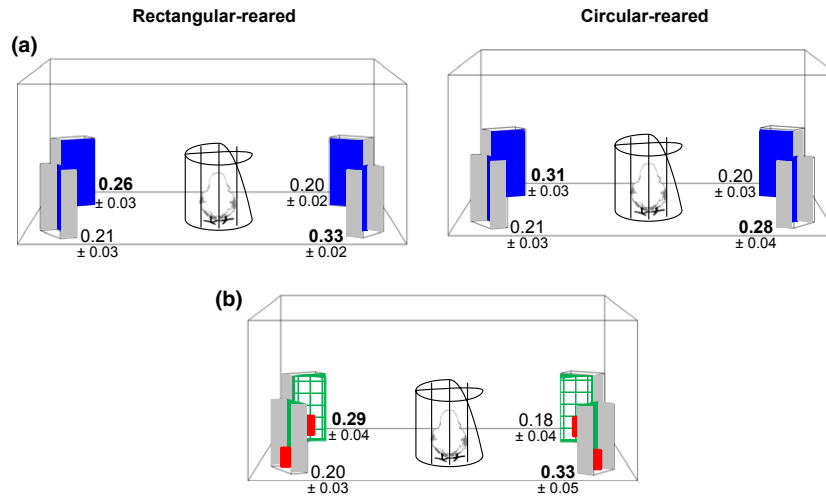
Test

On day 4, each chick was located in the middle of the testing apparatus inside the cylindrical grid (see Figure 1) and was shown the object approaching one of the four panels and going behind it. Then the opaque cylinder was lowered to prevent the chick from keeping track of the hiding location, and from detecting either the external rotation of the apparatus or the removal of the imprinting object. The apparatus was turned randomly by 90° to disorient the animal (see Chiandetti & Vallortigara, 2010a, for discussion of the equivalence of either subject- or environment-rotation for disorientation, but see e.g. Lourenco & Huttenlocher, 2006, for different results in humans). Finally, the chick was released to look for the imprinting object. Chicks were tested on 16 consecutive trials, with trial-by-trial variation in the hiding corner. A choice was scored when the chick went behind the panel or stopped in front of it, pecking at it or calling. Choices for both the correct hiding corner and the incorrect but geometrically equivalent corner were scored as correct. The side of the apparatus where the net was lifted to reposition the cylinder and chick was changed at random from trial to trial.

Results

A one-way analysis of variance (ANOVA) with Rearing cage (Rectangular vs. Circular) as the between-subjects factor and choices for geometrically correct positions as the dependent variable showed no difference associated with rearing conditions ($F_{(1, 21)} = .012$, $p = .912$). Chicks of both rearing groups chose significantly more often the correct hiding position (or its indistinguishable geometrical equivalent) at test (respectively Mean $\pm$ SEM, two-tailed one-sample *t*-test, rectangular-reared: $.589 \pm .025$, $t_{(9)} = 3.503$, $p = .007$; circular-reared: $.593 \pm .025$, $t_{(12)} = 3.668$, $p = .003$; Figure 1a).

A repeated-measures ANOVA with rearing (Rectangular vs. Circular) as the between-subjects factor and blocks of four trials (1–4, 5–8, 9–12 and 13–16) as the within-subjects factor revealed no differences associated with rearing conditions ($F_{(1, 21)} = .011$, $p = .916$) or test trials ($F_{(3, 63)} = .946$, $p = .424$) nor any significant interaction ($F_{(3, 63)} = 1.403$, $p = .250$).

Figure 1   *Chicks' start position under the cylindrical grid in the rectangular arena provided with (a) four identical blue opaque panels placed in each corner to test rectangular- (leftmost) and circular-reared (rightmost) chicks (Experiment 1); (b) four semi-hiding green panels with four identical imprinting objects (Experiment 2). Visits to geometrically correct corners (Means with SEMs below) are shown in bold.*

Experiment 2

Experiment 1 showed that at test the majority of chicks (Figure 2) used the available geometric information to reorient themselves irrespective of whether they had been exposed to geometry or not. However, it could be that the experience of being reared in a circular environment did provide the minimal experience needed to deal with geometry at test (e.g. by the perceptual information provided by cylindrical surfaces meeting the floor surface).

In the second experiment, we tested the reorientation abilities of chicks in the complete absence of any previous experience of navigating through extended surfaces. Chicks were hatched in the darkness and were exposed to the imprinting object directly in the testing environment; the working memory task this time exactly mimicked the one used with human children (i.e. the correct position was held constant), with the difference that, in contrast with human children, chicks saw for the very first time the array of surfaces of the geometric environment at the moment of test.

Subjects and apparatus

Twenty domestic chicks were obtained and hatched as described for Experiment 1, but they were kept completely in the dark in an almost square drawer of the incubator for 2 days post-hatching until the time of the test. This procedure enabled us both to avoid chicks' visual exposure to environmental features and to test them at an age when motor responses would be more likely to occur. When maintained in the darkness, newly hatched chicks spend most of the time sleeping and recovering from hatching, and they engage in little or no haptic exploration of the environment. Testing occurred in the same rectangular apparatus described before, except for the panels that this time consisted of a green net in a solid frame (see layout in Figure 1b). The semi-hiding net was preferred to opaque panels in order to keep chicks' motivation high due to the visibility of the objects, thus maintaining reaching behaviour comparable to that of Experiment 1.
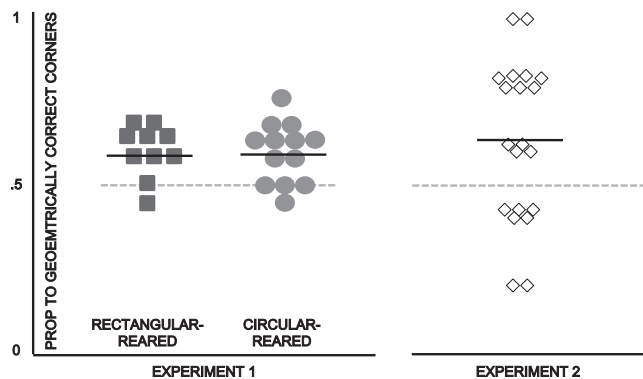
Figure 2   *Chicks' individual performance plotted for each condition. The dashed line indicates chance level and the solid lines represent the groups' means. The majority of chicks preferred the geometrically correct corners (p < .05, Binomial test).*

Procedure

On day 3, chicks were directly inserted into the testing apparatus as described for Experiment 1 and shown the object *quasi*-disappearing behind one of the panels while they were confined under the cylindrical grid. Then, the opaque cylinder was lowered and four identical objects were placed behind the panels at the corners. After disorientation in darkness (the cylinder was slowly turned 3–4 times clockwise and anticlockwise while the arena was rotated 90° anticlockwise), chicks were left free to spontaneously rejoin the imprinting object in five consecutive trials, holding the same hiding corner across trials as is often done with children and in previous work with chicks (Lee *et al*., 2012).

Chicks were immediately motivated to look for the object in the new environment since it was the only conspicuous object moving back and forth before stopping behind one semi-hiding panel. However, the entire test could last 30 to 50 minutes due to the fact that some chicks were slow and, despite their precocious ability to visually follow the object, the motor response could take some time to appear. Choices were scored as in the previous experiment. Whenever the chick took more than 10 minutes to make a choice, the trial was considered null and the chick was again confined under the cylindrical grid and given another trial. This happened with only four chicks, and they were given further trials, but never more than seven in total.

Results

A paired sample *t*-test showed that chicks directly chose significantly more often the correct hiding position or its geometrically indistinguishable rotational equivalent over the two diagonally opposite corners ($t_{(19)}$ = 2.218, *p* = .039), as seen in Figure 2, with no difference between the choices for the correct corner and its rotational equivalent ($t_{(19)}$ = .545, *p* = .592).

Due to the limited number of test trials, a one-sample chi-square test was calculated by dividing into two categories (geometric vs. non geometric) the choices in each single trial. The test confirmed that, overall, geometric choices were prevalent over non-geometric choices ($X^2_{(1)}$ = 5.76 , *p* = .016); moreover, no variation associated with trials was apparent ($X^2_{(4)}$ = 1.95 *p* = .745).

The majority of chicks (Figure 2) used the geometry of the environment to guide their choice between the corner locations, despite the absence of any prior experience navigating in a geometrically structured environment.

Discussion

In the longstanding debate over whether specific experiences underlie animals' use of environmental cues to move about in their habitat, we add new evidence for an innate sensitivity to the geometric properties of space in newborn animals. Experiment 1 showed that the early experience of living in environments with or without geometric features such as right angles and metrically distinct surfaces did not affect newly hatched chicks' ability to reorient on the basis of the shape of their enclosure. Although previous controlled rearing studies involved a reference memory version of the geometric reorientation task (Chiandetti & Vallortigara, 2008, 2010b; Vallortigara, Sovrano & Chiandetti, 2009), here we demonstrate equal performance in chicks previously exposed and not exposed to geometry by means of a working memory reorientation task, in which chicks have to encode spontaneously a new target position of the imprinting object on every trial.

In both Experiment 1 and in past research (Chiandetti & Vallortigara, 2008), chicks received exposure to an environment with at least minimal geometric structure during the period over which imprinting was established, allowing for a possible effect of learning on chicks' navigation. In Experiment 2, we eliminated this experience by confining all incidental exposure to geometric cues to the reorientation task itself. Chicks developed the filial attachment to the imprinting object directly during testing, allowing us to study the reorientation process in the absence of any previous exposure to geometry. Under these stringent conditions, chicks again spontaneously used the geometry of the enclosure to reorient themselves. They navigated to the object of imprinting, distinguishing it from three other featurally identical objects, by encoding the distances and/or the metric differences between the walls, and they used their directional sense to disambiguate between the correct and incorrect objects (Lee & Spelke, 2010; Spelke, Lee & Izard, 2010). It is noteworthy that in spite of the presence of four identically visible and indistinguishable imprinting objects, the majority of chicks systematically reoriented on the basis of the geometric location of the object observed before the disorientation delay.

These experiments provide, in an animal model, behavioural evidence for innate representations of space. Because of their highly precocial motor development, chicks may represent an appropriate model to test the issue of innateness of certain computational abilities by providing a sufficiently mature system at birth to allow behavioural testing in the absence of specific post-natal experiences. Indeed, our findings accord with evidence from neurophysiological experiments on infant rats. Rat

pups, tested at the onset of independent locomotion, showed functional head direction cells, border cells and rapidly maturing place cells, providing evidence for early-developing encoding of distance and direction (Bjerknes, Moser & Moser, 2014; Langston, Ainge, Couey, Canto, Bjerknes *et al.*, 2010; Wills, Cacucci, Burgess & O'Keefe, 2010). Here we show that chicks use the same information to reorient themselves the very first time that they encounter a geometrically structured environment. Even though it is of course impossible in principle to have learning without having at the same time (during the course of learning) sensory stimulation and therefore some form of experience, the crucial point is the specificity of the experience with respect to the capabilities the animals show. Thus, although they unavoidably have the opportunity to see the environment before starting to move and during movement itself, our naïve newly hatched chicks (and rats pups tested at the onset of independent locomotion) lacked experience of navigating in a geometrically structured environment.

Evidence from traditional societies suggests that human beings can deal with rudimentary geometric concepts such as points, lines, parallelism or right angles in the absence of schooling, experience with graphic symbols or maps or a specific language for geometrical terms (Dehaene, Izard, Pica & Spelke, 2006; Izard, Pica, Spelke & Dehaene, 2011). However, although these people lack any formal education in geometry, they have a lifetime of experience navigating in geometrically structured environments. It is possible, therefore, that their geometrical abilities depend not on a core system of knowledge but on a lifetime of learning, supported by general associative mechanisms, about this environmental structure and its geometry. Although the present experiments do not bear directly on the development of human cognitive capacities, they show, in controlled-reared chicks, that mastery of basic rudimentary geometry is possible without any involvement of associative learning mechanisms. Thus we provide existential proof that encoding of geometry is possible in a biological organism without any previous experience navigating in a geometrically structured environment.

Acknowledgements

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