ORIGINAL PAPER

L. Tommasi · G. Vallortigara · M. Zanforlin

Young chickens learn to localize the centre of a spatial environment

Abstract Young chickens were trained to find food by ground-scratching in the centre of a closed uniform arena and were then tested in arenas of similar areas but of different shapes. Chickens showed localized searching behaviour in the square-shaped arena, and maintained this behaviour when placed in a circular or triangular (both equilateral and isosceles) arena. With a rectangular-shaped arena, obtained by doubling the original square-shaped one, chickens showed more dispersed searching along the major axis, but searching tended to be concentrated around the centres of the composing squares and around the centre of the rectangle itself. When trained in a square- or triangle-shaped arena and then tested in an arena of the same shape but a larger area, chickens displayed searching behaviour at two different distances from the wall of the arena, one corresponding to the correct distance (i.e. centre) in the smaller (training) arena, the other to the actual centre of the test arena. On the other hand, in a circular arena, chickens searched mainly at a distance midway between the radius of the small (training) and of the large (testing) circular arena. These results suggest that, during training, chickens encoded information on both the absolute and the relative distance of the food from the walls of the arena, the latter information being more accurate when the arena displayed identifiable features such as corners.

Key words Spatial learning · Spatial memory · Spatial cognition · Birds · Chickens

L. Tommasi · M. Zanforlin
Dipartimento di Psicologia Generale, Università di Padova,
Via Venezia, 8, I-35131 Padova, Italy

G. Vallortigara (✉)
Dipartimento di Scienze Filosofiche e Storico-Sociali,
Laboratorio di Psicologia sperimentale,
Università di Udine, I-33100 Udine, Italy,
Fax: +39-432/556545, e-mail: giorgio.vallortigara@ifp.uniud.it

Introduction

Spatial learning has been studied extensively in a number of vertebrate and invertebrate species (reviews: Gallistel 1990; Etienne 1992; Etienne et al. 1996; Poucet 1993). Most species use visual landmarks as a means of navigation, e.g. insects (Wehner 1981; Collett 1996), birds (Sherry 1985; Sherry and Duff 1996), mammals (Morris 1981; Gallistel and Cramer 1996). Visual landmarks can fall into different classes (Collett et al. 1986) depending on their distance from the goal, ranging from the extremes of 'beacons' (objects so close to a goal that the animal can reach the goal simply by aiming for the beacon) and remote 'compass-marks' (very distant objects like the sun, stars and so on that allow the animal to establish direction but not the precise location of a goal). In between there are objects which are not very close to the goal, but nevertheless close enough to provide an accurate fix for the goal's position. Navigation using these objects as landmarks is possible provided that an animal can store an internal representation of the spatial arrangement of landmarks and goal.

Recently, an investigation has started into whether animals can store and use the geometrical relationships between objects in the environment. Cheng (1986) found that in place-finding tasks within a rectangular environment with distinct featural panels in the corners, rats systematically confused geometrically equivalent locations, i.e. locations standing in the same geometric relation to the shape of the environment but differing in nongeometric properties, such as brightness, texture or smell. Human adults use both geometric and non-geometric information for orientation, whereas young children, similar to mature rats, seem to rely only on geometric information (Hermer and Spelke 1994). Adult rats and young children appear to be impervious to all but geometric information when attempting to reorientate – whereas these limits seem to be overcome during human development. This fact has lead Hermer and Spelke (1994) to speculate that some representational

systems become more accessible and flexible over development and evolution. Vallortigara et al. (1990) tested young domestic chickens (*Gallus gallus*) in reference memory tasks similar to those employed by Cheng (1986) with rats, and Hermer and Spelke (1994) with humans. Chicks, similar to rats and young children, were found to be unable to use featural (non-geometric) information provided by distant landmarks, and tended to rely on geometric information. However, they also encoded featural information provided by close landmarks, and when faced with contradictory information, relied primarily on non-geometric cues. Thus, overcoming the (presumed) limits of informational encapsulation (Fodor 1983) is not confined to humans during ontogenetic development nor phyletically to mammals.

Evidence that chicks do possess good topographical abilities also comes from studies in which chicks were trained to find food using distant and nearby cues (Vallortigara and Zanforlin 1988; Rashid and Andrew 1989; Vallortigara 1996) and from detour studies (Regolin et al. 1994a, b, 1995). The finding that these birds are apparently capable of using the metric configuration of distances between surfaces in the environment, paves the way to previously uninvestigated spatial performances. For instance, a task which seems to be easily accomplished by humans is to localize and orient toward the perceptual centre of a closed environment. If the environment lacks distinctive landmarks, localization of the centre would require the use of abstract metric information concerning spatial relations and distances between surfaces in the environment. Here we present data on the ability of young chickens to localize the centre of closed, perceptually uniform environments.

Materials and methods

Subjects

The subjects were thirty Hybro (a local variety derived from the White Leghorn breed) chicks obtained from a commercial hatchery when they were only a few hours old. They were reared individually at controlled temperature (30–35 °C) in metal cages (35 × 35 × 38 cm) lit from above by fluorescent lamps with food and water *ad libitum*.

Apparatus and procedure

Behavioural procedures included two phases, one for training and one for testing. Chicks were trained daily for at least 1 week starting on day 8. Chicks were then tested when 15 days old.

During training, chicks had to find the central position within an arena of a certain geometrical shape. After their training performance was video-recorded on day 15 (below), they were tested in arenas of different shapes and sizes to check whether they searched for the central position in these novel environments.

The experimental arenas consisted of wooden, 40 cm high, walls, uniformly painted white, with light bulbs (25 W) placed at the corners and/or at random positions along the walls (see Fig. 1). Sawdust covered the floor (5 cm in depth). The arena was covered by a screen that prevented vision of the outside to the chick whilst allowing videorecording; the lights in the experimental room were kept off.

Fifteen hours before training, animals were food deprived to obtain the necessary motivational state. At the beginning of each training session, a small rectangular plastic box (5 × 10 × 2 cm) containing grains of food was placed in the central position of the arena floor. The box had a small hole in it (2 × 2 cm) through which food could be reached. Each chick was introduced into the arena at one of the corners; it was given time to reach the box, allowed to eat some food, and was then removed from the arena. Once the chicken had been taken out, the food box was buried a few millimeters in the sawdust. The animal was then placed in the arena again and the procedure was repeated following the same sequence. During the inter-trial period when the animal was removed from the arena, it was confined in a small closed cardboard box (10 × 15 × 10 cm) and slowly rotated to avoid subsequent usage of inertial or compass information. The corner by which it entered the arena varied randomly from trial to trial, and so was the position of the experimenter with respect to the arena in reintroducing the animal.

After a few trials the food box became almost invisible (hidden in the sawdust) and eventually it became completely invisible. When faced with complete or nearly complete submersion of the food box, chicks started to display a ground-scratching response to find the hidden food. Ground-scratching occurred with strong individual differences. Only those animals that produced the greatest amount of ground-scratching responses were used for further training (i.e. animals producing at least three responses within 1 min after placement in the arena).

When animals were 15 days old, their performance in the training arena was recorded with a video-camera fixed above the experimental environment. During video-recording, the small food box was removed and the sawdust was systematically mixed and moved about in order to rule out the use of olfactory cues. Recording lasted for 3 min. The videotape was subsequently analyzed and the positions of the scratches were reported on transparent cartesian grid paper superimposed on a TV monitor. For each of the animals a set of (x, y) coordinates was thus obtained, each representing the position of a scratch in the arena.

The subsequent test phase consisted of placing the animal in a novel environment with the same general features as the test arena except for changes in geometrical shape or size. The chicken's behaviour in the novel arena was video-recorded for 4 mins.

Seven chicks (three males and four females) were used in a shape-transformation experiment. They were first trained to find the center of a square-shaped arena (side 60 cm) and then tested in a single trial in four different arenas as follows: (i) a rectangular arena (sides 60 × 120 cm); (ii) a circular arena (diameter 50 cm); (iii) an equilateral triangle-shaped arena (side 60 cm); and finally (iv) an isosceles triangle-shaped arena (base 60 cm, side 110 cm). After each test in a novel arena, chicks were retrained in the
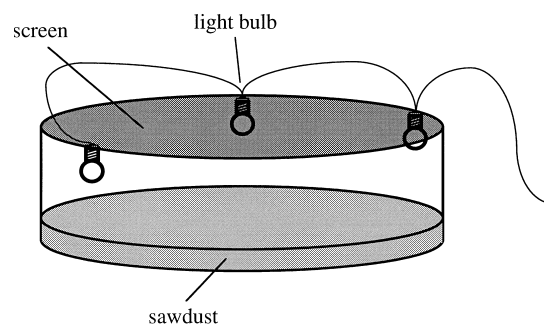

Fig. 1 Schematic representation of the test apparatus. The arena (circular in this case) was painted uniformly white and had sawdust on the floor where the food was hidden. A unidirectional screen covered the ceiling, and the chick's behaviour was video recorded with a camera mounted above the arena (not shown here). Illumination of the testing arena was provided by lamps the position of which was randomly varied from trial to trial and from one animal to the other

original square-shaped arena (one session) to avoid extinction of the ground-scratching response.

Twenty-three chicks were used in three size-transformation experiments. Six female chicks were first trained in a circular arena (diameter 50 cm) and then tested in a wider circular arena (diameter 100 cm). Seven male chicks were first trained in a square-shaped arena (side 70 cm) and then tested in a wider one (side 140 cm). Ten female chicks were first trained in a triangle-shaped equilateral arena (side 70 cm) and then tested in a wider one (side 140 cm).

Data analyses

Once the coordinates of the responses of all animals in the same arena were collected from the video-recording, they were rearranged in a spatially meaningful fashion. The floor of the arena was partitioned into equivalent areas: for each of these areas the weighted mean of the number of scratches was calculated (mean of all the response ratios, whereby the single animal's ratio was computed as the number of scratches in that area divided by the total number of scratches in the whole arena). The weighted means ranged between a minimum (always zero) and a maximum; these values were represented in a ten-level grey scale, where white stands for zero and dark grey for maximal proportion of scratches.

Results

Shape transformations

Results obtained from the chicks trained to find the centre of the square-shaped arena are shown in Fig. 2a. If searching behaviour had been randomly distributed, then the representation in this figure would have been homogeneously grey. This, however, is not the case. The chicks' searching behaviour was clearly concentrated around the centre of the training arena.

Searching behaviour in the arenas of different shapes is shown in Fig. 2b–e. With the circle-shaped (Fig. 2b)

Fig. 2a–d Results of the shape-transformation experiment. Chicks were trained within the square-shaped arena and then tested in the other arenas. The darker a cell, the more searching behaviour the chicks showed in that location. Chicks showed quite precise searching behaviour during training and good transfer to all testing arenas, with the exception of the rectangular-shaped one where searching behaviour was more diffuse

and equilateral triangle-shaped (Fig. 2c) arenas, searching was clearly concentrated in a restricted central area. In the rectangular-shaped arena (Fig. 2d), on the other hand, there was a three-modal distribution of responses: chicks searched either around the centres of one of the two (left and right) square-halves of the rectangle, or around the true geometrical centre. This suggests that although chicks remembered and used the distances between the walls and the centre of the training arena, they also tended to equalize relative distances between the walls and the centre of the novel (rectangular) arena. In the isosceles triangle-shaped arena (Fig. 2e), ground-scratching responses were concentrated in a rather limited central zone. Several possible mathematical centres can be computed for an isosceles triangle (the geometric centre, the gravity centre of the vertices, the intersection of bisectors), and these theoretical centres were statistically compared with the centre actually chosen by the animals. The y coordinates of the geometric centre and the bisector intersection were significantly different from the mean y empirical coordinate [$t(6) = -8.03$, $P < 0.001$, and $t(6) = 9.578$, $P < 0.001$, respectively]. The centre estimated by the chicks appeared also to differ from the centre of the training square – when one of its sides was superimposed on the isosceles triangle base [$t(6) = 4.16$, $P = 0.006$]. There was, on the other hand, no statistically significant difference with respect to the y coordinate of the gravity centre [$t(6) = 0.774$, $P = 0.473$].

Size transformations

The results of training within a circular arena and testing within a larger circular arena are shown in Fig. 3a–c. Although chicks did learn to search in the central region during training (see Fig. 3a), performance in a larger arena showed that animals did not search in the central position. A wide area ranging from perimeter to centre was visited and actively searched (Fig. 3b). We therefore present the animals' choices in another way, i.e. in concentric annuli of the same width (Fig. 3c): for each of them we calculated the weighted mean of the responses
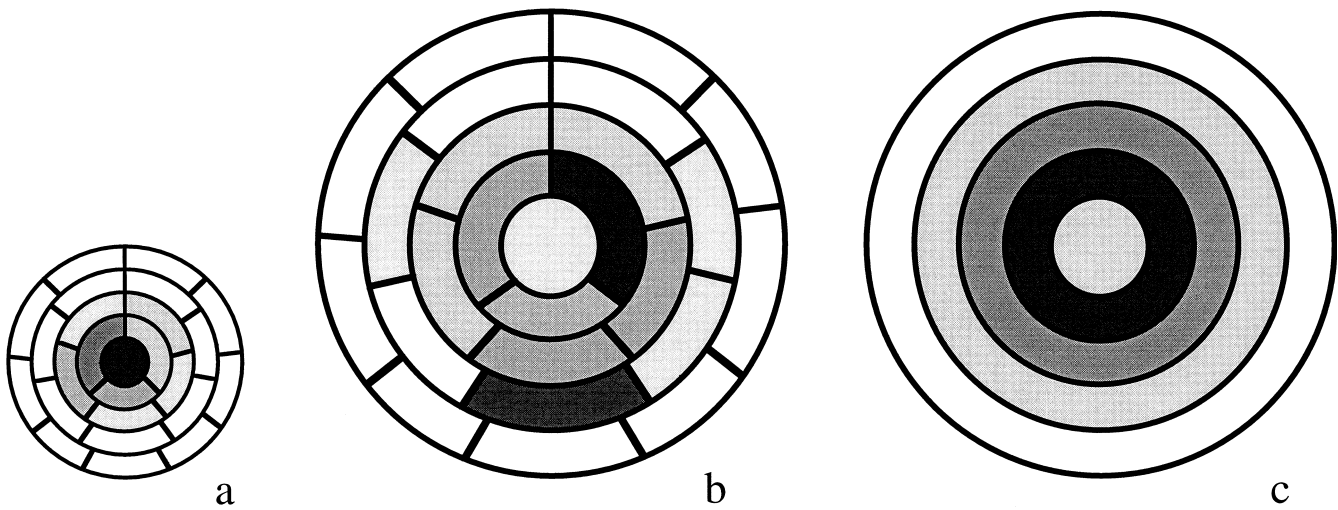

a

b

c

e

d
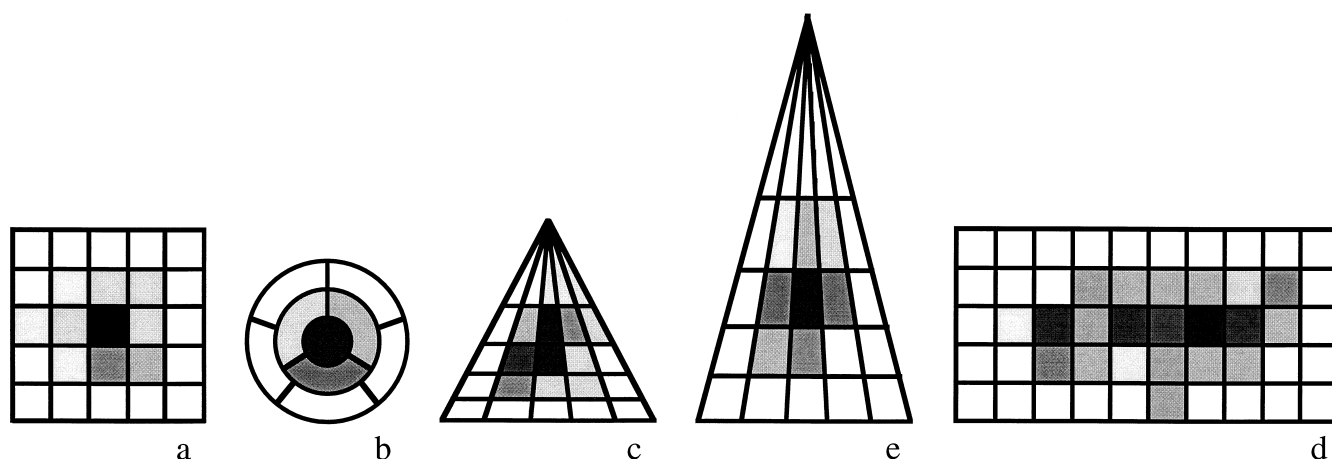
Fig. 3a–c Results of the size-transformation experiment with the circular arena. When tested within the larger arena, chicks searched prevalently at a distance from the walls which was midway between the centres of the smaller (training) and of the larger (testing) arenas

of all the animals and divided it by the area of the annulus. The grey gradient obtained in this case is a representation of search intensity as a function of distance from the centre. The rationale behind this procedure is that if the animals stored the absolute distance from the walls to the centre, then given that different animals can arbitrarily use different points on the walls to calculate this distance, a circular dark annulus centered at a distance equivalent to the distance from the walls to the centre of the training arena should emerge. As can be seen from Fig. 3c, however, the annulus of more intense ground scratching does not coincide with the absolute distance of the centre of the small arena: the animals' choices are actually a compromise between the old (small arena) and the novel (large arena) distances between the walls and the centre.

Similar data analyses were used for the animals trained in a square- (Fig. 4a) or in a triangle-shaped (Fig. 5a) arena and tested in a larger one (Figs. 4b,5b). In this case, however, chicks clearly searched in two

regions during testing, one region that corresponded to the centre of the training arena, and one that corresponded to the centre of the (larger) testing arena (Figs. 4c,5c).

Discussion

The results show that chicks can easily be trained to localize the centre of spatial environments lacking distinctive landmarks. Whether the 'centre' actually corresponds to a mere arbitrary-defined location or rather to a perceptually salient location (as seems to be the case in human perceptual experience) is an issue which requires further research. At any event, it is clear that chicks could use distances from the walls of the arena to localize the centre. They probably relied on a visual estimate of these distances from their actual positions. The

Fig. 4a–c Results of the size transformation experiment with the square- and the triangle-shaped arenas. When tested within the larger arenas, chicks searched in the centre of the novel arena but also in an annular region the distance of which from the walls corresponded to that of the centre of the smaller (training) arena
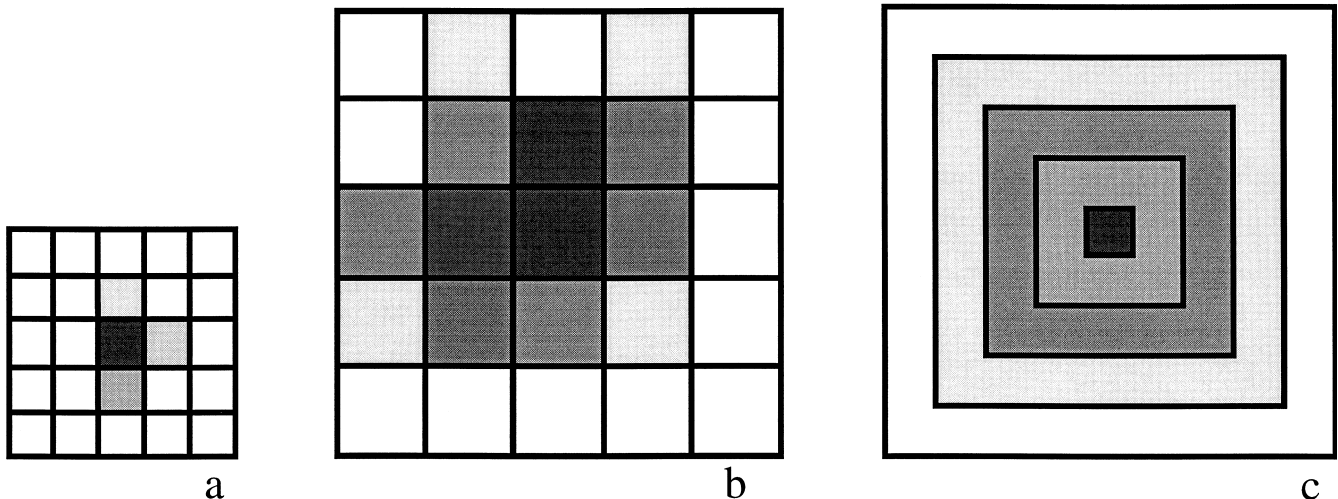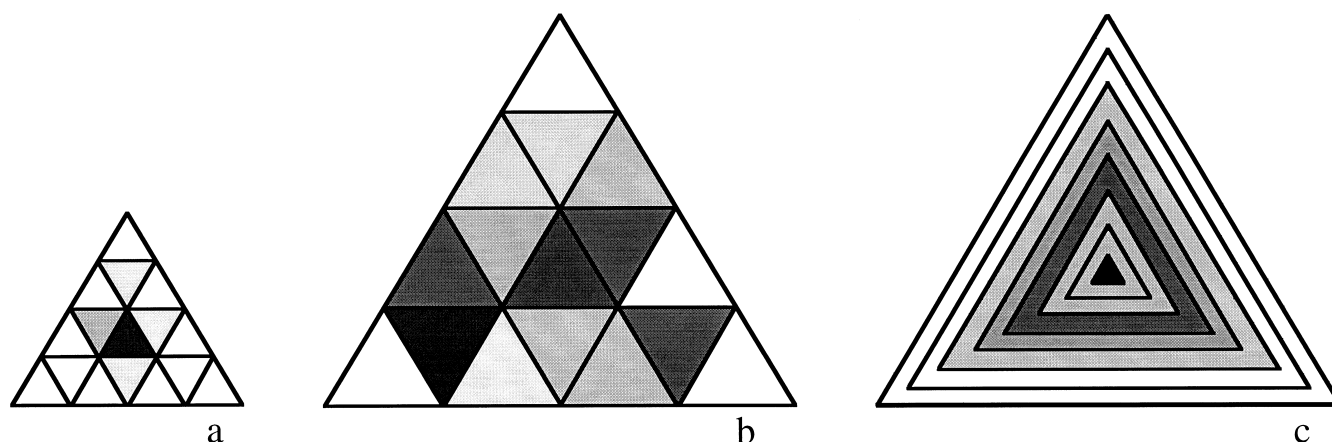
Fig. 5a–c Results of the size transformation experiment with the square- and the triangle-shaped arenas. When tested within the larger arenas, chicks searched in the centre of the novel arena but also in an annular region the distance of which from the walls corresponded to that of the centre of the smaller (training) arena

use of motor computations (e.g. number of steps) appears to be very unlikely, since chicks usually moved all around the cage before starting scratching, and selected no consistent trajectory from the releasing to the searching points.

It remains to be determined how the chicks actually measure distances in the task. The homogeneous walls can only provide visual distance information if the animals rely on the angular size of the wall's height, or if they orient to the speed of self-induced image motion perceived from the corners, or from the lamps (though placed at random positions, their distance from the centre was constant). However, even in the circular arena, chicks learned the task very well (Fig 3a).

Results of transfer tests suggest that during training chicks did not learn solely the absolute distance between the walls and the centre. It seems that they were able to take into account the fact that the relative distances between certain points located on the walls and the centre should be equal. This conclusion is supported by the finding that in transfer tests to larger square- and triangle-shaped arenas, chicks searched even in the centre of these novel larger arenas, and not only in locations which had the same absolute distances from the walls as in the training situation. Apparently, identifiable landmarks such as corners were needed to compute this centre, because chicks were unable to localize it in transfer tests using circular arenas.

The only previous work on centre localization in vertebrates of which we are aware has been carried out by Collett et al. (1986) with gerbils. These authors, however, studied planning of trajectories to a goal, and used distinct objects, rather than surfaces, as landmarks. Gerbils were trained to find seeds in the centre of an equilateral triangle formed by three identical cylinders, and their search patterns were evaluated when the light was turned off with the animals located at varying dis-

tances from the goal. The results showed that gerbils' visuo-spatial memories contain information relative to both distance and direction to a goal.

Recently, O'Keefe and Burgess (1996) have recorded 'place cells' from rats foraging in boxes of different shapes (a small and a large square and a rectangle). Most of the firing rate maps showed one contiguous region of firing with a single peak, and the locations associated with the peak firing rate were determined by fixed distances or proportions of distances to a box wall in the direction defined by the axes of the box. Most interestingly, place fields were not localized points, but rather areas: the shape of the fields varied systematically between boxes differing in length along one direction, either stretching or revealing a second peak along that direction when placed in a larger box. This finding strikingly resembles the distribution of searching locations we observed in our chicks, when arenas underwent similar transformations (e.g. from square-shaped to rectangular-shaped arenas).

The functions of the dorsomedial region of the avian brain (hippocampus and area parahippocampalis), which is thought to be homologous to the mammalian hippocampus, are not well documented. Hippocampal volume is positively correlated with food storing behaviour (Clayton and Krebs 1995), and the hippocampal system may play a role in navigation in pigeons (Bingman 1993). Nothing is known, however, about the possible presence of place cells in chickens' brain, nor has any role of the hippocampus in spatial learning been documented in this species (Sandi et al. 1992; Rogers 1995). Since spatial learning capabilities of chicks are now well-established (see Introduction), and given the increasing use of this species as a model system (Andrew 1991), it is time to supplement the behavioural data with neural investigations.

References

Andrew RJ (1991) (Ed) Neural and behavioural plasticity: the use of the domestic chick as a model. Oxford University Press, Oxford

Bingman VP (1993) Vision, cognition and the avian hippocampus. In: Zeigler HP, Bischof H-J (eds) Vision, brain and behavior in birds MIT Press, Cambridge, MA, pp 391–408

Clayton NS, Krebs JR (1995) Food-storing memory and the hippocampus. Curr Opin Neurobiol 5: 149–154

Collett TS (1996) Insect navigation en route to the goal: multiple strategies for the use of landmarks. J Exp Biol 199: 227–235

Collett TS, Cartwright BA, Smith BA (1986) Landmark learning and visuo-spatial memories in gerbils. J Comp Physiol A 158: 835–851

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

Etienne AS (1992) Navigation of a small mammal by dead reckoning and local cues. Curr Direct Psychol Sci 1: 48–52

Etienne AS, Maurer R, Séguinot V (1996) Path integration in mammals and its interaction with visual landmarks. J Exp Biol 199: 201–209

Fodor JA (1983) The modularity of mind. MIT Press, Cambridge, MA

Gallistel CR (1990) The organization of learning. MIT Press, Cambridge, MA

Gallistel CR, Cramer AE (1996) Computations on metric maps in mammals: getting oriented and choosing a multi-destination route. J Exp Biol 199: 211–217

Hermer L, Spelke ES (1994) A geometric process for spatial reorientation in young children. Nature 370: 57–59

Morris RGM (1981) Spatial localization does not require the presence of local cues. Learn Motiv 12: 239–260

O'Keefe J, Burgess N (1996) Geometric determinants of the place fields of hippocampal neurons. Nature 381: 425–428

Poucet B (1993) Spatial cognitive maps in animals: new hypotheses on their structure and neural mechanisms. Psychol Rev 100: 163–182

Rashid N, Andrew RJ (1989) Right hemisphere advantage for topographical orientation in the domestic chick. Neuropsychologia 27: 937–948

Regolin L, Vallortigara G, Zanforlin M (1994a) Perceptual and motivational aspects of detour behaviour in young chicks. Anim Behav 47: 123–131

Regolin L, Vallortigara G, Zanforlin M (1994b) Object and spatial representations in detour problems by chicks. Anim Behav 49: 195–199

Regolin L, Vallortigara G, Zanforlin M (1995) Detour behaviour in the domestic chick: searching for a disappearing prey or a disappearing social partner. Anim Behav 50: 203–211

Rogers LJ (1995) The development of brain and behaviour in the chicken. CAB International, Wallingford UK

Sandi C, Rose SPR, Patterson TA (1992) Unilateral hippocampal lesions prevent recall of a passive avoidance task in day-old chicks. Neurosci Lett 141: 255–258

Sherry DF (1985) Food storage by birds and mammals. Adv Study Behav 15: 153–188

Sherry DF, Duff SJ (1996) Behavioural and neural bases of orientation in food-storing birds. J Exp Biol 199: 165–172

Vallortigara G (1996) Learning of colour and position cues in domestic chicks: males are better at position, females at colour. Behav Process 36: 289–296

Vallortigara G, Zanforlin M (1986) Position learning in chicks. Behav Process 12: 23–32

Vallortigara G, Zanforlin M, Pasti G (1990) Geometric modules in animals' spatial representations: a test with chicks. J Comp Psychol 104: 248–254

Wehner R (1981) Spatial vision in arthropods. In: Autrum H (ed) Vision in invertebrates. Handbook of sensory physiology, vol. V11/6c. Springer, Berlin Heidelberg New York, pp 287–617