

View-based strategy for reorientation by geometry

Tommaso Pecchia* and Giorgio Vallortigara

Center for Mind and Brain Sciences, University of Trento, Corso Bettini, 31 38068 Rovereto, Italy

*Author for correspondence (tommaso.pecchia@unitn.it)

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SUMMARY

Human and non-human animals can use geometric information (metric information and left–right discrimination sense) to reorient themselves in an environment. The hypothesis that in so doing they rely on allocentric (map-like) representations has received wide consensus. However, theoretical models suggest that egocentric representations may represent efficient strategies for visuo-spatial navigation. Here, we provide, for the first time, evidence that a view-based strategy is effectively used by animals to reorient themselves in an array of landmarks. Domestic chicks were trained to locate a food-reward in a rectangular array of either four indistinguishable or distinctive pipes. In the key experimental series, the pipes had four openings, only one of which allowed the chicks to access the reward. The direction of the open access relative to the array was either maintained stable or it was changed throughout training. The relative position of the pipes in the array was maintained stable in both training conditions. Chicks reoriented according to configural geometry as long as the open access pointed in the same direction during training but failed when the positions of the openings was changed throughout training. When the correct pipe was characterized by a distinctive featural cue, chicks learnt to locate the reward irrespective of the stability of the direction to openings, indicating that place-navigation was dissociated from non-spatial learning. These findings provide evidence that view-based strategies to reorient by geometry could be used by animals.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/213/17/2987/DC1>

Key words: view-based navigation, geometric module, landmark, domestic chick, cognitive map.

INTRODUCTION

Seminal work by Cheng (Cheng, 1986) was the first systematic attempt to investigate geometric computation in vertebrate species. Rats were trained to locate a hidden food-reward at one of the corners of a rectangular arena. Distinctive panels were located at each of the corners providing featural information to distinguish the rewarded locations within the enclosure. Disorienting procedures between trials were administered to prevent rats from reorienting on the basis of inertial information. In a working memory task, rats systematically directed their searches towards the correct corner and its rotational equivalent, that is the corner diagonally opposite with respect to the goal. These two corners have the same geometrical relationship with respect to the shape of the enclosure and are, therefore, geometrically indistinguishable. Thus, rats apparently ignored the featural cues specified by the panels at the corners to reorient, and based their searches on the geometric information specified by the shape of the enclosure. It has been hypothesised that a cognitive module was responsible for the primacy of geometry in this task: the geometric module, encoding only metric properties and left–right relationships between surfaces, would lead the rats to commit the rotational error (Cheng, 1986).

There could be evolutionary advantages associated with use of geometric cues for navigation (Gallistel, 1990). Given the relational nature of the geometric cues, geometry is more stable when compared to the featural cues, thus providing reliable information for spatial reorientation. According to Gallistel (Gallistel, 1990), geometry would be encoded in allocentric coordinates, thus providing a metric frame to the ‘cognitive map’ (Tolman, 1948; O’Keefe and Nadel, 1978; Morris et al., 1982; Wang and Spelke, 2002).

Subsequent work has shown that fish [*Xenotoca eiseni* (Sovrano et al., 2002; Sovrano et al., 2003); *Carassius auratus* (Vargas et al., 2004)], birds [domestic chicks (Vallortigara et al., 1990); pigeons (Kelly et al., 1998)], rodents [rats (Golob and Taube, 2002)], non-human primates [rhesus monkey (Gouteux et al., 2001), tamarins (Deipolyi et al., 2001)] and humans (Hermer and Spelke, 1994; Hermer and Spelke, 1996) reoriented according to the geometric information (i.e. metric and the left–right discrimination sense) specified by the macroscopic layout of surfaces (reviewed by Wang and Spelke, 2002; Cheng and Newcombe, 2005; Vallortigara, 2009).

However, there is also evidence that vertebrate species fail to reorient by geometry under certain conditions (see Cheng, 2008), in particular in the case of arrays of separate landmarks. Gouteux and Spelke (Gouteux and Spelke, 2001), for instance, showed that children failed to reorient by geometry in an array of spatially isolated landmarks. In analogy to the Morris’s water maze, 3- and 4-year-old children were required to locate a hidden-toy in an array of boxes located centrally within a circular enclosure (Gouteux and Spelke, 2001). The participants could locate the toy by using either the visual aspects of hiding boxes (non-geometric information) or the geometric cues provided by the shape of the array. Since children could not perceive any extra-enclosure cues, positional information was entirely defined by the configural geometry. It was shown that the children were able to reorient in the array of distinctive boxes. However, children systematically failed to relocate the toy in the arrays of indistinguishable boxes, suggesting that they were unable to encode the geometric cues provided by the configuration (Gouteux and Spelke, 2001; Lee et al., 2006) (but see Garrad-Cole et al., 2001). Interestingly, children of comparable age successfully encoded the geometric cues specified by the macroscopic layout of extended

surfaces in a rectangular enclosure (Hermer and Spelke, 1994; Hermer and Spelke, 1996). It has been hypothesized that the availability of a macroscopic layout of surfaces may be crucial for computation of geometry (Lee et al., 2006; Lee and Spelke, 2008). According to several authors (for a review, see Vallortigara, 2009) extended surfaces are mostly represented by very stable and enduring cues in a natural environment, which, unlike featural cues, rarely undergo any substantial modification during the life-time of an organism, thus providing very reliable cues for navigational purposes (Gallistel, 1990; Lee and Spelke, 2008). Of course, several factors other than physical extension may be critical for estimating cues reliability for navigational purposes. Evidence in vertebrate species indicate that the apparent size of visual cues is a crucial feature for reorientation. It has been shown, for instance, that geometric information has a primacy within small enclosed spaces, whereas featural information is preferred as a cue to reorient within large enclosed spaces [domestic chicks (Vallortigara et al., 2005; Sovrano and Vallortigara, 2006; Chiandetti et al., 2007; Chiandetti and Vallortigara, 2008b; Sovrano et al., 2005; Sovrano et al., 2007), rats (Maes et al., 2009), humans (Hermer and Spelke, 1996; Learmonth et al., 2001; Learmonth et al., 2002)].

Results comparable to those obtained with children in landmark arrays have been found in non-human species. Domestic chicks trained to locate a reward in a rectangular array of indistinguishable landmarks failed to reorient but succeeded when the correct location was marked by a distinctive featural cue (Pecchia and Vallortigara, 2010). By contrast, in the absence of any featural polarizing cue, chicks efficiently reorient themselves on the basis of the macroscopic layout of surfaces provided by a small rectangular enclosure (Vallortigara et al., 1990). Results with chicks in the rectangular array apparently are in contrast to the hypothesis that avian species rely on vector strategies to reorient by landmarks [pigeons (Cheng, 1990; Spetch et al., 1992; Spetch et al., 1996; Spetch et al., 1997) (see also Cheng et al., 2006), Clark's nutcrackers (Kelly et al., 2008)]. If chicks were able to encode absolute distances and directions from the rewarded site and the surrounding cues, they would be expected to reorient by geometry in the rectangular array of landmarks. Caution is needed, however, in considering these findings as evidence for different navigational strategies in an array of landmarks in avian species. In a recent study by Kelly (Kelly, 2009), Clark's nutcrackers failed to locate a food reward in a rectangular array of four indistinguishable landmarks (Kelly, 2009). However, no data are available addressing the question of whether pigeons are indeed capable of reorienting according to the geometric cues provided by a rectangular array of separate objects.

Contrary to the results obtained with children and chicks, however, rodents are apparently able to encode the geometric cues specified both by an array of landmarks and by the shape of an enclosure. Collett, Cartwright and Smith (Collett et al., 1986) provided evidence that gerbils could locate a buried feeder using landmarks. Transformational tests also suggested that gerbils relied on absolute metric and directional estimation from the landmarks to accomplish the task (Collett et al., 1986). Further evidence in rats for geometric computation of an array of landmarks were obtained by Benhamou and Poucet (Benhamou and Poucet, 1998). Rats were trained to locate a submerged platform located midway between a pair of landmarks in a triangular array, arranged at the edge of a circular water maze (Benhamou and Poucet, 1998). After training, rats were tested in a mirrored version of the array used during training. Rats ignored the arrangement of the featural cues, and focused their searches at the correct geometric location in the array (Benhamou and Poucet, 1998), thus replicating the findings

by Cheng in the rectangular arena. Esber and colleagues (Esber et al., 2005) successfully trained rats to navigate towards a submerged platform in the vicinity of a landmark in a rectangular array, located close to the edge of a circular pool (Esber et al., 2005). Recently, Gibson, Wilks and Kelly (Gibson et al., 2007) trained rats to locate a food reward in a rectangular array of landmarks located centrally within a large experimental room. Rats learned the task in an array of four indistinguishable landmarks. Furthermore, rats trained in a rectangular array of four distinctive featural cues were able to retrieve the configural geometry when tested with an array of four indistinguishable landmarks (Gibson et al., 2007). Overall, these findings suggest that geometric computation in rodents are not restricted to the macroscopic layout of surfaces. There is therefore an apparent discrepancy with the data obtained in children and in birds.

Here we provide evidence that the use of a view-based strategy for spatial reorientation could provide a parsimonious explanation for the apparent discrepancies in the results obtained with chicks, rats and humans (see also Pecchia and Vallortigara, 2010). According to a view-matching strategy of reorientation, animals would navigate so as to minimize the difference between the panoramic image of the rewarded site and the panorama perceived from the current location (Collett and Collett, 2002). Comparative research on insects (Wystrach and Beugnon, 2009) and computer modelling (Miglino and Lound, 2001; Cheung et al., 2008; Stürzl et al., 2008; Dawson et al., 2010) suggest that a view-based strategy for reorientation could in principle be used by vertebrates as well. We have investigated this issue using the domestic chicks as an animal model. Chicks were trained in a woodpecker task to locate a food reward in a rectangular array of pipes. Chicks were trained to insert their heads through circular openings in the pipes to access a hidden food reward. The openings could act as local directional guides making it possible to control the panorama perceived by the chicks at the pipes in the array.

MATERIALS AND METHODS

One-hundred domestic chicks (*Gallus gallus* L.) of the Hybro strain (a local variety derived from the white leghorn breed) were used for the experiments. Chicks were obtained from a commercial hatchery on their first day of life and reared singly in cages (22.5 cm wide \times 30 cm high \times 40 cm deep) lit from above by fluorescent lamps (Philips Aquarelle 36 W) under controlled conditions (30°C; 67% relative humidity; 12 h:12 h light:dark cycle). Water and food were provided *ad libitum*. Chicks were deprived of food for ca. 10 h before every training session, during the dark phase of the photoperiod.

In all of the experiment, the apparatus consisted of a rectangular array (30 cm \times 60 cm) of four cardboard pipes, located centrally within a circular enclosure (130 cm \varnothing ; 50 cm height), the floor of which was covered with a layer of sawdust (6 cm in depth). A light bulb (75 W) hung above the centre, illuminating the enclosure. A one-way screen covered the top of the apparatus preventing the chicks from seeing outside. A digital camcorder (Panasonic NV-GS27, Osaka, Japan) was used to record the subjects' performances at the experimental tests.

In all of the experimental series, chicks were trained either in an array of four distinctive pipes or in an array of four indistinguishable pipes (see Table 1), which served as local landmarks to locate a food-reward. The reward in the array of identical pipes was hidden inside the pipes that occupied the geometrically equivalent locations. The position of the correct landmark was changed across the subjects in all of the experiments. The positions of the incorrect pipes in the

Table 1. Featural cues at the pipes

Featural cues	Experimental series		
	First	Second	Third
1 Homogeneous black masking tape	Non-rewarded features in the distinctive array	Rewarded feature in the distinctive array Featural cues in the identical array (training and test)	
2 Alternating white and red horizontal stripes		Non-rewarded features in the distinctive array	Not used
3a Dark green discs over an orange background			Not used
4a Homogeneous blue masking tape, with one yellow spiral stripe (2 cm wide)	Rewarded feature in the distinctive array Featural cues in the identical array (training and test)		Non-rewarded features in the distinctive array
3b Red discs over a green background	Not used	Not used	
4b Homogeneous blue masking tape, with four vertical yellow stripes (2 cm wide) located inbetween the pipe's openings	Not used	Not used	

distinctive pipes array were the same for a given subject, but were changed across the subjects.

In the first series of experiments, the pipes (7.5 cm $\varnothing \times$ 26 cm high) had one circular opening (\varnothing 2 cm) located 13 cm from the base and oriented toward the inner part of the array, bisecting the imaginary corners of the configuration. In the second experimental series, the pipes (8.3 cm $\varnothing \times$ 26 cm high) had four circular openings (\varnothing 2 cm) aligned at the same height from the base (13 cm) and spaced 90 deg from each other. The orientation of the openings relative to the array was maintained stable throughout the training and the test trials, bisecting the corners of the configuration. In the third series of experiments, the pipes had four openings also; however, a transparent sheet inside the pipes blocked three of the four openings on the pipes. Hence, only one of the openings allowed the chicks to access the contents of the pipes. The uncovered openings of the pipes were arranged symmetrically in the array and were either kept stable (fixed training condition) or changed between the training series (variable training condition; supplementary material Fig. S1). In the variable access condition of training, each of the four pipes' openings was maintained open for six non-consecutive training series. The direction of the uncovered opening in the fixed access condition was changed across the subjects.

Procedure

Chicks were trained to insert their head through the openings in the pipes in order to access the contents of the pipes, and gain a food reward in the case of a correct choice. Two pre-training sessions were given, on day 2 and day 3 post-hatch, respectively, with the reward available in all of the landmarks, in order to accustom the chicks to the testing environment. Then chicks were given 8 daily training sessions, starting from day 4 post-hatch, with one interruption on day 7. Each training session consisted of 30 trials equally distributed into 3 series of 10 trials. At every trial, chicks were released from the centre of the enclosure or from one of the four imaginary points determined by the intersection of the configural axis with the wall, facing different directions, and following a pseudo random schedule. A trial was considered ended as soon as the chick inserted its head through the opening in the pipe. In the case of a correct choice, the chick was allowed to consume the reward. Subsequently, the chick was placed outside the enclosure in a cardboard box (32 cm wide \times 13 cm high \times 21 cm deep) and was slowly rotated clockwise and counter clockwise to obtain a complete spatial disorientation.

To rule out the use of any uncontrolled external cue, the array of pipes was rotated between both training and test series. The relative position of the landmarks was changed whenever possible.

In both the second and the third experimental series, the pipes were vertically rotated, so that the same opening faced a different direction in the different training series. In the third series of experiment, the rotation of the pipes in the fixed access condition of training was compensated by rotating the transparent sheet inside the pipes in the opposite direction.

At the end of the training, chicks were observed in two series of six unrewarded trials in an array of four indistinguishable pipes. The experimental tests were administered following the same procedure as described for the training.

Data analyses

The first choice of chicks during training and test trials was considered for the analysis. The percentage of correct choices in a session was considered as the individual performance. A repeated measures analysis of variance (ANOVA), with rewarded position as the between-subjects factor and session as the within-subjects factor, was performed. In the third series of experiment, the access condition (fixed vs variable) was considered as the between-subjects factor for the analysis. Mauchly's test was used to assess for sphericity, and Greenhouse–Geisser correction was applied when necessary.

In the second series of experiments, directional analysis was performed on the bases of the direction through which the chicks accessed the correct pipes. The mean vector of the circular distribution of the correct choices at every training session was calculated from these scores, separately for each chick. A repeated measure analysis of variance (ANOVA), with the mean vector length as the dependent variable and session as the within-subject factor, was used to examine the direction through which the chicks accessed the pipes during training.

In order to ascertain whether chicks obtained the reward with comparable frequency from each of the four directions of opening, χ^2 analysis was performed in both the second and in the third series of experiments, separately for the two geometrically distinguishable positions in the array, on the pooled distribution of the correct choices made by the chicks to the four openings during the entire training period.

The path travelled by chicks during the test in both the first and the second series of the experiments were reconstructed. The route efficiency, calculated as the tracks' length divided by the distances separating the chick's starting point to the closest geometrically correct pipe, was considered as the individual performances. An analysis of variance was performed to evaluate the effect of the number openings on the efficiency of the paths.

A Wilcoxon signed-rank test was used to examine whether choices in the experimental test were equally distributed to the

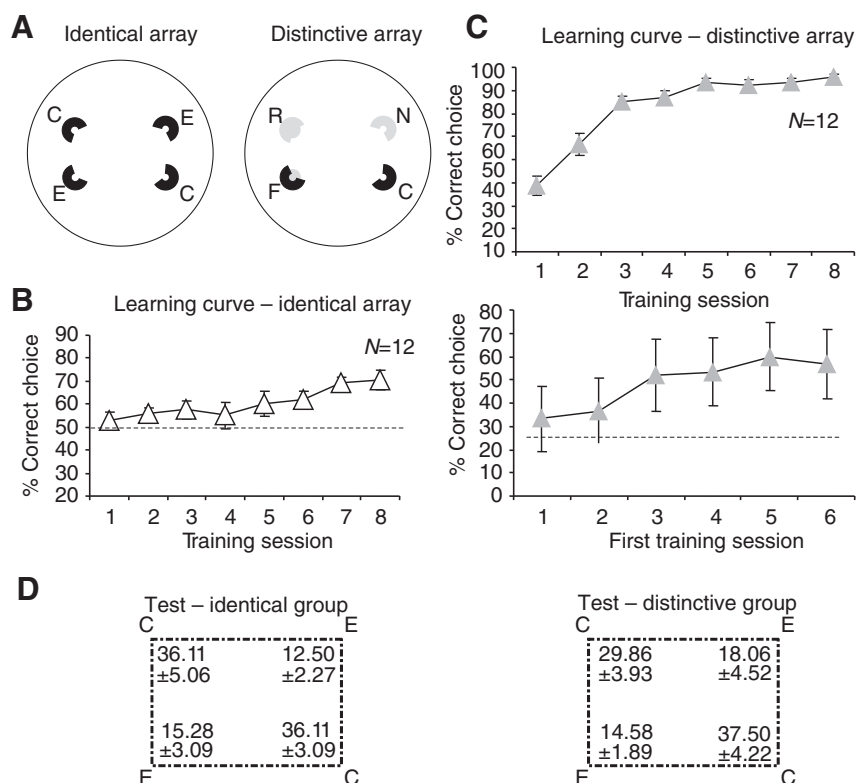


Fig. 1. Experimental series 1. (A) Schematic representation of the arrays. C, geometrically correct pipes; E, geometrically incorrect pipes; R, rotational error; N, near; F, far. (B,C) Percentage of the correct choices (\pm s.e.m.) during the training in the identical array (B) and in the distinctive array (C); dashed lines indicate chance performance. (D) Mean percentages (\pm s.e.m.) of choices to the geometrically correct and incorrect pipes in the array at the experimental test. For convenience, the rewarded position is represented at one position only.

geometrically correct and geometrically incorrect pipes, and to further examine whether choices were equally distributed between the geometrically equivalent landmarks in the array. Null hypotheses were always rejected with $\alpha < 0.05$.

RESULTS

First series of experiments

Chicks were trained to locate a food reward in a rectangular array of either four identical or distinctive pipes provided with single openings (Fig. 1A). In the array of four identical pipes, the subjects learnt the task, proving able to encode the configural geometry to relocate the reward (Fig. 1B). The analysis of variance revealed a significant main effect of the training session ($F_{7,70}=3.443$, $P=0.003$, $\eta_p^2=0.256$). The main effect of the reward position was not significant ($F_{1,10}=0.087$, $P=0.773$, $\eta_p^2=0.01$). There were no significant interactions between session and rewarded position ($F_{7,70}=1.284$, $P=0.271$, $\eta_p^2=0.114$).

The chicks trained in the array of four characteristic pipes (Fig. 1C) learnt to locate the reward on the basis of featural cues ($F_{3,31}=22.349$, $P<0.001$, $\eta_p^2=0.691$). There was neither significant main effect of the rewarded position ($F_{1,10}=4.212$, $P=0.067$, $\eta_p^2=0.296$), nor significant interaction of session by rewarded position ($F_{3,31}=0.311$, $P=0.946$, $\eta_p^2=0.030$).

After training, chicks were tested in an array of four indistinguishable pipes and in the absence of the reward. Chicks trained in the identical pipe array maintained their performances above chance (geometrically correct choices *versus* geometrically incorrect choices: Wilcoxon signed-rank test: $N=12$, $T^+=73$, $P=0.005$, Cliff's $d=0.875$), and their choices were distributed equally between the geometrically equivalent locations (Wilcoxon signed-rank test: correct *vs* rotational: $N=12$, $T^+=32$, Ties=2, $P=0.695$, Cliff's $d=0.056$; far *vs* near: $N=12$, $T^+=19$, Ties=5, $P=0.469$, Cliff's $d=0.062$). Chicks trained in the distinctive pipes

array chose the geometrically correct pipes significantly more often than the geometrically incorrect pipes in the array (Wilcoxon signed-rank test: $T^+=69$, $P=0.016$, Cliff's $d=0.778$), and their choices were distributed equally between the geometrically equivalent locations in the array (Wilcoxon signed-rank test: correct *vs* rotational: $N=12$, $T^+=42$, Ties=2, $P=0.160$, Cliff's $d=0.326$; far *vs* near: $N=12$, $T^+=24$, Ties=1, $P=1$, Cliff's $d=-0.139$).

Second series of experiments

The result of the first series of experiments showed that chicks could reorient according to the geometric information of a rectangular array of landmarks. This result stands in contrast to the previous findings in this avian species (Pecchia and Vallortigara, 2010). It has been shown that chicks trained in the ground scratching task failed to reorient by geometry in a rectangular array of landmarks. In the second series of experiments we examined the impact of the directional guides offered by the openings on the pipes on the chick's searching strategies. Chicks were trained to locate a food reward in a rectangular array of either four identical or four distinctive pipes provided with four openings, oriented in opposite directions with respect to the array.

The chicks' performances are reported in Fig. 2. In the identical pipes array, despite the presence of multiple openings on the pipes, chicks were able to locate the food reward, indicating successful geometric encoding (main effect of session: $F_{7,70}=4.628$, $P<0.001$, $\eta_p^2=0.316$). There was neither a significant main effect of the reward position ($F_{1,10}=0.075$, $P=0.790$, $\eta_p^2=0.007$), nor a significant interaction between session and reward position ($F_{7,70}=0.371$, $P=0.916$, $\eta_p^2=0.036$).

The analysis of variance of the circular distributions of the correct choices made by the subjects during the training around the correct pipes revealed, however, that the choices become progressively biased during the training towards openings oriented in a specific

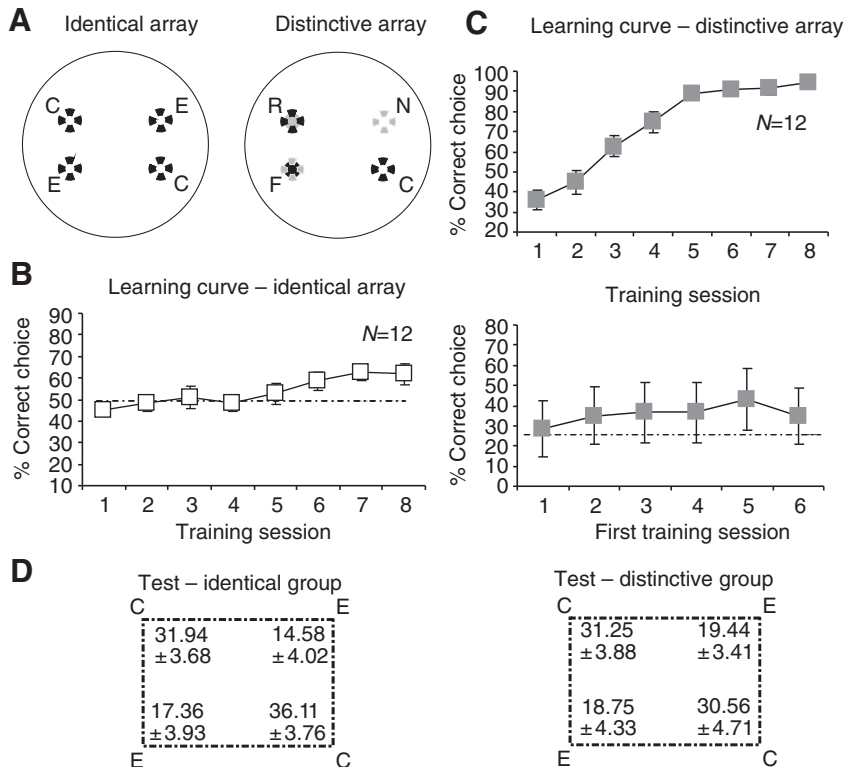


Fig. 2. Second experimental series. (A) Schematic representation of the arrays. C, geometrically correct pipes; E, geometrically incorrect pipes; R, rotational error; N, near; F, far. (B,C) Percentage of the correct choices (\pm s.e.m.) during the training in the identical array (B) and in the distinctive array (C); the dashed line indicates chance performance. (D) Mean percentages (\pm s.e.m.) of choices to the geometrically correct and incorrect pipes in the array at the experimental test. For convenience, the rewarded pipes are represented at one position only.

direction ($F_{7,70}=6.760$, $P<0.001$, $\eta_p^2=0.383$; Fig. 3B). A significant correlation was found between the mean vector length and the chick's accuracy ($F_{1,95}=6.288$, $P=0.014$, $R=0.25$; Fig. 3C).

In order to ascertain whether variable-trained chicks obtained the reward with comparable frequency from each of the four openings of different orientations, χ^2 analysis was performed on the pooled distribution of the correct choices made by the chicks to the four accesses during the entire training period. This analysis revealed that the distribution of the chicks' choices around the correct pipes was not randomly distributed [first diagonal: $\chi^2(3)=497.032$, $P<0.0001$; second diagonal: $\chi^2(3)=350.434$, $P<0.0001$; Fig. 4A], indicating systematic preferences for a specific direction to the openings.

Chicks trained in a rectangular array of four distinctive pipes readily learnt to locate the reward on the basis of the featural cues and approximated the optimal during the last training session. The analysis of variance revealed a significant main effect of session ($F_{7,70}=42.699$; $P<0.001$, $\eta_p^2=0.810$; Fig. 2C). There were neither a significant main effect of the rewarded position ($F_{1,10}=1.835$, $P=0.205$, $\eta_p^2=0.155$), nor a significant interaction between session and rewarded position ($F_{7,70}=0.447$; $P=0.869$, $\eta_p^2=0.043$).

In this training condition, chicks accessed the correct pipe from the same direction throughout the training (Fig. 3B). The correlation between the mean vector length and the mean proportion of the correct choices was not significant ($F_{1,95}=1.248$, $P=0.260$, $R=0.116$;

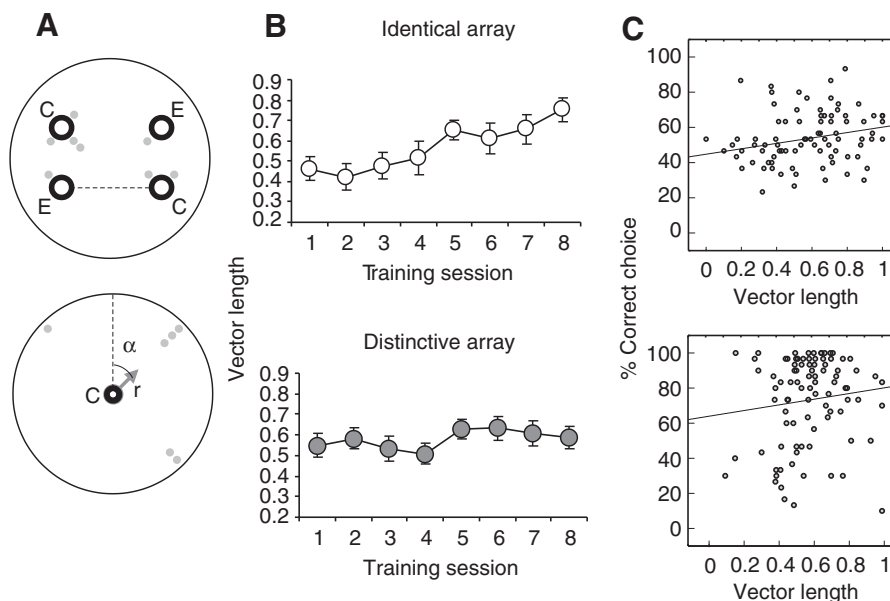


Fig. 3. Second experimental series. Directional analysis. (A) Schematic representation of the subject's choices (grey dots) at the pipes in an imaginary training series (top) C, geometrically correct pipes; E, geometrically incorrect pipes. Pooled distribution of the geometrically correct choices of this series (bottom). The arrow represents the mean vector of the circular distribution. The mean vector is characterized by the mean direction (α), as taken with respect to an arbitrary point of reference (dashed line), and the vector length (r). (B) Mean vector length (\pm s.e.m.) of the circular distributions of choices made by the chicks during the training. (C) Scatter plot of the mean vector lengths and the mean percentage of the correct choices in the corresponding sessions.

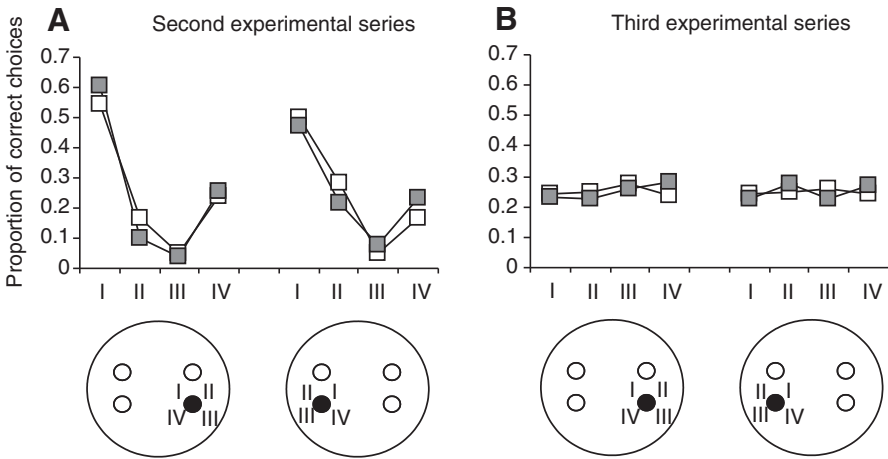


Fig. 3C). χ^2 analysis revealed that the pooled distribution of choices around the correct pipe was not randomly distributed [first diagonal: $\chi^2(3)=789.525$, $P<0.0001$; second diagonal: $\chi^2(3)=355.587$, $P<0.0001$; Fig. 4A], indicating systematic preferences for a specific direction to the openings.

After training, chicks were tested in an array of four indistinguishable pipes (Fig. 2D). Chicks trained in the identical pipe array maintained their performances above chance in the experimental test, even though the reward was no longer available. The mean percentage of choices directed towards the geometrically correct and incorrect pipes differed significantly (Wilcoxon signed-rank test: $N=12$, $T^+=67$, $P=0.013$, Cliff's $d=0.75$). Statistical

comparisons revealed that the choices were equally distributed between the geometrically equivalent locations in the array (Wilcoxon signed-rank test: correct vs rotational: $N=11$, $T^+=44$, Ties=1, $P=0.183$, Cliff's $d=0.181$; far vs near: $T^+=22$, Ties=4, $P=0.320$, Cliff's $d=0.160$).

Chicks trained in the array of four distinctive pipes retrieved the geometric information provided by the array at the experimental test. The difference between the mean percentage of choices directed toward the geometrically correct and incorrect landmarks was marginally significant (Wilcoxon signed-rank test: $N=11$, $T^+=51$, Ties=1; $P=0.061$, Cliff's $d=0.549$). There were no significant differences between the mean distribution of choices of the

Fig. 4. Proportions of choices around the correct pipe(s) over the total number of the correct choices during the training in the second (A) and the third (B) experimental series (white squares, identical pipes array; grey squares, distinctive pipes array). (Bottom) The values are plotted separately for the two geometrically distinguishable positions in the array (black circles). Latin numerals refer to the openings in the pipe.

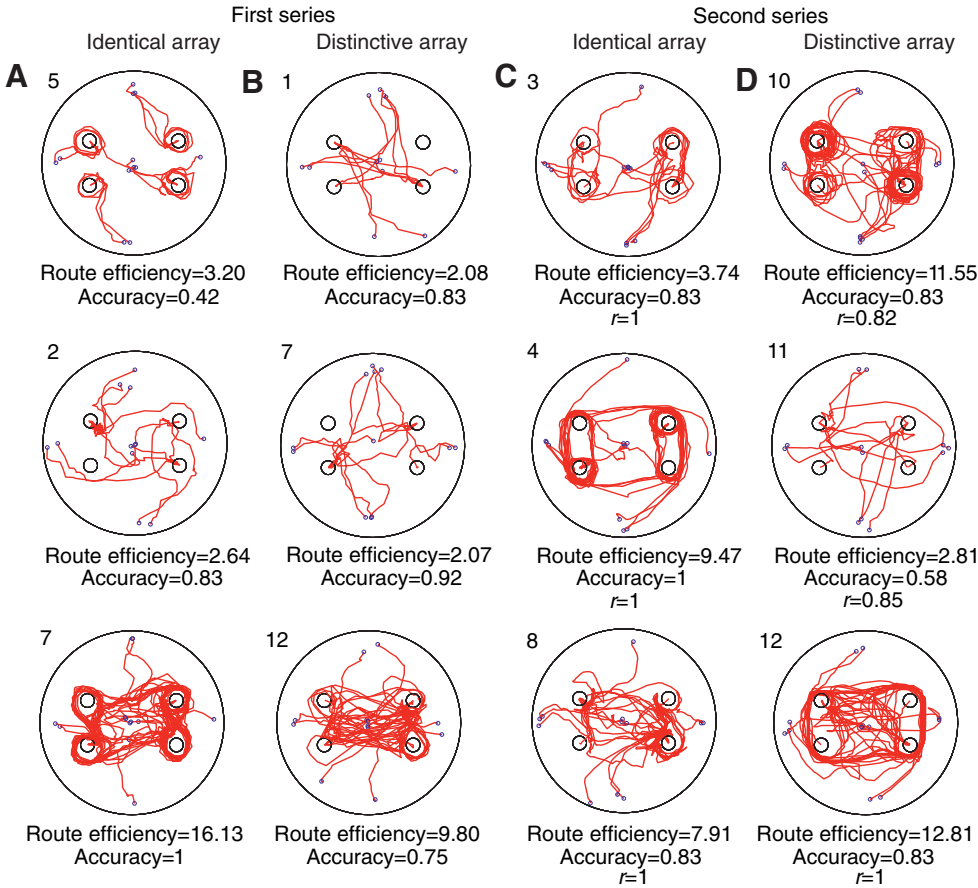


Fig. 5. Some representative tracks recorded during the test trials in both the first and the second series of experiments. The numbers on the top-left of the panels identify the subjects. The blue dots represent the starting location in the test trials. The mean efficiency of the routes (calculated as the length of the track divided by the distance between the starting point and the closest geometrically correct pipe), the accuracy (calculated as the percentage of the geometrically correct choices), and the mean vector length (r) of the circular distribution of the correct choices (ranging from 0 to 1, it represents the orientation of the chick's choices at the correct pipes) are given below the tracks.

landmarks which occupied the geometrically equivalent positions (Wilcoxon signed-rank test: correct vs rotational: $N=10$, $T^+=25$, Ties=2, $P>0.5$, Cliff's $d=-0.014$; far vs near: $T^+=17$, Ties=4, $P>0.5$, Cliff's $d=-0.083$).

Track analyses

The chick's paths at the experimental test in both the first and the second series of experiments were reconstructed (Fig. 5). From a qualitative analysis, the chick's path could be classified as follow: direct path: chick went directly to a pipe in the array and then make a choice; lateral movement: chicks approached, by a direct path, one of the pipe and then moved repeatedly towards the nearest pipes before making a choice; circling: chicks moved repeatedly around a single, a pair, or the entire array of pipes, following a stereotyped path, characteristic for each individual. Circling often results in a correct choice from a specific opening. Direct paths rarely terminated at the closest geometrically correct pipe. An analysis of variance was performed, with the number of pipe openings (one vs four) and the array's type (distinctive pipes array vs identical pipes array) as the between-subject factors, that revealed a significant main effect of openings on the path length ($F_{1,44}=5.616$, $P=0.022$, $\eta_p^2=0.113$). No other significant effects were apparent, suggesting that the chicks' paths were longer in the array of pipes with four openings than in the array of pipes with a single opening.

Third series of experiments

The second series of experiments showed that chicks were able to re-locate the reward in an array of pipes provided with multiple

openings. Directional analysis revealed that chicks accessed the pipes from specific directions, suggesting an egocentric strategy for spatial reorientation. In the third series of experiments, the chicks were experimentally guided to perceive either a stable or a variable panorama of the reward site. A transparent sheet was inserted inside each of the pipes in the array, blocking three out of the four openings. The remaining openings were either kept stable (fixed training condition) or changed throughout the training (variable training condition). If the chicks rely on an allocentric (map-like) representation to navigate, then they would be expected to reorient by geometry irrespective of the access conditions. Conversely, if chicks rely on a view-based strategy to locate the rewarded pipes, a failure to reorient in the variable access condition would be expected.

Chicks' performances in the array of four indistinguishable pipes largely depended on whether the orientation of the openings was maintained stable or changed during training (Fig. 6B). A main effect of session and access direction was apparent (session: $F_{4,59}=3.761$, $P<0.010$, $\eta_p^2=0.190$; access: $F_{1,16}=8.193$, $P=0.011$, $\eta_p^2=0.339$). Fixed- and variable-trained chicks differed significantly with respect to their learning progresses (session \times access: $F_{4,59}=3.761$, $P=0.039$, $\eta_p^2=0.148$). Trend analysis was performed, separately for fixed- and variable-trained chicks, in order to examine how performances changed during the training in the two groups. Only chicks trained to access the contents of the pipe from the same direction (fixed access) learnt to locate the reward [linear trend: $F_{1,8}=9.176$, $P=0.016$, $\eta_p^2=0.534$; mean percentage of the correct choices at the last training session=0.747, s.e.m.=0.063; $t(9)=3.922$, $P=0.004$, Cohen's

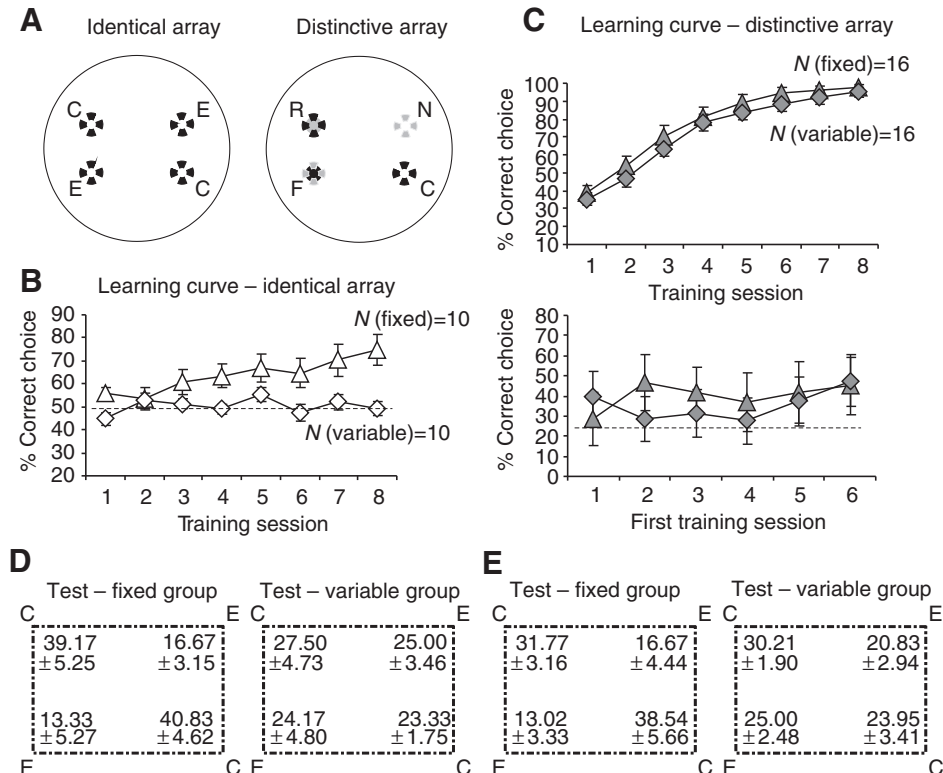


Fig. 6. Third experimental series. (A) Schematic representation of the arrays. C, geometrically correct pipes; E, geometrically incorrect pipes; R, rotational error; N, near; F, far. (B) The mean percentage of the correct choices (\pm s.e.m.) during the training in the identical array (B; white triangles, fixed; white diamonds, variable) and in the distinctive array (C; grey triangles, fixed; grey diamonds, variable). The dashed line in B and C indicates chance performance. (D,E) The mean percentage of choices directed to the four pipes (\pm s.e.m.) at the experimental tests (D, training identical; E, training distinctive). The experimental tests were conducted in the identical array. For convenience, the rewarded position is represented at one position only.

$d=1.240$]. By contrast, variable-trained chicks failed to learn the task [linear trend: $F_{1,8}=0.333$, $P=0.639$, $\eta_p^2=0.029$; mean percentage of the correct choices at the last training session: $=0.493$, $s.e.m.=0.023$; $t(9)=-0.242$, $P=0.814$, Cohen's $d=0.077$].

Chi-squared analysis was performed on the pooled distribution of the correct choices made by the chicks to the four accesses during the entire training period. Variable-trained chicks chose equally between the four opening orientations [first diagonal: $\chi^2(3)=4.481$, $P=0.214$; second diagonal: $\chi^2(3)=5.987$, $P=0.112$; Fig. 4B]. Since fixed-trained chicks accessed the reward from a fixed direction during the training, it could be argued that geometric learning occurred as long as chicks perceived a stable panorama at the reward locations.

With the distinctive array (Fig. 6C), chicks learnt to discriminate the correct landmark on the basis of the featural cues (session: $F_{4,99}=101.094$, $P<0.001$, $\eta_p^2=0.783$), irrespective of access condition (access: $F_{1,28}=1.362$, $P=0.253$, $\eta_p^2=0.46$). No significant interaction between access direction and session was apparent (session \times access direction: $F_{4,99}=0.219$, $P=0.910$, $\eta_p^2=0.008$). Chi-square analysis revealed that variable-trained chicks chose equally between the four openings at the correct pipe throughout the training [first diagonal: $\chi^2(3)=4.185$, $P=0.186$; second diagonal: $\chi^2(3)=0.966$, $P=0.810$; Fig. 4B], suggesting that the rotation of the opening did not affect featural learning.

After training, chicks were tested in an array of four indistinguishable pipes. Among chicks trained in the identical pipes array (Fig. 6D), fixed-trained chicks maintained their performances above chance (geometrically correct vs geometrically incorrect: Wilcoxon signed-rank test: $N=10$, $T^+=53$, $P=0.003$, Cliff's $d=0.97$), and equally distributed their choices between the geometrically equivalent locations in the array (Wilcoxon signed-rank test: correct vs rotational: $N=8$, $T^+=19$, Ties=2, $P=0.473$, Cliff's $d=0.18$; far vs near: $N=5$, $T^+=12$, Ties=5, $P=0.156$, Cliff's $d=0.24$). Conversely, variable-trained chicks chose equally among the pipes in the array (geometrically correct vs geometrically incorrect: Wilcoxon signed-rank test: $N=6$, $T^+=11$, Ties=4, $P=0.5$, Cliff's $d=0.20$). Among chicks trained in the distinctive pipes array (Fig. 6E), fixed-trained chicks retrieved the residual geometric information in the novel array (geometrically correct vs geometrically incorrect: Wilcoxon signed-rank test: $N=16$, $z=-2.438$, $P=0.015$, Cliff's $d=0.70$). By contrast, variable-trained chicks failed to retrieve the configural geometry (geometrically correct vs geometrically incorrect: Wilcoxon signed-rank test: $N=14$, $z=-1.350$, Ties=2, $P=0.177$, Cliff's $d=0.36$).

DISCUSSION

Chicks proved able to reorient in a rectangular array of indistinguishable landmarks, providing the first evidence for such a capability in an avian species. Comparable results were obtained with rats in a similar task [*Rattus norvegicus* (Gibson et al., 2007)], although they were not interpreted in the same theoretical framework. Chicks and rats are therefore able to reorient by geometry in an enclosed space as well as in an array of spatially isolated landmarks, confirming the primacy of geometry for spatial reorientation (see also Brown et al., 2007; Chiandetti and Vallortigara, 2008a; Chiandetti and Vallortigara, 2009; Vallortigara et al., 2009).

The results reported here provide direct support to the hypothesis that non-human vertebrates may rely on a (local) view-based strategy to reorient by geometry. According to a view-matching strategy of reorientation, animals would navigate so as to minimize

the difference between the panoramic image of the rewarded site, stored in memory, and the panorama perceived from the current location (Collett and Collett, 2002). Nevertheless, the overall pattern of findings reported here does not support the hypothesis of global matching in chicks (see also Wystrach, 2009; Sheynikhovich et al., 2009). In the third series of experiments, chicks appeared able to encode the configural geometry as long as the openings pointed in a fixed direction throughout training. Hence, geometric cues were encoded as long as chicks perceived a stable panorama from the reward pipe. By contrast, the chicks' performances in the array of distinctive featural cues were apparently not affected by the stability of the local views. No substantial differences emerged when comparing the performances of chicks trained in the array of distinctive pipes between the variable and fixed conditions, as if chicks encoded featural information about the rewarded pipe despite changes in the panoramic views. It could be speculated that chicks extracted higher-level features from stable local views, and matched those features to reorient according to configural geometry. Distances and directions would be implicitly encoded in the local views. Conversely, chicks did not necessarily rely on those features to reorient by featural cues, indicating therefore that place learning was dissociated from non-spatial learning. It is at present unclear what cues the chicks actually matched to reorient by geometry. Further experiments are needed to clarify this issue.

Results with chicks and rats in the rectangular room task (see Introduction) are consistent with the hypothesis that geometric information could be encoded in a local representation. The transformational approach revealed that the local cues could be used by rats and chicks to relocate the geometrically correct corners in a rectangular arena (Pearce et al., 2004; Tommasi and Polli, 2004), and that local information is likely to be preferred by rats to relocate the geometrically correct sites in a rectangular array of landmarks (Esber et al., 2005) (cf. Cheng, 2005). A view-dependent mechanism of reorientation has been proposed (Sovrano and Vallortigara, 2006) to explain the relative reliance of the geometric and the featural cues in enclosures of different sizes [domestic chickens (Vallortigara et al., 2005; Chiandetti et al., 2007; Chiandetti and Vallortigara, 2008b; Sovrano et al., 2005; Sovrano et al., 2007); rats (Maes et al., 2009); humans (Hermer and Spelke, 1996; Learmonth et al., 2001; Learmonth et al., 2002)]. View-matching strategy of reorientation was proved to account for many of the principal phenomena described by Cheng (Cheng, 1986) (see also Cheung et al., 2008; Stürzl et al., 2008; Dawson et al., 2010), and could be used by ants (*Gigantiops destructor*) to reorient in the rectangular arena task as well (Wystrach and Beugnon, 2009).

Intiguously, chicks proved able to encode the configural geometry of the rectangular array of pipes provided with multiple openings. Inertial guidance was unlikely because chicks were disoriented between trials and started from different locations, both during the training and the test sessions. Nevertheless, chicks showed remarkable directional preferences at the pipes and route (circling) stereotyped searching behaviour during the training. It is likely therefore that chicks encoded stable local views (heading- and location-dependent visual scenes) of the rewarded site to reorient by geometry in this condition.

It is unclear whether directional preferences in the second series of experiments, particularly in the array of distinctive pipes, would reflect the availability of the openings or rather a chick's searching strategy. We would like to stress, however, that chicks in the third series of experiment learned the configural geometry in the fixed access condition of training irrespective of whether the orientation

of the openings was towards the inner part of the array or the wall of the arena. This finding is consistent with the hypothesis that a stable local view is required in order to perform an appropriate visual matching.

The hypothesis of a view-based strategy for spatial reorientation apparently fails to predict the efficiency of chicks' paths, which remains far from optimal in both the first and the second series of experiments. Minimizing the differences between the current view and the target view, combined with continuous updating of the mismatch between visual information, would predict slightly direct path, particularly in the vicinity of the goal. Curiously enough, we observed that chicks sometimes moved toward an incorrect landmark in the array, despite their proximity to 'minimum' in image differences. It could be, therefore, that chicks did not continuously update their position within the arena. However, the openings on the pipes may have triggered the view-matching process in this task. The path length in the arrays of pipes with four openings were longer than the path length in the arrays of pipes provided with a single opening, as if chicks evaluated the mismatch between the current local view and the correct panorama from each of the openings at the pipes.

Laboratory studies have shown that Clark's nutcrackers establish stereotyped routes during seeds caching and recovery, similar to those described here for chicks (Kamil et al., 1999) (see also Bossema 1979). In an experiment by Kamil, Balda and Goodwas (Kamil et al., 1999) testing was carried out in a large room, in which there were thirty-two distinctive landmarks, providing multiple geometric and featural information for spatial reorientation. Stereotyped routes were apparent from the analysis of the bird's path between caching and recovery sessions. Stereotyped routes did not predict the nutcrackers' accuracy during cache recovery, suggesting that the cache sites were remembered in an allocentric (map-like) spatial representation (Kamil et al., 1999). However, the relative contribution of featural and geometric cues on the searching strategies of the nutcrackers was not ascertained. It could not be excluded, therefore, that the nutcrackers relied on a view-based strategy to reorient by geometry in that task.

Comparable findings were obtained in open field studies with pigeons (*Columba livia*). Homing experiments showed that pigeons established highly stereotyped navigational routes after repeated flights from the same release site (Biro et al., 2004; Meade et al., 2005). Results with chicks suggest that stereotyped routes may ensure successful navigation despite changes in the non-geometric cues in the spatial layout.

Results with young children (4- to 5-years old) suggest that they systematically fail to locate a hidden toy on the basis of the geometric cues specified by the spatial arrangement of an array of isolated landmarks (Gouteux and Spelke, 2001; Lee et al., 2006; Lee and Spelke, 2008), whereas they successfully encode the geometric information provided by the shape of a rectangular enclosure (Hermer and Spelke, 1996). Comparable findings were obtained in chicks using a ground scratching task in which animals searched for food hidden below sawdust on the floor of an arena. Although chicks were shown to be able to reorient on the basis of the featural cues in this spatial task, they failed to locate a buried feeder in a rectangular array of indistinguishable landmarks (Pecchia and Vallortigara, 2010). Nonetheless, chicks trained to locate the reward at the corner of a homogeneous rectangular enclosure reoriented successfully (Vallortigara et al., 1990). According to the results reported here, it is likely that chicks failed to reorient by geometry with the landmark arrays because the ground scratching task prevented them from perceiving a stable local-view of the correct

site (Pecchia and Vallortigara, 2010). By contrast, the circular openings on the pipes used in the present study provided a useful directional guide, facilitating appropriate visual matching.

Testing children with an analogous task to that developed for chicks may prove rewarding, and such a study is currently in progress in our laboratory. Furthermore, it seems likely that the directional guide provided by the openings at the landmark in the array study by Gibson (Gibson et al., 2007) made it possible for rats to encode the configural geometry. Of course, the walls at the corners of an enclosed space may also provide comparable directional cues, enforcing a view-based strategy for spatial reorientation in vertebrate species (see Sovrano and Vallortigara, 2006).

In conclusion, our results provide direct support to the hypothesis that non-human vertebrates may rely on a view-based strategy to reorient by geometry. The possibility that such a navigational strategy is also used by humans (particularly children) deserve careful empirical scrutiny.

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