

RESEARCH ARTICLE

Ontogenetic development of magnetic compass orientation in domestic chickens (*Gallus gallus*)

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SUMMARY

Domestic chickens (*Gallus gallus*) can be trained to search for a social stimulus in a specific magnetic direction, and cryptochrome 1a, found in the retina, has been proposed as a receptor molecule mediating magnetic directions. The present study combines immuno-histochemical and behavioural data to analyse the ontogenetic development of this ability. Newly hatched chicks already have a small amount of cryptochrome 1a in their violet cones; on day 5, the amount of cryptochrome 1a reached the same level as in adult chickens, suggesting that the physical basis for magnetoreception is present. In behavioural tests, however, young chicks 5 to 7 days old failed to show a preference of the training direction; on days 8, 9 and 12, they could be successfully trained to search along a specific magnetic axis. Trained and tested again 1 week later, the chicks that had not shown a directional preference on days 5 to 7 continued to search randomly, while the chicks tested from day 8 onward preferred the correct magnetic axis when tested 1 week later. The observation that the magnetic compass is not functional before day 8 suggests that certain maturation processes in the magnetosensitive system in the brain are not yet complete before that day. The reasons why chicks that have been trained before that day fail to learn the task later remain unclear.

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INTRODUCTION

Chickens have often been used as a model for spatial cognition research and its development (Rogers, 1995; Vallortigara et al., 1998). Immediately after hatching, domestic chicks learn to recognise their mother by an imprinting process (see Lorenz, 1935), a phenomenon guaranteeing that young precocial birds follow their mother and stay close to her (e.g. Bateson, 1987). However, if the hen is not within sight during the crucial period, young chicks can imprint on other moving or stationary objects (Eiserer, 1980; Bolhuis and Bateson, 1990). Using the motivation of young chicks to search for the imprinting stimulus when it is hidden, it was possible to train chicks to look for the stimulus in a specific magnetic direction, thus demonstrating their ability to obtain compass information from the geomagnetic field (Freire et al., 2005). Further experiments based on this test design showed that the magnetic compass of chickens works in the same way as described for European robins, *Erithacus rubecula*, a passerine migrant: it operates in a similar intensity window, is light dependent and can be disrupted by radio frequency fields in the MHz range, suggesting that the underlying mechanism is based on radical-pair processes (Wiltschko et al., 2007), and it is also lateralised in favour of the right eye system projecting primarily to the left brain hemisphere (Rogers et al., 2008).

Cryptochrome has been suggested as a candidate receptor molecule for magnetic compass orientation in birds (Ritz et al., 2000; see also Maeda et al., 2012). In chickens, as in other birds, there are at least four types of cryptochrome (Bailey et al., 2002; Haque et al., 2002; Liedvogel and Mouritsen, 2010; Watari et al., 2012). Of these, cryptochrome 1a has been found to be located at the disks in the outer

segments of the ultraviolet/violet cones of robins and chickens (Nießner et al., 2011), and thus at a location that is in agreement with a sensory function. The distribution of these cones across the entire retina, with their orientation in all spatial directions, meets the requirements of the radical pair model of magnetoreception (Ritz et al., 2000), and hence we take cryptochrome 1a to be the most likely candidate receptor molecule for sensing magnetic directions.

Because the behavioural studies demonstrating directional orientation by the magnetic field in domestic chickens had involved birds aged between days 10 and 23 after hatching (Freire et al., 2005; Freire et al., 2008; Wiltschko et al., 2007; Rogers et al., 2008; Denzau et al., 2013), it was not known at what age the magnetic compass became functional. In the present study, we combined immuno-histochemical and behavioural approaches to determine the ontogenesis of the magnetic compass. We investigated at what age cryptochrome 1a is present in the violet cones, at what age a task based on magnetic compass orientation could be successfully learned and how early experience might influence learning ability at a later age.

MATERIALS AND METHODS

The chickens used for the present study were Lohmann Brown chickens, a crossbreed of a Rhode Island Red cock and a White Plymouth Rock hen, obtained from the LSL Hatchery, Schaaflheim, Germany. We chose this strain because in an earlier study (Denzau et al., 2013) these chicks had readily used magnetic cues when searching for the imprinting stimulus. The experiments were conducted according to the rules and regulations of Animal Welfare in Germany.

Immuno-histochemistry of cryptochrome 1a and the violet opsin

In the immuno-histochemical part of the study, we used retinae of both eyes of six chicks, three of them 1 day old and three of them 5 days old. The retinae were taken under identical light conditions, fixed with paraformaldehyde (Morphisto, Frankfurt, Germany) and prepared using the procedure described by Nießner et al. (Nießner et al., 2011) for whole mounts.

Primary antibodies used in this study to immunolabel cryptochrome 1a and violet-opsin were as follows: (1) guinea pig cryptochrome 1a antiserum (designed in our laboratory and produced by GENOVAC, Freiburg, Germany), raised against amino acids 601–621 of cryptochrome 1a (N-) RPNPE EETQS VGPKV QRQST (-C), was used to mark cryptochrome 1a (characterized in Nießner et al., 2011); and (2) goat antiserum sc-14363 raised against a 20-aa N-terminal epitope of the human S (blue) cone opsin (Santa Cruz Biotechnology, Santa Cruz, CA, USA) was used to mark the ultraviolet/violet cones in birds (Schiviz et al., 2008; Nießner et al., 2011).

The retinae were viewed with a confocal laser scanning microscope (Zeiss LSM 510 META; Carl Zeiss AG, Oberkochen, Germany). We evaluated the entire retinae and compared the intensity of the immunolabeling of various areas between the two age groups. For a more detailed description of the procedures employed and the respective controls, see Nießner et al. (Nießner et al., 2011).

Behavioural experiments

For the behavioural experiments we used 72 chickens. They were incubated at the University of Frankfurt and kept in individual cardboard pens with food and water available *ad libitum*. Immediately after hatching, they were imprinted on a red table tennis ball that became their ‘mother’, following the established standard procedures, with the ball hanging on a nylon string in the centre of the cardboard box at a height where the young chick could easily touch and move it (e.g. Vallortigara et al., 1998).

Training and testing took place in a square arena (side length 80 cm, 70 cm high) with white screens (15 cm wide, 25 cm high) placed in each corner [see fig. 1 in Denzau et al. (Denzau et al., 2013)], using the standard procedure described in detail by Freire et al. (Freire et al., 2005). It began with visual displacements, in which the chick, confined in a transparent box, could observe the red table tennis ball disappear behind the screen in the training direction. The next step involved relocations, in which the table tennis ball was already hidden behind the screen in the training direction, with a second identical ball behind the screen in the opposite direction. This was done because chickens trained using this procedure do not discriminate between a direction and its opposite, but just show axial preferences (Freire et al., 2005). On finding one of the two balls without looking behind another screen, the relocation was scored as correct, and the chick was rewarded by being allowed to stay for 1 min with the ‘mother’. All training took place in the local geomagnetic field. To reach the criterion for the first test, each chick had to complete at least seven relocations, with at least the last three correct.

The critical tests were unrewarded, i.e. without table tennis balls behind the screens. They took place in a magnetic field with north shifted 90 deg to the east by Helmholtz coils so that chicks that used unavoidable non-magnetic ‘room’ cues would score incorrectly. After choosing one screen, the chick was immediately removed from the arena and brought back to its cardboard pen with the ball already hanging in the box. Every test was followed by at least one relocation, and after one correct relocation, testing continued until the chick had performed five critical tests.

Because we wanted to observe the ontogenetic development, six groups of 12 chicks each were tested; one group each was tested on days 5, 6, 7, 8, 9 and 12 after hatching. Training and testing of an individual chick took place within 1 day, starting with visual displacements in the morning, followed by relocations. Testing took place in late morning if a chick was very fast in reaching the criterion, but mostly testing took place in the afternoon. The chicks, especially the very young ones, often got tired during training and testing and took a brief nap; testing was interrupted for that time period. One week after its first testing day, on days 12–16 and 19, each chick was tested again five times, following the same procedure.

For statistical analysis, the number of correct directional choices of each chick was tested with the sign test to determine whether there was a significant preference of choosing either axis (see supplementary material Table S1). A two-sample *t*-test was used to test whether the number of correct choices differed from chance (chance level 50%) and to compare the performance on days 5, 6 and 7 with that on days 8, 9 and 12. The results of the first and second tests of each chick were compared using a paired *t*-test.

RESULTS AND DISCUSSION

Immuno-histochemical study

Fig. 1 shows retina whole mounts of a newly hatched and a 5-day-old chicken. In both samples the outer segments of violet cones containing violet opsin are marked in blue, indicating a similar number of violet cones in these parts of the retinae. Obviously, the visual system is already fully developed at hatching. This is not surprising, as visual imprinting on the mother must take place immediately after the chick leaves the egg.

The intensity of immunolabeling of cryptochrome 1a was very similar within each age group. It differed considerably, however, between the two groups: in newly hatched chicks, there are very few obvious markings, whereas in 5-day-old chicks the intensive labeling indicated a higher amount of cryptochrome 1a. This amount found on day 5 in the violet cones is very similar to that found in adult chickens (see Nießner et al., 2011), suggesting that the quantity of cryptochrome 1a, if it is indeed the crucial receptor molecule, would allow the physical processes of the radical pair mechanism to take place.

Compass orientation tests

The percentage of correct choices in the first and second tests of each chick at the various days are given in Fig. 2; for the results of the individual chickens, see supplementary material Table S1. The scatter is considerable, with some individuals apparently unable to orient using the magnetic field and instead using unknown non-magnetic cues, as their significant preference of the original training direction suggests (see supplementary material Table S1). Nevertheless, a clear trend emerges: on days 5, 6 and 7 after hatching, the choices of the young chicks were at chance level. From day 8 onward, however, the chicks showed a small, but significant, preference for the magnetically correct axis. Fig. 3, left diagrams, summarises the choices in all four corners of chickens tested on days 5 to 7 and of those tested on days 8, 9 and 12; the first group is randomly oriented ($t_{35}=0.59$, $P=0.558$), whereas the second group shows a significant preference for the magnetically correct axis ($t_{35}=3.03$, $P=0.005$).

All these birds were tested again 1 week later. The directional choices of these second tests are given in Fig. 3, right diagrams. The first group was now tested on day 12, 13 or 14, that is, at an age when, based on the performance of the second group, one would expect them to orient using the magnetic field. Yet their choices are still not different from chance ($t_{35}=0.308$, $P=0.760$). The chickens

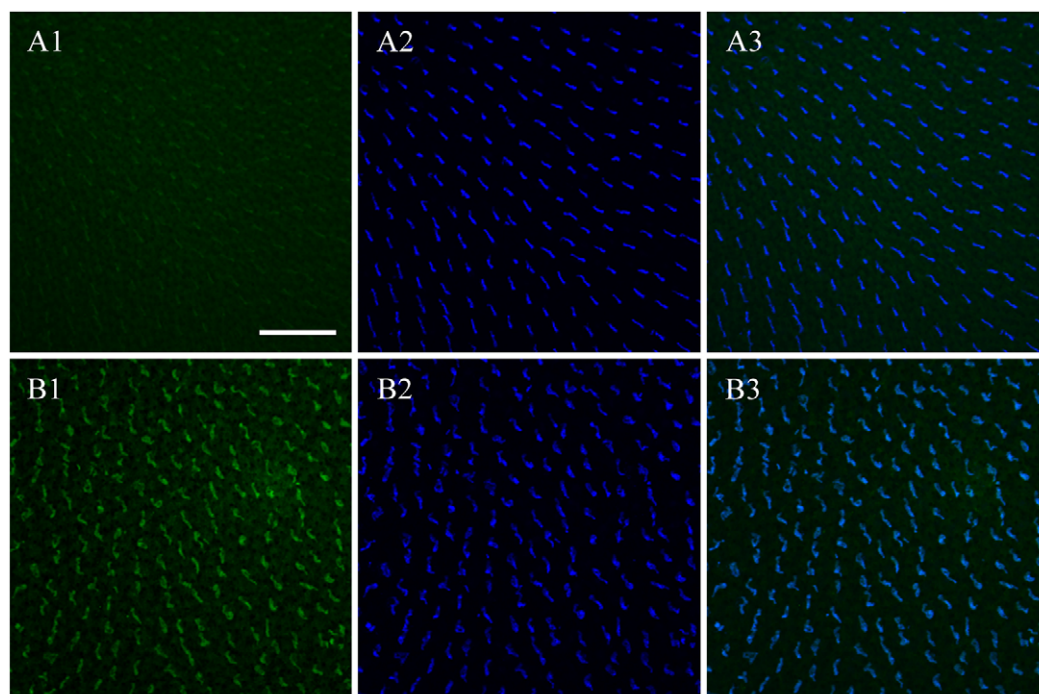


Fig. 1. Whole mounts of retinæ of a newly hatched (A) and a 5-day-old (B) Lohmann Brown chicken. (A1,B1) Cryptochrome 1a immunofluorescence in green. (A2,B2) Violet cone opsin immunofluorescence in blue. (A3,B3) A merge of both images, indicating that cryptochrome 1a, when present, is inside all violet cones. Scale bar, 50 μ m (applies to all panels).

tested a second time on days 15, 16 and 19 again showed a tendency to prefer the magnetically correct axis ($t_{35}=1.930$, $P=0.062$). A direct comparison of the tests on day 12 is presented in Fig. 4: the chicks that were tested for the first time solved the task by significantly preferring the magnetically correct axis ($t_{11}=2.283$, $P=0.0433$), whereas those tested for the second time failed to do so; their choices were disoriented ($t_{11}=1.232$, $P=0.244$). The performance of the two groups was significantly different ($t_{22}=2.545$, $P=0.019$). Apparently, chicks trained at an age when they are not yet able to learn the task using magnetic cues are not only disoriented during the test on that day but also when they perform the same task 1 week later. When all data from the first and second tests were combined and the performance of the two groups (i.e. group 1 trained on day 5, 6 or 7 compared with group 2 trained on days 8, 9 and 12) was compared, the performance of group 2 had a significantly higher percentage of correct choices than that of group 1 ($t_{142}=2.281$, $P=0.024$).

Ranging between 59 and 65%, the preferences of the magnetically correct axis observed in the present study in the birds tested from day 8 onward are not very pronounced. In our earlier study (Denzau et al., 2013), the same strain of Lohmann Browns had 75% correct choices. Compass orientation tests in Australia (Freire et al., 2005; Wiltschko et al., 2007; Rogers et al., 2008), testing a similar strain of chickens, a crossbreed including Rhode Island Red, in an identical test design usually showed between 72 and 78% choices along the correct axis. The reason for the comparatively poor performance in the present study is not entirely clear; it may lie, however, in the temporal constraint: because each chick had to complete the training and testing programme within 1 day, the critical tests usually took place in the afternoon, at a time when the young chicks are already rather tired. In the other experiments, without this constraint, training of the chicks had mostly begun in the afternoon with the birds trained until shortly before they had reached the criterion, so that the critical test usually followed on the next morning when the chicks were most alert. Also, in those experiments, the chicks normally had a night's sleep between the first part of the training and the tests. Sleep is known to enhance consolidation of memory; in birds, this has been found in pre-programmed learning such as song learning in passerines (e.g.

Dave and Margoliash, 2000; Derégnaucourt et al., 2005) or memorizing the imprinting stimulus (e.g. Jackson et al., 2008). Whether this applies to some extent to the direction learning of our study is not entirely clear. Yet the seemingly lower performance observed in the present study may not necessarily reflect a poorer ability to detect the magnetic field, but may, at least in part, be attributed to the temporal circumstances of testing. This is supported by the very first tests of each chick, which took place earlier in the day: for chicks of group 2, tested on days 8, 9, 12, 15 and 16, the percentage of correct choices is higher than average (see supplementary material Table S1).

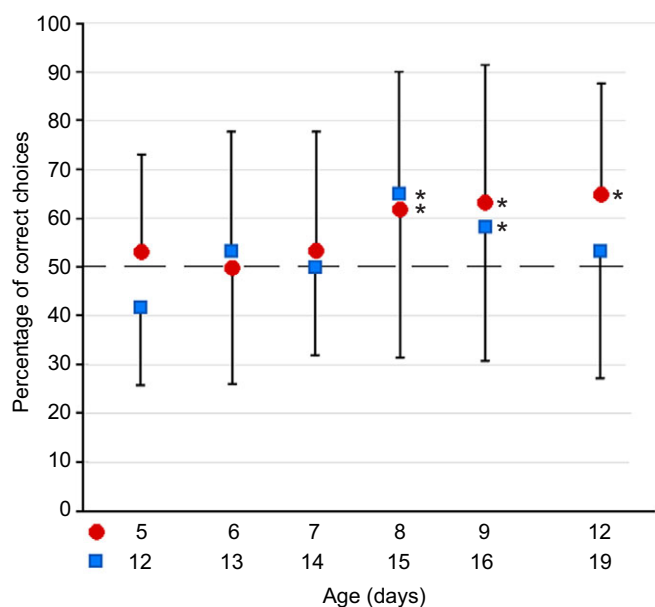


Fig. 2. Mean \pm s.d. percentage of choices in the first tests (red circles) and second tests (blue squares) of the same groups of chickens on the respective day. Chance level 50% is indicated by a dashed line. Asterisks indicate samples that deviate from chance.

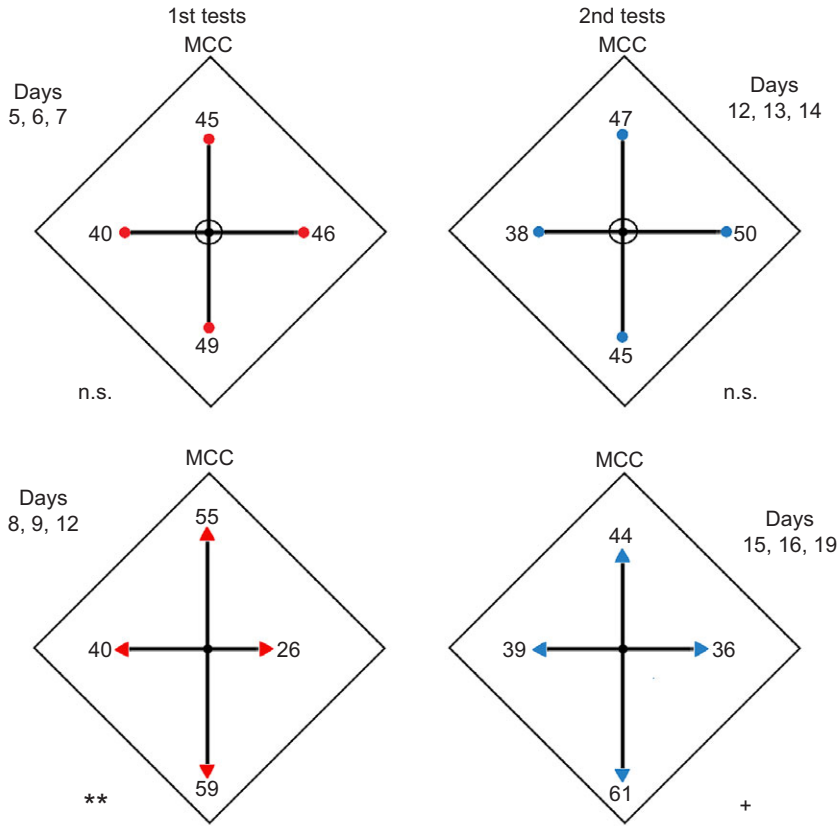


Fig. 3. Summarized results of directional choices of chicks when they were tested for the first time (left diagrams) and for the second time (right diagrams) on the days indicated. The magnetically correct corners (MCC) are at the top; the lines are drawn proportionally to the number of choices in the respective corner and are given numerically at the ends. Round endings and a circle around the centre indicate that choices were at chance level; arrows indicate a significant preference for the correct axis (** $P < 0.01$, + $0.10 > P > 0.05$).

General discussion

When we found that cryptochrome 1a, the protein we take to be the putative receptor molecule for sensing magnetic directions, was present in the retina on day 5 after hatching at a level similar to that in adult chickens, one of the basic prerequisites of magnetic compass orientation seemed to be fulfilled. Because at this age young chicks begin to make their first movements independent of the hen (Broom, 1968; Sherry, 1981; Workman and Andrew, 1989; see Rogers, 1995), we decided to start our behavioural tests at that age. Our results, however, indicate that the magnetic compass of chickens is not yet functioning on day 5 after hatching: we could not train chicks to search for the hidden social stimulus in a specific magnetic direction. This changed on day 8, when the chicks readily learned the task to find the stimulus using the magnetic field.

Day 8 is an important day in the development of young chickens, characterized by crucial changes. On that day, they start to turn their

attention to the environment, and watching the feeding behaviour of the hen is not so important any more (Rogers, 1995). They also begin to fixate their hen (or a human observer) with the right eye/left brain hemisphere (Workman and Andrew, 1989; Dharmaretnam and Andrew, 1994). Day 8 is a peak age for the use of the right eye and the left hemisphere for topographical cues in food searching (Rashid and Andrew, 1989); the categorization of the visual images is now done with the left hemisphere (Vallortigara and Andrew, 1991), in particular categorizing food as distinct from pebbles (Rogers, 1991; Rogers, 1995). The ability to sense magnetic directions was also shown to be a specialization of the right eye and left hemisphere (Rogers et al., 2008); hence the observation that the neuronal pathways processing directional information appear to be developed and become functional at the same age fits well into this general picture.

At the age of 10 days, the chicks begin to move around on their own, leaving their mother to explore independently for short

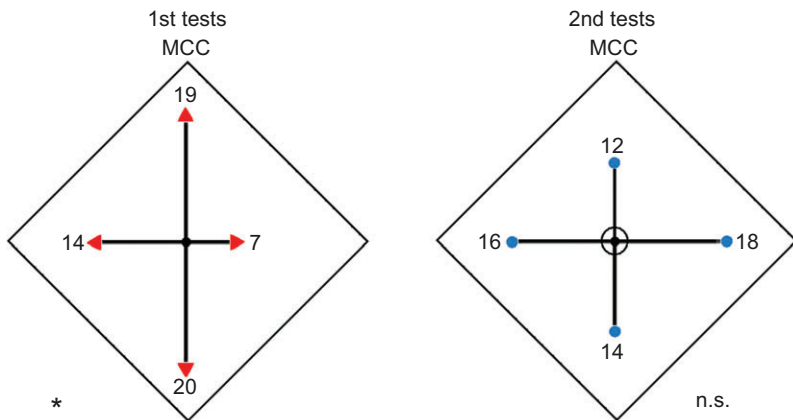


Fig. 4. Directional choices of chicks tested on day 12. Left: chicks tested for the first time; right: chicks tested for the second time on day 12 after they had been tested on day 5. For symbols and abbreviations, see Fig. 3.

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- periods, but always returning to her (Rogers, 1995; Vallortigara et al., 1997). The magnetic compass could be very useful during this phase: the young chicks could record the compass direction in which they move away from the hen and reverse it to return to her. Findings in young homing pigeons suggest a similar navigational strategy for their first spontaneous flights (Wiltschko and Wiltschko, 1978; Wiltschko and Wiltschko, 2009). In our tests, as in previous tests using the same technique (Freire et al., 2005; Freire et al., 2008; Wiltschko et al., 2007; Rogers et al., 2008), young chicks showed axial behaviour, not distinguishing between the direction towards the imprinting stimulus and the direction opposite. An axial compass would be of limited use only, and hence the axial preferences may be an artefact resulting from the artificial testing situation in the very symmetrical, almost featureless arena. Also, under natural circumstances, the young chick would actively move away from the hen and return to her by moving in the opposite direction; our test paradigm, in contrast, requires the chick to move only towards the 'mother' without having actively moved away from her, which may lead to a confusing of the two directions.
- The finding that the chicks trained and tested first on days 5, 6 or 7 seemed unable to rely on magnetic compass direction in their searching behaviour 1 week later was unexpected, as the other group of chicks trained and tested on day 12 used magnetic directions. Also, Freire et al. (Freire et al., 2005), who tested their chicks twice, once at the age of 10 to 14 days and a second time at 19 to 23 days, found a preference for the magnetically correct axis during both periods. The after-effect of early training and testing that we found seems to suggest that subjecting the chicks to a training and testing procedure when they were probably unable to use the direction of the magnetic field prevented them from using the magnetic field as a cue in that particular context in the future. In their first test on days 5 to 7, they may have learnt to use non-magnetic 'room' cues and persisted to use these when they were tested later. However, their individual performance does not support such a strategy, as chicks that had shown a preference for the original training direction in the first tests did not do so in the second tests and *vice versa* (see supplementary material Table S1). They may have simply adopted a random search strategy and persisted to do so even though they could have used magnetic cues later.
- In conclusion, the ability to process and learn to follow magnetic directions develops between day 7 and 8 of post-hatching life. Although the retinal pigments probably used to detect the magnetic field by the radical pair mechanism are present in the violet cones by day 5, the association of their input with the central mechanisms of learning using magnetic information does not occur until 3 days later. This finding suggests that the maturation of the necessary cognitive mechanisms takes place after the development of the relevant cellular and subcellular structures in the retina.
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- AUTHOR CONTRIBUTIONS**
- S.D. and W.W. conceived the study; S.D. and C.N. performed the study, S.D., C.N., W.W. and L.J.R. interpreted the findings, with L.J.R. contributing substantially to the discussion; S.D. drafted and W.W. revised the manuscript.
- COMPETING INTERESTS**
- No competing interests declared.
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