



The use of spatial and local cues for orientation in domestic chicks (*Gallus gallus*)

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Received: 7 October 2019 / Revised: 18 December 2019 / Accepted: 19 December 2019 / Published online: 1 January 2020
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Abstract

Birds have been widely used to study spatial orientation. However, since different birds rely on different types of visual information to find goal locations (such as spatial information from free-standing objects or local cues, i.e. characteristics of a goal location like color and shape), it is important to investigate this aspect in each model species. The aim of the present study was to clarify whether domestic chicks, a ground-living bird and a widely used model for the comparative study of spatial orientation, are able to reorient in relation to free-standing objects and if they preferentially follow local or spatial cues. Furthermore, we also investigated whether monocular eye occlusion influences the ability of chicks to use spatial or local cues. Chicks were trained and tested in a large circular arena with free-standing objects providing relational spatial information, to find food in one of the feeders. We found that dark-incubated male chicks were able to reorient in relation to distinct, free-standing landmarks (Experiment 1), but when local and spatial cues were put in conflict, chicks significantly preferred local cues over spatial cues (Experiment 3). Moreover, while the use of one eye system only was not sufficient to orient by spatial cues (Experiment 2), the preference for local over spatial cues was independent of monocular occlusion (Experiment 4). The results are discussed in relation to our general knowledge of spatial information processing in domestic chicks.

Keywords Spatial orientation · Spatial cues · Local cues · Lateralization · Monocular eye occlusion · Domestic chicks (*Gallus gallus*)

Introduction

Bird species are often excellent travellers and have been widely used as animal models for studying spatial orientation (Jouventin and Weimerskirch 1990; Wallraff 2005; Egevang et al. 2010; Tommasi et al. 2012; Gagliardo 2013; Mayer et al. 2013, 2016; Wilschko and Wilschko 2017; Bingman 2018; Mouritsen 2018). To find the correct course when traveling long distances, birds use different types of information, such as the sun and star compasses, the Earth's magnetic field and the polarization pattern of the sky (Moore 1987; Ossenkopp and Barbeito 1978; Wilschko and Wilschko 2005). However, this information provides only the direction of the goal location and not its exact location. Small-scale navigation can be accomplished using geometrical information provided by the spatial arrangement of

objects and expanded surfaces surrounding the goal location to create a navigational map. The localization of the specific goal position can be based on the local cues associated with the goal location itself (such as its shape, color and texture), which can be used as a beacon for localization (review in Vallortigara 2009). The preference for using local or spatial cues for finding food locations varies across different bird species. For example, some food storing birds prefer to use spatial cues over local cues (Brodbeck 1994; Clayton and Krebs 1994a, b), whereas other non-storing birds, such as zebra finches (*Taeniopygia guttata*), use both strategies equally often (Mayer and Bischof 2012). However, this difference could also depend on the test conditions, since food storing birds, contrary to zebra finches, were tested in well-oriented environments, without being subject to disorientation procedures. Compared to local cues, the use of spatial cues provides more reliable information in a changing environment, where local cues could be displaced or covered (e.g. by leaves or snow). The preference of food hoarding birds to use spatial cues may thus be a result of adaptation (Brodbeck 1994; Brodbeck and Shettleworth 1995; Clayton

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and Krebs 1994a, b). On the contrary for other bird species, such as hummingbirds, it may be adaptive to rely preferentially on local cues over spatial cues, given their different foraging ecology (Hurly et al. 2014), despite being also tested in well-oriented environments. Thus, it is important to investigate the preferences for different types of information in each model species. This is especially true for tasks involving reorientation, which are commonly used in laboratory settings and may reveal the processes supporting the formation of a navigational map.

The domestic chick (*Gallus gallus*) has been frequently used to study spatial orientation, demonstrating chicks' abilities to find hidden food by a single beacon (Regolin et al. 1995), from arrays of local cues (Pecchia and Vallortigara 2010), by using egocentric information (Vallortigara 1996), distances (Vallortigara and Zanforlin 1986; Chiesa et al. 2006) or by using environmental geometry (Vallortigara et al. 1990; Chiandetti et al. 2007, 2015; Mayer et al. 2016, 2018). Also, view matching strategies has been proposed for this species (Dawkins and Woodington 2000; Pecchia and Vallortigara 2010, Pecchia et al. 2011; but see Lee et al. 2012). Relevantly, chicks are able to use relational information for orientation, as proven by their ability to find the centre of a rectangular enclosure in relation to the walls (Tommasi et al. 1997; Chiesa et al. 2006). Overall, environmental geometry can be considered a property that defines the position of a surface, line or point relative to the location of other objects or surfaces (Gallistel 1990). The ability of animals to use the shape ("geometry") of a small-scale environment is typically tested in a classical paradigm that was initially developed for rats (Cheng 1986) and later adopted for chicks (Vallortigara et al. 1990). This task involves a rectangular enclosure. Here, the initially disoriented animals learn to find a reward in one of the corners by using the global enclosure shape as a reference for their initial reorientation (recalibration of a spatial representation in reference to allocentric spatial information after a disruption of the egocentric reference system). In this test, the animals choose equally often the geometrically correct corner and the geometrically equivalent corner on the opposite side of the rectangular arena. Based on this finding, it has been proposed that animals possess a geometric module, which enables a representation of the overall shape of an environment and which can be used to find goal locations (Cheng 1986; Cheng et al. 2013, but see Sutton and Newcombe 2014). Although most of the spatial orientation studies in chicks were performed using this paradigm (Vallortigara et al. 2010), in this task it is difficult to disentangle the precise nature of the information used by the animals to orient (Duval 2019). At the same time, orientation in relation to distinct objects has not been well studied. However, in the natural habitat of a ground-living species such as domestic chickens, the availability of large surfaces is not guaranteed, thus making it vital for

chicks to be able to orient also in relation to distinct free-standing objects, such as trees, stones or other similar cues present in the environment. Orientation by free-standing objects has been studied in many bird species (e.g. pigeons: Legge et al. 2016; Spetch et al. 2003; Clark's nutcrackers: Kelly et al. 2010; European jays: Bennett 1993), but such tasks have never been adapted to chickens.

In domestic chicks, brain lateralization plays an important role for cognitive performance (see reviews: Vallortigara and Rogers 2005; Daisley et al. 2009; Rosa-Salva et al. 2012; Rogers et al. 2013). Not surprisingly, their spatial orientation behavior is also considered to be affected by functional lateralization (Vallortigara et al. 2010). Chicks' eyes are placed laterally, determining a wide monocular visual field. Moreover, the information coming from each eye stimulates mainly the contralateral brain hemisphere, since fibers almost completely decussate at the optic chiasm and the telencephalon lacks a corpus callosum serving as a bridge between hemispheres (Cowan et al. 1961). Therefore, monocular occlusion has been frequently used in chicks as an indirect measure of brain hemispheric specialization for a number of functions (Tolman 1948; Rogers 1996, 2008; Rosa-Salva et al. 2012; Manns and Ströckens 2014; Rogers and Vallortigara 2015). In chicks, asymmetries in the performance of social, spatial and object recognition tasks are influenced by light exposure during incubation of the eggs (Rogers and Bolden 1991; Rogers and Deng 1999; Rogers et al. 2013). During the late stages of egg incubation, light penetrating through the shell stimulates exclusively the right eye of the embryo, which faces the eggshell, while the left eye is occluded by the body, causing asymmetries of the visual pathways and of a number of behaviors (Johnston et al. 1997; Johnston and Rogers 1999; Andrew et al. 2004; Chiandetti et al. 2005; Dharmaretnam and Rogers 2005; Rogers 1990; Rogers and Bolden 1991; Rogers and Deng 1999; Rogers 2005, 2008; Rogers et al. 2013; Rugani et al. 2015). However, since some forms of lateralization do not depend on light exposure of the embryo, it is important to further investigate the presence of asymmetries also in dark-incubated chicks, for each given task (Deng and Rogers 2002; Rogers et al. 2004, 2013; Ocklenburg and Güntürkün 2012; Manns and Ströckens 2014; Mascetti and Vallortigara 2001).

Regarding spatial cognition, the general belief is that, in chicks like in humans, global information is predominantly processed by the right hemisphere (left eye system) and local information by the left hemisphere (right eye system) (Vallortigara 1996, 2000; Rogers and Andrew 2002; Chiesa et al. 2006). The contribution of the two hemispheres for orientation based on local or global information has been well studied, in tasks in which the global information was provided by the geometrical shape of the environment (Tommasi et al. 1997; Vallortigara et al. 2005; Chiesa et al. 2006; Sovrano and Vallortigara 2006). However, so far, no

lateralization studies done in chicks used tasks in which relational information for orientation was provided exclusively by distinct, free-standing objects. Only in two cases, distant relational cues were provided, located outside the arena (Chiandetti et al. 2005; Rashid and Andrew 1989). In the earlier of these works, it was found that male chicks (presumably light incubated, even though this was not specified in the paper) prefer to orient by spatial cues if the left eye is in use, while right-eye chicks use mainly local features to find the reward (Rashid and Andrew 1989). However, in this study it was unclear what kind of distant cues were present outside the arena, making it difficult to rule out that the shape of the experimental room might have played a role. In the study of Chiandetti et al. (2005), dark-incubated binocular and monocular chicks showed a strong preference to local over global cues, while this was reduced by embryonic light stimulation in chicks using the left eye system. While the approach of this study is highly commendable, not all aspects of the results are of straightforward interpretation. In particular, in this context it is worth noting that object-specific features were provided multiple times in the testing arena, which might have increased the probability that chicks would base their choices on this local information. Moreover, the test was carried out in a rectangular arena, which could have played a role for reorientation.

The aim of the current study was, thus, to systematically investigate the ability of dark-incubated chicks to orient in relation to free-standing objects and to locate the goal using local cues as a beacon. Concurrently, we also wanted to clarify the contribution of the two eye systems in these tasks. To do so we adapted for chicks an orientation task, similar to the one used in pigeons (Fremouw et al. 1997) and in our studies with zebra finches (for a review see: Mayer et al. 2013). However, in the current study, landmarks were placed inside the arena, which was surrounded by a curtain to eliminate external cues. In this task, chicks can reorient in relation to the position of three free-standing objects (spatial information) or they can directly locate the reward (baited feeder) based on its distinct features (local information). In fact, the most important conceptual point in the current context is that the presence of the free-standing objects provides exclusively relational information for orientation (e.g. the objects must not be located exactly in front of the goal location, acting as a beacon).

We performed four experiments: in experiment one we tested if chicks were able to orient only on the basis of the relational information provided by the free-standing objects. Experiment two investigated if, in dark-incubated chicks, orientation by free-standing objects was affected by monocular occlusion, which limited most of information processing to one of the eye systems. The third experiment assessed the preference of chicks to use local or spatial cues, when these two sources of information were in conflict, while

experiment four investigated if the choice to orient by conflicting local or spatial cues was influenced by monocular eye occlusion.

General materials and methods

Subjects

Fifty-one male domestic chicks (*Gallus gallus*) of the Aviagen ROSS 308 strain were used. Fertilized eggs were obtained from a commercial hatchery (Agricola Berica, Montegalda, VI, Italy). During incubation and hatching, eggs and chicks were maintained in complete darkness. After hatching chicks were housed individually in metal cages (28 cm wide × 32 cm high × 40 cm deep) with food and water available ad libitum, at a constant room temperature of 30–32 °C and a constant light–dark regime of 14 h light and 10 h dark. On each training day, chicks were transported to a heated room (28 °C) next to the experimental room, where they were placed individually in custom-made transportation cages (see below), which were also used to transport and to release the animal into the experimental arena, without directly manipulating them. All chicks were food deprived for 3 h before the training. During the training, chicks received mealworms as reward and water was available ad libitum. After the end of the training, chicks returned to their home cages in the animal house, where they remained with food and water ad libitum until the subsequent day of training. After the end of the experiments, all chicks were donated to local farmers. All experiments were carried out in accordance with the ethical guidelines current to European and Italian laws. The experiments and experimental procedures were licensed by the Ministero della Salute, Dipartimento Alimenti, Nutrizione e Sanità Pubblica Veterinaria (permit number 560/2018-PR).

Apparatus

The transportation cages (26 cm wide × 32 cm high × 40 cm deep) were made out of black polypropylene sheets (Poliplak®). Each cage was illuminated with LED lamps (16 W) positioned on their ceilings. One of the shorter walls contained a sliding door to allow the release of the animals into the arena without touching them. The experimental apparatus (Fig. 1) consisted of a large circular arena (270 cm diameter) surrounded by 30 cm high walls made of black polypropylene sheets. The floor was uniformly covered by black rubberized fabric, which was cleaned after each trial. The walls contained four entrances (12 cm wide × 14 cm high) at equal distances of 218 cm between each other (measured along the circumference). Every entrance was connected to a small

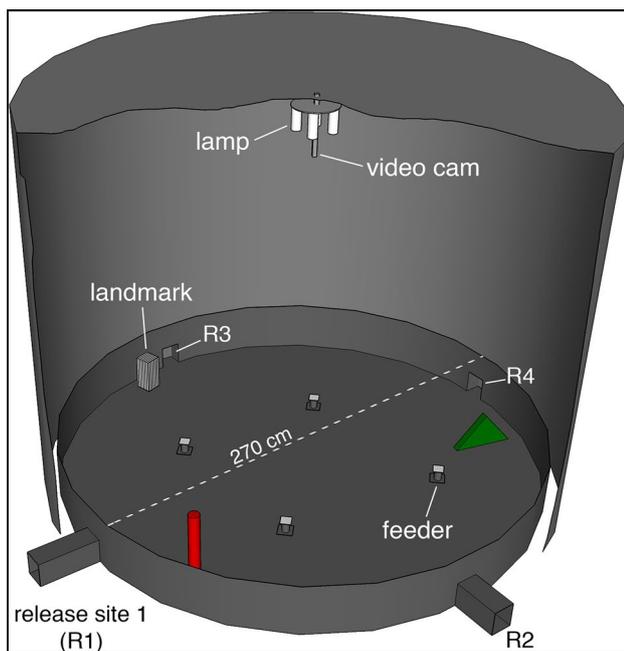


Fig. 1 Experimental setup: the circular arena with three spatial landmarks and four feeders. The chicks entered the arena from one of the releasing sites (R1, R2, R3, R4) and were trained to find a mealworm inside the rewarded feeder

corridor (12 cm wide \times 14 cm high \times 25 cm long) on the outer side, to which the individual transportation cages were attached. The arena was covered by a circular black tent (275 cm diameter, 220 cm high) to prevent chicks from seeing outside the arena. The setup was placed in a dark experimental room with constant temperature of 28 °C. Homogeneous illumination of the experimental arena was provided by four LED lamps (64 W) hanging at the centre inside the tent at 180 cm above the floor of the arena arranged in a square shape with 8 cm between the nearest neighbors. Between the four lamps, a camera (ELP USB camera module, 8 megapixel with a fisheye wide angle lens of 180°) was placed and connected to a computer outside the tent in the same experimental room, enabling the experimenter to score behavior online during the training and test. The visual landmarks inside the arena consisted of three differently shaped and distinguishably colored objects: a red cylinder (6 cm diameter, 35 cm high), a green triangle (34 cm long \times 20 cm high \times 4 cm wide) and a striped black–white box (20 cm high \times 9 cm wide). Each landmark was placed at a distance of 90 cm from the centre of the arena and 30 cm distance from the walls. The red cylinder was placed 20° on the left from the release site 1, the green triangle 20° on the right from the release site 3 and the striped black–white box was placed 20° on the left of the release site 4 (see Fig. 1).

Habituation training

All chicks underwent habituation training starting at post-hatching day 5 that aimed to familiarize the animals with the testing environment, to train them to enter the arena, to access a mealworm (*Tenebrio molitor* larvae) by pecking at a grey plastic sheet (4 \times 4 cm) that covered a feeder placed inside the arena and to return back to their transportation cage. The habituation training started 1 week after hatching and lasted for 2 days. Each chick performed four training sessions per day, with six trials per session. For each session the chick was transported to the experimental room inside its transportation cage, which was placed at one of the four entrances (randomized between the sessions). Once chicks became confident with the mealworms (administered directly in the plastic cages), they were attracted with a worm to enter and to explore the illuminated arena. After 2–5 min of exploration, the light in the experimental arena was turned off, whereas the light in the plastic cage was still on. In this situation, most of the subjects returned spontaneously to the illuminated cage; otherwise, they were attracted towards the cage with a mealworm. If needed, to further encourage the chicks to go back to their illuminated cage, the experimenter produced noise by clapping hands outside the arena, which encouraged them to escape in the opposite direction towards the illuminated cage. In the second session, each trial started by opening the sliding door allowing chicks to run towards a baited feeder placed in front of the entrance. One mealworm was placed on the feeder lid to encourage the chicks to peck on it, thus removing the lid and reaching another mealworm located inside the feeder. After all worms were found and eaten, the light in the arena was turned off and chicks returned back to the transportation cage that was still illuminated. In the third session, the worm on the top of the feeder was removed and chicks had to uncover the feeder to get the mealworm placed inside it. During each trial of the fourth session, the baited feeder was gradually moved towards the middle of the arena. During the additional four consolidation sessions, the baited feeder was always placed in the centre of the arena and in each trial the animal was released from a different entrance. By the end of the eighth session, each animal was reliably entering the arena when the sliding door was opened, it was eating the mealworm from the feeder in the centre of the arena and quickly coming back to the illuminated starting cage when the light in the arena was turned off.

Discrimination training

Discrimination training started 1 day after the habituation training. During this phase, chicks had to learn to recognise the baited feeder out of the four feeders present. Only the baited feeder could be opened and contained a mealworm.

In contrast, the non-baited feeders were made inaccessible to chicks. They did not contain a mealworm and were covered with a lid that was attached to them. The discrimination training continued for four training sessions per day, with six trials per session. In each trial the animal was released from a different entrance (disorientation). The trial ended when the subject found the mealworm (or if it was not able to find the correct feeder within 2 min, in which case the trial was considered invalid and repeated). Training continued until chicks reached a learning criterion of four correct out of six trials for two consecutive sessions (8/12, binomial test: $p < 0.003$).

Test session

Testing took place 1 h after the learning criterion had been reached and was composed of four trials lasting 2 min. each. In the first testing, trial chicks were released from release site 1 (R1) (see Fig. 1). At each of the following testing trials, chicks were released from the other entrances (R2, R3, R4), respectively. During the test all feeders were closed and did not contain any worms. Testing conditions are described in detail for each experiment. The test session was video recorded and analysed off-line.

Data analysis

The behavioural data were scored off-line from the videos of the test sessions. For each trial, four behavioural measures were scored: absolute first choice and its latency, cumulative first choices and total choices. Absolute first choice: for this measure the first feeder pecked or touched by the chick during the very first test trial was scored; only the first peck or touch performed during each trial was considered. Touching and pecking of feeders were both clearly visible on videos and easily scorable. The distribution of the absolute first choices for each feeder (i.e. the number of animals that chose it) was compared to chance level with a binomial test. To track paths followed by the animals during the test, we used the software Ethovision 3.1 (Noldus Information Technology, Leesburg, VA, USA; see also Noldus et al. 2001, Spink et al. 2001) on the video recordings. This provided the x and y coordinates of the animal positions over time. These coordinates were then plotted with Matlab (2018a). The tracks were overlaid with the background image of the arena in Adobe Illustrator (v.24), which was used for the schematic reconstruction of the arena and the alignments of the landmarks, feeders and releasing sites.

Cumulative first choices: for this variable the first choice of each trial was scored. Then the first choices for each feeder in all the four test trials were summed up, so that each of the four feeders could receive a score ranging from 0 (feeder never chosen first) to 4 (for a feeder that was chosen

first in all the 4 test trials). Total choices: for this measure the overall number of choices (pecks/touches) that the chick directed towards each of the feeders during the whole 2 min duration of the test trial was computed. The values scored for each trial were then summed to obtain the total value for the whole test session. For both these variables, a repeated measure ANOVA was employed to compare the choices obtained for the four different feeders, while comparisons between different feeders were conducted with paired sample t tests. All statistical analyses were performed with the software IBM SPSS Statistic for Windows (Version 22.0).

Experiment 1: spatial orientation

The aim of this first experiment was to investigate if chicks were able to orient in relation to free-standing objects.

Subjects and procedure

Ten domestic chicks were used for this experiment. During the discrimination training, four identical feeders were placed in the arena (Fig. 2a). Only one feeder, positioned between the ‘striped box’ and the ‘green triangle’ (position D, Fig. 2a), was covered with a removable lid and contained a mealworm as reward. Chicks were trained to find the rewarded feeder in relation to the landmarks, until they reached the learning criterion. At test, all the three free-standing objects were rotated by 90° counterclockwise and none of the feeders was rewarded. The aim of the test was to investigate whether chicks would reorient according to the new position of the landmarks, in which case they should choose the feeder placed between the ‘striped box’ and the ‘green triangle’, now at position A (Fig. 2b). On the contrary, if they used any other source of information they should have chosen the previously rewarded position D (Fig. 2b).

Results

During training, all ten chicks reached the learning criterion within 6.7 ± 0.9 sessions (mean \pm SEM, rounded numbers). In regard to the absolute first choice, during the first trial of the test after the landmark rotation, seven out of ten animals went first to the feeder at position A, which is the ‘new correct’ position relative to the landmarks. The preference for position A is significantly above chance level (binomial test: $p < 0.002$), whereas approaches to the other positions were not different from chance level: two animals went to position B ($p = 0.500$), none of the animals chose position C ($p = 0.072$) and only one animal went to the ‘old’ position D ($p = 0.232$). The latency to the first choice was on average 4.1 ± 0.3 s (mean \pm SEM, rounded numbers).

Experiment 1

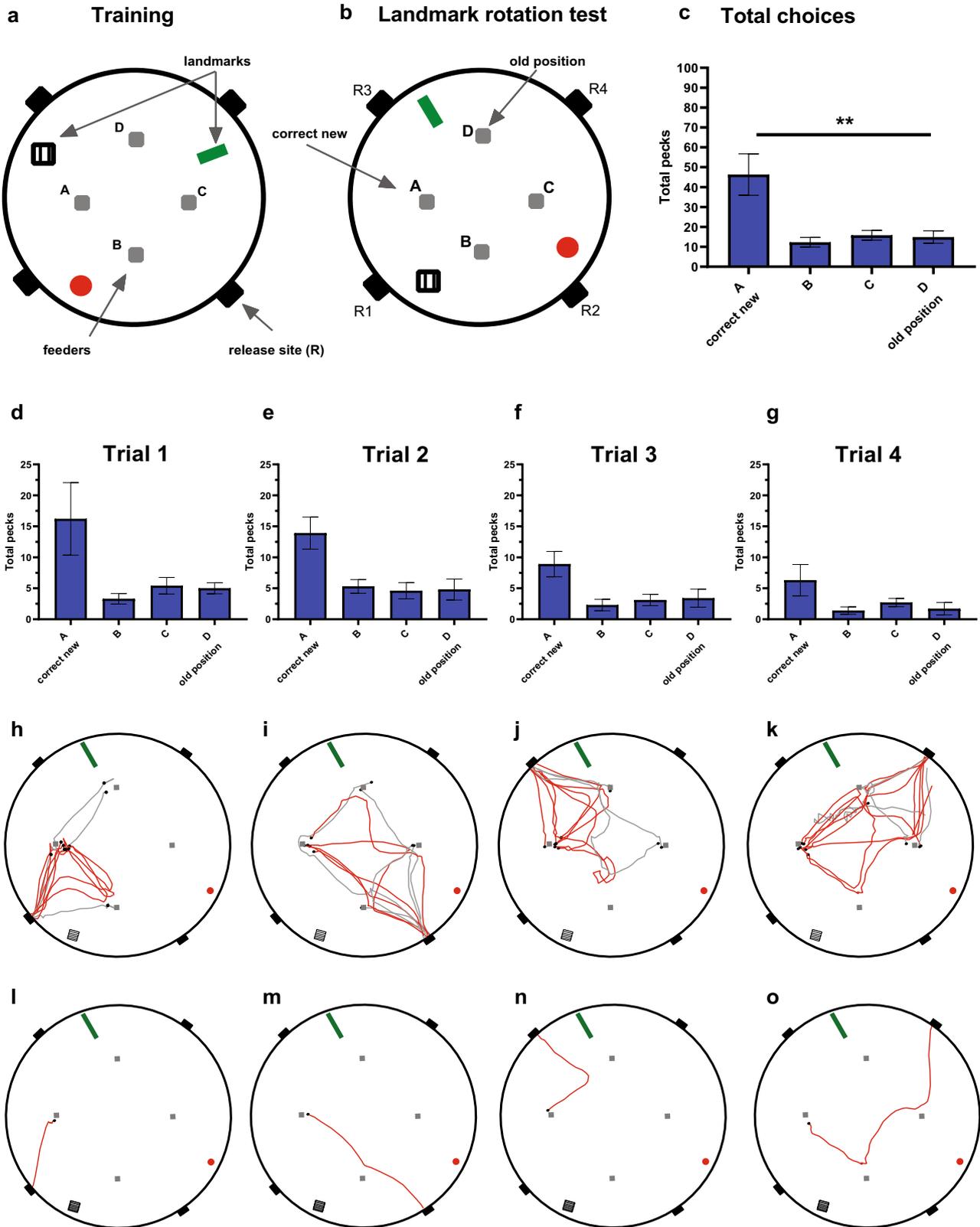


Fig. 2 Spatial orientation in binocular chicks (experiment 1). **a** Schematic representation of the arrangement of the landmarks during training. **b** At test the landmarks were rotated 90° counterclockwise. **c** Total number of pecks made during the four testing trials. **d–g** Total number of pecks for each testing trial. **h–k** Overlaid walking paths of all chicks until first choice was made (pecking position is marked as black dot). Paths are represented separately for each trial. The paths of chicks that chose the ‘correct new’ position are indicated in red, while the paths of chicks doing a wrong first choice are indicated in grey. **l, m** Example of paths of a single chick choosing the ‘correct new’ location in all trials, with no indication of view-matching behaviour (see general discussion). Bar plots show mean and sem. Asterisks (**) represent a significant difference ($p < 0.01$)

The analysis of the cumulative first choices made by the individuals during the four testing trials confirmed the preference for the feeder located at the ‘correct new’ position A (Table 1). A repeated measures ANOVA revealed a significant difference in the choices for the feeders at different positions ($F_{(3,27)} = 20.647; p < 0.001$). A paired samples *t* test revealed a significantly higher number of choices at the ‘new correct’ position A compared to the previously rewarded position D ($t_{(9)} = 5.438; p < 0.001$).

The chicks’ individual walking tracks until the first choice of each trial are represented in Fig. 2h–k. In all trials, chicks are initially attracted by the first feeder they see either on their left or on their right. However, without pecking on it, they correct their trajectory towards the correct feeder, on which most of them peck. Overall, the total number of choices per trial (Fig. 2d–g) shows that chicks decrease the number of pecks among trials, while the exploration is increased, leading to less direct tracks (Fig. 2h–k).

Finally, the significant preference for the feeder at position A was also confirmed by the analysis of the total choices emitted at the test (Fig. 2c; Table 1). A repeated measures ANOVA revealed a significant difference between the different positions ($F_{(1,170,10,529)} = 11.128; p = 0.006$. Greenhouse–Geisser corrected values are reported, since Mauchly’s test indicated that the assumption of sphericity had been violated, $W_{(5)} = 0.036, \epsilon = 0.390, p < 0.001$). A significantly higher number of choices was directed at the ‘new correct’ position A, compared to the previously rewarded position D ($t_{(9)} = 3.466; p = 0.007$; Fig. 2c).

Table 1 Values of the three dependent variables and the four test positions in Experiment 1

	Positions			
	A (correct new)	B	C	D (old position)
Absolute first choice	7	2	0	1
Cumulative first choices	2.7 ± 0.3	0.3 ± 0.5	0.6 ± 0.2	0.4 ± 0.2
Total choices	46.3 ± 10.4	12.3 ± 2.4	15.8 ± 2.5	14.9 ± 3.1

For the absolute first choice, the values represent the number of chicks emitting each choice. For the cumulative first choices and the total choices mean and SEM are reported

Discussion

In this first experiment, we found that chicks are able to learn the position of the rewarded feeder based only on the relational allocentric information that was provided by the location of the three landmarks inside the large arena. Chicks were able to reorient after the rotation of the landmarks and this was independent of the releasing site of the animal in the arena. Thus, chicks are able to use the spatial arrangement of the free-standing objects for reorientation, which requires a memorized representation of the configuration of the landmarks in the environment, acquired during the training session.

Experiment 2

The aim of this experiment was to investigate if monocular occlusion, limiting vision only to either the left or the right eye system, has an impact on spatial orientation in this task (orientation in relation to the position of free-standing objects inside a large arena).

Subjects and procedure

Eleven males were trained to discriminate the position of a baited feeder in relation to the position of the three landmarks until reaching the learning criterion, as described for Experiment 1 (Fig. 3a). However, in this second experiment, 1 h before the test, half of the chicks were right eye occluded and the other half was left eye occluded. The patch consisted of a white cone-shaped folded paper tape, applied gently on the eye of the chicks. The shape of the eye patch ensured that chicks could freely open and close the eyelid behind it. For the test, the three landmarks were rotated 90° clockwise (Fig. 3b) and the chicks were allowed to orient using either their left eye system (LES) or their right eye system (RES). After the test, the patch of each chick was removed and subjects were placed back in their home cages. On the following day, the same chicks underwent additional training until they reached again the learning criterion, after which they were tested again with the other eye occluded. Therefore, in this

Experiment 2

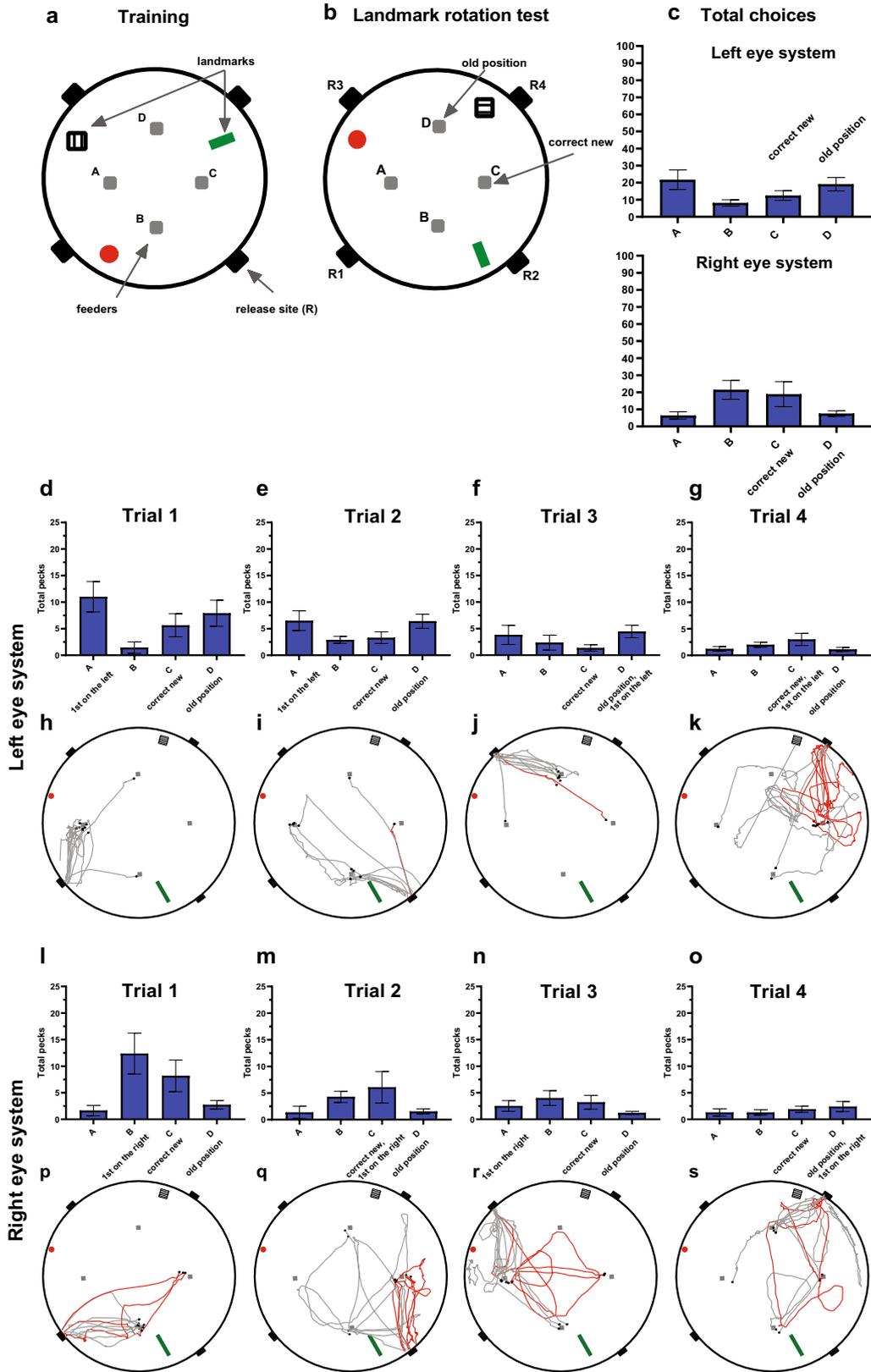


Fig. 3 Spatial orientation in monocular chicks (experiment 2). **a** Schematic representation of the arrangement of the landmarks during training. **b** At test the landmarks were rotated 90° clockwise. **c** Total number of pecks for the LES and RES conditions. **d–g** Total number of pecks for each testing trial in the LES condition. **h–k** LES chicks’ walking paths. **l–o** Total number of pecks for each testing trial in the RES condition. **p–s** RES chicks’ walking paths. The paths of chicks that chose the ‘correct new’ position are indicated in red, while the paths of chicks doing a wrong first choice are indicated in grey. Bar plots show mean and SEM

experiment each chick underwent two testing sessions (each session consisting of 4 trials), during which either their left or right eye was occluded. The order of the eye occlusion was counterbalanced between animals.

Results

All 11 chicks reached the learning criterion within 7.5 ± 0.9 sessions. During the first trial of the test, monocularly occluded chicks did not show any significant preference for the feeder at the new “spatially correct” position C. Instead, the absolute first choice of chicks using their left eye system (LES) showed a significant preference for position A, which was the first feeder the animals encountered on their left in that trial. Overall, 9 out of 11 animals went to position A (binominal test: $p < 0.001$). None of the animals went to the ‘new correct’ position C ($p = 0.058$), one animal went to position B ($p = 0.19$) and one to position

D ($p = 0.19$). Similar results were provided by the chicks using their right eye system (RES). During their absolute first choice, 8 out of 11 animals of the RES condition went to the feeder at position B, the first feeder they could see on their right ($p < 0.001$). Only three animals went to the ‘new correct’ position C, which was thus not chosen above chance level ($p = 0.431$). The feeders at positions A ($p = 0.058$) and D ($p = 0.058$) were not chosen by any of the animals. The latency to the first choice of the chicks in the LES condition was 16.1 ± 3.5 s and in the RES condition 7.5 ± 2.3 s. A paired *t* test comparison revealed a non-significant trend for a difference between the two conditions ($t_{(10)} = 2.122$; $p = 0.060$). On average (11.8 ± 2.2), the monocular chicks in this experiment needed significantly more time to approach the first feeder compared to the non-occluded chicks of experiment 1 ($t_{(19)} = 3.2726$; $p = 0.004$).

Likewise, the cumulative first choices did not show any significant preference for the feeder at the new “spatially correct” position C (Table 2). In both occlusion conditions, chicks preferred the first feeder they saw with their non-occluded eye. A repeated measures ANOVA revealed a significant interaction between two within-subject factors, eye occlusion and position ($F_{(3,30)} = 4.927$; $p = 0.007$), indicating that the eye occlusion had an effect on the cumulative choices for the feeders at the four positions. No main effects of the factors position ($F_{(3,30)} = 0.678$; $p = 0.433$) and eye occlusion ($F_{(1,10)} = 0.313$; $p = 0.588$) were present. Also in this case, neither chicks tested in the LES or in the RES

Table 2 Values of the three dependent variables and the four test positions in Experiment 2

	Positions			
	A	B	C (correct new)	D (old position)
Left eye system				
Absolute first choice	9	1	0	1
Cumulative first choices	1.3 ± 0.2	0.8 ± 0.2	0.6 ± 0.2	1.0 ± 0.1
Total choices	21.7 ± 5.8	8.1 ± 1.8	12.5 ± 2.8	19.1 ± 3.9
Right eye system				
Absolute first choice	0	8	3	0
Cumulative first choices	0.5 ± 0.16	1.6 ± 0.3	1.3 ± 0.3	0.6 ± 0.2
Total choices	6.5 ± 2.1	21.5 ± 5.5	18.9 ± 7.3	7.6 ± 1.6
Restructured data, left eye system				
	Feeder L (1st on the left)	Feeder R	Feeder III	Feeder IV
Cumulative first choices	2.5 ± 0.2	0.3 ± 0.1	0.3 ± 0.1	0.7 ± 0.2
Total choices	19.8 ± 4.0	9.2 ± 2	14.8 ± 2.7	16.8 ± 2.6
Restructured data, right eye system				
	Feeder L	Feeder R (1st on the right)	Feeder III	Feeder IV
Cumulative first choices	0.4 ± 0.2	2.2 ± 0.4	0.7 ± 0.2	0.5 ± 0.3
Total choices	9.7 ± 2.2	22.9 ± 4.4	14.5 ± 3.5	8.2 ± 2.3

Data are presented separately for the RES and LES conditions. In the lower half of the table, the data are restructured based on the position of the feeders with respect to the chick (see results)

conditions revealed any preference for the ‘new correct’ position C compared to the ‘old’ position D (paired samples t test: LES $t_{(10)} = -1.305$; $p = 0.221$; RES $t_{(10)} = 1.698$; $p = 0.120$).

Likewise, the individual walking tracks until the first choice do not show any preference for the correct feeder at the new position A. Instead, in all trials chicks of both LES and RES conditions tend to choose first the feeder they see with their non-occluded eye (see Fig. 3h–k for LES and Fig. 3p–s for the RES conditions). Moreover, as in experiment 1, chicks of both conditions increased exploration in later trials, while the number of total pecks decreased (LES: Fig. 3d–g; RES: Fig. 3l–o).

A further analysis was then run, to account for the tendency of the chicks to approach the first feeder on the side of the non-occluded eye (this depended also on the releasing site used in each trial). To do so, the data were restructured and the feeders were assigned to different labels. The two feeders closer to the animals were called ‘feeder L’ = first on the left and ‘feeder R’ = feeder on the right. The remaining two feeders were called ‘feeder III’ and ‘feeder IV’, counterclockwise. Thus, in the LES condition chicks saw first the ‘feeder L’ with their left eye and in the RES condition chicks saw first the ‘feeder R’ with their right eye. A repeated measures ANOVA with two between-subjects factors (feeder and eye occlusion) was run on these data (Table 2, restructured data). This revealed a significant effect of the feeder ($F_{(3,30)} = 5.244$; $p = 0.005$) and a significant interaction of the two factors ($F_{(3,30)} = 24.242$; $p < 0.001$). Thus eye occlusion had an effect on the feeder preferences. No significant main effect of eye occlusion was found ($F_{(1,10)} = 0.313$; $p = 0.588$). Indeed, in the LES condition, chicks’ preference for the feeder L was significantly higher compared to feeder R (paired samples t test: $t_{(10)} = 9.639$; $p < 0.001$) and in the RES condition they preferred the feeder R compared to feeder L ($t_{(10)} = -4.100$; $p = 0.002$).

Finally, the analysis of the total number of choices confirmed the lack of preference for the spatially correct position C. Again, eye occlusion had a significant effect on chicks’ preferences for the different feeders (Fig. 3c, Table 2). A repeated measures ANOVA (within-subjects factors: eye occlusion and position) revealed a significant interaction of the two factors ($F_{(3,30)} = 8.372$; $p < 0.001$), but no significant main effect of position ($F_{(3,30)} = 0.080$; $p = 0.970$) or eye occlusion ($F_{(1,10)} = 0.403$; $p = 0.540$). In both eye occlusion conditions, there was no difference in the preference for the ‘new correct’ position C compared to the ‘old’ position D (LES: $t_{(10)} = -1.673$; $p = 0.125$; RES: $t_{(10)} = 1.625$; $p = 0.135$).

In sum, independently of which eye was occluded, chicks were not able to find the correct position in relation to the landmarks. However, the left and right eye occlusion had

an impact on chicks’ preferences for the feeders at different positions. Therefore, this data (total number of choices) was also re-analysed, after being restructured as described above (Table 2, restructured data). The repeated measures ANOVA revealed a significant interaction of eye occlusion and position ($F_{(3,30)} = 9.278$; $p < 0.001$), meaning that the eye occlusion had an effect on the feeder preferences. There were no significant main effects of eye occlusion ($F_{(1,10)} = 0.216$; $p = 0.652$) or position ($F_{(3,30)} = 0.918$; $p = 0.444$). While chicks in the LES condition showed a non-significant trend towards the feeder L compared to feeder R ($t_{(10)} = 2.172$; $p = 0.055$), in the RES condition they significantly preferred the feeder R ($t_{(10)} = -3.216$; $p = 0.009$).

Discussion

With this second experiment, we found that visual input from both eyes was needed for spatial orientation in the present task. Monocularly occluded, dark-incubated male chicks were not able to reorient in relation to the free-standing objects in the large arena, regardless of which eye was occluded. Instead, at the beginning of each trial chicks went first to the first feeder they saw with the non-occluded eye. Also taking into account the whole test duration, we did not obtain any evidence of a preference for the spatially correct location, despite the fact that chicks explored all of the feeders.

Experiment 3: spatial vs. local

The aim of the third experiment was to investigate whether domestic chicks search for a goal location preferentially by local or spatial cues, if the two types of information are put into conflict.

Subjects and procedure

Eleven chicks were trained to discriminate a rewarded feeder. During training, the reinforced feeder was placed always at position D (between the ‘striped box’ and the ‘green triangle’) and was marked by distinguishable local features. The rewarded feeder had a white stripe (2 cm wide paper ring in the middle of the black feeder) and it was covered with a black and white striped lid. In contrast, the other three feeders were uniformly black and they were covered with a checked lid (Fig. 4a). For the test session, spatial and local cues were put in conflict by displacing the distinguishable “striped” feeder from position D to position B (Fig. 4b). If the animals follow local cues, they would peck at the “striped” feeder at the new position B, whereas if they oriented by spatial cues (i.e. in relation to the free-standing objects), they should choose the feeder at position D.

Experiment 3

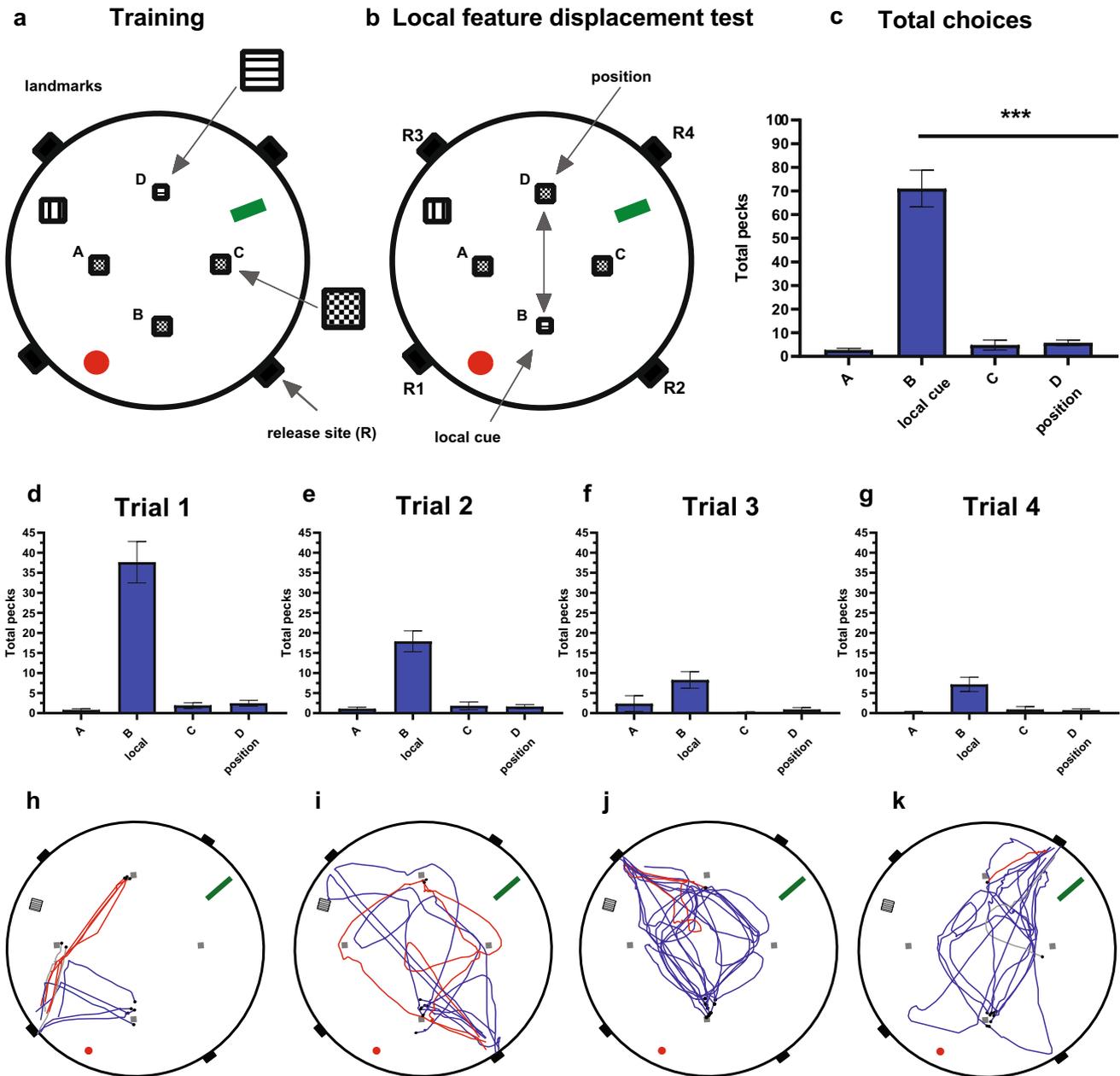


Fig. 4 Use of spatial vs. local cues in binocular chicks (experiments 3). **a** Schematic representation of the local cue position during training. **b** At test the local feature was displaced from position D to position B. **c** Total number of pecks. **d–g** Total number of pecks for each testing trial. **h–k** Chicks’ walking paths. The paths of chicks that

chose the ‘correct new’ position are indicated in red, of those that chose the local feature in blue and the paths of chicks doing a wrong first choice in grey. Bar plots show mean and sem. Asterisks (***) represent a significant difference ($p < 0.001$)

Results

All 11 chicks reached the learning criterion within 6.7 ± 0.4 sessions. At test, five animals went first to the locally distinguishable “striped” feeder at the new position B, showing a non-significant trend for choosing this feeder above

chance level ($p = 0.08$). The other four animals went to the previously rewarded, spatially correct position D, which was not chosen more than expected by chance ($p = 0.172$). Only two animals went to position A, never rewarded at training ($p = 0.258$), while none of the chicks went to position C, also never rewarded ($p = 0.042$, below chance level).

Table 3 Values of the three dependent variables and the four test positions in Experiment 3

	Positions			
	A	B (local cue)	C	D (position)
Absolute first choice	2	5	0	4
Cumulative first choices	0.3±0.1	2.8±0.4	0.1±0.1	0.8±0.2
Total choices	2.7±0.7	71.0±7.8	4.8±2.1	5.7±1.2

The average latency to the first choice of the chicks was 6.3 ± 1 s.

Clearer evidence of a preference for the “striped” feeder at the new position B was obtained for the cumulative first choices (Table 3). A repeated measures ANOVA revealed a significant difference in the choices for the different feeders ($F_{(1.330,13.303)} = 23.089$; $p < 0.001$, Greenhouse–Geisser corrected values are reported, since Mauchly’s test indicated that the assumption of sphericity had been violated, $W_{(5)} = 0.056$, $\epsilon = 0.443$, $p < 0.001$). A paired samples t test revealed a significant preference for the feeder with the previously rewarded local features at the new position B, compared to that at the spatially correct position D ($t_{(10)} = 3.597$; $p = 0.005$).

Qualitative investigation of the walking tracks to the first choice of the first trial revealed three different profiles of correct choices (Fig. 4h). Some chicks went directly to the spatially correct position, while others to the local feature. Chicks of the third type initially went towards the correct position and then changed their trajectory towards the local feature, which they approached and pecked. This profile disappears, however, in the later trials (Fig. 4i–k). Likewise, if all the choices emitted during the full 2 min of the trial are analysed, it is clear that in each trial chicks show a clear preference for the local feature (Fig. 4d). As in the other experiments, in later trials all chicks explored more (Fig. 4 h, j, k) and pecked less (Fig. 4d–g).

The total choices showed a significant preference for the local feature at the new position B (Fig. 4c, Table 3). A repeated measures ANOVA revealed a significant difference in the choices for the different feeders ($F_{(1.121, 11.210)} = 62.522$; $p < 0.001$, Greenhouse–Geisser corrected values are reported, since Mauchly’s test indicated that the assumption of sphericity had been violated, $W_{(5)} = 0.012$, $\epsilon = 0.374$, $p < 0.001$). The preference for following local features was also confirmed by the higher number of choices for the striped feeder at the new position B compared to the feeder at the spatially correct position D ($t_{(10)} = 8.017$; $p < 0.001$).

Discussion

In this third experiment, in a situation of choice, chicks preferred to use local features for finding the goal. The locally correct feeder was chosen significantly more often than the feeder located at the previously rewarded spatial position. However, in their first choices, less than half of the chicks went to the local feature at a new location, whereas a nearly equal number of chicks went to the previously rewarded spatially correct position. This suggests that at least some of the chicks might have learnt both strategies and used relational spatial information to direct their first choices. Nevertheless, if more time was given for exploration, chicks significantly preferred to use local cues over spatial cues, showing that local cues are more relevant for chicks in this task.

Experiment 4

The aim of this last experiment was to investigate if the tendency of chicks to locate the baited feeder predominantly by local cues, when spatial and local cues are put in conflict, is influenced by monocular eye occlusion.

Subjects and procedure

Seventeen chicks were trained and tested exactly in the same way as in experiment 3 (Fig. 5a, b), with the only exception that 1 h before the test, chicks were randomly assigned to two experimental groups and monocular occluded (RES group: $n = 9$, LES group: $n = 8$). We decided to use two different groups instead of testing the same animals twice (as we did in Experiment 2). This was because the results of Experiment 3 revealed that our test chicks prefer to find the goal based on local features rather than by spatial information. Multiple testing of the same individuals would thus compromise the conflict test, which requires that left- and right-eye-occluded chicks have a balanced experience with spatial and local information. By using two independent groups we avoided this confounding. As in Experiment 2, the animals were allowed to habituate to monocular occlusion for 1 h before the test was performed. For the test session, spatial and local cues were put in conflict by displacing the distinguishable “striped” feeder from position D to position B. This allowed to verify if the monocular occluded chicks would prefer to use local over spatial cues.

Results

All 17 chicks reached the learning criterion within 5.2 ± 0.4 sessions. During the first trial of the test, the LES group did not reveal any preference either for the locally distinguishable “striped” feeder at the new position

B or for the one at the previously rewarded, spatially correct, position D. The analysis of the absolute first choices revealed that four LES chicks went first to the feeder at position A, the first they encountered on the side of their non-occluded eye ($p = 0.087$). Of the remaining LES animals, two went to the locally distinguishable feeder at the new position B ($p = 0.5$) and two to the spatially correct position D ($p = 0.5$), while none of the chicks went to position C ($p = 0.11$). On the contrary, eight chicks in the RES group went first to the locally distinguishable feeder at the new position B (binomial test: $p < 0.001$). However, this was also the first feeder that the animals encountered on the side of their non-occluded right eye, during the first trial of the test. Only one RES chick went to the never rewarded position C ($p = 0.282$), while none of the chicks chose the spatially correct position D ($p = 0.089$) or the never rewarded position A ($p = 0.089$). The latency to the first choice of the chicks in the LES group was 15.9 ± 2.7 s and in the RES group 19.7 ± 6.9 s, with no significant difference between the two groups ($t_{(10,324)} = -0.514$; $p = 0.618$). Monocular chicks ($n = 17$, 17.9 ± 3.8) needed significantly more time to approach the first feeder compared to the non-occluded chicks from experiment 3 ($t_{(26)} = 2.4280$; $p = 0.022$).

The ANOVA on cumulative first choices did not reveal any interaction of the between-subject factor eye occlusion and the within-subject factor position ($F_{(3,45)} = 0.586$; $p = 0.627$) or any effect of the factor eye occlusion ($F_{(1,15)} = 0.126$; $p = 0.728$). However, there was a significant main effect of position ($F_{(3,45)} = 46.861$; $p < 0.001$). Since the two treatment groups (LES and RES) did not differ in their feeder preferences (see also Table 4), for post hoc analyses of the cumulative first choices, the LES and RES groups were combined (position A: 0.35 ± 0.1 ; position B: 2.6 ± 0.2 ; position C: 0.3 ± 0.1 ; position D: 0.5 ± 0.1). This analysis confirmed the preference for the local features: a higher number of cumulative first choices went to the feeder with distinguishable local feature at the new position B than to the feeder in the spatially correct position D ($t_{(16)} = 7.164$; $p < 0.001$, Fig. 5c).

The walking trajectories to the first choice (LES: Fig. 5i–k; RES: Fig. 5p–s) reveal that also, in this experiment, chicks showed an initial tendency to walk towards the first feeder they saw with their non-occluded eye. However, contrary to experiment 2 their behaviour was affected by the presence of the local feature. If the first feeder they saw did not present the correct local feature, most of the chicks started to explore the arena until they found the striped feeder. In fact, there were even three animals that were seemingly attracted by the black and white striped landmark visible on the side of their non-occluded eye (Fig. 5h). This landmark presented a similar pattern as the feature of the local feeder, which was also composed of black and white

stripes. As in all the other experiments, chicks of both groups increased their exploration among trials and decreased the total pecks (LES: Fig. 5d–g; RES: Fig. 5l–o).

Also, the total choices did not reveal any significant interaction between the position and eye occlusion, indicating that the two groups did not differ in their preference for the various feeders ($F_{(3,45)} = 0.710$; $p = 0.551$). Also, no effect of the factor eye occlusion ($F_{(1,15)} = 0.140$; $p = 0.713$) was found. However, there was a significant main effect of position ($F_{(1,184,17,761)} = 77.814$; $p < 0.001$, Greenhouse–Geisser corrected values are reported, since Mauchly’s test indicated that the assumption of sphericity had been violated, $W_{(5)} = 0.026$, $\epsilon = 0.395$, $p < 0.001$). For post hoc analyses of the total choices, the LES and RES groups (see Table 4 for the segregated data and Fig. 5d–g, l–o, for segregated data trial by trial) were combined (position A: 4.4 ± 1.5 ; position B: 54.1 ± 5.3 ; position C: 4.8 ± 1.3 ; position D: 3.1 ± 0.7 , see Fig. 5c). The preference for the feeder marked by the distinguishable local features was confirmed by the higher number of choices for the “striped” feeder at the new position B compared to the feeder at the spatially correct position D ($t_{(16)} = 9.465$; $p < 0.001$).

Discussion

In this last experiment, chicks using either only their right or only their left eye system were equally able to use distinguishable local features to find the goal. Regardless of which eye was occluded, chicks of both groups chose the feeder marked by the previously rewarded pattern. This indicates that one eye system is enough to process local information. Interestingly, contrary to what was the case for Experiment 2, in this last experiment we did not find a clear bias in favour of the first feeder seen by the non-occluded eye (with a possible exception of the absolute first choice of RES chicks). Thus, the availability of local information for orientation was enough to override the tendency to choose the first feeder encountered on the side of the seeing eye.

General discussion

In the present study, we performed four experiments testing the orientation abilities of dark-incubated male domestic chicks in a large circular arena. In the first experiment chicks were able to orient on the basis of relational information provided by free-standing objects inside the arena. However, in the second experiment, monocular occlusion had a dramatic impact on this spatial orientation ability. Regardless of which eye was occluded, chicks did not reorient in relation to the free-standing objects, but instead chose the first feeder they saw with the non-occluded eye. The third experiment

Experiment 4

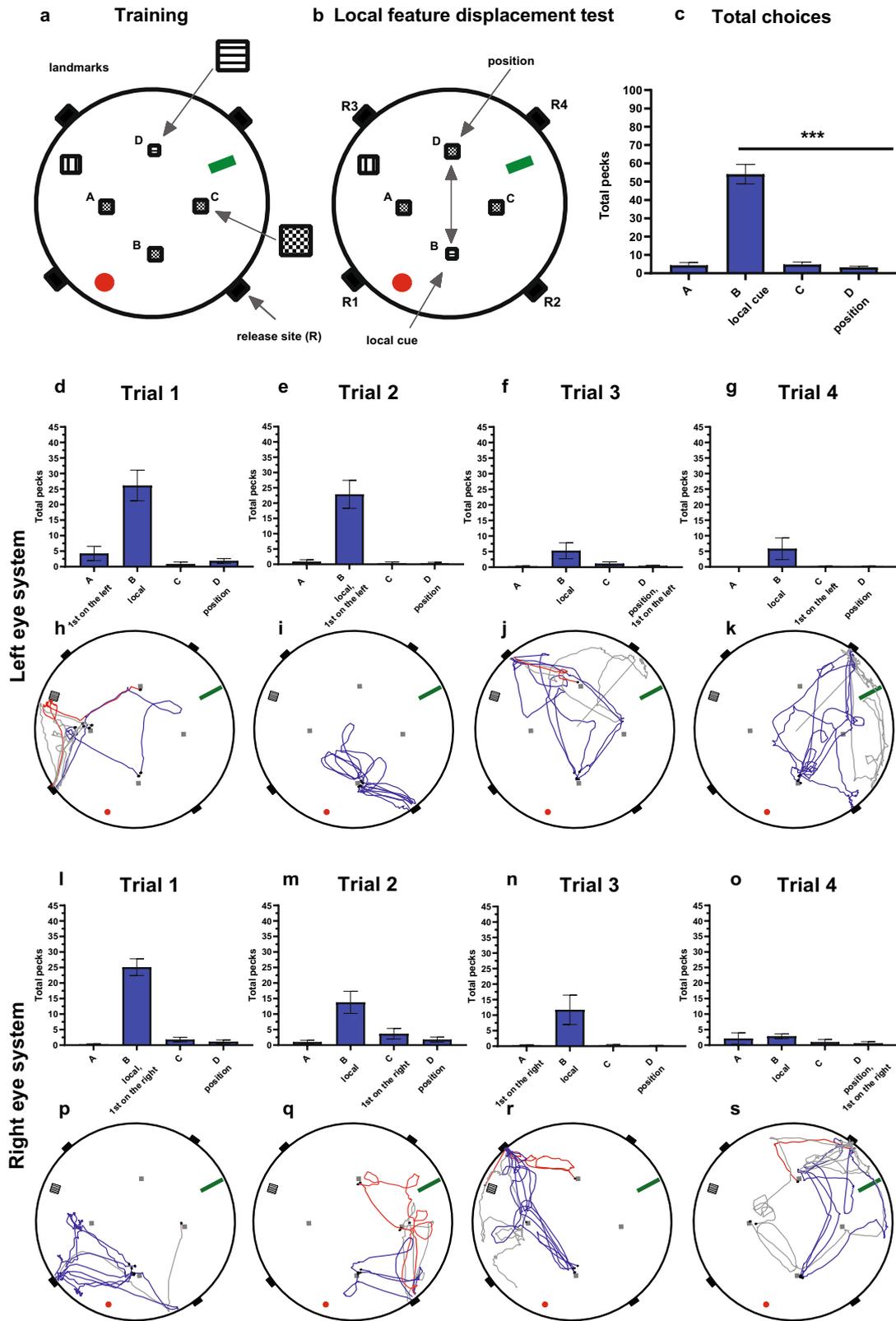


Fig. 5 Use of spatial vs. local cues in monocular chicks (experiment 4). **a** Schematic representation of the local cue position during training. **b** At test the local feature was displaced from position D to position B. **c** Total number of pecks. **d–g** Total number of pecks for each testing trial in the LES condition. **h–k** LES chicks’ walking paths. **l–o** Total number of pecks for each testing trial in the RES condition. **p–s** RES chicks’ walking paths. The paths of chicks that chose the ‘correct new’ position are indicated in red, of those that chose the local feature in blue and the paths of chicks doing a wrong first choice in grey. Bar plots show mean and sem. Asterisks (***) represent a significant difference ($p < 0.001$)

Table 4 Values of the three dependent variables and the four test positions in Experiment 4

	Positions			
	A	B (local cue)	C	D (position)
Left eye system ($n=8$)				
Absolute first choice	4	2	0	2
Cumulative first choices	0.5 ± 0.2	2.6 ± 0.3	0.1 ± 0.1	0.5 ± 0.2
Total choices	5.4 ± 2.8	58 ± 10	2.8 ± 1.2	2.6 ± 0.8
Right eye system ($n=9$)				
Absolute first choice	0	8	1	0
Cumulative first choices	0.2 ± 0.2	2.6 ± 0.3	0.4 ± 0.2	0.4 ± 0.2
Total choices	3.4 ± 1.5	50.6 ± 5.3	6.6 ± 2.2	3.6 ± 1.1

Data are presented separately for the RES and LES conditions

revealed that, in the present task, local cues were more relevant for chicks when spatial and local cues were in conflict. Finally, with the last experiment we found that the preferential use of local cues was not influenced by monocular eye occlusion, indicating that both eye systems were equally able to process local information.

In the landmark rotation test of our first experiment, chicks clearly used the three distinct free-standing objects for reorientation. Independently of where they were released in the arena, they were able to find the correct location. This orientation ability requires a memorized representation of some crucial information provided by the layout of the three landmarks, acquired during the training sessions. Such a mental representation can be referred to as a ‘cognitive map’. The concept of ‘cognitive map’ was introduced by Tolman (1948) and has been a source of extensive debates in later literature (Shettleworth 2010). Although ‘cognitive map’ means different things to different people, it can be broadly defined as ‘... any orientation based on implicitly computing distances and directions is evidence of a cognitive map.’ (Gallistel 1990). Under this definition, the learnt information provided by the three landmarks that chicks used for orientation in our experiment can be referred to as

forming a ‘cognitive map’. More specifically, in the current task chicks had to rely on relational information. For example, they could have encoded the food location in relation to two or more conspicuous landmarks (e.g. the baited feeder was positioned between the striped black–white box and the green triangle). This would be in line with evidence that chicks are able to use relational information to find encoded locations, such as the centre of a square-shaped arena (Tommasi et al. 1997). However, chicks are also able to encode locations based on absolute and relative distances (Tommasi and Vallortigara 2000). Indeed, one could argue that in the present study it would be enough to encode the distance between one landmark and the correct feeder, following the ‘standard model’ suggested for pigeon navigation in small-scale environments (Cheng et al. 2006). However, the use of absolute distance is unlikely in our experiments, since it would require the animals to approach one landmark and then to walk a memorized distance to the feeder. Such behaviour has been described in bees (Collett and Rees 1997). However, we did not observe it with chicks. Instead, most of the chicks were walking almost directly to the correct feeder, independent of the release site from which they entered the arena. Some other chicks were initially attracted by one of the feeders either on their left or on their right of the release site. However, from there these chicks were also going directly towards the spatially correct feeder without approaching any of the landmarks (Fig. 2h–k). This means that if they used distances for orientation, they estimated them directly from visual input, in line with the vector sum model proposed in pigeons (Cheng 1988, 1989, 1990). This is associated with an additional complication: the size of the retinal projection of the distance between two objects depends on how far they are from the animal. Thus, to reliably estimate the distance between the landmark and the feeder, chicks would need to compute relative distances, taking into account also their own position. This is not unlikely, since the ability to use relative distances has been demonstrated in chicks (Tommasi and Vallortigara 2000) and also in other birds (Gray et al. 2004; Gray and Spetch 2006; Kelly et al. 2008, 2010). However, for the interpretation of our results, this means that chicks had in any case to rely on relational information to find the correct feeder: either by using relative distances or the relative position of the feeder between the free-standing objects. It is quite possible that both orientation strategies are based on the same mechanism, for which the hippocampus is likely to play a vital role (Mayer et al. 2013, 2010; Mayer and Bischof 2012; Watanabe et al. 2008). This suggests the importance of investigating the involvement of the chick’s hippocampus in encoding relative distances and locations in future studies.

An alternative explanation of how chicks could have used the three landmarks to orient in our experiment is by using a template matching between the currently perceived

visual scene and a ‘snapshot’ memory of the same. Template matching strategies have been initially proposed for invertebrates (Cartwright and Collett 1983; Durier et al. 2003; Wehner et al. 1996; Zeil 1993; Collett et al. 1992; Collett 1995). The first similar evidence in a bird species has been found in chickens (Dawkins and Waddington 2000). In later studies, view-based strategies have been proposed also for reorientation in a rectangular array of landmarks in domestic chicks (Pecchia and Vallortigara 2010), pigeons (Pecchia et al. 2011) and hummingbirds (Pritchard and Healy 2018; Pritchard et al. 2018). However, in contrast to these findings, at least reorientation by layout geometry in rectangular-shaped environments has been found not to be based on image matching in domestic chicks and in children (Lee and Spelke 2011; Lee et al. 2012). In line with that, we could not see any evidence in chicks’ paths that single individuals released from different sites tried to match the visual scene to a specific view before performing their choice (see Fig. 2d–g for an example of the tracks followed by a single chick). However, we cannot exclude that chicks might have learnt multiple view-based strategies, to reach the goal from multiple directions, as it has been proposed for invertebrates (Graham et al. 2010). Therefore, the potential use of view-based strategies in our experimental setup requires further investigations. For example, in future studies chicks could be trained by being released in the arena from only three sites and tested from the forth, unfamiliar, release site.

Previous studies with monocular occlusion indicated that, in chicks, place learning is predominantly processed by the left eye system, and thus presumably by the right hemisphere (Rashid and Andrew 1989; Tommasi and Vallortigara 2000, 2004). Similar asymmetries have been reported also for marsh tits, blue tits, jays and jackdaws (Clayton and Krebs 1994a, b). Moreover, it has been reported that right-eyed chicks mainly attend to absolute distances, whereas left-eyed chicks mainly attended to relative distances (Tommasi and Vallortigara 2000, 2001). Remarkably, in the present study we did not find a similar effect of eye occlusion. Neither the left-eye-occluded nor the right-eye-occluded chicks chose the feeder in the correct relative spatial position. These results suggest that the visual input from both eyes was needed to retrieve spatial locations in relation to the landmarks. However, these seemingly contradicting findings can be explained considering the lack of embryonic light stimulation in our study. In chicks, the development of structural and behavioural asymmetries is strongly influenced by embryonic light stimulation. Even during binocular vision, cognitive performance of dark-incubated chicks can be different from that of light-incubated chicks (Daisley et al. 2010). The studies on spatial orientation mentioned above used chicks that were hatched at local commercial hatcheries (Rashid and Andrew 1989; Tommasi and Vallortigara 2000, 2001,

2004), which normally do not control for light exposure. It is thus likely that the eggs were exposed to light during the critical time period, inducing stronger asymmetries compared to the well-controlled dark-incubated chicks employed for the present study. Indeed, there are hints in the literature suggesting that, in chicks, embryonic light stimulation is crucial for the development of the left-eye-system advantage for spatial orientation. For instance, as regard the chicks tested monocularly in the study of Chiandetti et al. (2005), only light-incubated chicks using the left eye system were attentive to the global cues. On the contrary, dark-incubated chicks tested in monocular vision conditions neglected the spatial cues regardless of the eye in use. Our results are in line with the results of Chiandetti et al. (2005) and confirm that dark-incubated male chicks tested in conditions of monocular vision tend to neglect the allocentric environment for orientation. It is also worth mentioning that, during the binocular training, the chicks used in the second experiment had already successfully learnt the correct spatial location of the rewarded feeder. So, these individuals were able to orient by spatial cues, if information from both eyes was available. Thus, we can conclude that monocular eye occlusion significantly affects the spatial orientation abilities of dark-incubated male chicks and that information from both eyes is needed for this task.

To further assess how eye occlusion influenced chicks’ behaviour, we compared the latency of first approach between experiments involving monocular testing and their binocular counterparts. Chicks were significantly slower in the two monocular experiments. This might be interpreted as an indication that the novel challenge that chicks had to face, due to the reduction of their visual field, created a sufficient disturbance to prevent us from observing lateralization effects. However, we believe this to be unlikely because multiple previous studies (e.g. Rashid and Andrew 1991; Tommasi and Vallortigara 2000; Chiandetti et al. 2005, in the field of spatial cognition) used a similar procedure to successfully reveal functional lateralization.

Interestingly, in the second experiment chicks chose the first feeder they saw with their non-occluded eye. A similar tendency has already been reported in the literature for monocularly occluded chicks (Rugani et al. 2011, 2016). It is quite possible that by seeing only half of the global scene, chicks’ attention is more easily attracted by the first conspicuous local feature that appears in their visual field, one of the feeders in this case. Indeed, monocular occlusion should cause greater mismatch of the current view with respect to the information memorised for the entire visual scene, than for the appearance of a single object. If what was seen with one eye is missing, the appearance of the global scene is severely modified, whereas the appearance of a single object is still well matched between binocular and monocular vision

conditions. This could explain why in monocular vision conditions there is a stronger reliance on local cues. Similarly, in experiments 3 and 4, chicks showed a strong preference for local features by neglecting the spatial features, regardless of whether they were tested in monocular or binocular vision conditions. This is in line with the results of Chiandetti et al. (2005), where dark-incubated chicks focused on local cues, while only the light-incubated chicks using their left eye did not show a clear choice between global or local cues, taking both into account. Overall, our results confirm that local features, but not relational spatial information, can be processed by both eye systems independently in dark-incubated chicks. Whether orientation in relation to distinct landmarks would be possible in light-incubated chicks using only one eye system remains to be investigated in future studies.

It is particularly interesting to compare our results on the lateralization of cue use with those found in pigeons. There are reports of several species-specific differences in the lateralization of spatial and featural encoding between chicks and pigeons (for reviews see Prior 2006; Manns and Strökens 2014). Nevertheless, the present study suggests that there are at least some similarities between those two species. For example, in pigeons, landmark shift tests in square-shaped enclosures revealed that both eye systems can encode featural information. Moreover, they rely more on landmarks than on geometrical information if tested monocularly (Wilzeck et al. 2009). In the current study we have confirmed both these features in chicks. Finally, it has been reported that pigeons using both eye systems encode a greater amount of geometrical information than when they are using either eye system alone (Wilzeck et al. 2009; see also Prior and Güntürkün 2001 for similar evidence in a different task). Although we did not find evidence that monocular chicks were able to encode geometric information in our task, monocular occlusion clearly impaired chicks' ability to use spatial landmarks (Experiment 2 and 4). One could argue that the lack of encoding of spatial information by single eye systems reflected monocular chicks' impossibility to see all the three free-standing objects simultaneously. Chicks have a visual field of about 165° for each eye (Andrew and Dharmaretnam, 1993), which would allow them to see at least two of the visual landmarks from the release site also after monocular occlusion, when looking in the correct direction (Figs. 3, 5). This is theoretically sufficient information to orient, if chicks had acquired a complete representation of the environment at training. Moreover, chicks can move their eyes, they can flexibly turn their heads and they were able to explore the arena freely. However, it is possible that chicks did not always acquire such a representation, and that accuracy would increase if all the three landmark would be always visible at the same time also to monocular chicks. In this case, the performance of monocular chicks could depend on their ability to combine information from

different views. With regard to the comparison with pigeons, in the study of Wilzeck et al. (2009) the animals could encode relational information even in monocular conditions, despite being impaired. However, contrary to our chicks, for pigeons the relational information was provided by the shape of the arena borders. This could have made the relational information available within smaller portions of the visual field. Overall, this pattern of results suggests that at least monocularly occluded, dark-incubated male chicks might behave comparably to pigeons. It would be interesting to test how dark-incubated male chicks would encode the centre of a square-shaped arena. Up to now, this task has been used only with chicks that were likely to have received light during egg incubation (Tommasi and Vallortigara 2001).

There are several other factors that might have contributed to the preference for local over spatial information in our experiments. One such factor is the size of the environment. In experiments using rectangular enclosures of different sizes, chicks showed better retention of geometrical information when tested in small enclosures than in large enclosures (Chiandetti et al. 2007; Vallortigara et al. 2005). They were also more attentive to local features in larger compared to smaller environments (Chiandetti et al. 2007; Vallortigara et al. 2005). In the present study, we used a large circular arena with distinct landmarks for orientation. The relatively large distance between the landmarks in the present study (about 160 cm) indeed exceeds the size of even the largest enclosures (70 cm deep, 35 cm wide) previously used to investigate the effect of space size on reorientation in chicks (Chiandetti et al. 2007; Vallortigara et al. 2005). The use of a larger arena in the current study aimed at increasing the ecological validity of the task, making it more comparable in scale to the orientation behaviour in the natural habitat of a ground-living galliform. However, if the encoding of geometrical relationship between distinct landmarks and continuous surfaces is based on the same mechanism, it is possible that chicks in our study relied more on local traits than on spatial due to the size of the geometrical space.

Another factor that might have biased the choice towards local information is the sex of the animals tested. In the present study we used exclusively male chicks. There is quite a lot of literature investigating the sex difference in spatial orientation abilities in different species (Newcombe 2007). In chicks it had been initially reported that males are better at position encoding, while females are better in colour discriminations (Vallortigara 1996). However, this study did not involve reorientation after disorientation and the rewarded position could be identified both by egocentric (left right location of the feeder) and allocentric information (position in relation to the walls of the enclosure) (Vallortigara 1996). Indeed, contradicting findings were obtained in a later study, where chicks of both sexes were trained to reorient and encode the centre of a rectangular enclosure marked

with a local feature (Tommasi and Vallortigara 2004). In this case, males were less precise than females at searching in the centre and they relied upon the local information (beacon) more than females (Tommasi and Vallortigara 2004). Likewise, the male chicks in our study showed a clear preference for the familiar beacon, which was unaffected by conflicting positional information. However, whether females would behave different in the given task is an empirical question for future studies.

Other potential factors for the preferential use of spatial or local cues may be related to the training duration. Green finches, for example, have been shown to switch their preference depending on the number of training trials (Herborn et al. 2011; for similar results with rats see also Packard and McDaugh 1996). Moreover, the saliency of local or distal cues, the complexity of the pattern and the surrounding environment could also affect the ratio of decisions. For example, in pigeons cue preferences can be experimentally manipulated by changing the salience or values of the cues (Kelly et al. 1998). In fact, in the current study the global information available was well controlled (provided only by the three free-standing objects) and thus very minimal. It is quite possible that in a more complex surrounding, chicks would be more attentive to the allocentric environment. Such availability of multiple sources of information should increase search accuracy as proposed by the multiple bearing hypothesis based on studies with Clark's nutcrackers (Kamil and Cheng 2001). Biases towards particular cue types may be generated by experimental design, if some cues are easier to learn (Shettleworth 2005) or more conspicuous than others (Cheng et al. 2007; Gray et al. 2005). Overall, the flexibility in cue use challenges the hypothesis that natural selection favoured a preferential use of spatial information only in food-catching birds. According to this hypothesis, non-storing birds like chicks should not show a preference between local and spatial cues (e.g. Krebs 1990; Brodbeck 1994; Clayton and Krebs 1994a, b; Clayton and Krebs 1994b; Sherry and Vaccarino 1989; Brodbeck and Shettleworth 1995; Hampton and Shettleworth 1996; Herz et al. 1994). This is clearly contradicted by our data. Moreover, other studies were unable to find the expected differences between storing and non-storing species in their cues use (Healy 1995; Healy and Krebs 1992; Hodgson and Healy 2005; LaDage 2009). Altogether, these findings suggest that a simple categorization of food storers vs. non-storers does not reliably predict the preferential use of spatial or local cues. Nevertheless, it is still plausible to consider foraging strategies in the light of species-specific adaptations. One could speculate that domestic chickens (or their ancestors) are adapted to search for food that is dispersed in their natural habitat. This requires a preferential attention to local features. In contrast, spatial cues are less informative for finding food and are used mostly for general orientation.

This would explain chicks' preferential use of local feature for food localization in the present study and also in Chiangetti et al. (2005).

Overall in the present study, dark-incubated male domestic chicks were able to rely on relational information from distinct landmarks for reorientation. However, they preferred to use the local features, as beacons if this strategy was available. We were not able to find any lateralization effect in the use of the two strategies. While positional encoding required input from both eyes in this task, local features were processed equally well by either eye system. Future studies are needed to disentangle whether the use of spatial or local cues is influenced by embryonic light exposure, the size of the geometrical space or sex of the animals.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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