

Orientation and lateralized cue use in pigeons navigating a large indoor environment

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Summary

The pigeon's use of different visuo-spatial cues was studied under controlled laboratory conditions that simulated analogous aspects of a homing situation. The birds first learned the route to a goal that was not visible from the starting location, but became visible as it was approached. Birds could orientate within a mainly geometric global reference frame, using prominent landmarks within their range, or by 'piloting' along local cues. After learning the route, the birds were tested from familiar and unfamiliar release points, and several aspects of the available cues were varied systematically. The study explored the contribution of the left and right brain hemispheres by performing tests with the right or left eye occluded. The results show that pigeons can establish accurate bearings towards a non-visible goal by using a global reference frame only. Furthermore, there was a peak of searching activity at the location predicted by the global reference frame. Search at this location and directedness of the bearings were equally high with both right and left eye, suggesting that both brain hemispheres

have the same competence level for these components of the task. A lateralization effect occurred when prominent landmarks were removed or translated. While the right brain hemisphere completely ignored such changes, the left brain hemisphere was distracted by removal of landmarks. After translation of landmarks, the left but not the right brain hemisphere allocated part of the searching activity to the site predicted by the new landmark position. The results show that a mainly geometric global visual reference frame is sufficient to determine exact bearings from familiar and unfamiliar release points. Overall, the results suggest a model of brain lateralization with a well-developed global spatial reference system in either hemisphere and an extra capacity for the processing of object features in the left brain.

Key words: orientation, lateralized cue use, brain, pigeon, *Columba livia*.

Introduction

The capability of pigeons to find places such as their loft over long distances has been studied extensively. In a typical homing experiment, pigeons are brought from their loft to release sites ranging from a few to tens of kilometres away, and their homing performance is measured. Standard parameters measured include the direction taken by the birds at the release site, the time until they vanish from the release site, and the time they take to return to their loft. Pigeons successfully home from totally unfamiliar sites. It is assumed that they can sense the direction of the loft by using a navigational map and that they use mechanisms such as a sun compass to keep their course. It is, however, still debatable which cues are used with the navigational map, and to what extent, and how the pigeons use visual cues related to prominent landscape features when homing through familiar terrain.

Several studies support the view that visual aspects of the landscape are used during homing. When pigeons have the opportunity to preview a familiar landscape before departing

they home faster than birds without this visual information (Braithwaite and Guilford, 1991; Braithwaite and Newman, 1994; Burt et al., 1997). Pigeons, however, tend to deviate in a predictable manner from the correct direction at familiar release sites if their sun compass is altered by clock-shifting (cf. Füller et al., 1983; Wiltschko and Wiltschko, 1998). Whether such findings are inconsistent with the pigeons' use of visual information depends on the way they process this information. If they were 'piloting' by heading towards prominent landmarks, they should not deviate after a clock-shift. If, however, they were using visual information just to recognize the site, they should show a systematic deviation. For example, when clock-shifted, pigeons with lesions to the hippocampus and released at familiar sites (Gagliardo et al., 1999) deviated to the full extent predicted by the clock-shift, whereas control pigeons showed only a small deviation from the home direction. This suggests that intact control birds derived directional information directly from the landmarks, while birds with hippocampal lesions used the landmark

information to recognize the site and to recall a bearing associated with that site. Fairly clear-cut evidence for the use of visual information at the release site was obtained in a recent study using a circular arena that confined the pigeons for a brief moment before departure (Gagliardo et al., 2001b). This design permitted assessment of the pigeons' bearings while the visual cues were strictly controlled. Pigeons that were rendered anosmic to prevent them from using olfactory cues, but could see the surrounding landscape, were well oriented towards home. When the landscape was screened from view by curtains, the pigeons were oriented randomly. Apart from the dependence of performance on visual information, this study demonstrated the translation of landscape information into a bearing under conditions controlled by what the pigeons could see. Although evidence from field studies for the use of visual information is increasing, it is still not clear which aspects of landmark information are used by the pigeons and how this information is processed.

A quite different line of research investigated the use of visual landmark information by pigeons searching for food in the laboratory. The environments were rather small, but as the conditions in the laboratory allowed for controlled manipulations of visual cues, these studies provided important insights into the way pigeons process landmark information. In a typical experiment, the birds searched for hidden food, and changes in their searching activity after systematic changes of the visuo-spatial cues were assessed. Such studies have shown that the size of the landmarks appears to be of minor importance (Cheng, 1988). Typically, pigeons appear to remember distances and directions to landmarks following a two-step process. In the first step, the landmark matching process, pigeons recognize landmarks or an array of landmarks. In the second step, the search place matching process, they establish the direction to individual landmarks (Spetch et al., 1996, 1997). If a symmetric landmark array was learned and then transformed during a test, for example by extending the array from a square into a rectangle, pigeons used a spatial strategy quite different from that of humans. While humans encoded a kind of rule in terms of the overall array (e.g. 'search in the middle'), pigeons tended to encode the distance and direction to single landmarks or a small subset of the landmark array.

To understand how pigeons might use such information in the real world, two points in particular need further evaluation. Firstly, which aspects of visual information do the pigeons use to determine a bearing upon being released? Do they recognize the release site by local features, or are they able to use the overall geometry of the surrounding landscape, which might provide a global reference frame accessible from a number of sites within a given area? For example, the area around Pisa in Italy, where many important homing studies take place, is characterized by a global reference frame consisting of a straight coastline in the west, the wall of the Apuan Alps in the north east, and the Tuscan hills in the south east. If a pigeon is released within this area, after gaining some height it will always be exposed to this global reference frame. The

perspective might differ, but it will see this spatial reference frame, at familiar as well as at unfamiliar sites. On the other hand, local features and prominent landmarks might differ completely at different release sites. So, in principle, a mainly geometric global reference frame could guide the birds visually when released from familiar and unfamiliar places at short to medium distances.

A second important point arises from the fact that the multi-component task of spatial orientation is based on different contributions from the left and right brain hemisphere. In order to understand what spatial information is processed and how, it is crucial to evaluate the unique role of each hemisphere. In birds, tests for lateralization can be carried out conveniently by temporary occlusion of one eye. As the fibres of the avian optic nerve cross over completely, visual input through the right eye is mainly processed by the left brain hemisphere and *vice versa* (cf. Güntürkün, 1997). On the basis of early findings, a complementary pattern of avian visual lateralization had been suggested in which the right brain hemisphere is mainly concerned with the processing of topographical information, while the left brain hemisphere deals with recognising and categorising the properties of objects (Andrew, 1991; Bradshaw and Rogers, 1993). Several studies were consistent with this hypothesis (Rashid and Andrew, 1989; Clayton and Krebs, 1994). There is, however, increasing evidence that both hemispheres contribute to spatial cognition, so as things stand now, the challenge is to determine which specific aspects of spatial information processing are contributed by the right or the left brain hemisphere (Ulrich et al., 1999; Tommasi and Vallortigara, 2001). Pigeons show lateralization of object discrimination, but not of spatial performance, when subjected to a working memory task in a maze (Prior and Güntürkün, 2001), and the left hemisphere is superior during homing from remote release sites (Ulrich et al., 1999; H. Prior, R. Wiltschko, K. Stapput, O. Güntürkün and W. Wiltschko, manuscript submitted for publication). Furthermore, a lesion study suggested lateralized learning of the navigational map (Gagliardo et al., 2001a). There are several possible explanations for a left hemispheric superiority during homing. As pigeons have a better long-term memory for visual patterns in the left brain hemisphere (von Fersen and Güntürkün, 1990), it might be more competent in recognizing landmarks, which could be particularly important as pigeons approach the loft. Also, the left and the right avian brain might differ in rather fundamental aspects of spatial information processing. From experiments where the shape of an indoor arena was varied during food searching by chicks, Tommasi and Vallortigara (2001) concluded that the right avian brain is mainly concerned with relational spatial information, while the left avian brain encodes absolute metric information.

The present study considered both the role of different cues and perspectives and the question of lateralization. A large laboratory arena was used, and several aspects of a natural homing situation were simulated. There were three levels of visuo-spatial information. (1) A global reference frame was provided by the outer walls of the arena. An artificial 'horizon'

(see Materials and methods) prevented the pigeons from seeing straight ahead for more than 1–2 m from any place when walking through the arena. The global reference frame could be seen from anywhere. (2) Four prominent landmarks, tall enough to be seen from any place within the arena, formed an array around the target region. (3) There were many local cues, which were only visible from a very short distance. In principle, a pigeon could successfully find the goal along the familiar training route by ‘piloting’ from one local cue to the next. Pigeons were tested with the original configuration of spatial cues from familiar (experiment 1) and new (experiment 2) release sites. Then how removal of landmarks and local cues affected the pigeons’ performance was assessed (experiment 3). Finally a dissociation experiment was carried out (experiment 4). The landmark array was moved so that the target region predicted by the landmark array differed from the target region predicted by the global reference frame.

All experiments included testing for lateralization. Apart from the more general question of whether pigeons can determine accurate bearings from new places and whether the two brain hemispheres contribute differentially to this, we formulated several more specific hypotheses. If the pigeon’s orientation guided by global cues does not show lateralization, as suggested by the maze study (Prior and Güntürkün, 2001), their performance should be the same for tasks in which a global reference frame allows for orienting and is not in conflict with local cues (experiment 1). If there is lateralization in the processing of object-specific cues, performance with the right eye/left hemisphere should be impaired when prominent landmarks or local cues are removed (experiment 3). If there were, as in chicks, a pattern of lateralization in which the left brain hemisphere specializes in object information and the right brain hemisphere is mainly concerned with geometric relational cues (cf. Andrew, 1991), the right hemisphere should outperform the left hemisphere when the birds approach the goal from new points in different directions (experiment 2). Furthermore, in a case of conflicting information, birds using the right eye should search in a target area predicted by prominent landmarks, and birds using the left eye should search at the area predicted by the global spatial reference frame (experiment 4).

Materials and methods

Animals

The subjects were 15 experimentally naïve pigeons (*Columba livia* L.) approximately 1 year old, obtained from local breeders. They were housed in individual cages in a colony room at 21 ± 1 °C and subjected to a 12 h:12 h light:dark cycle. Birds were kept at approx. 85 % of their free feeding weight during the experiments. Water and grit were available *ad libitum*. Before the beginning of training and testing, about one-half of the birds’ flight feathers were clipped, so that the birds could only become airborne with great effort and would walk through the arena without trying to fly (cf. Prior and Güntürkün, 2001).

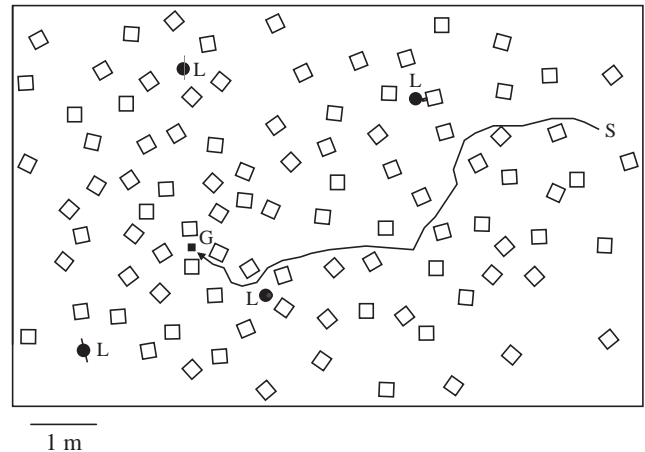


Fig. 1. View of the arena with the cardboard containers making up the ‘horizon’ shown as white squares. S, starting location during training, experiments 1 and 3; G, goal; L, prominent landmarks. The arrow from start to goal depicts a typical search path in experiment 1.

Experimental environment

Experiments took place in a large indoor room, within which a rectangular arena (6.5 m × 10 m) was set up (see Fig. 1). The outer walls of the room were 4 m high and provided two of the arena walls. The other two arena walls were wooden separations 2.5 m high. The room was brightly lit by fluorescent lamps at the ceiling. Black curtains covered all windows so that no sunlight entered the room. Approximately 100 cardboard containers (25 cm × 22 cm × 31 cm, length × width × height) were distributed randomly within the arena and provided an artificial ‘horizon’ for birds moving on the floor. The goal G was not visible until birds were 1–2 m away from it. Four big landmarks, poles 140–200 cm high and at different distances and directions from the goal, were visible above the artificial horizon. At the top of each pole was fixed a piece of cardboard, 40–60 cm wide and 60–80 cm high, with a unique shape and colour pattern for each landmark. Local cues were drawings and prints on the cardboard containers, which differed in size, shape and colour.

Monocular occlusion

Before training and testing began, birds were prepared for wearing eyecaps as described (Ulrich et al., 1999). In brief, a ring of Velcro was fixed around each eye with water-soluble, non-toxic glue after clipping a circular strip of feathers. The counterpart of the Velcro ring was glued to a circular cardboard eyecap (26 mm diameter). The eyecap could be bent easily, to ensure a tight fit on the pigeon’s head. The eyecap was fixed about 10 min before starting a monocular test, and was removed immediately afterwards.

General procedure

Birds were first trained to find the route to the goal from a start position that was the same during all trials. In order to prevent the birds from visiting sites to be designated as new sites during later tests, they learned the final route from the starting position stepwise during the very first trials. Birds

started by finding a short route approximately 0.5 m from the goal, and during subsequent training trials the route was elongated by moving the start position further away until the birds began at the designated start position, which was used during late training trials and tests in experiments 1 and 3. Reaching the goal directly four times in a row was taken as the criterion that the birds had learnt each step of the route. After achieving this from the final start position, ten further training trials were done. The four experiments described above were then performed, each addressing a specific question. Every trial was videotaped, and a clock integrated into the video recorder displayed the time to 0.1 s resolution, which allowed for frame-by-frame analysis of the birds' performance. The following parameters were derived for all experiments: the bearing of the birds after they had moved 1 m from the starting point, the time they took to reach the goal, and the length of the path taken. Individual paths were traced with tracking software (*Wintrack*; cf. Wolfer et al., 2001).

Statistical analysis

Analogous to a homing study in the field, our statistical analysis focused on how the birds were oriented upon leaving the starting site and how efficiently they reached the goal. For the initial orientation, we assessed: (1) the mean direction, (2) the extent of directedness, (3) the observed direction with respect to the goal direction, (4) the observed direction of monocular birds with regard to binocular controls, and (5) dispersion variation within the different treatments. Mean directions were calculated as mean vectors. The length of the mean vector, ranging from 0 to 1, gives an estimate of the birds' directedness. In homing studies, orientation in a predicted (e.g. home) direction is usually analysed by the *V*-test. Although the arena we used was fairly large, there might have been spatial constraints, e.g. due to the distance of the starting locations to the outer walls, so the *V*-test would have overestimated the direct flight of the birds towards the goal. Therefore, a rather conservative and robust approach was chosen. For each sample, linear confidence intervals of coefficient $Q=0.99$ were calculated (cf. Batschelet, 1981), and whether they included the goal direction was checked. Similarly, we tested whether the mean direction of binocular controls was within the confidence limits of monocular birds. We calculated angular differences with regard to the goal direction as a measure of dispersion. 'Homing performance' was the average speed of each bird calculated from the path length and the time taken to reach the goal. Angular differences and 'homing' speeds were compared by analysis of variation (ANOVA) after checking for normality and homogeneity of variances. A Fisher's LSD test was used for pairwise comparisons after significant overall ANOVAs if the number of comparisons was small (approximately 3), because in that case the test provides a good trade-off between power and security. For higher numbers of comparisons, a Tukey's HSD test was used. Directional data from experiment 4 were analysed the same way as in the other experiments, but there were some differences in other performance parameters. As the

search time was fixed, the path lengths rather than the 'homing' speeds were compared. In addition, search activity at different locations was compared, and for this the arena was divided into 0.5 m squares. The time spent in any of these squares was measured, and for each bird data were combined to obtain the distribution of search activity along the long and small axes of the arena. As this measure had a non-parametric distribution, comparison between eyecap conditions was done using Wilcoxon matched pairs tests.

Experiment 1

After learning one particular route, each pigeon was tested on two consecutive days. On the first day, half of the birds were treated in the order 'left – binocular – right', and the other half 'right – binocular – left'. On the second day the order was reversed. The reason for two tests was to identify differences between the first and the second monocular trial, as it is known from other studies with monocular birds that they tend to show systematic deviations towards the side of the uncovered eye during first tests.

Experiment 2

In this experiment, the birds were tested from four new positions (cf. Fig. 4), which were balanced in route length and direction. In addition to a binocular trial from each of the new starting sites, each bird completed four tests with eyecaps. Tests with the same eye were made from release points at the same distance from the goal, and the combination of release points and eyecap conditions was balanced between subjects. Thus, for each position there was a within-subject comparison binocular *versus* monocular and a between-subject comparison between use of the left and the right eye.

Experiment 3

In this experiment, the role of landmarks and local cues within the arena was tested. In a first test (3a), the four prominent landmarks were removed from the arena, and the birds were tested from the original start location. In a second test (3b), all local cues were removed by using blank cardboard containers for the 'horizon' and relocating the containers randomly. Thus, the containers had no defining features and were only used as a 'horizon'. Both tests were performed for all conditions and the order of eyecap treatment was balanced for each experiment.

Experiment 4

Experiments 1, 2 and 3 tested whether the pigeons headed accurately for a non-visible goal, independently of the eye/brain hemisphere used. Once in the vicinity of the goal, however, they could see the goal. Experiment 4 tested for the searching location of the pigeons after dissociating possibly relevant cues. The two aspects that were of some importance in the earlier tests, i.e. the global reference frame and the prominent landmarks, were arranged so that two predicted different goals. The local cues, which apparently had no effect on the searching activity of the pigeons, were randomised

throughout the entire arena so that they could not signpost the location of the goal. The prominent landmarks were moved (cf. Fig. 8) so that the overall configuration of the landmark array and its orientation with regard to the global reference frame were preserved, but the goal location predicted by the prominent landmarks (G') was different from the goal position predicted by the global reference frame (G). In this test we were interested not only in the first choice of the birds but also the subsequent search. There was therefore no goal. Thus, we could evaluate how the birds would distribute their search behaviour guided by the global reference frame and/or big landmarks only. The searching behaviour of the birds was observed for a period of 5 min. All birds started from two new sites (A and B) at opposite walls of the arena. Eight of the birds used the right eye from site A and the left eye from site B, and seven birds received the opposite treatment. We measured the time the birds took to reach an area within a radius of 0.5 m around G or G' on their first choice, the length of the search paths during a 5 min period, and the distribution of searching activity among different patches in the arena.

Results

All the birds learned the original route easily. During stepwise route learning they usually achieved the criterion with the minimum number of trials, so that the birds completed 25 training trials in total. On subsequent tests they began with very directed bearings from familiar as well as from new locations. Although monocular birds took longer to reach the goal, they performed fairly well. There was no difference between birds with left eye or right eye occluded using the original landmark array, regardless of whether the starting location was familiar (experiment 1) or unfamiliar (experiment 2). There was, however, a difference in how the birds responded to changes in prominent landmarks. The birds appeared to completely ignore such changes if using the left eye; when using the right eye, they were distracted if the prominent landmarks were missing (experiment 3), or allocated some of their searching activity to the site predicted by the prominent landmarks when this site differed from that predicted by the global reference frame. Under both eyecap conditions the global reference frame was the predominant cue guiding the search of the birds.

Experiment 1

Experiment 1 tested the effect of monocular occlusion and possible differences between the right and left brain hemisphere when navigating a highly familiar route. The results of experiment 1 are given in Figs 2 and 3. All bearings had long vectors ($r > 0.95$ for all) indicating a high degree of directedness. Despite being highly directed, the bearings showed two types of bias. Firstly, on average the direction of the bearings would have led the birds to a place closer to the short wall near the goal than to the actual goal position. Except for the mean bearing of birds using the left eye on the second test, the home direction was outside the confidence intervals of

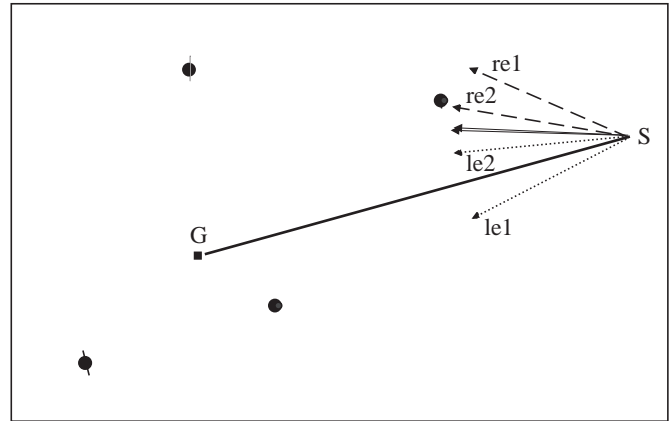


Fig. 2. Mean bearings during experiment 1 in the binocular (solid arrow), left eye (dotted arrow) and right eye (broken arrow) condition. le1, le2, first and second test, respectively, with the left eye; re1, re2, first and second test, respectively, with the right eye. For comparison, the most direct path to the goal G is indicated by a bold line. 'Horizon' not shown. Other symbols as in Fig. 1.

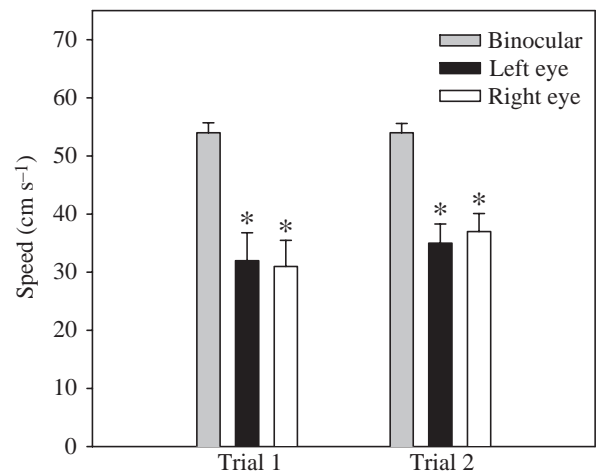


Fig. 3. Speed of reaching the goal from a familiar location in experiment 1 (means \pm S.E.M., $N=15$). Performance was higher in the binocular condition, but similar with the left and the right eye. *Significant difference from binocular condition ($P < 0.0001$).

the mean bearings. Secondly, there was a systematic bias in monocular conditions. Birds using the right eye tended to deviate to the right side, and birds using the left eye tended to deviate to the left side. This tendency was profound in the first trial, but considerably reduced in the second trial. Accordingly, the mean bearing of controls was outside the confidence intervals of the bearings of either eyecap group in the first test, while there was no difference in the second test. The dispersion for the monocular conditions on the first and second trial was symmetric. Analysis of the angular differences by ANOVA, with eyecap treatment and trial order as repeated measures, showed a significant effect of trial order ($F_{1,14}=24.21$, $P < 0.0005$), but no effect of eyecap condition ($F_{1,14}=0.10$, $P > 0.75$), and no interaction ($F_{1,14}=4.05$, $P > 0.05$). Birds

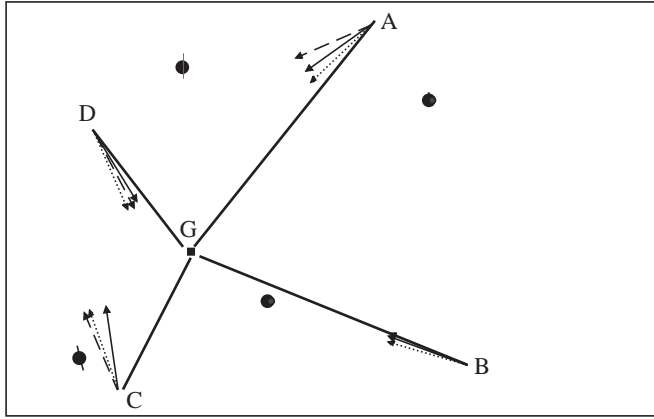


Fig. 4. Mean bearings from new starting points A–D during experiment 2 in the binocular (solid arrow), left eye (dotted arrow), and right eye (broken arrow) conditions. From each location a similar ‘release site bias’ occurred in the different visual conditions. Other symbols as in Figs 1, 2.

reached the goal sooner when they could use both eyes (Fig. 3), but there was no difference between the left and right eye, and the patterns in the first and second trials were the same. Accordingly, an eyecap condition \times trial order ANOVA revealed a significant effect of eyecap condition ($F_{2,26}=36.92$, $P<0.0001$), but no effect of trial order ($F_{1,13}=1.73$, $P>0.2$), and no interaction ($F_{2,26}=0.72$, $P>0.4$). Pairwise comparisons of the conditions of viewing showed that the birds deviated from the binocular condition with the left ($P<0.0001$) and the right ($P<0.0001$) eye, but that there was no difference between the monocular conditions ($P>0.75$).

Experiment 2

Experiment 2 tested for directedness of the initial orientation and for possible differences in navigation performance between the right and left brain hemisphere when the birds started from new positions. The results from experiment 2 are given in Figs 4 and 5. All bearings were highly directed. In the binocular condition, the vector length was $r>0.95$ from all new starting locations. For the left-eye only condition, vector length was $r=0.91$ from point A; from the other points it was $r>0.95$. In the right-eye only condition, vector length was $r=0.94$ from point A, $r=0.99$ from point B, $r=0.95$ from point C, and $r=0.88$ from point D. As in experiment 1, there appeared to be some general tendency to head for a location which was slightly closer to the short wall of the room than the actual goal. This bias was smallest from starting point B and largest from point C, but it was in the same direction from all starting points and under all eyecap conditions. Accordingly, confidence intervals of the mean bearings of birds using the left or right eye always included the mean direction of binocular controls. Confidence intervals included the goal direction from starting locations B and D. From A, only the bearings of the left-eye only group did not differ from the goal direction, and from location C all bearings were different from the goal direction. As in experiment 1, birds reached the goal sooner in the binocular condition than in the

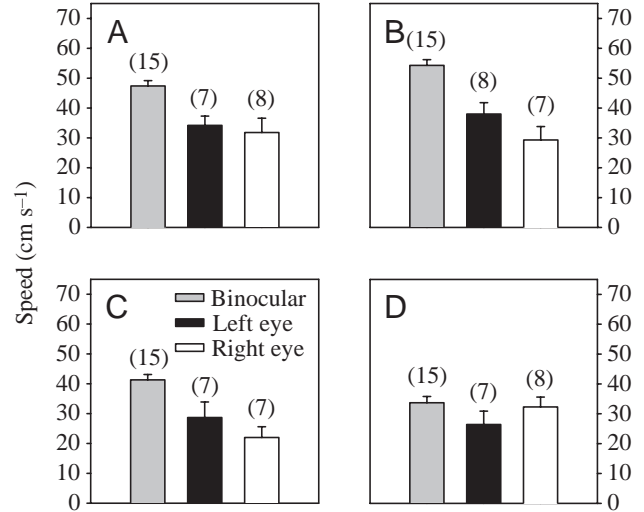


Fig. 5. Speed of reaching the goal from four new locations (A, B, C, D) in experiment 2 (means \pm S.E.M., N as indicated in parentheses). Differences between the left and right eye were not significant, but performance of binocular *versus* monocular vision at positions A–C were significantly different. See text for details.

monocular condition. Although the extent by which the monocular speed differed from the binocular speed varied among places, the difference between the monocular conditions was never significant. ANOVA with the eyecap condition as independent variable and binocular *versus* monocular vision as a repeated measure showed no difference between the right and the left eye for any starting position (A: $F_{1,13}=0.01$, $P>0.9$; B: $F_{1,13}=1.16$, $P>0.3$; C: $F_{1,12}=0.42$; $P>0.5$; D: $F_{1,13}=0.17$, $P>0.6$). There was a significant effect of binocular *versus* monocular performance at three positions (A: $F_{1,13}=30.62$, $P<0.0001$; B: $F_{1,13}=32.83$, $P<0.0001$; C: $F_{1,12}=24.62$; $P<0.0005$). From position D, this effect was not significant ($F_{1,13}=2.25$, $P>0.1$), but there was a significant interaction ($F_{1,13}=5.81$, $P<0.5$), which was due to a difference between the binocular condition and the left eye ($P<0.05$), but not the right eye ($P>0.4$).

Experiment 3

The effects of removing prominent landmarks (experiment 3a) and local cues (experiment 3b) were tested. As in experiments 1 and 2, the bearings were highly directed and were closely similar in experiments 3a and 3b; therefore, only bearings from experiment 3a (Fig. 6) are shown. Vector lengths were $r>0.95$ for all conditions. All confidence intervals included the goal direction, and all bearings of monocular trials were the same as those of binocular control trials. There were no differences in angular dispersion in experiments 3a ($F_{2,24}=0.92$, $P>0.4$) or 3b ($F_{2,28}=3.28$, $P>0.05$). In experiment 3a, when the prominent landmarks were removed for the first time, the birds took longer to reach the goal when they were using the right eye (Fig. 7a). ANOVA with eyecap treatment as a repeated measure revealed a significant effect of eyecap condition ($F_{2,28}=59.52$, $P<0.0001$). Pairwise comparisons showed a difference between the binocular and the monocular

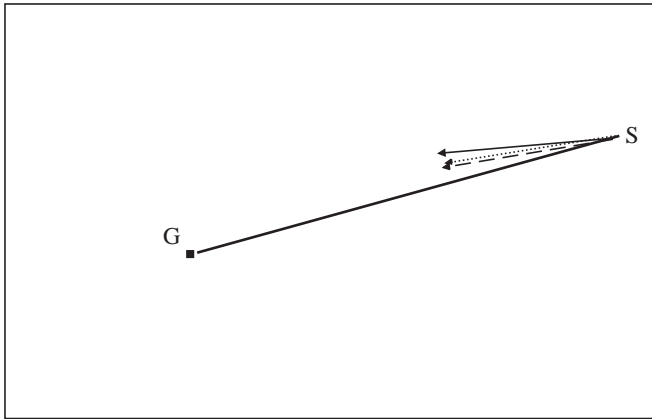


Fig. 6. Mean bearings after removal of landmarks during experiment 3 in the binocular (solid arrow), left eye (dotted arrow), and right eye (broken arrow) condition. Other symbols as in Figs 1, 2.

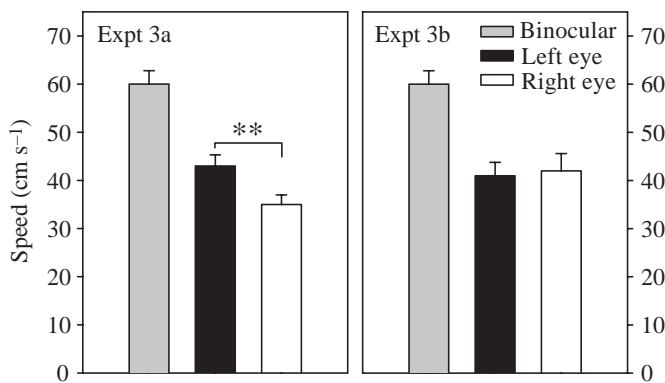


Fig. 7. Speed of reaching the goal after removal of prominent landmarks (experiment 3a) and after removal of local cues (experiment 3b) (means \pm S.E.M., $N=15$). Removal of prominent landmarks impaired the birds when they used the right eye. **Right-eye only condition in experiment 3a was significantly different from all other monocular conditions in 3a and 3b ($P<0.01$). There was no difference between the other monocular conditions. See text for details.

conditions ($P<0.0001$ for both), and a difference between the left and the right eye occluded ($P<0.005$).

Removal of the local cues in experiment 3b had no differential effect on the left and right eye. In the right-eye only condition, birds quickly adjusted to the changes of prominent landmarks experienced in experiment 3a, and under both monocular conditions performed at a similar level to the left-eye only condition in experiment 3a (cf. Fig. 7a,b). Accordingly, ANOVA with eyecap treatment as a repeated measure revealed a significant overall effect of eyecap condition ($F_{2,28}=16.73$, $P<0.0005$), but pairwise comparisons showed no difference between the monocular conditions ($P>0.75$) (although both differed from the binocular condition: $P<0.0005$ for both).

Combined analysis of experiments 3a and 3b with both experiment and eyecap treatment as a repeated measure

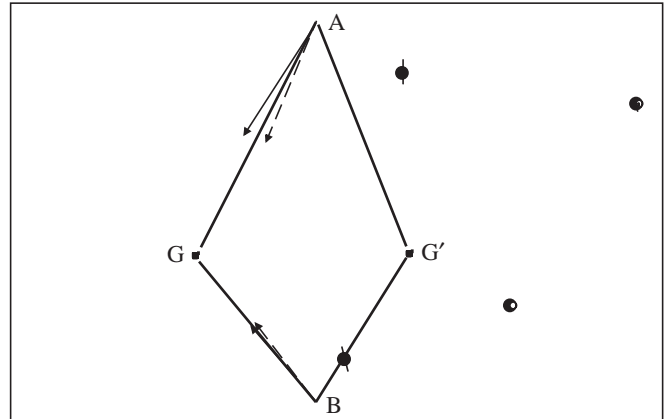


Fig. 8. Mean bearings from two new starting points A and B with the left eye (broken arrow) and right eye (solid arrow) after translation of the landmark array in experiment 4. G, goal predicted by the global reference frame; G', goal predicted by the translated landmarks. For comparison, the direct routes to G and G' are indicated by a bold line. Other symbols as in Figs 1, 2.

showed no overall difference between experiments 3a and 3b ($F_{1,14}=1.65$, $P>0.2$), but there was a difference between the eyecap conditions ($F_{2,28}=36.82$, $P<0.0001$), and a significant interaction ($F_{2,28}=4.48$, $P=0.02$). Further comparison of the monocular conditions revealed a difference between right-eye only performance in experiment 3a and all other monocular scores (right-eye only, experiment 3b: $P<0.005$; left-eye only, experiment 3a: $P<0.005$; left-eye only, experiment 3b: $P<0.01$). Left-eye only performance in experiment 3a did not differ from left-eye only ($P>0.5$) or right-eye only ($P>0.95$) performance in experiment 3b.

Experiment 4

Experiment 4 tested the performance of the left and the right brain hemispheres after moving the landmark array so that different goal positions were predicted by the global reference frame and the prominent landmarks. Birds started from two new positions, and they had highly significant bearings from both positions that were directed towards the goal location predicted by the global reference frame (G, Fig. 8). With the left-eye only, vector lengths were $r=0.89$ from point A and $r=0.96$ from point B, and with the right-eye only, vector lengths were $r=0.87$ from point A and $r=0.95$ from point B. All confidence intervals included the goal direction G, but not the alternative direction G', and the mean bearings predicted the location of G almost perfectly. Consistent with this, the birds reached the goal region quickly, and there was no difference between the left and the right eye occluded ($F_{1,14}=0.57$, $P>0.4$) in the time the birds needed (Fig. 9). There was, however, a considerable difference in the subsequent search pattern between the two monocular conditions. When the birds used the left eye, they stayed close to the area of the goal predicted by the global reference frame during the whole search period. When using the right eye, birds tended to continue to search further away from G, and much of this

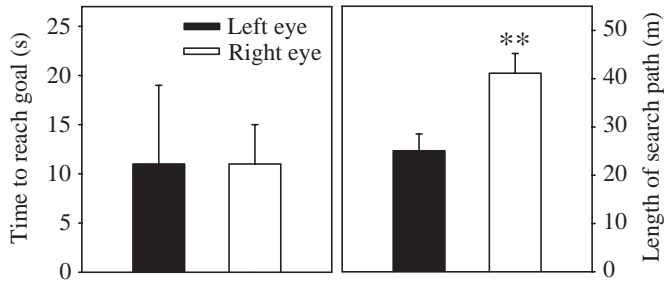


Fig. 9. Time to reach an area within a 0.5 m radius of goal G and length of the search path during the whole search period in experiment 4 (means \pm s.e.m., $N=15$). The search paths using the right eye only were considerably longer (** $P<0.01$).

additional search was near the location of the goal predicted by the prominent landmarks. This difference in search activity was reflected in a path length that was about 60% greater in searches with the right eye only ($F_{1,14}=10.57$, $P<0.01$) (Fig. 9). Fig. 10 shows the distribution of search activity along the two main axes of the arena. Along the short axis, where the predicted peak of activity was the same for G and G', the peak for the left-eye only condition was sharper, but the difference of activity allocated to the target region was not significant between the right and the left brain (Wilcoxon test: $Z=-1.36$, $P>0.1$). Along the long axis of the arena, birds almost exclusively searched at and around the location predicted by the global reference frame when using the left eye only, and there was virtually no search at the site predicted by the prominent landmarks. When the right eye only was used, the peak of search was at G, but the birds also searched at G'. Statistical comparison of the search activity at both possible goal locations showed no difference at G ($Z=-0.540$, $P>0.5$), but there was a significant difference between use of the left and the right eye only at G' ($Z=-2.557$, $P<0.01$).

Discussion

These results show that pigeons can use a global reference frame to determine exact bearings towards a non-visible goal from familiar as well as from unfamiliar locations. The ability to do so did not show any hemispheric differences. When systematic deviations from the direction of the goal occurred, the effect was the same for all eyecap conditions. Hemispheric differences emerged when changes to prominent landmarks were made. When they were missing, the performance was temporarily impaired in birds using the right eye only, and when an array of prominent landmarks was moved to predict a different target location than the global reference frame, birds completely ignored the landmarks when using the left eye only, but spent some time searching at the target location predicted by the landmark array when using the right eye only.

The ability of pigeons to determine fairly exact bearings from new locations is of interest with regard to other laboratory studies as well as to the possible role of visual cues during homing under natural conditions. Laboratory studies have

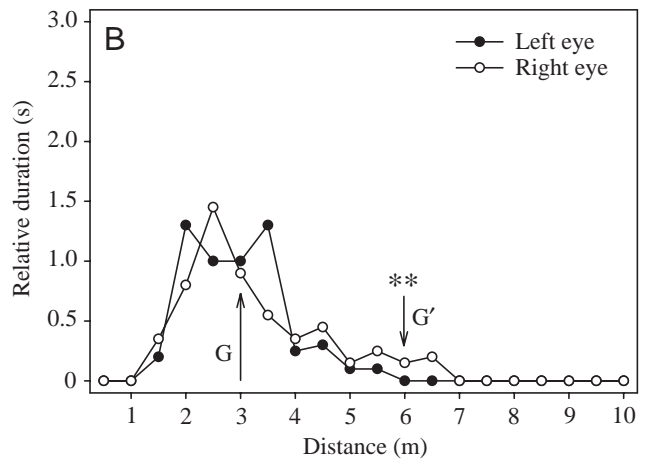
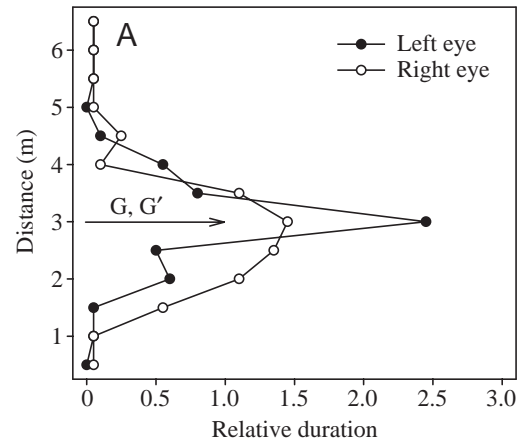


Fig. 10. Search activity parallel to the short axis (A) and the long axis (B) of the arena in experiment 4. The arrows indicate the position of the goal as predicted by the global reference frame (G) or the translated landmarks (G'). With either eye, search maximum was at G. With the right eye, there was also search at G', while there was virtually no search at G' with the left eye. **Significant difference between use of right and left eye only at G' (Wilcoxon test, $Z=-2.557$, $P<0.01$).

shown that the distances and directions to individual landmarks are of paramount importance for the pigeon's use of landmark information (Cheng, 1988). The present study shows that not only can pigeons find places at a certain distance and direction from landmarks, but also that they can determine the direction towards a place of interest from new remote locations. This raises the possibility that pigeons use a global reference frame (for example, with coast lines and mountain chains as boundaries) to visually determine the home direction from new places in the field.

In experiments 1, 2 and 3, which tested performance not only with the right or left eye, but also with both eyes, binocular performance was clearly better than monocular performance. This differs from the pattern observed when discriminating for natural food (Güntürkün et al., 2000), but resembles findings observed when orientating in a maze (Prior

and Güntürkün, 2001), suggesting that, at least in a rather complex spatial environment, performance levels might profit from a panoramic view that integrates visual input from both eyes. This does not preclude the possibility that under certain natural or experimental conditions the cues available to one hemisphere might be sufficient for maximum performance, or that binocular performance could even be impaired if environmental cues provide conflicting information.

The high directedness in experiment 1 is not surprising, because the pigeons had been trained in that direction, and the possibility could not be excluded that the pigeons simply learned to move parallel to the long axis of the arena until they came close to the goal. However, the results from experiments 2 and 4 suggest the learning of a very accurate representation of where the goal is located relative to the global reference frame or the prominent landmarks.

An interesting finding from experiments 1 and 2 is that the pigeons appeared to misrepresent the exact goal position in a manner that resembles a classical 'release site bias' (Keeton, 1973). Such a bias can apparently develop on the basis of a purely visual relational framework. It is not yet clear why this bias was small or virtually absent from some positions and fairly strong from others. Based on the bias observed at the new site C, one might be tempted to assume that orientation from a new site might be more difficult if the direction is approximately opposite to the training direction. But the bearings from the corresponding site D show nearly perfect orientation towards the goal.

Overall, two points about the 'release site bias' are noteworthy. Firstly, the pigeons appeared to improve their directional orientation during repeated testing from different positions. While there was a systematic bias in departures from the familiar start position in experiment 1, directional orientation was almost perfect in experiment 3. Similarly, birds show almost perfect directional orientation from two new locations in experiment 4. Secondly, if a bias occurred it had the same direction and degree under the different eyecap conditions.

Regarding the question of lateralization, the results provide a clear-cut picture. Firstly, neither hemisphere appears to make use of local visual cues. Changing local features had no effect, perhaps because birds are predisposed to learn cues, which are more reliable under natural conditions. Local cues at short range, provided by the colour of the vegetation, can change rapidly. In terms of a differential contribution of the left and right brain hemisphere, the results do not support a pattern of contrasting hemispheric specialization. Experiment 2, where the birds had to orient from new places, showed that the left hemisphere is quite skilled in using a global geometric frame or prominent landmarks to determine the direction to the goal. Of course, determining a direction could be done by different processes, so the strongest evidence for analogous mechanisms in both hemispheres is the virtually identical 'release site bias' under all conditions of viewing. Also in the peak of search activity with no goal, the parameter usually evaluated in other laboratory studies, the left hemisphere demonstrated high competence in finding this place immediately by means of a

relational, mainly geometric reference frame. The difference between the hemispheres was that the left brain hemisphere attended to conspicuous object cues and the right brain hemisphere did not. Based on these findings the following model of visuo-spatial lateralization in pigeons is likely. Both brain hemispheres have a module that enables the birds to determine the direction to places, and to find places by means of a global reference frame, but the left hemisphere is considerably more specialized for the processing of object properties. Consequently, the choice of cues to be followed during monocular tests depends on intrahemispheric competition. If the right hemisphere is tested, global spatial cues are the only salient clues. If the left hemisphere is tested, the module for global spatial cues and the module for object cues compete for control of the task. If both types of cues predict the same location, they act in synergy. If the predicted locations differ, either a mixed pattern is observed, or the orientation along object cues might become dominant.

The results from experiment 4 are quite revealing. There was a similar tendency for both hemispheres to use the global spatial reference frame in the first place. With either eye/hemisphere the birds demonstrated an exact bearing from a new starting location towards the (non-visible) target area predicted by the global reference frame. Only later did a clear hemispheric difference emerge. For the right brain hemisphere, the location predicted by the global reference frame was the only site of interest. When the goal was not found at the expected site, they continued to search in the close vicinity. This led to a comparatively short search path and a plateau-like search maximum along the long axis of the arena, which included the location of the expected target and closely adjacent patches. For the left hemisphere, an alternative location was possible, and when the expected goal (G) was not found, the search was extended to the site predicted by the alternative cues (G'). The amount of search activity at G' is clearly smaller than the amount of search activity at G as both hemispheres initially preferred the area of G. But since the birds did at least some searching at G' when using the right eye and virtually no searching when using the left eye, a clear and significant dissociation between the conditions emerged.

One note of caution: although the results clearly show that both hemispheres are highly competent in finding a place by a global reference frame only, there is still the possibility that the overall importance of the prominent landmarks would have been higher and the tendency of the left brain hemisphere to attend to them would have been greater if the global reference frame had been less stable. Previous studies on the use of landmarks often tried to diminish the salience of a global reference frame by shifting the landmark array during training (e.g. Spetch et al., 1997). And it has been shown that the reliability and stability of local *versus* global cues do have an influence on the choice of cues by the birds (Gould-Beierle and Kamil, 1996; Kelly et al., 1998). Similarly, there is the question of whether the birds would have responded differently to local cues if there had been landmarks of natural vegetation, such as little shrubs. On the other hand, the basic design of the present

study corresponds to a natural situation, with a highly stable global reference frame, less reliable prominent landmarks, and frequently changing local cues. That pigeons showed no evidence of using the short-distance local cues might reflect a natural readiness to use of cues, which are probably reliable. Therefore, the pattern of hemispheric contribution observed in the present study is likely to occur in natural environments.

The pattern of lateralization suggested by the findings of the present study and supported by the findings from maze learning in pigeons (Prior and Güntürkün, 2001) indicates a well-developed capacity for orientation according to global cues in both hemispheres and an additional capacity for attending to and memorizing conspicuous objects in the left hemisphere, in contrast to suggestions that the right avian brain shows general superiority for topographical information (Andrew, 1991; Bradshaw and Rogers, 1993). Therefore, a brief comparison with the main findings in other avian models is appropriate. There are three avian models of cerebral asymmetry in spatial memory: the pigeon, the chick, and pairs of food-storing and non-storing passerine birds. Evidence in chicks is mixed. An early study with rotation of the experimental array during tests suggested that orientation according to global topographical cues when using right eye/left hemisphere is random, whereas when using left eye/right hemisphere orientation is good (Rashid and Andrew, 1989). However, later studies indicated that orientation along global spatial cues using right eye/left hemisphere is also possible. A recent study using a test similar to experiment 4 of the present study, in that the subjects had to recall a site from reference memory after a landmark was moved so that global geometric information and landmark information predicted different sites, birds using the right eye only searched in a slightly larger area after landmark translation, but nevertheless showed fairly good orientation according to global geometric cues (Tommasi and Vallortigara, 2001). Thus, the searching pattern of the chicks was similar to that of the pigeons in the present study, and fairly consistent with the model of lateralization we propose. On the other hand, studies in chicks using a working memory task (Vallortigara, 2000) suggested a pattern of lateralization resembling those observed in a working memory task in passerine birds (see below). Therefore, further studies are needed to clarify the extent by which differences between avian studies are due to the species or due to specific task demands.

Comparisons with studies in passerine birds require caution as the tasks conducted by these birds are not equivalent in the type of spatial memory involved. In experiments with passerine species, birds had to relocate sites with food items unique to the trial. In some studies with food-storing birds, food items had been stored by the experimental subjects themselves. In other studies, mainly designed to compare storing and non-storing species, birds learned the location of a food item placed by the experimenter. In terms of lateralization, both procedures yielded similar results, so they will be discussed together. In a first series of experiments (Clayton, 1993; Clayton and Krebs, 1993), which did not evaluate in detail the nature of the spatial cues involved, it was

shown that after retention intervals of up to 3 h, information could be retrieved with the right as well the left eye, but that after 24 h or longer, information was only accessible when the right eye/left hemisphere was in control of the task. There was a difference between a storing species, the marsh tit, and a non-storing species, the blue tit, in that marsh tits remembered information acquired *via* either eye while blue tits only remembered information acquired with the right eye. If a similar pattern also occurred during long-term retention of a particular site, as required in the food-searching tasks in chicks and in the present study, passerine birds should be able to relocate the goal when using the right eye, but not when using the left eye, i.e. they should show a pattern different from both chicks and pigeons. It has to be considered, however, that remembering a trial-unique feeding location (the passerine's working memory task) and retention of a stable site in reference memory might involve different brain systems.

A second series of experiments with storing and non-storing passerine birds evaluated the role of different cues that might guide the birds' relocation of a feeding site. In brief, birds had to remember where a food item was placed in one of several feeders. Each feeder could be identified by one of two types of cue, a global topographic cue (location within the experimental room) and a colour cue on each feeder. Short retention intervals of 5 min were used. In phase 1 of a trial, birds learned which feeder contained food. Before phase 2 of a trial, two of the feeders were swapped so that the positions predicted by global spatial and colour cues were different. When using the left eye, birds of all four species tested (marsh tit, blue tit, jay, jackdaw) made their first choice according to the global cues. When using the right eye, all species used the colour cues (Clayton and Krebs, 1994). Data from the first choice made by the birds were consistent with the assumption that both brain hemispheres show good orientation according to global cues, and that the left brain has an extra capacity for processing local cues, which may guide searching behaviour if they are salient enough. A consequence of this assumption, however, would be that birds using the right eye should search at the correct spatial location on their second choice (as the right-eyed pigeons in this study, which searched at the correct landmarks after not finding the goal at the location visited first). This was not the case, however, as the second choice of passerines with the right eye was random (Clayton and Krebs, 1994). Again, possible differences in the type of task have to be considered. It might be that passerines have a different pattern of lateralization of spatial capabilities than chicks and pigeons. Together, the results from different studies suggest that both species and task are important for the pattern of lateralization observed. Therefore, further comparative studies with different species and tasks are needed for a more detailed understanding of avian brain lateralization.

Overall, the results from the present study further support the view that lateralization of spatial orientation in birds depends on a complex interplay of mechanisms in the left and right brain hemisphere. The present study shows that, at least in pigeons, visuo-spatial orientation along a global reference frame is performed skilfully by either brain hemisphere.

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