

Research report

Left-hemispheric superiority for visuospatial orientation in homing pigeons

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Abstract

To test for lateralisation of visuospatial orientation during homing, pigeons who had binocularly learned the homeward route from remote release sites were tested monocularly on either their left or their right eye for homing performance. In two experiments with three different release sites, birds using their right eye showed considerably better homing performance. If sun compass information was available, there was no difference in the direction of vanishing. Without this information, a difference between pigeons using their left or right eye emerged. Results show that visuospatial orientation in birds can be lateralised in favour of the left brain hemisphere and lend further support to the view that vision is important for pigeons homing on a familiar route. Cognitive mechanisms which might account for the observed pattern of lateralisation are discussed. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

From laterality patterns of visual information processing in humans it has been concluded that the left and right brain hemispheres differ fundamentally in their specific contribution to visuospatial cognition [22,36,37]. Similarly, findings in birds, particularly chicks, provide evidence for a difference between the left (right eye system 'sensu' Andrew [2]) and the right brain hemisphere (left eye system), in that the right hemisphere of the avian brain constructs a detailed organisational and topographical map of the environment, whereas the left hemisphere is mainly concerned with discriminating and categorising stimuli [8].

In humans, many studies are consistent with the hypothesis of a right-hemispheric advantage in spatial

information processing, such as perception of line orientation [5], recognition of complex patterns [54], and identification of objects from unusual viewpoints [60]. However, several recent studies indicate that both brain hemispheres contribute to spatial cognition [34,42]. As in birds, human spatial orientation appears to be a multi-component task [32,33]. This view is supported by computational models [35,39–41]. Recent studies in humans additionally stress the importance of real world information. For example, an activation of the right hippocampus was found if subjects had to make use of real world topographical information [46,47], but not if virtual environments were used [1].

In birds, there is by now good evidence for left-hemispheric superiority in visual discrimination learning (review in [30]), but lateralisation of spatial cognition is still a moot point. Although some studies support a role in spatial tasks for the right hemisphere [19,48,55], findings in food-storing birds show both right- and

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left-hemispheric superiority for visuospatial memory [18,19], perhaps due to different retention intervals. As only a few species have been tested for visuospatial memory, it is not yet clear as to whether differences between avian studies are due to the species used, the retention interval used, or the type of task.

In the homing pigeon (*Columba livia*), one of the most studied models of spatial orientation in vertebrates, there is now considerable evidence for a superiority of the right eye/left hemisphere in discrimination of food objects and visual patterns [27,28,57]. These findings are due to differences in central visual processing and not to differences in peripheral vision since left and right eye visual acuity is equal in pigeons [29]. It has also been demonstrated that pigeons show a preference for the position rather than the colour of two otherwise identical home lofts, indicating selective processing of stimulus components [53]. The latter study, however, did not include testing for laterality and so far no investigation has been carried out on possible lateralisation of visuospatial behaviour in adult pigeons. Also no study has addressed lateralisation of spatial orientation of birds or any other vertebrate in complex large scale environments.

Thus, the aim of our study was two-fold: first, to obtain information on the possible lateralisation of visuospatial behaviour in pigeons within a complex real world environment; and second, to obtain further information on the role of vision in pigeon homing which is still a matter of discussion [12,58].

Though many details concerning the environmental cues and the mental representations used by homing pigeons remain to be resolved (see Ref. [6] for a recent review), what a pigeon does during a typical homing experiment can be outlined briefly as follows:

When released at a remote site, pigeons depart in a direction which is often close to the homeward direction. This direction is calculated by the pigeons by estimating their displacement using sensory cues (presumably olfactory and/or magnetic ones) and by determining the homeward direction against a general directional reference. If the sun is visible, the position of the sun and an internal clock are used to establish a sun compass, although other compass systems cannot be excluded. As indicated by at least some evidence, homing can be increasingly guided by vision if pigeons are released repeatedly from the same place [7].

Thus, the first important point in the design of our study was that the pigeons should be sufficiently familiar with release site and homeward route since under this condition homing is likely to be at least in part visually guided. To test for visual asymmetry, binocular training was subsequently followed by monocular testing [8]. Monocular occlusion in pigeons allows for selective visual input to the left or right brain hemi-

sphere since fibres of the optic nerve of birds cross almost completely. Thus, both of the pigeon's brain hemispheres can compete freely for control of visually guided behaviour during the binocular training stage of the experiment. If one of the brain hemispheres establishes a more accurate representation of the visual scenery and/or is dominant in the job of handling these visual representations, a clear prediction can be made with regard to subsequent monocular tests: birds using the eye contralateral to the dominant hemisphere should show superior homing performance.

In experiment 1, pigeons learned the route from a release site south-eastern (ESE) from their loft. After establishing left-hemispheric superiority of visually guided homing, experiment 2 was designed to test whether this effect would occur independently of the release site used. Although lateralisation of visuospatial long-term memory was the most likely explanation for the results of experiment 1, several alternatives should be evaluated: (1) when pigeons home on a familiar route from a south-eastern release site at roughly the same time of day (between noon and late afternoon in experiment 1), the sun is predominantly seen by the birds with their left eye; (2) predominant landmarks might be available to a different extent on the left and right side of the direct route to the loft; and (3) the earth's magnetic field, which can provide an alternative cue to sun compass information and landmark based navigation, shows local variability and different average variation along the east–west and the north–south axis. To control for these environmental factors, in experiment 2 pigeons were trained and tested from two new release sites arranged along the north–south axis. Furthermore, experiment 2 provided a serendipitous control for the possible effect of sun-compass information. While the weather was sunny with no or only a few clouds during all tests of experiment 1, there was complete overcast during all tests of experiment 2.

2. Materials and methods

2.1. Experiment 1: south-eastern release site, clear skies

2.1.1. Animals

Forty-one homing pigeons from the breeding stock of the Schweizerische Briefftaubenstiftung SBS were tested, 21 using their right eye during monocular testing and 20 using their left eye. Eighteen birds were born during the years 1993–1996 in Switzerland and were pre-experienced in returning to mobile lofts from different sites [45]. Twenty-three birds hatched in April and early May 1997 at the place of the experiment. The birds were housed in two mobile lofts placed on a large meadow on Bochum University campus. Water was

available ad lib. They were fed a standard pigeon diet once or twice a day. On days of releases regular feeding was done after the birds had returned.

2.1.2. Procedure

After arrival of the mobile lofts at Bochum, pigeons were first habituated to the new site by remaining confined to their loft with access to the wire-mesh outdoor aviary. After 2 weeks, a familiarisation program started during which the birds were brought to nearby release sites up to 7 km and released. Young birds hatched at Bochum were included into the training program as soon as they were independent and commenced regular flights around the loft.

For binocular and monocular releases during the main experiment, pigeons were collected from their lofts in the morning and put in pigeon baskets with free circulation of air. They were brought by car to a release site ESE from Bochum near the city of 'Iserlohn' (distance 32 km, homeward direction 300° with regard to north). Birds were released in groups of five to ten on the first binocular releases, then pairwise, and finally, for three to four releases, singly. The total number of binocular training releases per bird was 10.1 ± 0.27 (mean \pm SEM).

Birds then made a binocular and subsequently a monocular test release. For monocular testing, eyecaps were adjusted 1 day or several days before a test, and after fixing the eyecaps birds made a test flight around the loft. If they could fly and orient without problems, they were considered for a test release. The eyecap was removed and fitted again when the birds were collected for the test. Older birds had been adjusted to eyecaps in Switzerland before transport to Bochum in order to prevent a conditional discrimination of location and eyecap condition. The eyecaps were circular caps of cardboard (diameter 25 mm). They were fixed to a ring of Velcro that was attached to the skin around the eye by means of a non-toxic and water-soluble glue after clipping a circular strip of feathers. When birds had entered the loft after a monocular test, eyecaps were removed by the experimenter. All birds for which exact homing times are available were observed arriving with eyecaps fitted. Two birds who came late and were checked the next morning had their eyecaps off, but the eyecaps were found at the loft (eyecaps were labelled with the birds' numbers). Thus, all birds made the homeward journey with eyecaps on.

Before training and test flights, birds stayed at the release site for at least 30 min and were then released singly by tossing them randomly from the hand of the experimenter. Vanishing bearings were taken by observing the pigeons with 10×40 glasses using a standard procedure. Vanishing times were taken as the times between releasing the birds and disappearing from the release site. An observer at the loft checked the incom-

ing individuals which were labelled by a unique pattern of coloured leg rings. Arrival of individual birds at the loft was electronically measured using a TIPES™ system. Since all birds entered the loft promptly after returning, performance scores are based on electronically measured times. Binocular releases were carried out during July and August 1997 and subsequent monocular tests on August 25, 27 and 31. Different subgroups of birds were released on each monocular test day. During the binocular and monocular tests weather conditions were similar, with bright sunny weather, no or only a few clouds, and a light to moderate wind from SE to SSE.

2.1.3. Statistics

Average vanishing directions were calculated as mean direction and angular deviation. The preference for the mean direction by birds of a certain group is indicated by mean vector length. Significant preferences for the homeward direction were evaluated with *V*-tests and differences between the experimental groups were assessed using Watson's *U*²-test [4]. Vanishing times and homing times were calculated as mean \pm SEM. Mean vanishing times during monocular tests were compared by one way-ANOVA. Homing times were analysed by three-way ANOVA (release date \times group \times test; group = tested on left or right eye; test = repeated measure binocular versus monocular test) followed by planned comparisons (Fisher's LSD) between the experimental groups (left eye/right eye) in the binocular and monocular tests, and between the binocular and monocular test for each group.

2.2. Experiment 2: northern and southern release site, overcast

2.2.1. Animals

Like in experiment 1, pigeons from the breeding stock of the Schweizerische Brieftaubenstiftung SBS were used. Birds were housed in two mobile lofts at the same site as in 1997 and, again, about half of the birds were experienced birds hatched in the years 1993–1997 and the other birds hatched in spring 1998 at the site of the experiment. Pretraining and feeding were done as in 1997.

2.2.2. Procedure

Training from the release site of the main experiment and testing were done as in experiment 1 except for that two new release site along the north-south axis were used. The northern release site was between the cities of 'Haltern' and 'Recklinghausen' (distance to the loft 25 km, homeward direction 170°) and the southern release site was near the city of 'Wuppertal' (24 km, 8°). In contrast to the weather conditions during experiment 1, on both test days there was complete overcast with

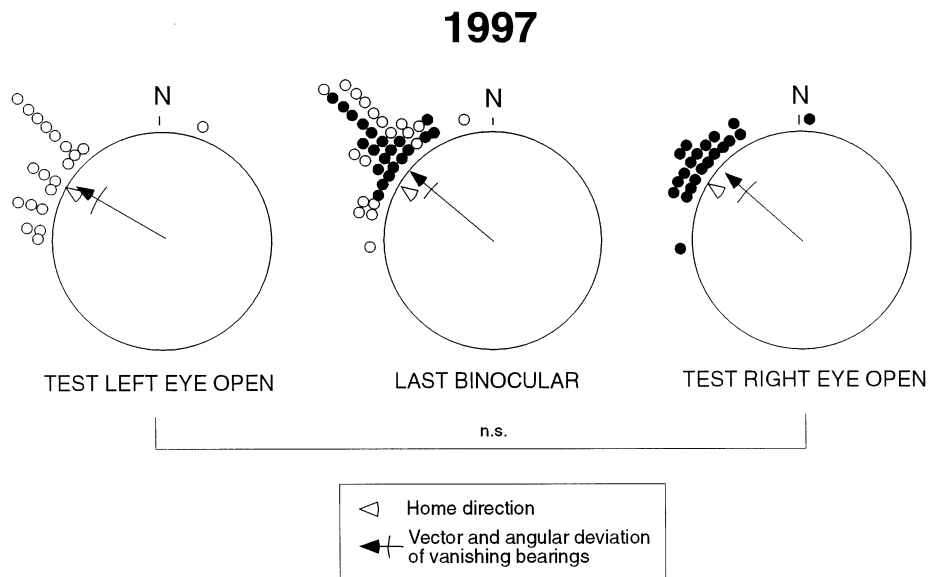


Fig. 1. Vanishing bearings during last binocular release and monocular test release from south-eastern release site under clear skies. Individual vanishing points are indicated by small circles. There were no differences between the left eye (open circles, $n = 20$) and right eye (filled circles, $n = 21$) group during binocular and monocular test flights. A significant preference for the homeward direction was present in both groups during binocular as well as monocular testing (all: $P < 0.0001$). N = north. Azimuth of the home direction (open arrowhead) = 300° . Vector diagrams by program VECTOR ROSE 3.0™ (P.A. Zippi, PAZ Software, Garland, Texas, paz@airmail.net).

spells of rain. Tests were carried out on August 25 (binocular) and August 27 (monocular), simultaneously from the northern and southern release site.

2.2.3. Statistics

The same statistics were used as for the data of experiment 1, with two exceptions: In one case (left eye group, monocular test flight) where no significant preference for the home direction was found in the V -test, a Rayleigh test was used to evaluate whether there was any directional preference at all. As all birds performed the binocular or monocular test on the same day, but from two different release sites, design of the three-way ANOVA analysing homing times was release site \times group \times test (release site = northern vs. southern release site; group = tested on right vs. left eye; test = binocular vs. monocular test flight (repeated measure)).

3. Results

3.1. Experiment 1: south-eastern release site, clear skies

Results from the tests on different days showed a similar pattern with regard to measured parameters and were thus combined for further analysis. On monocular test flights, birds equipped with eyecaps flew without visible problems. Usually, they approached the loft with high speed without circling over the loft before landing. They landed on the loft very precisely (smooth landing

on top of the aviary with maximum distance of 150 cm to the entrance), even if their last turn was toward the covered eye.

During binocular and monocular tests, most of the birds took a vanishing direction close to the homeward direction (300°). Birds tested with their right eye ($n = 21$) vanished in a mean direction of 312° (angular deviation: 9.8° , mean vector length: $r = 0.986$) on the last binocular release and 312° (19.7° , $r = 0.943$) on the monocular test release. In birds tested with their left eye, the respective values are 309° (19.3° , $r = 0.945$) on the last binocular release ($n = 19$, one missing value) and 306° (23° , $r = 0.923$) on the monocular test release ($n = 20$). Analysis of vanishing bearings revealed no significant difference between pigeons using the left or the right eye (Watson's U^2 -test, $U^2 = 0.069$, $P > 0.5$) and a significant preference for a vanishing direction close to the homeward direction in both groups under the binocular as well as under the monocular condition (V -tests, all: $P < 0.0001$, Fig. 1).

Birds using their right eye ($n = 21$) vanished after 2.9 ± 0.32 min whereas individuals using their left eye ($n = 20$) were out of sight after 4.1 ± 0.75 min. This difference is not significant ($F_{1,39} = 2.215$, $P > 0.1$).

Except for one bird (left eye seeing), all birds returned home. Two pigeons (one per group) came back late after end of electronic time measuring. Thus, exact homing times are available for 38 birds. Homing times (Fig. 2) of birds using their right eye were 55.2 ± 8.1 min. They are somewhat (36%) longer than on the last binocular release (40.3 ± 2.8 min). By contrast, homing

times of pigeons using the left eye (116.7 ± 25.7 min) were more than twice as long as in the right eye group as well as in comparison to the last binocular release of the same birds (129%). Three-way ANOVA revealed no significant main effect of release date ($F_{2,32} = 0.009$, $P > 0.9$), a significant main effect of experimental group ($F_{1,32} = 6.306$, $P < 0.025$), and a significant difference between binocular and monocular tests ($F_{1,32} = 5.966$, $P < 0.025$). There were no significant interactions of release date \times group ($F_{2,32} = 0.128$, $P > 0.8$), release date \times test ($F_{2,32} = 0.323$, $P > 0.7$), and no significant three-way interaction ($F_{2,32} = 0.128$, $P > 0.8$). There was a trend for an interaction experimental group \times test ($F_{1,32} = 2.261$, $P < 0.1$). Planned pairwise comparisons show a significant difference in birds using their left eye between the binocular and monocular test ($P < 0.01$), but not in birds using their right eye ($P > 0.4$), and a significant difference between both experimental groups in the monocular test ($P < 0.025$), but not in the binocular test ($P > 0.6$).

3.2. Experiment 2: northern and southern release site, overcast

Like in experiment 1, birds equipped with eyecaps flew without visible problems. Although the overall pattern of vanishing bearings from both release sites was similar, there appeared a slight difference in the divergence of the monocular groups (Fig. 3). Therefore, vanishing bearings were analysed separately for the northern and southern release site. As both comparisons between the left eye and right eye group tested the same hypothesis, a sequential Bonferroni correction (Dunn–Sidak method) was used. Vanishing times and

homing times showed no difference between both sites and were combined for further analysis. Except for three pigeons (two using their left eye, one using the right eye), all subjects returned home. After excluding birds returning late after end of electronic time measuring from homing times analysis and those without vanishing bearings in both tests from analysis of vanishing bearings, a data set of 47 pigeons (northern release site: using left eye $n = 13$, right eye $n = 11$; southern release site: left eye $n = 12$, right eye $n = 11$) was available for analysis of vanishing bearings and vanishing times, and of 42 pigeons (left eye $n = 24$, right eye $n = 18$) for evaluation of homing times.

From the northern release site (home direction 170°), birds of the left eye group vanished in a mean direction of 215° on the binocular test (24.5° , $r = 0.819$, V -test: $u = 2.9516$, $P < 0.005$) and birds of the right eye group had a mean vanishing bearing of 230° (35.5° , $r = 0.808$, $u = 1.8946$, $P < 0.05$). During monocular testing, birds of the left eye group disappeared in a mean direction of 154° (21.3° , $r = 0.931$, $u = 4.562$, $P < 0.0001$) and in birds of the right eye group the mean direction was 194° (47.2° , $r = 0.660$, $u = 2.828$, $P < 0.005$). While there was no difference between the left eye and right eye group in the binocular test ($U^2 = 0.0274$, $P > 0.5$), a significant difference was present in the monocular test ($U^2 = 0.1999$, $P < 0.05$).

From the southern release site (home direction 8°), birds of the left eye group vanished in a mean direction of 341° on the binocular test (50.0° , $r = 0.620$, $u = 2.7055$, $P < 0.005$) and birds of the right eye group had a mean vanishing bearing of 346° (35.0° , $r = 0.813$, $u = 3.5365$, $P < 0.0001$). During monocular tests, birds of the left eye group disappeared in a mean direction of 289° (29.4° , $r = 0.869$). There was no significant preference for the homeward direction ($u = 0.8120$, $P > 0.1$), but a significant preference for the mean direction (Rayleigh test: $z = 9.062$, $P < 0.001$). In birds of the right eye group the mean direction was 2° (56.8° , $r = 0.508$, $u = 2.3716$, $P < 0.01$). While there was no difference between the left eye and right eye group in the binocular test ($U^2 = 0.0659$, $P > 0.5$), a significant difference was present in the monocular test ($U^2 = 0.3961$, $P < 0.001$).

Birds using their left eye ($n = 25$) vanished after 3.2 ± 0.68 min whereas pigeons using their right eye ($n = 22$) were out of sight after 2.3 ± 0.21 min. This difference is not significant ($F_{1,45} = 1.260$, $P > 0.25$).

Homing times (Fig. 4) of birds using their right eye were 41.0 ± 5.0 min during binocular testing and 63.7 ± 9.9 min on the monocular test (+ 55%). Homing times of pigeons using their left eye (102.5 ± 18.4) were much longer than in the right eye group as well as in comparison to the last binocular release of the same birds (39.0 ± 4.1 min, + 163%). Three way ANOVA revealed no significant main effect of release site

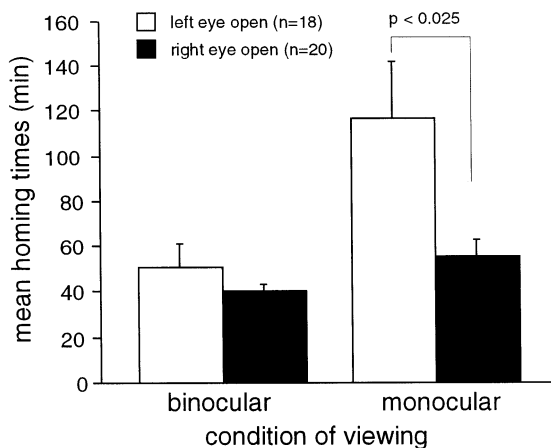


Fig. 2. Homing times from last binocular release and monocular test release. Mean and SEM. Homing times of birds using the right eye ($n = 20$) were somewhat, but not significantly higher as compared to binocular performance, whereas homing times of pigeons seeing with their left eye ($n = 18$) were more than twice as high as compared to binocular performance ($P < 0.01$). Left eye and right eye group differ significantly on the monocular test ($P < 0.025$).

($F_{1,38} = 0.196$, $P > 0.6$), and no significant interactions of release site \times group ($F_{1,38} = 0.366$, $P > 0.5$), release site \times test ($F_{1,38} = 0.000$, $P > 0.9$) as well as no significant three-way interaction ($F_{1,38} = 0.508$, $P > 0.4$). There was a trend for a main effect of experimental group ($F_{1,38} = 2.227$, $P < 0.1$), a significant difference between binocular and monocular test ($F_{1,38} = 14.067$, $P < 0.0001$), and a significant interaction group \times test ($F_{1,38} = 3.207$, $P < 0.05$).

Planned pairwise comparisons showed a significant difference in birds using their left eye between the binocular and monocular test ($P < 0.01$), but not in birds using their right eye ($P > 0.2$), and a significant

difference between both experimental groups in the monocular test ($P < 0.025$), but not in the binocular test ($P > 0.9$).

4. Discussion

Results from both experiments showed that pigeons homing monocularly on a familiar route evinced a considerable increase in homing times if using the left eye. This pattern emerged similarly under different environmental conditions (release site, weather). Whether the direction of vanishing differs between

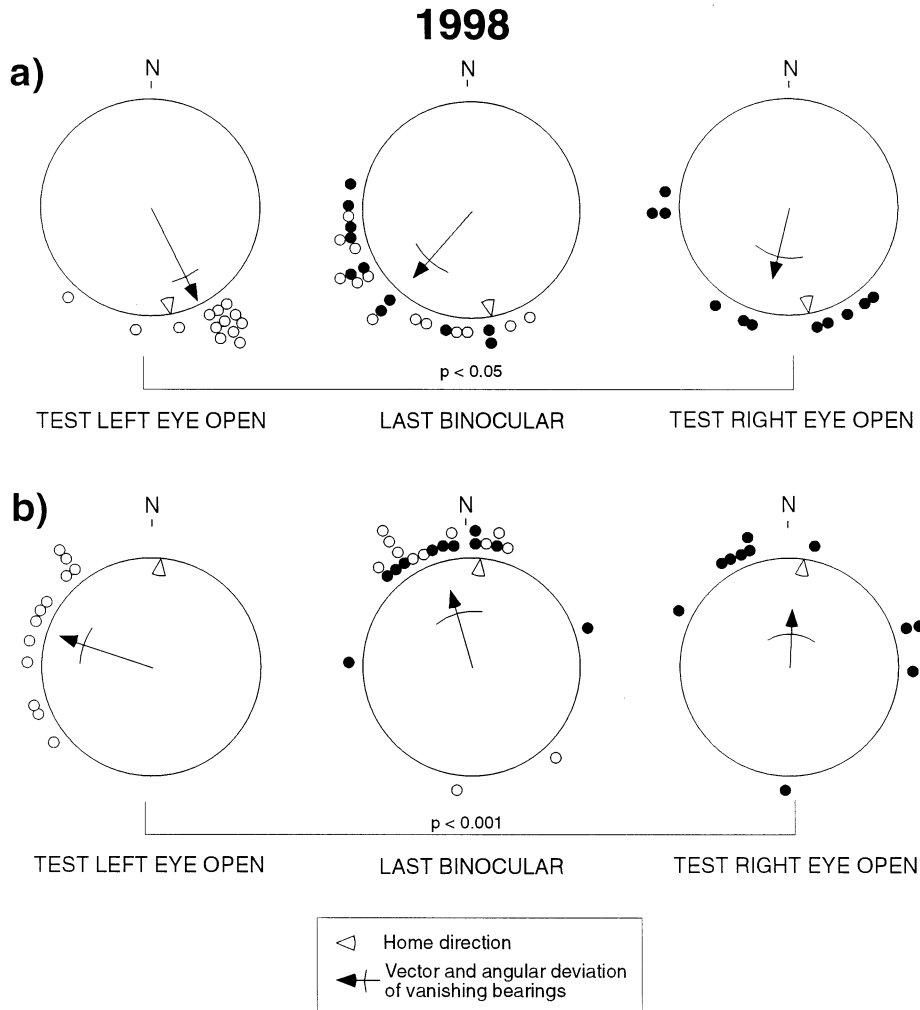


Fig. 3. Vanishing bearings during last binocular release and monocular test release from northern (a) and southern (b) release site under overcast. Individual vanishing points are indicated by small circles. (a) Northern release site, homeward direction (open arrowhead) = 170° . While there was no difference between both groups during binocular testing, a difference in directional preference between the left eye (open circles, $n = 13$) and right eye (filled circles, $n = 11$) group occurred during monocular testing ($P < 0.05$). Both groups had a significant preference for the homeward direction during binocular (left eye: $P < 0.005$; right eye: $P < 0.05$) as well as monocular testing (left eye: $P < 0.0001$; right eye: $P < 0.005$). (b) Southern release site, homeward direction (open arrowhead) = 8° . Whereas there was no difference between both groups on the binocular test flight, a difference between the left eye (open circles, $n = 12$) and right eye (filled circles, $n = 11$) group emerged on the monocular test ($P < 0.001$). Both groups had a significant preference for the homeward direction on the binocular test while on the monocular test only the right eye group significantly preferred the home direction. Birds using their left eye had, however, a significant preference for this group's mean direction ($P < 0.001$). N = north.

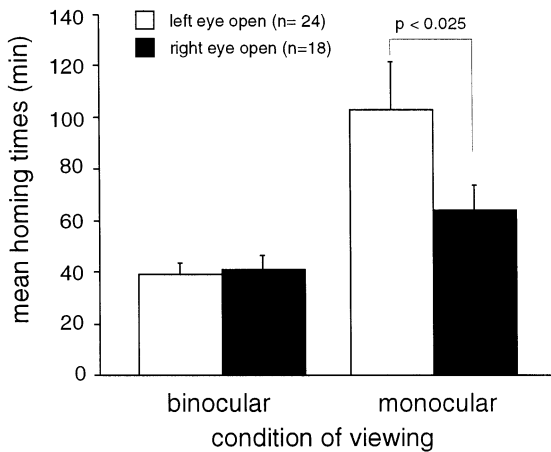


Fig. 4. Homing times from last binocular and monocular test releases. Mean and SEM. Homing times of birds using the right eye ($n = 18$) were somewhat, but not significantly higher as compared to binocular performance, whereas homing times of pigeons seeing with their left eye ($n = 24$) were more than twice as high as compared to binocular performance ($P < 0.0002$). Left eye and right eye group differed significantly on the monocular test ($P < 0.025$).

birds using their left or right eye appears to depend on environmental factors.

Consistent with findings from earlier studies which manipulated visual input in homing pigeons [49,50] results hint at two different and partially independent mechanisms contributing to homing performance. The first is a sun compass which is not visually lateralised. The second mechanism is lateralised and vision-based. It facilitates homing while tracking the route and/or while approaching the loft.

A role for vision under conditions of familiarity is supported by studies which used the method of pre-viewing familiar landscapes [9–12] or other controls for visual information [26,58]. Whereas the support for the use of visual cues might sometimes be confounded by experimental co-manipulation of other sensory input [12], the present findings provide methodologically independent and rather clear-cut evidence since they are based on different conditions of visual input. The slight difference between binocular and right eye performance is consistent with earlier findings on complex visual behaviour in birds indicating that co-operation of the neural systems fed by both eyes yields the best results [20,57,61].

4.1. Visual lateralisation during homing

The main effect of the present study is a lateralisation of homing times. The difference in homing times could have arisen at different stages of the journey. If birds had flown directly to the area of their loft by means of non-visual cues and then—after visually recognising the loft—had steered directly towards it, the difference between the experimental groups could be due to a

combination of dead reckoning [23] and use of landmarks near the loft. However, though not reaching significance, the difference in vanishing times between pigeons using their right eye and those using their left eye (experiment 1: +41%; experiment 2: +43%) rather indicates that a factor in favour of the right eye system was already present at the release site. This suggests that pigeons were using visual information derived from topographical cues along the whole homeward route and were thus relying on a navigational process generally referred to as familiar landmark navigation [6].

At the present stage of knowledge, two types of visual cognitive processes are likely candidates which might—alone or together—account for left-hemispheric superiority for visual orientation during homing: (1) processing of direction information related to landmarks; and (2) visual ‘snapshot’ memory for landmarks and landscapes.

(1) The importance of directional information for spatial orientation in pigeons was demonstrated in the field [59,63] as well as in laboratory studies [13–17,51,52,64]. As laboratory studies [15,16] indicate use of directional information also in small-scale environments well known to the birds, directional information could play an important role for vision in the loft area only or along the whole route. Therefore, left-hemispheric superiority for visually guided homing might indicate lateralised processing of directional information in birds and perhaps other vertebrate species, including humans [38].

(2) In addition or alternatively, pigeons might have memorised multiple locations along the homeward route and the loft area by taking ‘snapshots’ and forming associations between these snapshots and the homeward direction (using their sun compass or magnetic compass as reference). It can be assumed that compass readings are available continuously so that every ‘snapshot’ can be associated with unique directional information. Left-hemispheric superiority in homing performance would then be due to left-hemispheric specialisation for visual long-term memory of landmark features. Regarding the direction of lateralisation, this interpretation is fairly consistent with results showing left-hemispheric superiority for visual long-term memory for complex patterns in discrimination learning [57]. High capacity of the pigeon’s memory for such patterns [56] and the pigeon’s ability to discriminate two-dimensional stimuli (photographs) showing familiar places [62] are consistent with a role of this cognitive feat in visually guided homing. Since pigeons in the present study were trained for a sufficient number of times on the homeward route, a stable, long-lasting memory for topographical cues could have been formed and stored predominantly in the left brain hemisphere. If so, in terms of the direction of lateralisation, present results

would square quite well with findings in food-storing birds which showed a right-hemispheric preference for spatial memory after a short retention interval of 5 min [19], but a left-hemispheric advantage after long-term memory formation (e.g. 24 h retention interval) [18]. Thus, remembrance of cache sites in food-storing birds and of landscape features in homing pigeons would both involve visual long-term memory processes primarily left hemisphere based. Superiority of the left brain hemisphere in avian visual long-term memory is also indicated by findings of unilateral memory and unilateral memory transfer to the left hemisphere in chicks [3,24,25]. As in chicks [21], a possible neuronal basis of lateralised representation in pigeons is an asymmetric organisation of the visual system [31].

4.2. Sun compass information

The most likely account for the lateralisation difference in vanishing bearings between experiments 1 and 2 is the availability of sun compass information in experiment 1 (clear skies), but not in experiment 2 (complete overcast). This suggests that under clear skies a highly precise compass orientation can be established via either eye and hence by either brain hemisphere. Under overcast, pigeons have to rely upon alternative compass mechanisms as well as to a higher degree upon visual information stemming from the surrounding landscape. Compared to the mean direction of both monocular groups, birds using their left eye slightly deviated to the left side and vice versa. Compared to the home direction, mean orientation of birds homing from the southern release site (Fig. 3(b)) was close to the direction of the loft. This should, however, not be taken as better orientation in birds using their right eye, since left monocular and binocular data suggest a general release site bias towards the left side. As under overcast, in monocular indoor experiments birds often show a slight turning bias towards the open eye. The sun compass can obviously completely suppress this tendency, regardless of whether the right or the left brain hemisphere controls behaviour.

4.3. Future perspectives

Homing in pigeons is a complex process requiring the integration of sensory, motivational and environmental factors. For example, homing performance can vary according to weather conditions and peculiarities of individual release sites. Successful replication of the main findings from experiment 1 in the second experiment in which several environmental variables differed, indicates a fairly robust effect of lateralised visual input on overall homing performance. A next important step in analysing the underlying cognitive processes will be a more detailed analysis of homing patterns using ad-

vanced route recording techniques. This will permit to observe the part of the home route in which the pigeons using the left eye only have difficulties. Similarly, it might be of interest to test homing at night, when pigeons returning on familiar routes appear to use little visual information [44].

5. Conclusions

To summarise, the results of this study provide the first evidence for a left-hemispheric superiority for visuospatial orientation during piloting in homing pigeons and lend further support to the view that vision is used by pigeons when orienting in familiar areas. Together with recent studies on humans and rats [43], present findings indicate that the notion of right-hemispheric superiority for 'spatial' memory or behaviour should be reconsidered and replaced by models considering different visuospatial processes which may constitute different patterns of lateralisation depending on task and species.

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