

Research report

# Effects of monocular viewing on orientation in an arena at the release site and homing performance in pigeons

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## Abstract

Orientation and homing performance of pigeons with the left or right eye occluded were assessed in an arena at the release site and during the subsequent homing flight. Three release sites near Pisa, Italy, were used. Compared to binocular controls, monocular birds showed a bias in orientation towards the side of the viewing eye. In the arena, this bias was considerable and the mean deviation corresponded to the angle of the optical axis, suggesting a systematic error in visual representation during directional orientation. During flight after leaving the arena the directional bias decreased and the homeward orientation increased. While there was a slight lateralization of overall homing performance in favour of the right eye, there was no lateralization in directional orientation in the arena or at vanishing. Our results show that navigational mechanisms in either brain hemisphere profit from information obtained before take off and while flying over the release site. The existence and degree of lateralization is discussed in comparison to other studies that investigated homing under monocular viewing conditions. © 2002 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

Most studies on bird navigation have adopted one of two standard methods. They investigated how pigeons home from remote release sites, or they tested the behaviour of migratory birds in orientation cages. These studies have revealed a host of intriguing facts, in particular, regarding the cues and the sensory systems involved in navigation. So far, however, they have provided little insight into how and where the avian brain processes information during homing or migration. During the past years two methods have, nevertheless, led to some advancement in the understanding of the neural basis of avian navigation.

The first approach used targeted brain lesions. By investigating the effects of lesions to brain regions that

are promising candidates for navigation information processing it was evaluated which brain regions might compute certain components of homing behaviour. The most clear-cut findings concerned the piriform cortex and the avian hippocampus. After ablation of the piriform cortex both the learning [9] and the operation [17] of the navigational map were disrupted. Lesions of the hippocampal formation have suggested that this region is involved in spatial learning based on visual landmarks [2,25]. Furthermore, specific aspects of spatial information processing were separated. Pigeons with hippocampal lesions were capable of using landmark information to recall the home direction as a compass bearing, but they could not use visual landmarks at the release site to establish the home direction directly from landmark information [10].

The second approach was testing for cerebral lateralization by means of monocular occlusion. The fibres of the avian optic nerve cross over completely. Inter-hemispheric commissures are comparatively small, and a corpus callosum, which represents the major connection

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in the forebrain of primates, is lacking. Therefore, visual input into the right eye is mainly processed by the left brain hemisphere and vice versa. By temporarily covering the right or left eye with an eye-cap, the functions of each brain hemisphere can be tested separately. In birds, a number of visual asymmetries have been studied, revealing specializations of either hemisphere for different tasks [13,22,28]. In chicks, studies using this method have suggested right hemispheric processing of topographic information [21]. In food-storing and non-storing passerine birds, there also was a right hemisphere/left-eye preference for using topographical information when retention intervals were brief [6]. With longer retention intervals (24–51 h), in at least one species, the marsh-tit, information was transferred to the right eye/left hemisphere [5]. More recent studies suggest that the right and left brain hemisphere might control different aspects of spatial information processing [26].

In the first study on visual lateralization during spatial orientation in large-scale environments in any vertebrate, Ulrich et al. [27] investigated the influence of monocular occlusion on homing pigeons and found superior performance as measured in homing time when the birds were using the right eye/left hemisphere. In addition, under both monocular conditions pigeons' vanishing bearings deviated to the side of the uncovered eye. A recent study with highly experienced adult and less experienced young pigeons demonstrated similar effects and, furthermore, suggested a strong lateralization of directional orientation. Birds using the right eye were as well directed as BI, while performance of birds using the left eye was considerably poorer [19]. The exact nature of the sensory information acquired with the left or right eye, which is accountable for this lateralization, is not yet known. Also, it is not clear at which stage of the return flight lateralized processing mechanisms come into play. Is there, in accordance with the pigeon's lateralized memory for two-dimensional patterns [29], a lateralized recall of landmark information already before the pigeons take off? Does the deviation towards the side of the open eye depend on the perception of optic flow or other dynamic perceptions that birds acquire during flight? For an understanding of the nature of visual information used by the pigeons at the release site and in order to evaluate the contribution of the left and right brain hemisphere to the processing of this information it would be important to know whether the orienting behaviour of the birds differs between a situation, in which the pigeons can only see a static image of the landscape from a certain viewpoint, and a situation, in which the pigeons fly around, sense optic flow, perceive depth cues like parallax, and see landmarks from different viewpoints.

The present study combines testing for lateralized orientation in an arena and during the homing flight. This allows separating two stages of orientation beha-

viour. In the first stage, pigeons within the arena can view the familiar landmarks at the release site, but only as more or less static images. It is known that previewing the landscape from a confined place at the release site can enhance homing speed [3,4] and affects directional orientation before take off [11]. This suggests that some aspect of visual landmark information is used, but it is not known whether the processing of this information in the pigeon's brain is lateralized. If so, the bearings and/or the take off times in the arena should differ between birds with the left or right eye occluded. During the second stage, the pigeons can see the familiar landmarks from different perspectives by flying around over the release site as soon as they leave the arena. Again, differences in vanishing intervals and bearings between birds with the left or right eye occluded should indicate lateralization of perceptive and cognitive processes crucial during this stage. In addition, any differences in lateralization between measures in the arena and at vanishing will indicate by which time and under which conditions a possible lateralization emerges. To confine the pigeons before departure, we used a circular arena that allowed for a full panoramic view of the surroundings [11,14]. Although pigeons further refine their course after leaving, they tend to be already home directed within the arena.

Since, as predicted by the olfactory navigation hypothesis [16,30], homing pigeons might use olfactory cues for determining the direction of displacement even at familiar locations [11], anosmic pigeons were used in order to increase the probability of visually guided orientation. Moreover, it has been shown that navigation performance of olfactory deprived pigeons is unimpaired at familiar sites [31].

## 2. Materials and methods

Forty-three experienced adult homing pigeons housed in the Arnino Field Station and allowed to perform spontaneous flights were used in the experiment. These birds took part, about 2 months earlier, in another experiment [11]. In that experiment they had been trained to exit from a circular arena [14] and had been tested at three very familiar release sites, all under binocular conditions.

In the present experiment all birds were trained three times from each of these already familiar release sites in flocks before the first test release. Training from the release sites occurred always in binocular condition. Before the tests, all birds were made anosmic by washing their olfactory mucosae with a 4% ZnSO<sub>4</sub>·7(H<sub>2</sub>O) solution, according to the procedure described in Ref. [12]. The birds were released singly from a circular arena (1.8 m diameter) which allows to determine the orientation during take-off. The release procedure and techni-

cal details of the arena are described by Mazzotto et al. [14]. Briefly, the arena consisted of an aluminum frame, which was placed on a rack 1.2 m above the floor. The bottom of the arena was made of opaque plastic. It was covered by a net allowing full sight of the sky. The surrounding edge of the arena consisted of hinge aluminum bars, spaced 20 cm apart, which birds could easily push up when exiting the arena. Each bird was placed in a start booth (30 cm diameter) encircled by a net in the center of the arena. After lifting the net of this enclosure, which was done remotely by an experimenter placed underneath the arena, the bird was free to leave the arena.

Before the experimental releases the birds were prepared to be eye-patched during the experiment. A thin Velcro ring was glued for half of the birds around the left eye and for the other half around the right eye with non-toxic, water-soluble glue after clipping a circular strip of feathers. For the first release, the birds were assigned into a binocular, a monocular left and a monocular right group. Therefore the birds of the binocular group also received a Velcro ring around either their left or right eye. This served as a control for the extra handling involved and a possible inconvenience of wearing such a Velcro ring.

In the first experiment, one third of the pigeons was prevented to see with the right eye by means of right eye-caps (RC), one third was treated with left eye-caps (LC), and one third were BI. Subsequently, each group of pigeons was divided, and in the second and third releases each half of each group was assigned to one of the two visual conditions not experienced before. As a consequence of this experimental plan, each pigeon was tested in three different visual conditions during the three releases.

All the experimental releases took place in sunny conditions, with light wind. Each bird was kept in the release box of the arena for 2 min, which allowed the bird to scan the environment. The bird was then released from the box. The outer part of the arena was logically divided into four quarters, one of them centred on the home direction, and it was recorded, which quarter was entered by the birds immediately after the inner booth opened by lifting the net. The escape bearing was recorded by using a compass referring to the mid-point between the bars lifted by the pigeon. After take-off the pigeon's flight was observed using 10 × 40 binoculars and the azimuth of the vanishing bearing was recorded. Both the time spent by each individual in the arena before taking off and its vanishing time were recorded. If a bird spent more than 15 min before exiting the arena, it was put back to the waiting cage in order to release it later. The homing speed was calculated by recording the time of arrival of each bird at the loft. For each release two bearing distributions were obtained: one referring to the pigeons' directions of take-off when

exiting the arena and the second referring to the birds' vanishing bearings. These distributions were tested for randomness by means of both the V and the Rayleigh test [1]. For each release, between group differences were tested by means of the Kruskal-Wallis ANOVA [24] applied to the angular difference between individual direction of take-off or vanishing bearing and the home direction (to test for group differences in orientation), and to the angular difference between the direction of take-off or vanishing bearing and the group mean direction. Paired group multiple comparisons were performed with the Dunn's test [7]. Group differences in homing performance and vanishing times were also tested using the Kruskal-Wallis ANOVA and the Dunn's test. The directional choices of the pigeons with respect to home (setting the home direction at 360°) in different visual conditions were compared by using the Hotelling test for paired samples of angles [32].

### 3. Results

#### 3.1. Single tests

The data relative to the orientation in the arena are given in Table 1 and Fig. 1. Pigeons in the BI condition displayed a significant orientation in the arena in two out of three releases according to the Rayleigh test, and in all releases according to the V test. Monocular pigeons were generally more scattered than controls: in fact, according to the Rayleigh test, the RC and LC birds were significantly oriented only from La Costanza and Calambrone respectively. In all the releases, the BI pigeons were oriented close to the home direction, while the RC and LC pigeons tended to deviate counter-clockwise and clockwise respectively, depending on the side of the covered eye (see  $\Delta$ BI in Table 1). These differences in the side of the bias were significant at Calambrone ( $P < 0.01$ ) and La Costanza ( $P < 0.05$ ), but not at Arnaccio ( $P > 0.30$ , Fisher's exact tests). However, due to the scattering of the monocular birds distributions, among group differences in orientation with respect to the home direction were not statistically significant (Kruskal-Wallis,  $P > 0.05$  for all releases). Also the dispersion around the mean vector direction did not differ significantly among treatments (Kruskal-Wallis,  $P > 0.05$  for all releases).

A difference in directional orientation was already present in the inner booth of the arena. When the net was lifted, RC and LC birds entered the quarter oriented towards the home direction with the same frequency, but RC birds made their first move more often into the adjacent quarter on the left side of the home direction, whereas LC birds predominantly moved into the adjacent quarter on the right side of the home direction ( $P < 0.02$ , Fisher's exact test).

Table 1  
Directional choices in the arena

| Release                                    | Group | <i>N</i> ( <i>n</i> ) | $\alpha$ | $\Delta$ BI | <i>r</i> | <i>P</i> (R) | <i>P</i> (V) | hc    | at    |
|--|-------|-----------------------|----------|-------------|----------|--------------|--------------|-------|-------|
| Calambrone<br>26/09/2000<br>356°, 7.4 km   | BI    | 9 (9)                 | 347°     |             | 0.68     | *            | **           | +0.67 | 0'03" |
|  | RC    | 15 (15)               | 279°     | −68°        | 0.39     | ns           | ns           | +0.09 | 5'32" |
|  | LC    | 14 (14)               | 083°     | +96°        | 0.50     | *            | ns           | +0.03 | 5'22" |
| Arnaccio<br>27/09/2000<br>270°, 12.7 km    | BI    | 13 (12)               | 259°     |             | 0.60     | *            | **           | +0.59 | 0'03" |
|  | RC    | 11 (11)               | 222°     | −37°        | 0.43     | ns           | ns           | +0.29 | 1'22" |
|  | LC    | 12 (11)               | 339°     | +80°        | 0.48     | ns           | ns           | +0.17 | 3'04" |
| La Costanza<br>29/09/2000<br>185°, 18.1 km | BI    | 10 (10)               | 200°     |             | 0.39     | ns           | *            | +0.38 | 0'03" |
|  | RC    | 11 (11)               | 151°     | −49°        | 0.57     | *            | *            | +0.47 | 2'23" |
|  | LC    | 10 (10)               | 250°     | +50°        | 0.28     | ns           | ns           | +0.12 | 5'23" |

Release site: name of the release site, date of the experiment, home direction and distance; BI, binocular pigeons; RC, right eye-cap; LC, left eye-cap; *N*, birds released; *n*, birds for which the orientation in the arena was recorded;  $\alpha$ , mean vector direction;  $\Delta$ BI, angular difference between  $\alpha$  and the BI mean vector direction; *r*, mean vector length; *P*(R), results of the Rayleigh test; *P*(V): results of the V test; \**P* < 0.05, \*\**P* < 0.01 and \*\*\**P* < 0.001 respectively; hc, homeward component =  $r \cos(\alpha - \beta)$ , where  $\beta$  is the home direction.; at, median time spent in the arena.

The data relative to the time elapsed between the opening of the starting cage and the moment in which the birds took off is shown in Table 1 for each release. The time spent by the pigeons in the arena before exiting is significantly different among groups in all releases (Kruskal-Wallis: Calambrone, *P* < 0.001; Arnaccio, *P* < 0.005; La Costanza, *P* < 0.05). The two groups of monocular pigeons spent a longer time in the arena than the BI birds (Dunn's test: RC vs. BI and LC vs. BI, *P* < 0.05; RC vs. LC, *P* > 0.05).

The orientation data at vanishing are reported in Table 2 and Fig. 2. At vanishing the pigeons were significantly oriented according to both the Rayleigh

and the V test in all visual condition in the three tests. Moreover in all releases the three groups showed a similar degree of dispersion around the mean vector direction (Kruskal-Wallis, *P* > 0.05). Similarly to what happened in the arena, also at vanishing RC pigeons tended to deviate towards the left and LC pigeons towards the right as compared to the mean direction of the binocular group. The bias in turning to the left or right side was significant at Calambrone (*P* < 0.005) and Arnaccio (*P* < 0.001), but not at La Costanza (*P* > 0.40, Fisher's exact tests). However, angular differences between vanishing bearings of monocular and binocular pigeons and home direction were small and the orienta-

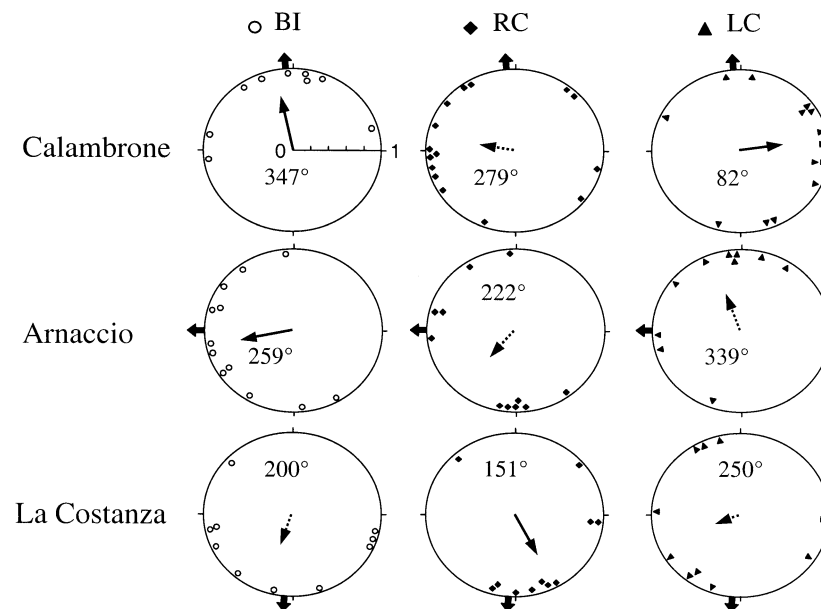


Fig. 1. Orientation in the arena at the release sites of Calambrone, Arnaccio, and La Costanza. Small symbols (circle, diamond, triangle) refer to individual bearings. BI, binocular controls; RC, cap on the right eye, left eye viewing; LC, cap on the left eye, right eye viewing. The arrow in the centre of each plot gives the direction and the length (full radius = 1.0) of the mean vector. Solid arrows indicate significant directedness of the group (dashed arrows, not significant). The arrow at the outer line of the plot indicates the home direction.

Table 2  
Orientation at vanishing

| Release                                    | Group | N (n)   | $\alpha$ | $\Delta$ BI | r    | P(R) | P(V) | hc    | vt    |
|--|-------|---------|----------|-------------|------|------|------|-------|-------|
| Calambrone<br>26/09/2000<br>356°, 7.4 km   | BI    | 9 (9)   | 340°     |             | 0.95 | ***  | ***  | +0.92 | 2'01" |
|  | RC    | 15 (15) | 324°     | -16°        | 0.87 | ***  | ***  | +0.74 | 2'44" |
|  | LC    | 14 (14) | 004°     | +24°        | 0.86 | ***  | ***  | +0.85 | 2'19" |
| Arnaccio<br>27/09/2000<br>270°, 12.7 km    | BI    | 13 (13) | 262°     |             | 0.81 | ***  | ***  | +0.81 | 3'15" |
|  | RC    | 11 (11) | 224°     | -38°        | 0.85 | ***  | **   | +0.59 | 3'43" |
|  | LC    | 12 (12) | 319°     | +57°        | 0.93 | ***  | **   | +0.61 | 3'23" |
| La Costanza<br>29/09/2000<br>185°, 18.1 km | BI    | 10 (10) | 215°     |             | 0.98 | ***  | ***  | +0.85 | 2'18" |
|  | RC    | 11 (11) | 198°     | -17°        | 0.98 | ***  | ***  | +0.95 | 3'24" |
|  | LC    | 10 (9)  | 229°     | +14°        | 0.87 | ***  | **   | +0.63 | 3'14" |

Vt, median vanishing time. For the other abbreviations see Table 1.

tion with respect to the home direction was significantly different among groups only in the test at Calambrone (Kruskal-Wallis,  $P < 0.05$ ).

The pigeons in the three visual conditions took a similar amount of time in vanishing in the tests at Calambrone and Arnaccio (Kruskal-Wallis,  $P > 0.05$ ). On the contrary, at La Costanza the vanishing times were different among treatments (Kruskal-Wallis,  $P < 0.05$ ). In particular, the RC pigeons were significantly slower in vanishing than the BI birds (Dunn's test, RC vs. BI,  $P < 0.05$ ; RC vs. LC,  $P > 0.05$ ; LC vs. BI,  $P > 0.05$ ).

The homing performance differed among treatments in all releases (Kruskal-Wallis,  $P < 0.05$ ; Fig. 3). All the BI pigeons homed, while a few birds released in the monocular condition were lost in each experiment (see Fig. 3 for details). In the tests at Calambrone and La

Costanza, only the RC pigeons displayed significantly poorer homing performances than the BI birds (Dunn's test: RC vs. BI,  $P < 0.05$ ; LC vs. BI  $P > 0.05$ ). In the test from Arnaccio, both monocular groups performed worse than controls (Dunn's test,  $P < 0.05$ ).

### 3.2. Pooled data

The directional choices in the arena were pooled setting the home direction equal to 360°. The distributions and the relative mean vectors of the pigeons tested in the three visual conditions are reported in Fig. 4a.

When tested without eye-caps the pigeons were significantly oriented in a direction close to the home direction (Rayleigh test,  $P < 0.001$ ; V test,  $P < 0.001$ ,  $hc = +0.54$ ). Although the same pigeons when tested under RC condition displayed a counter-clockwise

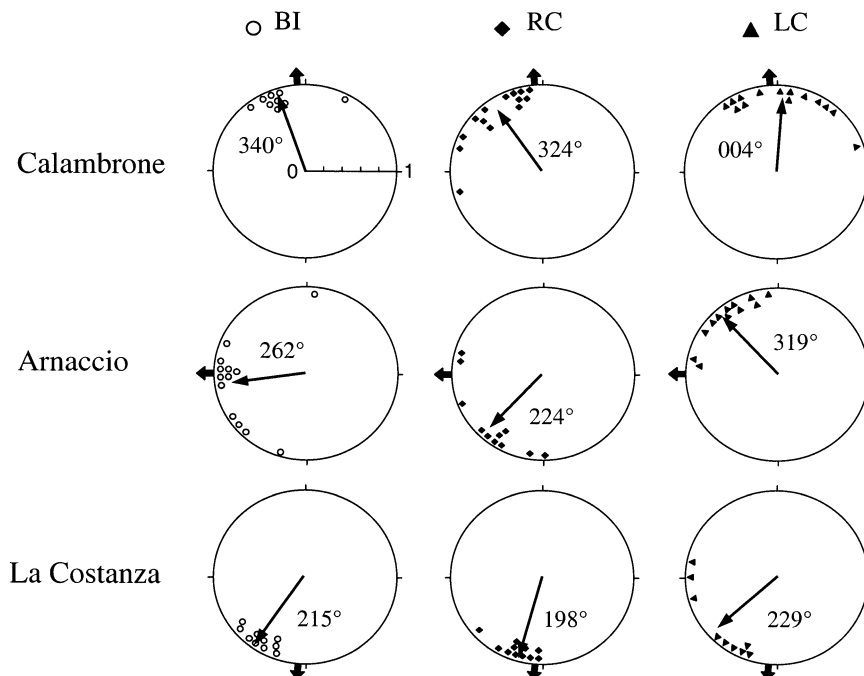


Fig. 2. Vanishing bearings at the release sites of Calambrone, Arnaccio, and La Costanza. Details as in Fig. 1.

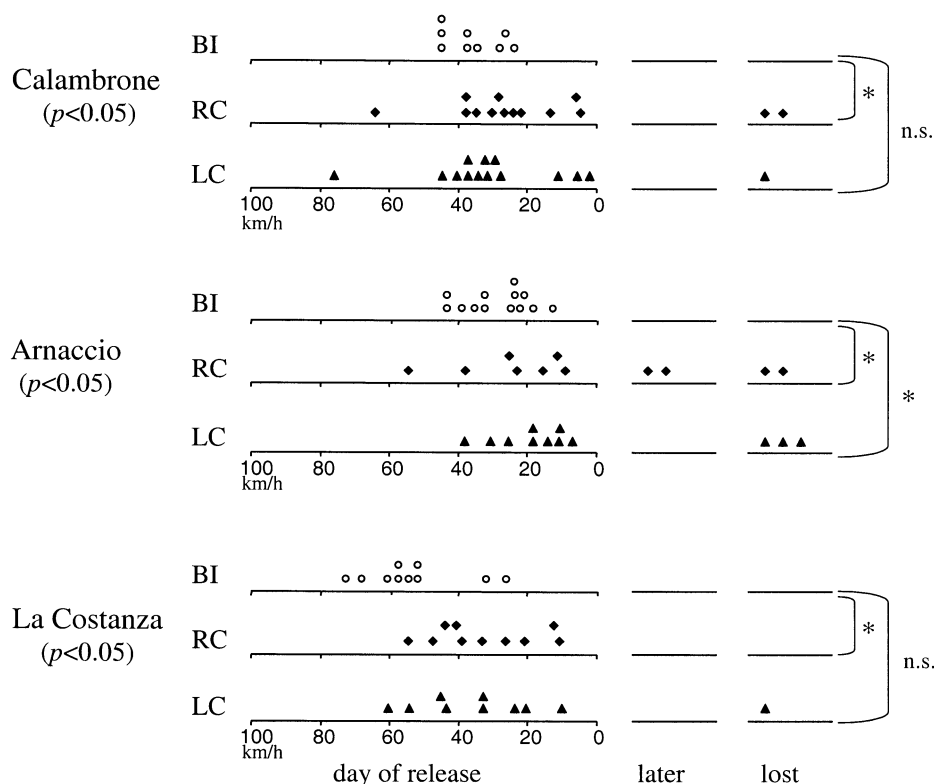


Fig. 3. Homing performance at the three release sites. Left parts of the plot show number and homing times of birds returned on the day of release; the middle parts show the number of birds arriving during the following days; the right parts show the number of lost birds. Birds with a cap on the right eye were slower than BI on all releases, while birds with the left eye covered only differed from controls at the site of Arnaccio.

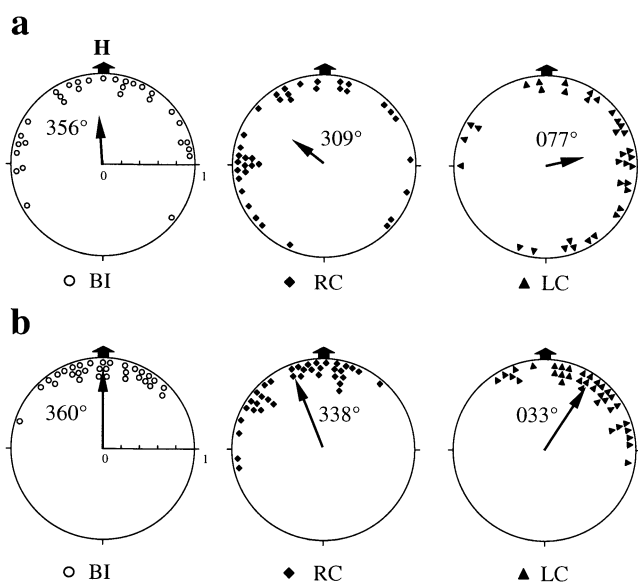


Fig. 4. Data on orientation in the arena (a, top) and during vanishing (b, bottom) pooled over all releases. Other detail as in Fig. 1.

deviation ( $-47^\circ$ ) with respect to the orientation in the BI condition, they were significantly oriented both according to the Rayleigh ( $P < 0.001$ ) and the V test ( $P < 0.01$ ,  $hc = +0.35$ ). When tested under LC condition, these birds deviated clockwise as compared to their

orientation under BI condition ( $+80^\circ$ ). The LC distribution turned out to be significantly oriented according to the Rayleigh test ( $P < 0.01$ ), but not according to the V test ( $P > 0.05$ ,  $hc = +0.10$ ) which takes into account the home direction. Comparing the two monocular conditions, pigeons showed a greater deviation when tested in the LC condition than when tested in the RC condition.

However the Hotelling test for paired data revealed a significant effect of the monocular occlusion on the orientation of the pigeons in the arena in both visual conditions (LC vs. BI  $P < 0.005$ ; RC vs. BI  $P < 0.05$ ).

The effect of the monocular treatment on the amount of time spent by the pigeons in the arena before take off was tested by means of the analysis of variance for repeated measures, by pooling the data relative to the three experimental tests. In accordance to what emerged from single releases, the pigeons spent different amounts of time in the arena depending on their visual condition (Friedman repeated measures ANOVA on ranks,  $P < 0.001$ ). In particular, the pigeons were slower in exiting the arena when tested in monocular condition if compared to the BI condition (Student-Newman-Keuls test: RC vs. BI,  $P < 0.05$ ; LC vs. BI,  $P < 0.05$ ; RC vs. LC,  $P > 0.05$ ).

The BI, RC and LC distributions, obtained by pooling the vanishing bearings with respect to the

home direction, and the relative mean vectors are reported in Fig. 4b.

Looking at the distributions at vanishing it can be observed that the deviation produced in the arena by the monocular occlusion still persists, but to a lesser extent. Interestingly, the Hotelling test for paired data revealed a significant difference in orientation with respect to the control condition only by consequence of the monocular vision with the right eye (BI vs. LC  $P < 0.025$ ; BI vs. RC  $P > 0.05$ ). Not surprisingly the initial orientation distributions relative to the LC and RC conditions were significantly different (Hotelling test for paired data,  $P < 0.001$ ). On the contrary, the monocular treatments seem not to have affected the vanishing time, according to the Friedman repeated measures ANOVA on ranks ( $P > 0.10$ ).

#### 4. Discussion

Results demonstrate a profound effect of monocular occlusion at all stages of homing. Pigeons with one eye occluded took longer than BI to depart from the arena and showed an orientation bias towards the side of the uncovered eye. This directional bias was already present when the birds entered the arena from the small circular cage in the centre of the arena. During the time between leaving the arena and vanishing, the systematic bias decreased and homeward orientation increased. The degree of the orientation bias at vanishing was the same in each eyecap treatment. Until vanishing, monocular birds took longer than BI. BI homed faster than birds with one eye occluded. Although the difference between controls and birds with caps on the right eye was significant on all releases, while LC birds differed from controls only once, there was no lateralization in any of the parameters based on direct comparisons of the monocular groups. Thus, a strong lateralization of overall homing performance that had been observed in earlier studies in Germany [19,27] was not found in the present study. Thus, the main questions are (1) what caused the strong systematic deviation during initial orientation, (2) which factors led to a better homeward orientation after leaving the arena, and (3) what might be the critical factors that led to a strong lateralization of directional orientation at the release site and a moderate lateralization in homing speed in some experimental conditions but not in others.

##### 4.1. Directional bias in the arena

Although deviating from homewards, the orienting behaviour of the pigeons within the arena was different from random. The mean directions of birds with the right and the left eye covered deviated to opposite sides, but to approximately the same degree. If the mean

directions of the birds from either treatment are combined, the mean bearing is not distinguishable from the home direction or the direction taken by BI. Apparently, the direction of monocular arena bearings is the resultant of two factors, one that enables the pigeons to determine the home direction, and a second one that leads to a systematic bias. What was the nature of the first process? In anosmic pigeons, orientation in an arena is homeward directed, if the birds can see the surrounding landscape, but is scattered randomly when the view of the landscape is screened [11]. Thus, the birds were relying on visual cues related to landmark features when they determined the home direction. In principle, they can use the view of the surrounding at the release site and 'en route' either determine a landmark placed about in the home direction or, more probably, recognise the release site and recall the home direction. In both cases they will head in a specific direction and it is at this stage that a systematic deviation occurs. During 'normal' binocular flight a straightforward means to keep course is to determine the compass direction and to orient towards the centre of the (binocular) visual field. If the pigeons apply the same method during monocular flight, they should systematically deviate as the centre of the visual field is now close to the visual axis of the one or other eye. Interestingly, the degree of the average deviation from home ( $65^\circ$ ) very closely corresponds to the angle of the optical axis ( $70^\circ$ , [15]).

One might ask whether the systematic deviation could be due to a simple visuo-motor response resulting from the birds' avoidance of flying into a direction where they cannot see. However, a role of visual representation rather than a pure visuo-motor bias is supported by the fact that the deviation decreased during flying over the release site and that it was already present when the birds were still confined in the small inner cage of the arena, i.e. before they began to move around in the arena. Furthermore, comparison with other studies supports the view that the systematic deviation is a matter of visual representation. Although the bias found in the arena under monocular conditions was fairly strong, a similar tendency also was observed in vanishing bearings [19,27] and during orientation in a large indoor arena where no sunlight was present [20]. Therefore, this phenomenon per se is not dependent on use of the sun compass. It appears to occur regularly if pigeons visually determine their direction with one eye covered.

##### 4.2. Directional bias in the arena

During stage two of the homeward journey, the period from leaving the arena until vanishing from the observer's view, the directedness of the pigeons increased. The systematic error decreased, but it was still

present in the vanishing bearings. A profound (symmetric) increase in directedness had also been observed in an earlier study using an arena of the same type [14]. While flying over the release site birds appear to obtain additional information, which enables them to sense the home direction with greater accuracy. Thus, the change from a strong bias in the arena bearings to a moderate bias in the vanishing bearings is probably due to a stronger homeward directed component and a still present lateral component. At the present stage of knowledge it is not possible to say what additional information pigeons profit from. We took great care that the position of the arena was exactly the same as during training so that the pigeons had experienced the view from the arena before. Nevertheless, during flying after leaving the arena they had access to a number of cues not contained in the restricted view from the arena. They could see and recognize a higher number of landmarks at the release site and so become more sure at which place they were. They had access to a panoramic view from above, which might be the typical way of how release sites are seen and remembered. Furthermore, by seeing the landmark array from different viewpoints, they could switch from a static, largely two-dimensional representation of the landscape to a three-dimensional relational representation of the landmark array. Thus, the considerable improvement in orientation might be due to a shift from site-specific compass orientation to piloting based on information on the relative position of landmarks.

#### 4.3. Lateralization of orientation and homing performance

None of the performance measures showed clear evidence of lateralization. In particular, the bearings in the arena and the vanishing bearings were not lateralized. This is different from earlier findings [27] and results from a recent study with monocular occlusion in the Frankfurt area where clear lateralization of vanishing bearings and a moderate lateralization of homing performance as measured in homing speed were found [19]. The tendency for slightly longer homing time in RC birds than in LC birds in the present study might hint at a similar, although weaker, effect. Regarding directional orientation at the release site, however, present findings clearly differ from those reported earlier [19,27]. One difference between the studies was that pigeons were anosmic in the present study, but not in the other two studies. However, a follow-up experiment with pigeons not made anosmic also did not show strong lateralization of directional orientation (unpublished data). Therefore, differences in environmental factors rather than differences in the treatment of the birds are a likely explanation for differences in directional orientation. Comparisons of the pigeons' performance in Germany

and Italy (e.g. [8]) have shown that the different environments have an influence on the pigeons performance, which overall tends to be better in Italy. Obviously, a lateralization effect occurs in the more difficult conditions in Germany, but does not appear in Italy. From human studies on lateralization it is well-known that detection of hemispheric asymmetries can depend on differences in task difficulty [18,23]. Another factor might be that the distance from the release sites was considerably shorter during the present study. This also could have contributed to facilitated performance and a ceiling effect regarding the monocular conditions. Finally, there could be qualitative differences in the pigeon's cue use. The design of the present study explicitly tested for visually guided homing. In one of the studies in Germany a strong lateralization of orientation during vanishing was found at unfamiliar release sites, suggesting that visual factors not related to landscape features were involved [19].

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