

Research report

Visual lateralization and homing in pigeons

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Abstract

The aim of our study was to analyse the components of visual lateralization in pigeon homing, a large-scale spatial task. In a series of 13 releases, birds were tested as binocular controls or monocularly with the right or left-eye covered. Occlusion of either eye had a significant effect on initial orientation and homing performance. Vanishing bearings were deflected to the side of the open eye, vanishing intervals were longer, and homing speed was reduced. These parameters were affected to a different degree. Initial orientation was markedly lateralized, with birds using their right-eye deviating less from the mean of control birds and showing significantly less variance. One minute after release, the deviation and variance were similarly large in both monocular groups. However, while the right-eyed birds improved their performance until leaving the release site, the left-eyed birds failed to do so. Vanishing intervals were similar in both monocular groups, but homing speed was reduced to a lesser extent in pigeons using the right-eye. The degree of lateralization varied across different releases, but superiority of the right-eye/left hemisphere prevailed. Lateralization did not depend on familiarity with the release site. This suggests that the crucial processes involved the eyes, but did not depend on visual memory of landscape features at the release site. Results reveal, for the first time, asymmetries of directional orientation as an essential component of lateralized homing performance. As likely mechanisms we suggest hemispheric differences in magnetic compass orientation and in the adjustment to optic flow.

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1. Introduction

Hemispheric specialization of brain function, as known from human handedness and language capabilities, is not restricted to our species, but appears to be rather widespread among vertebrates. Preceded by a long period of interest in the question of footedness in parrots (review [16]), systematic studies on hemispheric asymmetries in birds began with the finding of lateralized motor control for singing in chaffinches [22]. Since then, a large number of lateralized behaviours have been identified.

Among the best-studied cases are visually guided behaviours and the underlying perceptive and cognitive abilities (reviews in [13,27,31]). In birds, fibres of the optic nerves cross over completely, interhemispheric commissures are small, and a corpus callosum, the major connection be-

tween the left and the right forebrain of placental mammals, is lacking. Hence the immediate transfer of information between the two hemispheres is rather limited. As a consequence, visual input to the right eye is mainly processed by the left brain hemisphere and vice versa. This provides an easy access to analysing phenomena of visual lateralization. By temporarily covering one eye the capabilities of each brain hemisphere can be assessed separately.

Studies on the discrimination of natural food objects, mainly in pigeons and chicks, have fairly consistently found a superiority of the right eye/left hemisphere [13]. A similar lateralization pattern was found for the discrimination of two-dimensional black/white patterns [32]. This suggests a general superiority of the left avian brain in discriminating object-related cues. From studies involving spatial tasks [6,7,25,30] a division of labour between the two brain hemispheres had been suggested, with the right eye/left hemisphere specializing in the discrimination and categorization of individual stimuli and the left eye/right hemisphere specializing in spatial tasks [1,2,5]. However, evidence is

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accumulating that both brain hemispheres are involved with spatial cognition. Thus, it is appropriate to ask what specific aspects of spatial information processing are carried out by the left or right brain hemisphere [24,28,29]. To this end studies are needed that address the full complexity of the natural tasks the brain mechanisms have evolved for.

A seminal field study with monocular pigeons released at three familiar sites [29] demonstrated a striking superiority of the right eye/left hemisphere in homing performance measured as overall homing speed. Differences in vanishing bearings between experimental groups were greater under overcast than in sunny conditions. It was, however, not clear to what extent the differences were caused by factors associated with different locations or due to differences in visibility of the sun or of landscape features. Therefore, we performed a more extended study releasing pigeons at distances of 40 to 55 km and in different directions from the loft. In order to assess a possible role of familiar landmarks, we also released, within the same test release, pigeons that were familiar and pigeons that were unfamiliar with the release site and compared their performance.

2. Materials and methods

The experiments were performed in summer 2000 under sunny conditions, using five release sites 40 to 55 km from the loft at Frankfurt am Main (50°08'N, 8°40'E). For details of the release sites see Table 1.

2.1. Animals

2.1.1. Adult pigeons

Ten releases were performed using adult, experienced pigeons between 1 and 9 years of age that had participated in their first year in a standard training program of flock tosses from up to about 40 km in different directions; they also had homed singly in various experimental releases. Thus, all birds were more or less familiar with the release sites, which were close to earlier training release sites. In addition, many of the birds had homed singly from the same release sites before or had overflowed them when homing from greater distances. Prior to the second test from a site, the birds were released once more as a flock from the respective site in order to refresh their memory.

2.1.2. Young pigeons

Three releases involved young pigeons born in spring 2000. They were 4 to 5 months of age and had been trained from up to 25 km in the cardinal compass directions. Thus, they were able to use site-specific cues and their navigational 'map' [4,35]. For studying a possible influence of familiarity with the release site, half of the birds were given training flights as a flock from the release sites in the East and in the North, while the other half were released from the site in the West and an equally distant site in the South. So all

young pigeons had equal flying experience prior to critical tests, but one group was familiar with the test site, while the other was not.

2.2. Monocular occlusion

The pigeons were prepared for wearing eyecaps by clipping some feathers and fixing a ring of Velcro around one eye with water-soluble, non-toxic glue [29]. The counterpart of the Velcro ring was glued to a circular cardboard cap, 26 mm in diameter. The cap could be bent easily, which allowed for a tight fit over the pigeon's eye. Before the first test in any eyecap condition, birds were fitted with eyecaps for a brief training flight around their loft in order to familiarize them with flying with one eye covered. For the critical tests, the pigeons were equipped with eyecaps at the loft immediately before they were transported to the release site. Before release, the correct placement of the eyecap was checked again, and when the pigeons returned to the loft, this was checked once more before the eyecap was removed. Binocular control (Bi) birds also wore a Velcro ring around one eye (side balanced).

During the releases with adult pigeons, the eyecap treatment changed from right eye to left eye or left eye to right eye and back. Each of the birds was given the three eyecap conditions—binocular control, left-eye open (LE; eyecap right) and right-eye open (RE; eyecap left)—in a balanced design. In addition, we avoided to release birds with the same eyecap condition twice from the same site. Young birds were tested with the same eyecap condition in all three consecutive releases. Familiar and unfamiliar birds were allocated to one of the three eyecap conditions so that six experimental groups were tested from either site.

2.3. Release procedure

The releases followed standard procedures: the pigeons were released singly, alternating between treatments, and followed by two observers with 10 × 40 binoculars (Zeiss Diallyt). The vanishing bearings, i.e. the directions where the birds were lost from sight, were recorded with a compass to the nearest 5°. The vanishing intervals were recorded with a stopwatch. We proceeded until 10 valid bearings in each eyecap condition had been obtained. Additionally, the bearings after 1 min were taken. An observer recorded the time when individual pigeons arrived back at the loft.

2.4. Data analysis and statistics

For each release, the vanishing bearings of the three experimental groups were calculated as a mean vector and tested with the Rayleigh test for significant directional preference [3]. We also calculated mean vectors based on the bearings recorded 1 min after release. For analysing the differences between the vanishing bearings of the eyecap conditions in a single release, the Watson Williams test

Table 1
Initial orientation and homing performance in the release experiments

Site position datum	Treatment	n_r (n_b)	Mean vector vanishing bearings		Difference to		Vanishing interval (min:s)	Return rate (%)	Homing speed (km/h)
			α_m (°)	r_m	Bi (°)	RE (°)			
Old, experienced pigeons									
Hattenheim	Bi	10	87	0.82***			4:59	100	60.3
77°, 44.2 km	RE	10	96	0.95***	+9		4:34	100	40.8***
16/6/2000	LE	12 (10)	62	0.42	-25	-34**	5:55	75	40.2**
Lich	Bi	13 (10)	226	0.87***			3:19	100	40.6
192°, 40.6 km	RE	11 (10)	254	0.90***	+28		4:20	91	38.1
18/6/2000	LE	10	192	0.83***	-34*	-62*	4:58	100	32.9
Gernsheim	Bi	11 (10)	2	0.69**			4:05	100	58.6
16°, 42.0 km	RE	10	18	0.90***	+16		3:53	100	63.0
21/6/2000	LE	12 (10)	338	0.65*	-24	-40	6:06*	92	34.1**
Linsengericht	Bi	15 (10)	238	0.88***			4:52	100	40.7
262°, 40.0 km	RE	11 (10)	267	0.67**	+29**		8:36*	82	37.5
27/6/2000	LE	12 (10)	232	0.91***	-6	-35**	5:01	100	40.7
Lich	Bi	10	206	0.92***			5:56	100	65.8
192°, 40.2 km	RE	10	206	0.76**	0		9:40**	100	36.9**
21/7/2000	LE	10	187	0.89***	-19	-19	4:40	100	39.9**
Hattenheim	Bi	10	96	0.98***			4:16	100	60.3
77°, 44.2 km	RE	11 (10)	103	0.97***	+7		5:20*	100	48.5*
7/8/2000	LE	12 (10)	81	0.94***	-15	-22*	7:03**	100	41.4**
Gernsheim	Bi	10	9	0.90***			4:49	90	56.0
16°, 42.0 km	RE	11(10)	36	0.94***	+27		4:19	91	51.4
11/8/2000	LE	12(10)	308	0.48	-61	-88***	6:46*	100	37.6**
Linsengericht	Bi	11 (10)	265	0.90***			3:34	100	61.5
262°, 40.0 km	RE	10	284	0.93***	+19		4:44*	100	40.0**
14/8/2000	LE	11 (10)	218	0.86***	- 47**	-66***	5:17**	91	33.8***
Lorsch	Bi	10	314	0.95***			4:04	100	40.5
6°, 55.3 km	RE	10	337	0.82***	+23		4:24	100	36.9
24/8/2000	LE	10	287	0.73**	-27	-50*	3:53	100	40.0
Lorsch	Bi	11 (10)	338	0.79***			4:07	100	56.2
6°, 55.3 km	RE	11 (10)	351	0.89***	+13		5:17*	100	29.9**
29/8/2000	LE	10	313	0.93***	-25	-38**	6:40*	100	41.5**
Young pigeons									
Linsengericht	F-Bi	10	250	0.90***			4:16	100	58.5
262°, 40.0 km	F-RE	12 (10)	280	0.87***	+30*		5:57	91	51.1
18/8/2000	F-LE	10	229	0.79***	-21	-51*	5:13	90	44.4
	U-Bi	10	255	0.79***			5:00	90	47.1
	U-RE	12 (10)	283	0.81***	+28		6:19	75	33.3*
	U-LE	11 (10)	209	0.84***	-46*	-74***	9:46**	82	19.2**
Hattenheim	F-Bi	12 (10)	107	0.92***			4:46	100	45.7
77°, 44.2 km	F-RE	11 (10)	112	0.98***	+5		6:15*	100	44.9
22/8/2000	F-LE	12 (11)	99	0.53*	-8*	-13*	4:54	92	41.4
	U-Bi	10	109	0.74**			5:24	100	29.1
	U-RE	10	132	0.75**	+23		5:58	80	16.9
	U-LE	12 (10)	30	0.36	-79*	-102*	8:34*	75	32.3
Lich	F-Bi	12 (10)	212	0.92***			4:20	100	48.7
192°, 40.2 km	F-RE	12 (10)	234	0.92***	+22		8:13	83	38.1*
30/8/2000	F-LE	10	196	0.76**	-16	-38**	6:58	100	23.4***
	U-Bi	12 (10)	207	0.84***			4:42	100	49.7
	U-RE	11 (10)	233	0.70**	+26		6:57	91	31.2*
	U-LE	10	201	0.66**	-6	-32	5:52	80	20.5**

Home direction and distance are indicated under the name of the release site. Treatment: Bi, binocular control; RE, right eye viewing–eyecap left; LE, left eye viewing–eyecap right; young pigeons: F and U before Bi, RE and LE indicate that the birds were familiar or unfamiliar, respectively, with the release site. n_r (n_b) is the number of pigeons released (number of valid bearings, if different); α_m , r_m , direction and length of mean vector of the vanishing bearings, with asterisks at r_m , indicating significance by the Rayleigh test. The columns ‘Difference to’ give the angular difference to the mean of the binocular controls and birds with their left-eye covered, respectively, (+) clockwise, (-) counterclockwise; significant differences by the Watson Williams test or the Mardia Watson Wheeler test are marked with asterisks. Asterisks at vanishing intervals and homing speeds indicate differences from the binocular controls (Mann Whitney *U*-test). Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

indicating differences in preferred direction (if $r_m > 0.7$) and Mardia Watson Wheeler test indicating differences in distribution were used [3].

In addition to comparing the performance of the experimental groups, we analysed the vanishing bearings using within-subject comparisons. In adult pigeons, which had experienced all eyecap treatments on subsequent releases in balanced order, this allowed for a subject-based comparison of the different conditions of viewing. In young birds we used a within-subject design for analysing the possible role of familiarity on orientation at the release site. Angular differences, which reflect dispersion as a parametric measure, were calculated with the mean bearing of controls at a given release as a reference and were subjected to repeated measurements ANOVA. In adult birds, eyecap treatment was the within-subject factor, and in young birds eyecap treatment was a between-subject factor and familiarity with the release site was a within-subject factor.

Vanishing intervals (time elapsed between the moment of release and vanishing from sight) and homing speeds, which are not normally distributed, were compared using the non-parametric Mann Whitney *U*-test.

For analysing the effect of monocular occlusion, we performed a second order analysis, using the Wilcoxon test for joint samples to compare the traditional parameters characterizing the behaviour of pigeons in experimental releases, namely: (1) the mean direction: we used the angular deviation from the mean of the binocular controls, $\Delta\alpha$, with (+) indicating clockwise and (–) counterclockwise deviations ($|\Delta\alpha|$ is used for calculating lateralization indices, see below); (2) the length of the mean vector, r_m , which reflects the variance of the vanishing bearings (it is close to 1 if the birds' bearings agree well and approaches 0 if the bearings are distributed randomly); (3) the median vanishing interval; (4) the median homing speed; and (5) the return rate in percent. The Wilcoxon test was also used to compare the

data of the first and the second release of adult birds from the same site.

To characterize the degree of lateralization in the birds' performance, we calculated lateralization indices for the variables listed above based on the mean or median performance of the groups for each release according to the formula $(RE - LE)/(RE + LE)$ or $(LE - RE)/(LE + RE)$ – the first formula was applied to r_m and homing speed where high values indicate good performance, the second to $|\Delta\alpha|$ and the vanishing intervals where high values indicate poor performance. This results in indices between –1 and +1, with positive values indicating superiority of the right eye/left hemisphere, negative values indicating superiority of the left eye/right hemisphere and values close to 0 indicating no lateralization.

3. Results

Table 1 lists the data from the releases. Although initial orientation and homing performance were fairly good in all three treatments, with significant mean vectors and return rates of or close to 100%, occlusion of one eye had a marked effect. We frequently observed significant differences in mean vanishing bearings, vanishing intervals and homing speed between the binocular and the monocular birds in single releases; they are indicated in Table 1. Table 2 compares the means of the three groups, giving the distribution of differences and the test statistic of the Wilcoxon test.

3.1. Effect of occluding one eye

In general, the following pattern emerged (Table 2): both monocular groups deviated significantly to the side of the uncovered eye from the mean of the binocular controls (Fig. 1).

Table 2
Means of variables and differences between treatments

Variable	Age	Binocular control (Bi, mean)	Right eye open, RE			Left eye open, LE			Monocular comparison	
			Difference RE – Bi			Difference LE – Bi			Difference LE – RE	
			Mean	+:0:–	<i>T</i> , sign?	Mean	+:0:–	<i>T</i> , sign?	+:0:–	<i>T</i> , sign?
$\Delta\alpha$	ad.	–	+17°	9:1:0	0**	–25°	0:0:10	0***	9:0:1	7*
	juv.	–	+22°	6:0:0	0*	–29°	0:0:6	0*	3:0:3	10; ns
r_m	ad.	0.87	0.87	6:0:4	25; ns	0.76	2:0:8	8.5*	3:0:7	15; ns
	juv.	0.85	0.84	3:1:2	8; ns	0.66	1:0:5	1*	1:0:5	1*
van. int. (min:s)	ad.	4:23	5:31	7:0:3	8*	5:38	8:0:2	6*	7:0:3	21; ns
	juv.	4:45	5:31	6:0:0	0*	6:52	6:0:0	0*	2:0:4	11; ns
Speed (km/h)	ad.	54.0	42.3	1:0:9	1**	38.2	0:1:9	0**	4:0:6	18; ns
	juv.	46.5	36.0	0:0:6	0*	30.2	1:0:5	1*	1:0:5	5; ns
Return rate	ad.	99%	96%	0:8:2	–	96%	1:6:3	–	3:4:3	10; ns
	juv.	98%	87%	0:1:5	0*	87%	0:1:5	0*	2:0:2	–

Variables: $\Delta\alpha$, angular difference to the mean of the binocular controls; r_m , lengths of mean vector; van. int., vanishing interval; speed refers to homing speed. Age: ad., adult pigeons between 1 and 9 years old; juv., young pigeons born in the year of testing. Difference: the numbers under +:0:– indicate how often the difference indicated is positive, zero or negative. The column '*T*, sign?' gives the test statistic of the Wilcoxon test, and indicates whether or not the differences show a significant trend. Significance levels as in Table 1; ns, not significant.

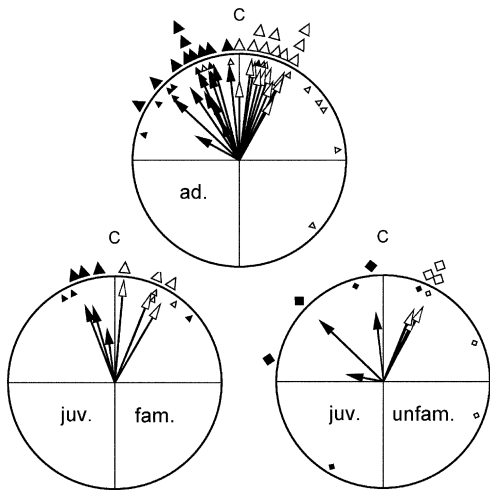


Fig. 1. Mean vectors of pigeons wearing an eyecap drawn with respect to the mean of corresponding binocular controls (C). Top: experienced adult birds; bottom left: young pigeons familiar with the release site; bottom right: young birds unfamiliar with the release site. The mean bearings are indicated at the outer periphery with a symbol; the length of the vector is drawn proportional to the radius of the circle = 1. The smaller symbols at the inner periphery of the circle mark the mean bearings 1 min after release. Open symbols: RE-birds with the left eye covered; solid symbols: LE-birds with the right eye covered.

Vanishing intervals were significantly longer, and homing was significantly slower in both monocular groups than in the control birds (Fig. 2). The effect on return rate was rather small: in the experiments with adult birds, only 1 of 111 control birds failed to return, compared to 4 of 105 RE-birds and 5 of 111 LE-birds. Of the young pigeons, 1 of 66 control birds got lost, compared to 9 of 68 RE-birds and 9 of 65 LE-birds (Table 1).

The effect of monocular vision described above was found in adult and juvenile birds alike (Table 2). It appears to be independent from the pigeons' familiarity with the release site: the data of the second releases of adult birds that had recently refreshed their knowledge of the release site were not different from those of the first releases ($P > 0.05$, Wilcoxon test for all parameters), and we also found the same pattern in young pigeons familiar and unfamiliar to the release site (Table 1).

3.2. Comparison of the two monocular treatments

Regarding lateralization, the crucial comparison involves differences between the two monocular groups. The respective data are included in Table 2 in the columns to the right.

In initial orientation, we observed a clear difference between groups of adult RE-birds and LE-birds: Fig. 1 gives the mean vectors of their vanishing bearings with respect to the mean of the binocular controls. The deviation to the side of the open eye was significantly greater in adult LE-birds. Young birds unfamiliar with the release site showed a similar tendency (Fig. 1), but overall the difference between young

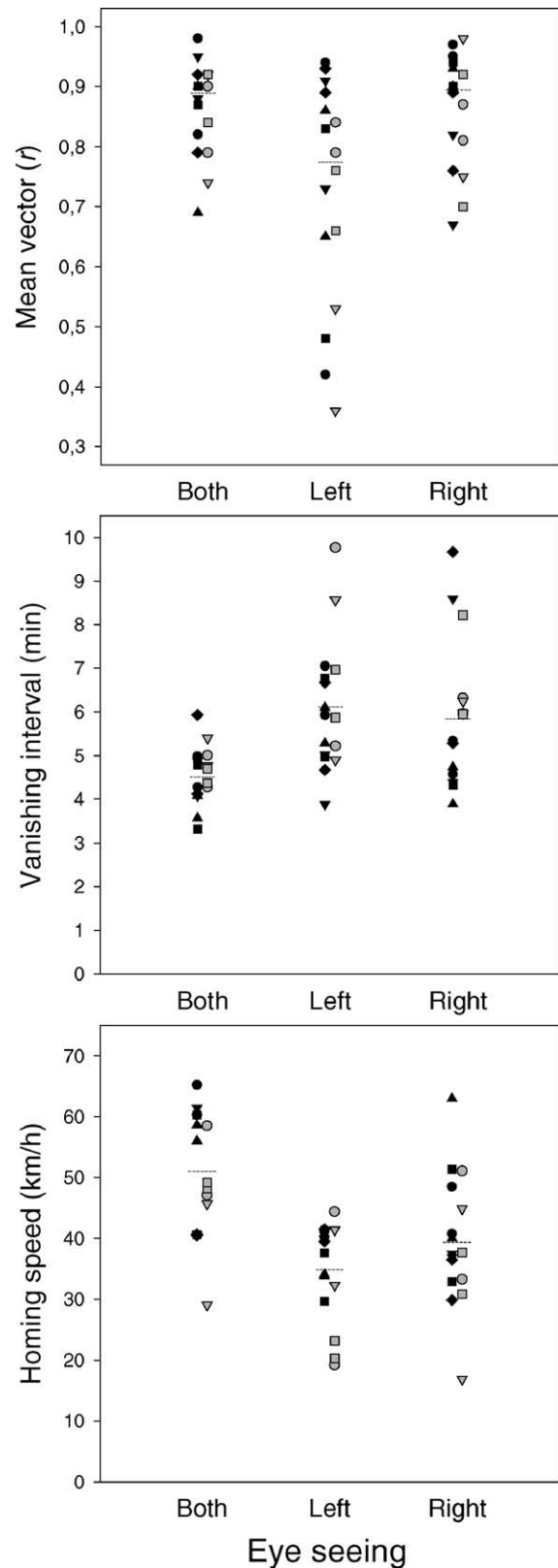


Fig. 2. Scatter graph of vector lengths (top), median vanishing intervals (middle), and median homing speeds (bottom). Black symbols indicate the data of adult birds and grey symbols those of young birds. The small perpendicular lines indicate the medians from all samples.

LE-birds and RE-birds did not reach significance (Table 2). At the same time, while the RE-birds had long vectors like the control birds, the LE-birds' vectors were shorter (Table 1 and Fig. 2), with this tendency being significant in the young birds (Table 2) and also in the combined sample ($N = 16$, $T = 25$, $P < 0.05$, Wilcoxon test).

The 1-min bearings (Fig. 1), although considerably scattered, point out how this asymmetry emerges. With few exceptions, the 1-min bearings already deviated to the side of the uncovered eye, but the mean vectors were short and often non-significant. At this stage, all three treatments showed the same great amount of scatter. Interestingly, there was no significant difference in the average degree of the deviations from the control birds 1 min after release, neither in adult nor in young birds—the number of cases of the LE-birds showing the greater deviation to that of the RE-birds showing the greater deviation being 5:5 and 3:1:2, respectively (both $P > 0.05$, Wilcoxon test). Between 1 min after release and vanishing from sight, however, adult RE-birds significantly improved in their orientation: their deviations from the mean of controls decreased, and their vector lengths increased significantly (Table 3). Adult LE-birds, in contrast, showed no consistent change in deviation, and the increase in vector length was less pronounced. In young pigeons, only controls and RE-birds showed a significant increase in the lengths of the vanishing vectors; the deviations from the control direction did not show a significant trend (Table 3). This means that both monocular groups started with the same marked deviation and short vectors immediately after release. The observed asymmetry in initial orientation emerged because the RE-birds, and here in particular the adult RE-birds, were able to improve their performance significantly as long as they were still within sight of the observers, while the LE-birds failed to do so.

The within-subject analysis also showed clear differences between the experimental treatments (Fig. 3A). Overall, there was a significant difference between treatments ($F(2, 60) = 9.25$, $P < 0.001$). Pairwise comparisons showed that performance with the left eye was considerably poorer than with the right eye ($P < 0.005$) or binocularly ($P < 0.001$). By contrast, there was no such difference

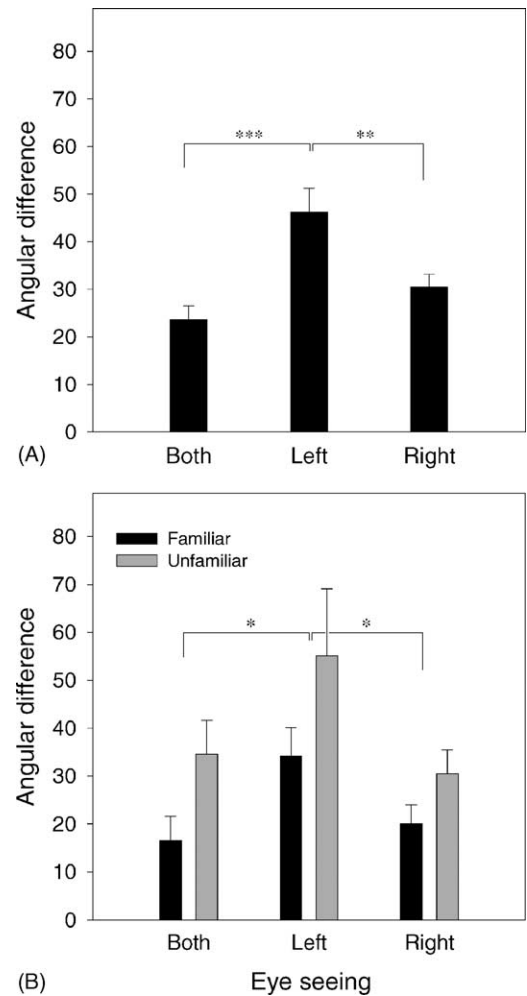


Fig. 3. Mean angular differences of individual vanishing bearings from the mean bearings of controls. For each release, individual angular differences were calculated and then combined for each bird over all releases with the same eyecap treatment in adult birds (A, top) and over all releases with the same familiarity treatment in young birds (B, bottom). Deviation was greater when birds used their left eye, while there was no significant difference between use of both eyes and the right eye only. The same pattern of laterality emerged at familiar and unfamiliar sites.

Table 3
Orientation 1 min after release

Variable	Binocular control			Left-eye covered			Right-eye covered		
	Bi, mean	Improved at vanishing ?		RE, mean	Improved at vanishing?		LE, mean	Improved at vanishing?	
		+:–	T, sign?		+:–	T, sign?		+:0:–	T, sign?
Adult pigeons									
$\Delta\alpha$				+ 41°	8:2	3.5**	–34°	7:3	12.5; ns
r_m	0.63	10:0	0**	0.61	10:0	0**	0.67	8:2	6.5*
Young pigeons									
$\Delta\alpha$				+48°	4:2	5; ns	–25°	4:2	11; ns
r_m	0.62	6:0	0*	0.62	5:1	1*	0.66	2:4	10; ns

Improved at vanishing indicates whether the variable improved between 1 min after release and the moment of vanishing from sight. Positive signs indicate an improvement (i.e. smaller deviations from the controls, longer vectors), while negative signs indicate a deterioration. Otherwise as in Table 2.

between the binocular control condition and the use of the right eye ($P > 0.2$).

Regarding the other variables, adult and young birds showed the same trends (see Fig. 2): the vanishing intervals of the RE-birds and the LE-birds were not different, and the same is true for the return rates. Homing speed tended to be higher in the RE-birds than in the LE-birds, with this difference reaching significance in the combined sample ($N = 16$, $T = 34$, $P < 0.05$).

3.3. Role of familiarity with the release site

In general, pigeons familiar and unfamiliar with the release site were similar in their behaviour, with a slightly lower level of performance in the unfamiliar birds (Table 1). However, the crucial question was whether the pattern of lateralization differed between familiar and unfamiliar sites (Fig. 3B). As expected, ANOVA with the factor eyecap treatment and familiarity as a repeated measure revealed a main effect of familiarity ($F(1, 31) = 7.98$, $P < 0.01$). In addition, there was a main effect of eyecap treatment ($F(2, 31) = 3.59$, $P < 0.05$). The absence of an interaction between these factors ($F = 0.28$, $P > 0.75$) indicates that the effect of occluding the left or right eye was the same at familiar and unfamiliar sites. Pairwise comparisons of the angular differences revealed that at familiar as well as at unfamiliar sites, LE-birds showed significantly more scatter than controls and RE-birds (both: $P < 0.025$), while there was no difference between latter groups ($P > 0.95$). In summary, birds showed the same pattern of lateralization in vanishing bearings at familiar and unfamiliar release sites.

3.4. Lateralization indices

Fig. 4 gives the lateralization indices for the variables discussed above for each release, together with the mean later-

alization indices. They varied considerably, with means between +0.020 and +0.172, with a grand mean of +0.084. Although all means are positive, indicating a superiority of the right eye/left hemisphere, only the indices calculated from $\Delta\alpha$ and r_m and the mean indices show a significant trend towards the positive side ($P < 0.05$, sign test). This indicates a clear difference in the extent to which the different parameters were lateralized. Overall, initial orientation was more affected by lateralization than vanishing intervals and homing speed.

4. Discussion

Our results demonstrate an effect of monocular occlusion on all homing parameters. The pattern, however, was different for the various parameters studied: (1) with either eyecap treatment, pigeons deviated towards the side of the open eye at the beginning of their homing flight, a tendency that was largest shortly after release and that was compensated in a lateralized way; (2) monocular birds had longer vanishing intervals than binocular controls. Finally, (3) monocular birds had slower homing speeds, with birds using their right eye being overall faster than birds using their left eye.

The marked effect of wearing an eyecap per se is not surprising. Complex tasks usually require input from both eyes for optimum performance, probably due to the integration of different types of information, initially processed by the left or right hemisphere alone, into a combined percept. This was demonstrated for foraging in a maze [23] or a large indoor arena [24], and may also be relevant in navigation and homing. In contrast to the laboratory studies, our experimental birds were flying, and normal visual flight control involves both eyes [10].

As occluding one eye disrupts binocular optic flow, difficulties with forward and rotational movements may arise

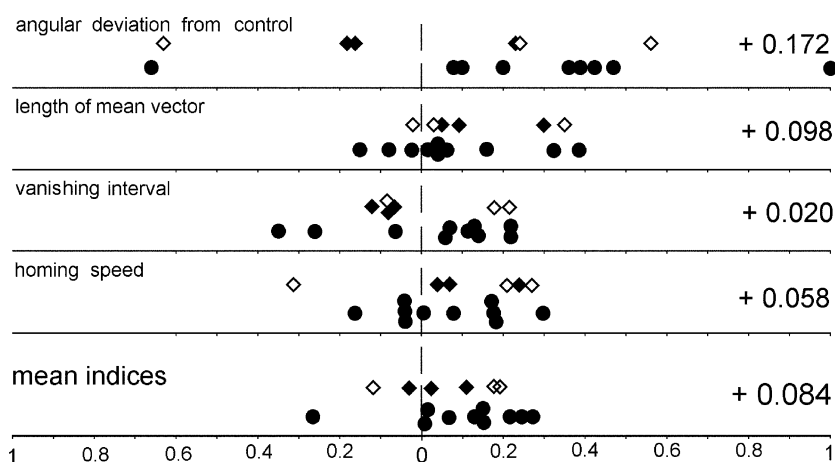


Fig. 4. Lateralization indices calculated for each release from the difference in performance of the RE and LE-pigeons. Positive values indicate right-eye superiority, negative values left-eye superiority and values at 0 no lateralization. Solid circles, scores of adult pigeons; solid diamonds, scores of young pigeons familiar with the release site; open diamonds, scores of young pigeons unfamiliar with the release site. The mean of the indices is given numerically on the right side.

[10]. The consistent deviation to the side of the open eye shortly after becoming airborne in birds with eyecaps might reflect such difficulties. It also could reflect a spontaneous reluctance to head into unseen territory and thus to prefer the visually scanned side [33]. Despite having a small binocular visual area of 22–40°, pigeons are essentially monocular with a complete panoramic view of 316° [18,19]. In resting position, the optic axis of pigeons points 64 to 70° away from the midsagittal plane [19], and monocular pigeons confined to an arena at the release site showed lateral deviations within this range [8]. If pigeons would take a compromise between their intended heading and the optic axis of their open eye, they would deviate about 35° to the seeing side. This is very close to the 37° we observed as the mean of all deviations 1 min after release. On the other hand, the smaller deviation might indicate a first successful step in compensating for unilateral optic flow. The decrease in deviation from the first minute until vanishing after 3–6 min suggests that birds might require some time to fully cope with the asymmetric visual input. How pigeons do this is not yet clear. Nalbach et al. [20,21] described that pigeons can enlarge their frontal binocular field dramatically during pecking by combining yaw, pitch, and roll movements of the eyes in the skull, reshaping their visual field in a way that a larger frontal field below the beak is present even under monocular conditions. However, it is highly unlikely that pigeons can use this strategy during flight: flying pigeons maintain a position where the horizon is about 39° above the beak [9], and the enlarged binocular field below the beak is considerably myopic and thus of little help during flight [17]. Probably, our pigeons adjusted themselves gradually to the asymmetric optic flow and reduced the discrepancy between their initial heading and their intended home course.

The observation that the compensatory improvement did not reach significance in young monocular birds suggests that they might need more time than adult birds to cope with unilateral visual input. Being older than 4 months, they had a mature navigational system yet still lacked the extensive homing experience of older pigeons. Also, we cannot exclude that the brain systems compensating for monocular visual input undergo changes during juvenile development as reported for aspects of visual lateralization in other avian species [27].

Aside from the effect of occluding either eye, we observed lateralization of overall performance, with pigeons using their right eye performing consistently better, indicating a superiority of the right-eye/left hemisphere. The lateralization indices for all parameters except vanishing intervals were larger than 0.051, the mean index found for a sample of more than 100 pigeons discriminating grain from grit [15]. Thus, most homing parameters in the present study showed a more pronounced lateralization than that observed in visual discrimination tests in the laboratory. Angular deviation from the mean of the controls showed the largest degree of lateralization. Interestingly, this asymmetry in

vanishing bearings appears to arise from a lateralized tendency to compensate the larger initial deviation. Although the birds forced to use their left eye only finally reached home in similar numbers, the faster homing speed of the right-eyed birds indicates that lateralization in favour of the right eye/left hemisphere continued after leaving the release site.

What is the cognitive and neuronal basis of this effect? Numerous laboratory tests had revealed lateralization of object recognition, with superiority of the right eye [13]. Considering this evidence, Ulrich et al. [29] discussed their results in view of lateralized memory for visual landmarks at the release site and en route. Our present data, while indicating a slightly lower level of performance in unfamiliar birds, which is normal in pigeon releases [34], clearly show the same lateralization pattern in birds released at familiar and unfamiliar sites. This precludes recognition of familiar landmarks at the release site as a reason for the lateralization of vanishing bearings. A recent series of homing studies in Italy confirmed that lateralized vanishing performance does not depend on familiarity with the release site: birds familiar with the sites were not lateralized during vanishing, whereas birds not familiar with the release sites exhibited lateralization with better performance when the right eye was used (Prior et al., unpublished observations; [8]). Furthermore, Gagliardo et al. [11,12] studied the influence of lesions targeted on the hippocampus on homing performance in pigeons. The finding of participation of both brain hemispheres in familiar landmark navigation [11] also suggests that memory for visual landmarks is not crucial for lateralized homing performance. This is further supported by a study involving lesions early in life before the birds could learn a navigational map. Directional orientation was good with an intact left brain hemisphere (lesion to the right hippocampus), but poor with an intact right brain hemisphere [12]. Taken together, the data suggest that the factor relevant for lateralization is mediated by the eye, but does not depend on visual memory for landscape features at the release site.

This leaves general processing of visual input and the two compass mechanisms used by homing pigeons, both of which involve retinal receptors. As visual motion is important for structuring a bird's environment [10] and as the visual tectofugal system, which is of paramount importance for visual motion analysis, is asymmetric [14], lateralized visual motion processing involved with flight control might have been one of the reasons for the observed pattern of lateralization. An involvement of the sun compass, on the other hand, appears less likely. If monocular occlusion interfered with sun compass use, we would have expected the effect to depend on the side of the open eye with respect to the sun and thus on the direction the monocular birds had to fly while homing. This was not the case. We cannot rule out that sun compass information can be acquired without direct view on the sun, but only experiments testing specifically for lateralization of the sun compass can give a final answer.

Magnetic compass orientation in birds is also based on light-dependent processes in the eye [26,37]. The avian magnetic compass was recently found to be strongly lateralized [38]: migratory European robins, *Erithacus rubecula*, using their right eye were well oriented in migratory direction, while they failed to show any directional preference using the left eye. That is, the magnetic compass of robins also involves a superiority of the right eye/left hemisphere, which was markedly stronger than the effect observed here in pigeons. Interestingly, Ulrich et al. [29] reported a stronger difference between the right-eyed and left-eyed performance under overcast than under clear skies, which suggests that in pigeons, too, the magnetic compass is lateralized in favour of the right eye. In the present study, weather conditions allowed our birds to use the sun compass in all releases. However, a recent analysis of the interaction of sun compass and magnetic compass [36] suggests that pigeons normally use information from both compass mechanisms together. There was no obvious deficit when the magnetic compass was impaired by a small bar magnet under clear skies, but this impairment could have been of short duration only, as birds might quickly learn to overcome the effect of an added static field. Hence birds with magnets might regain access to the geomagnetic field after a short interval, while our pigeons were deprived of magnetic compass information during the entire homing flight. Also, lack of magnetic compass information might prove more severe when birds are otherwise handicapped, so that an interference with the magnetic compass is indeed a possible reason for the poorer performance of the left-eyed birds.

In summary, the observed lateralization in favour of the right eye/left hemisphere during homing might be caused by a combination of two effects. First, superiority of the right eye for the processing of visual stimuli enables right-eyed pigeons to overcome the problems of asymmetric optic flow considerably faster. And second, due to a strong lateralization of the avian magnetic compass in favour of the left brain hemisphere magnetic compass information is available for right-eyed, but not for left-eyed birds. In combination these factors lead to lateralization of initial orientation and homing speed.

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