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Growing up in an Altered Magnetic Field Affects the Initial Orientation of Young Homing Pigeons

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Summary. To test whether the sun compass of pigeons is calibrated by the magnetic field, a group of young pigeons was raised in an altered magnetic field in which magnetic north was turned ca. 65° (in 1974 and 1975) and 120° (in 1980) clockwise. They could see the sun only in an abnormal relation to the magnetic field, since they were released for exercise flights or training flock tosses only when the sky was totally overcast.

On their first flight in sunshine these experimental birds deviated clockwise from the mean of their controls; the amount of this deviation was, however, only about half of the shift in magnetic north. On their second flight in sunshine the clockwise deviation changed to counterclockwise. This change occurred after an exercise flight in sunshine as well as after a homing flight. On later flights in sunshine the differences in orientation between experimentals and controls seemed to disappear.

These findings indicate that the magnetic compass is involved in the learning process to establish the sun compass, but the relation between the two systems is more complex than the calibration hypothesis assumed.

Introduction

Numerous clock-shift experiments have documented that under clear skies experienced homing pigeons use the sun compass to localize directions – a mechanism based on the relationship of sun azimuth, time, and geographic direction (Schmidt-Koenig 1958; for summary see R. Wiltschko 1980, 1981). When we found that the birds' knowledge of this relationship is not innate but has to be established by experience (W. Wiltschko et al. 1976), we began a series of experiments to study the development of the sun compass in young homing pigeons. It became evident that the birds could not derive a geographic direction from the sun at a time of day when they had never seen it before (R. Wiltschko and W. Wiltschko 1980; R. Wiltschko et al. 1981). Apparently they must observe large portions of the sun's arc to find out at what time the sun is in which position. Their ability to generalize or to extrapolate seems to be much smaller than, for example, that of honey bees (Lindauer 1959). This leads to the question of how the birds judge the sun's motion to associate it with geographic direction and what they use as points of reference.

There are three obvious possibilities:

(1) The birds observe the sun's position from a fixed location and record its progress relative to visual landmarks. This would result in a sun compass completely independent of all other means of detecting direction.

(2) The birds record the sun's changing azimuth relative to the magnetic compass, a possibility that appears most likely since recent findings indicate that the magnetic compass is used by young pigeons before the sun compass is established (R. Wiltschko and W. Wiltschko 1981; R. Wiltschko et al. 1981). Such a mechanism has been found in night-migrating birds, where the star compass can be calibrated by information from the earth's magnetic field (cf. W. Wiltschko 1980).

(3) In pigeons, sun compass orientation is always part of the homing process. Thus it is possible that the birds when establishing their navigational 'map' (see W. Wiltschko and R. Wiltschko 1982) learn how the sun's azimuth varies relative to the directions of the gradients for bicoordinate navigation in the course of the day. In this case,

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the sun compass would be connected directly with the navigational 'map', a possibility first suggested by Wallraff (1974).

All three possibilities would have the same result, and therefore we cannot tell by simple observation which method is used. The most promising approach lies in experimentally manipulating the learning process. We began testing the hypothesis that the sun compass is calibrated by the magnetic compass: We raised a group of young pigeons in such a way that they always viewed the natural sun in an abnormal relation to the magnetic field. The results clearly indicate that the birds' orientation is affected by this treatment, but they leave many questions about the interrelation of sun orientation and magnetic compass unanswered. Nevertheless, because this type of experiment will not be continued in the near future, our findings are reported here.

Materials and Methods

The experiments were conducted in the summers of 1974, 1975 and 1980 at the Cornell pigeon loft at Ithaca, New York, USA (42°26′N 76°26′W).

The 'Magnetic Loft'

The birds were housed in a small portable loft (1.5 m × 1.2 m × 1.4 m) that provided space for up to 50 young pigeons and was equipped with an open aviary covering the roof where the inhabitants had a full view of the sky (Fig. 1). It was placed in the center of a pair of Helmholtz coils (2.7 m diameter, 1.35 m clearance, 40 windings of copper wire) aligned in such a way that the horizontal component of the resultant magnetic field was rotated clockwise to geographic east, while total intensity and inclination were approximately the same as in the geomagnetic field. In 1974 and 1975 the shift in magnetic north was ca. 65°, to ENE, and in 1980 it was ca. 120°, to ESE.

The setup was technically rather imperfect; the magnetic field was not completely homogeneous in the range of the loft. Conditions as described above existed only in the center of the coils, with distortions (distributed more or less symmetrically) near the windings. In the aviary from which the birds could observe the sun, the field was roughly homogeneous except at the edges where intensity, declination and inclination varied. In particular the inconstant directional information might be expected to add a certain scatter to the orientation of the experimental birds. Their vector lengths, however, were not regularly shorter than those of the controls.

In 1975 and 1980, the controls lived in a small portable loft similar in size and construction to the experimental loft including a roof top aviary. Only in 1974 were the control birds housed in a section of a normal pigeon loft which, among other things, differed from the magnetic loft in having only a small aviary on its south side and in being much more shielded from wind etc.

Experimental Birds

In early spring 1974, 11 pairs of adult pigeons were moved into the magnetic loft where they laid eggs and raised youngsters. These young birds and additional birds that had been

Fig. 1. The experimental loft within Helmholtz coils; the inhabitants could see the sun only in altered relationship to the magnetic field

put into the magnetic loft after they had been separated from their parents at an age of ca. 24 days were raised together. Since there was no difference in behavior between the two groups, in 1975 and 1980 we used only experimental birds that had been living in the magnetic loft from the age of ca. 24 days. The control birds were of equal age and experience; in 1975 and 1980, most of them were siblings of the experimental birds.

When the young pigeons were ready to fly, the control and the experimental groups were settled in their respective lofts and were released together for exercise flight. Since the experimental birds were to see the sun only in the altered magnetic field at their loft, all the settling and exercise flights took place *only under totally overcast* skies when a solid cloud cover could be expected to last for several hours. Those experimental birds that were to be tested as trained birds were given a series of training flights when the sky was completely overcast – 10 flights up to 8 km in 1974 – while the control birds had the corresponding flight in sunshine. In 1980, experimentals and controls were trained together under overcast skies; they had 17 flock tosses from up to 8 km in all directions, the birds of groups IV and V (see below) had three additional flights before being tested. Thus, the experimentals had gathered all their flying experience in magnetically natural conditions under overcast conditions, presumably using their magnetic compass. The only difference from the controls was that they had to pass a distorted magnetic field when leaving and entering their loft, and – most important – that when they stayed in their aviary they saw the sun in an abnormal directional relation to the magnetic field.

When releasing the experimental birds for exercise or training flights, we faced the problem of having them back in the altered magnetic field before the sun came out. This proved to be not too difficult. Because of the structure of the loft, the birds usually landed on top of their aviary, i.e. inside the altered magnetic field, and by carefully rationing the birds' food on days when overcast was expected, we were normally able to trap them in time. Any latecomers were easily identified by the large numbered band, and their accidental sun exposure was noted. Since a large number of experimental birds was required, those pigeons whose exposure could be considered negligible (i.e. when it was very short, mostly sitting and had occurred at an early age during the process of settling the birds at their loft) had to be included in the critical tests. In these cases, the exposure did not appear to affect their behavior, as their vanishing bearings did not differ from those of 'clean' experimentals, in contrast to the effect of a later extended exercise flight in bright sunshine (see below). The controls were treated similarly, though not quite as strictly as the experimentals.

Experimental Procedure, Data Analysis and Statistics

The critical tests were performed on sunny days. Each bird was released singly from the hand and watched by one or two observers using 10 × 40 or 10 × 50 binoculars until it vanished from sight. Experimentals and controls were released alternately so that both groups were exposed equally to any temporally changing environmental conditions. The vanishing bearings were recorded with a compass to the nearest 5°; bearings 1 min, 2 min and 3 min after release were also taken. The interval between release and vanishing was recorded with a stop watch, and observers at the loft recorded the arrival times of the birds successfully homing.

The mean vector of each set of bearings was calculated by vector addition. This vector was used in testing the distribution of the bearings for non-uniformity by the Rayleigh test. Vanishing bearings of experimentals and controls were compared using the Watson-Williams test (Batschelet 1965), and the vanishing intervals and the homing times were compared using the Mann-Whitney test.

Results

The hypothesis to be tested was that the sun compass is calibrated by the magnetic field. If this is true, and provided that the birds only need to see the sun while sitting at their home loft to calibrate the sun compass, we should expect the experimental birds to show a deviation from the controls corresponding to the shift of magnetic north at their loft, i.e. ca. 65° *clockwise* in 1974 and 1975, and ca. 120° *clockwise* in 1980, at least for their first flight under sun. On later flights the experience they obtained while flying in the sun might lessen any effect.

This prediction is based on the assumption that our experimental birds had a normally developped navigational system because of their experience gathered during the numerous exercise and training flights in magnetically natural conditions under totally overcast conditions. Alternatives will be discussed. Table 1 gives the data of the individual releases.

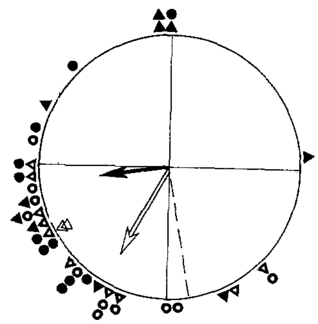

Fig. 2. On their first flight in sunshine, inexperienced experimental birds showed a significant ($P < 0.05$) *clockwise* deviation from the mean of their controls. In this and all following figures, the vanishing bearings of control birds are given as *open symbols* and those of experimental birds as *solid symbols* at the periphery of the circle. An *open* and a *solid arrow*, respectively, give the mean vectors with their length drawn proportional to the radius of the circle ($r = 1$). The home direction is marked by a *dashed line*, and home plus the deviation of magnetic north is marked by a *double triangle* inside the circle. *Triangles*: test 75-1, *dots* 75-2 (see Table 1a (1))

First Flights Under Sun

In 1975, we performed two tests with untrained young pigeons that were ca. 16 and 20 weeks old and whose only flying experience consisted of infrequent exercise flights under overcast skies at the loft. The vanishing bearings of these tests 75-1 and 75-2 are given in Fig. 2. Pooling the two releases, the experimentals' mean lies 44° *clockwise* from the mean of the controls; the difference is statistically significant ($P < 0.05$, Watson-Williams test). Figure 3 presents the vanishing bearings of three tests performed with experimental birds that had completed a short training program under totally overcast skies. In these tests, we found a clockwise deviation, which is significant for the two 1980 tests (Fig. 3b, c). It was, however, always markedly smaller than the shift in magnetic north, at the most only about half of it.

In summary, on their first flight in sunshine, the experimental birds showed a deviation in the expected direction, but in most cases this shift did not correspond to the shift in magnetic north.

A study on the development of sun orientation (R. Wiltschko and W. Wiltschko 1981) had clearly shown that the timing of the establishment of the sun compass strongly depends on the birds' flying experience, which normally means flying mostly in sunshine. In a first test 74-1, untrained experimentals only 13 weeks old had shown a non-significant counterclockwise deviation (Table 1); today we know that these young birds with their limited flying experience could not be expected to use the sun compass. To check whether our 1980 test birds

Table 1. The data of the individual releases, including age and experience of the test birds are given: Roman numbers mark test groups (a group of experimentals plus the corresponding group of controls) whose successive performances can be followed up in the series of tests. Treatment (*tr*) indicates whether the sample were controls (*C*) or experimentals (*E*); the indices indicate which flight in sunshine the respective flight was. CS_f = a sample of controls whose internal clock was shifted 6 h fast. α_m = direction of mean vector; r_m = length of mean vector, *asterices* indicate significance by the Rayleigh test. ΔC = difference in mean direction between experimentals and controls; + = clockwise, and − = counterclockwise. *Asterices* at ΔC indicate that this difference is significant by the Watson Williams test. *Median van. int.* median vanishing interval; *median hom. int.* median homing interval; *asterices* indicate that these data from experimentals and controls differ significantly by the Mann Whitney test. Significance: * $P<0.05$, ** $P<0.01$, *** $P<0.001$

Test group	Date and age	Release site, home direction, distance	tr	Birds released (bearings)	α_m	r_m	ΔC	Median van. int. (min:s)	Homed day 1 (later)	Median hom. int. (h:min)
a) First flight under sun										
(1) Untrained pigeons:										
74-1	17.7.74	West Mountain	C	9 (9)	341°	0.79**		4:05	6 (1)	1:03
	13 weeks	288° 19.1 km	E_1	10 (10)	309°	0.68**	(−32°)	6:33	9 (–)	0:32
75-1	15.7.75	Auburn	C	12 (10)	222°	0.74**		8:04	– (2)	2 days
	16 weeks	170° 66.2 km	E_1	11 (10)	283°	0.31	+61°	8:44	1 (1)	1 day
75-2	9.8.75	Auburn	C	13 (11)	215°	0.76***		6:10	1 (3)	2 days
	20 weeks	170° 66.2 km	E_1	14 (11)	255°	0.76***	+40°	6:15	– (2)	2 days
(2) Pigeons that had completed a short training program:										
74-2	29.7.74	West Mountain	C	9 (9)	296°	0.49		4:09	8 (1)	0:58
I	15 weeks	288° 19.1 km	E_1	12 (9)	342°	0.53	+46	4:45	12	0:58
80-1	27.7.80	Langmuir	C	11 (10)	157°	0.97***		3:52	11	0:14
III	16 weeks	158° 5.9 km	E_1	11 (10)	186°	0.92***	+29°**	4:19	11	0:16
			CS_f	11 (10)	103°	0.71**	−54°*	3:55	10 (–)	0:24
80-3	22.8.80	South Danby	C	10 (10)	313°	0.89***		6:52	10	0:48
IV	20 weeks	14° 12.1 km	E_1	12 (10)	18°	0.92***	+65°***	5:47	12	0:57
b) Second flight under sun										
(1) First flight had been a *homing flight* under sun the previous day:										
80-2	28.7.80	Level Green	C	11 (8)	3°	0.69*		4:36	11	1:09
III	16 weeks	309° 15.4 km	E_2	11 (10)	290°	0.60*	−73°*	5:02	11	0:51
80-4	23.8.80	West Mountain	C	13 (12)	351°	0.97***		3:37	12 (–)	1:19
IV	20 weeks	288° 19.1 km	E_2	12 (12)	313°	0.73***	−38°*	3:46	12	1:07
(2) First flight had been an *exercise flight* at the loft under sun:										
74-3	31.7.74	Auburn	C	13 (12)	128°	0.64**		5:13	4 (1)	2:11
II	15 weeks	170° 66.2 km	E_2	12 (12)	34°	0.46	−94°**	3:35	4 (3)	7:10
80-4	23.8.80	West Mountain	C	13 (12)	351°	0.97***		3:37	12 (–)	1:19
V	20 weeks	288° 19.1 km	E_2	8 (7)	286°	0.85***	−67°***	6:17	7 (2)	2:03
c) Later flights under sun										
74-5	19.8.74	Weedsport	C	9 (8)	176°	0.90***		3:57	8	not rec.
I		173° 73.3 km	E_2	13 (10)	157°	0.20	−19°	5:45	10	not rec.
74-6	19.8.74	Orwell, Pa.	C	8 (6)	290°	0.81*		5:06	6	not rec.
II		348° 65.2 km	E_3	11 (7)	311°	0.95***	+21°	5:04	7	not rec.
80-5	25.8.80	West Mountain	C	11 (10)	328°	0.86***		7:00	11	0:57
III		288° 19.1 km	E_3	11 (11)	275°	0.80***	−53°**	8:13	10 (1)	1:06
80-6	3.9.80	Perry City	C	11 (9)	307°	0.60		5:50	5 (5)	5:20
III		104° 23.0 km	E_4	11 (8)	237°	0.53	−70°	7:32	6 (5)	2:49
80-7	6.9.80	Locke	C	11 (10)	213°	0.91***		3:31	10 (1)	1:39
IV, V		170° 26.8 km	E_3	14 (10)	230°	0.57*	+17°	4:50	14	1:19*
80-8	28.9.80	Virgil	C	7 (5)	225°	0.88*		6:21	7	not rec.
IV, V		250° 21.8 km	E_4	18 (4)	226°	0.98**	+1°	2:32	18	not rec.
80-9	1.10.80	Ecklor Road	C	12 (8)	269°	0.91***		2:55	5 (7)	2 days
IV, V		349° 30.9 km	E_5	12 (8)	304°	0.62*	+35°	3:13	8 (4)	ca. 4:00

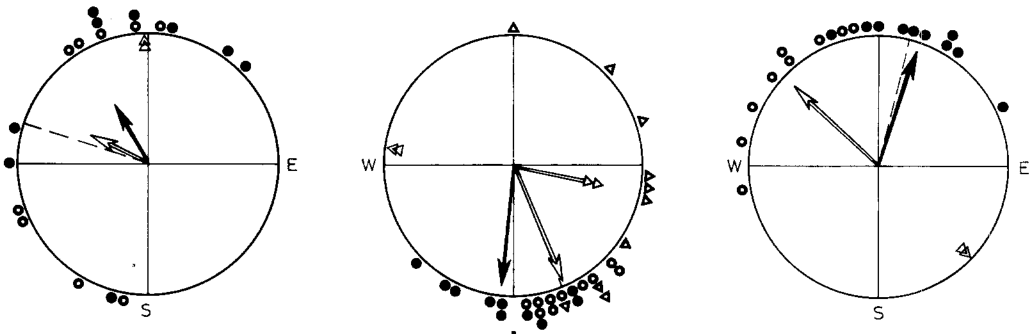

Fig. 3a–c. On their first flight in sunshine, experimental birds that had been trained under overcast conditions showed a *clockwise* deviation from their controls. **a** Test 74-2, **b** test 80-1; *open triangles* and the *open arrow* with a triangle tip mark the bearings and the mean vector of a group of control birds whose internal clock had been phase-shifted 6 h fast (see text). **c** Test 80-3 (see Table 1 (2))

Table 2. Differences in the mean directions of the experimentals and controls 1, 2, and 3 min after release. *Sign. sample* indicates which sample – controls (*C*) and experimentals (*E*) – are significant by the Rayleigh test with at least $P<0.05$. ΔC gives the difference in mean direction, see Table 1

Test number	1 min		2 min		3 min		Van. bearings	
	Sign. sample	ΔC	Sign. sample	ΔC	Sign. sample	ΔC	Sign. sample	ΔC
a) First flights under sun								
75-1	None	+90°	None	−121°	None	−54°	*C*	+61°
75-2	*E*	+19°	*E*	+36°	*E*	+26°	*C, E*	+40°
74-2	*C, E*	+42°	None	+69°	None	+64°	None	+46°
80-1	*C, E*	− 9°	*C, E*	−28°	*C, E*	+ 7°	*C, E*	+29°**
80-3	*C, E*	− 9°	*C, E*	+52°*	*C, E*	+14°	*C, E*	+65°**
b) Second flights under sun								
80-2	*C, E*	− 9°	*E*	−30°	*C, E*	−54°*	*C, E*	−73°*
80-4	*E*	−37°	*C, E*	−22°	*C, E*	−24°	*C, E*	−38°*
74-3	*C*	−153°	None	−113°*	None	−71°	*C*	−94°**
80-4	None	−47°	*C, E*	−55°	*C, E*	−38°	*C, E*	−67°***

were using the sun compass, we released in test 80-1 as a third group control birds whose internal clock had been phase-shifted 6 h fast (marked CS_f in Table 1, a). These birds, aged 16 weeks, produced vanishing bearings deviating significantly ($P<0.05$) from those of the untreated controls (Fig. 3b, open triangles); yet the 54° deviation was only roughly half the expected amount for a 6 h fast shift at this time of the year. The distribution of the bearings seems to suggest that possibly some birds made full use of the sun compass, while others showed only a slight shift. Altogether, this clock-shift test seems to indicate that birds knowing the sun only from sitting in their loft are able to establish a sun compass, but apparently not all of our birds had completed this process. This must be considered when the amount of deviation between the experimentals and the controls is interpreted.

Table 2 lists the differences in bearings at 1, 2, and 3 min after the five releases in which the test birds were experienced enough to use their sun compass. The clockwise deviation observed in the vanishing bearings seems to manifest itself only slowly during the departure of the birds.

Second Flights in Sunshine

In the two 1980 tests, all trained birds returned from their first flight in sunshine on the day of release, and they were released again in sunshine the following day from a new site. Their vanishing bearings are given in Fig. 4. The experimental birds now show a pronounced *counterclockwise* deviation from their controls, which is significant in test 80-4 ($P<0.05$, Fig. 4b).

This switch from a clockwise deviation on the first flight to an counterclockwise deviation on the second flight is also found when the first flight in sunshine was not a homing flight but merely an exercise flight at the loft (see Fig. 5). In test 74-3 (Fig. 5a), the birds had had a sun flight for ca. 10 min the day before, and in test 80-4 (Fig. 5b) the birds had had a sun flight for ca. 30 min a week before they were tested. In both cases, the counterclockwise deviation of the experimentals from the controls is significant ($P<0.01$).

The differences in bearings at 1, 2, and 3 min for these releases are listed in Table 2. Here the experimentals tended to show the counterclockwise deviation immediately after their release.

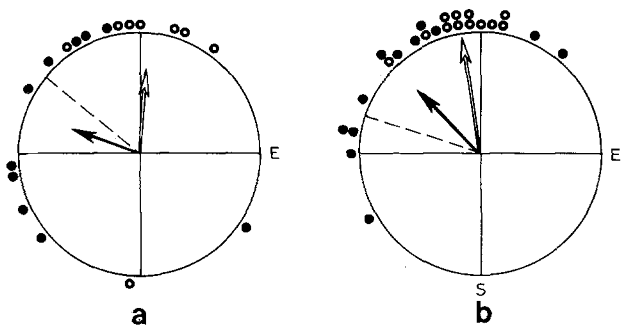

Fig. 4a, b. Experimental birds that had homed in sunshine the previous day from test 80-1 and 80-3 showed an *counterclockwise* deviation from their controls on their second flight in sunshine. **a** Test 80-2, **b** test 80-4 (see Table 1b (1))

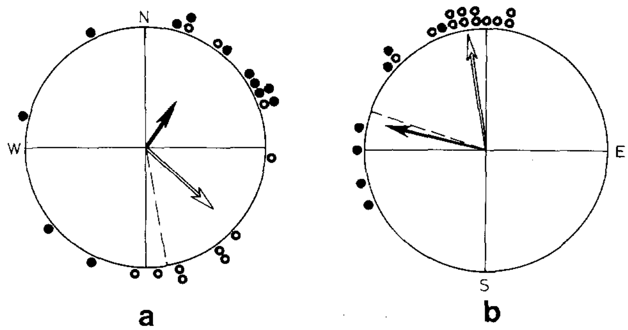

Fig. 5a, b. Experimental birds that had previously had one exercise flight at their loft in sunshine also showed *counterclockwise* deviation from their controls when released in sunshine for a second flight. **a** Test 74-3, **b** test 80-4 (see Table 1b (2))

Later Flights in Sunshine

The experimental birds returning from their first two flights continued to live in the magnetic loft and were repeatedly released in sunshine. Their later behavior, however, does not form a uniform picture. In 1980, the birds of group III continued to show a marked counterclockwise deviation at least on their third and fourth flights in sunshine (Fig. 6a, b). The experimental birds of the other groups, however, appeared to orient more or less like their controls on their third (Fig. 6c) and later flights (Table 1). This seems to indicate that the difference in orientation between experimentals and controls eventually disappeared.

We never found a consistent difference between the experimentals and the controls in vanishing intervals and homing times.

Discussion

Growing up in the loft from which they could observe the sun only in an abnormal directional relationship to the surrounding magnetic field affected the birds' orientation in sunshine: On their first flight in sunshine the experimental pigeons deviated from the controls in the direction in which magnetic north had been turned. However, the amount of the deviation was generally smaller than

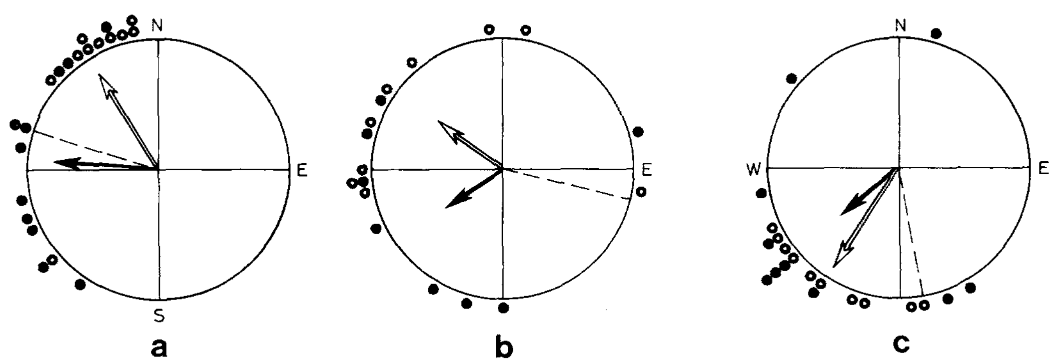

Fig. 6. One group of experimental birds continued to show counterclockwise deviation from their controls on their third (**a** test 80-5) and fourth (**b** test 80-6) flight in sunshine, while the other groups did not (**c** test 80-7). See also Table 1c

that predicted by the calibration hypothesis. This is difficult to interpret. The magnetic field in the aviary that was not completely homogenous may have played a role. But, as the clock-shift test 80-1 seems to indicate, it is also possible that some of our young, unexperienced test birds may not have completed the process of establishing their sun compass. Likewise, it is possible that our test birds not having been able to calibrate their sun compass in a normal way i.e. during flight, gave less weight to it than normal birds. Faced with a discrepancy between their magnetic compass and their sun compass, they may have chosen a compromise.

Another finding is even more puzzling: One experience of flying in the sun – during an exercise flight a the loft just as on a homing flight – changed the clockwise deviation into an counterclockwise one. This reaction looks like over-compensation and can hardly be explained in terms of a simple re-calibration of the sun compass, but appears to suggest a much more complex relationship between the sun compass and the magnetic field.

The good homing success of the experimental birds is not surprising: Realizing that their sun compass did not agree with the true situation, they may have easily switched to their magnetic compass, since all their exercise and training flights had been exclusively under overcast conditions (see Keeton 1969).

So far we have discussed our results in view of the development of the birds' sun compass. As an alternative explanation, an effect on the birds' 'map' must be considered: Wallraff (1974) discussed whether birds learn the directional characteristics of the factors used for bicoordinate navigation during exposition at their home loft (several types of aviary experiments support such an assumption, see Papi 1976, Wallraff 1979 and others). Living in an altered magnetic field might have resulted in an abnormal connection between the 'map' factors and the magnetic compass. There is no direct evidence that we indeed observed an effect on the sun compass, since vanishing bearings of birds released under overcast conditions were not recorded, but our findings seem to support this idea.

The experimental birds had all their flying experience – including 8 km training flights for most groups – in the natural local geomagnetic field. It was always the *first flight in sunshine* which changed their behavior from a clockwise to an counterclockwise deviation. Why this one flight should be different from the numerous previous flights under overcast conditions cannot be explained by assuming that the directional relation of the 'map' factors to the magnetic field is affected. It seems to argue strongly in favor of an abnormal sun compass caused by the altered magnetic field.

By indicating a connection between the sun compass and the magnetic compass our findings do not support the other possible ways of establishing the sun compass mentioned at the beginning: Estimating the sun's position relative to landmarks and a direct coupling of the sun compass with 'map' factors, as Wallraff (1974) proposed, should not be affected by an altered magnetic field at the loft.

Our data on the birds' behavior during later flights in sunshine are rather inconsistent, but they seem to suggest that eventually, after repeated flights in the sun, the experimental birds' orientation ceased to differ from that of the controls. This would mean that they learned to ignore their experience in the altered magnetic field at the loft and at last based their orientation solely on experience gathered during actual flights. However, we do not know whether these birds finally used a normal sun compass or why one group appeared to take longer than the other groups to normalize its orientation.

In summary, our findings support the assumption that the magnetic field is involved in the learning process establishing the sun compass in young pigeons. But this process does not appear to be as simple as the calibration hypothesis describes. Sun compass and magnetic compass seem to be related in a much more complex way, which we do not completely understand yet.

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