THE EFFECT OF DIRECTIONAL EXPERIENCE ON INITIAL ORIENTATION IN PIGEONS

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IN a review article (Wallraff 1967) I reported that the individual experience gained from previous homing flights is one of the various factors determining the initial bearings of displaced pigeons. This conclusion was based both on earlier published results (Wallraff 1959a, Graue 1965) and on further findings of which some examples were shown. I emphasized that, at least in birds with limited experience, even a single flight can influence the initial direction in a following flight, depending on the relation between the two homeward directions. I also emphasized that the magnitude of the deflection varies within a very wide range.

Recently Alexander and Keeton (1972) reported that they failed to find effects of directional training on initial orientation in pigeons of their loft in Ithaca, New York. As they also doubted the conclusiveness of the data I had thus far presented, I feel bound to discuss the matter again and to publish all the data I have that may be especially relevant to deciding the question.

MATERIAL AND METHODS

From the records of all the pigeon releases I and/or my co-workers conducted between 1956 and 1972, I selected 14 releases that met the following criteria: At the same date and place two groups of pigeons were released, each of them consisting of at least five birds. One of the groups, called *L*, had had its last preceding flight from a place with homeward direction 90 ± 45 degrees *left* of the homeward direction in the test release, while for the other group, *R*, this former direction was 90 ± 45 degrees to the *right*. (I assume that the 14 releases are really all those fitting these criteria, but I may have overlooked one or more releases among the mass of records filed under other topics. At any rate, the selection was entirely independent of the results.)

Table 1 lists the most important data of the releases, designated by letters A to N. Comments will be restricted to additional information that cannot be deduced from the table.

In the first ten releases (A–J), the preceding flight was the first release the participants had ever had; thus all were second-flight birds. In release K, most of the group *L* birds had returned from three earlier flights (22 September 1956, 23 km west; 23 September 1956, 69 km south; 26 September 1956, 23 km east), and most of the group *R* birds from four (16 September 1956, 23 km east; 19 September 1956, 23 km west; 23 September 1956, 69 km south; 30 September 1956, 23 km west); all the pigeons had participated in the last preceding flight mentioned in Table 1. Releases L, M, and N are parts of a sequence in which the same two groups of birds, A and B, were utilized. The sequence consisted of the following releases: (1) 13 and 15 July 1960, both groups 23 km east (first

TABLE 1

DATA OF TESTS, LAST PRECEDING RELEASES, AND MEAN BEARINGS AT VANISHING[1]

Test release					Preceding release			Test release		
		Towards home				Towards home		Number of bearings	Mean vector	
No.	Date	Dir.	Dist.	Group	Date	Dir.	Dist.		Dir.	Length[2]
A	17–10–57	358°	20	L	23– 8–57	268°	23	12	223°	0.28
				R	2–10–57	95°	23	15	89°	0.88★★
B	5– 9–58	95°	23	L	24– 8–58	358°	20	5	9°	0.76+
				R	24– 8–58	144°	22	9	93°	0.36
C	5– 9–58	268°	23	L	24– 8–58	144°	22	9	143°	0.78★
				R	24– 8–58	358°	20	6	55°	0.52
D	4–10–64	204°	160	L	26– 8–64	83°	157	6	75°	0.82+
				R	27–8–64/24–9–64	269°	45	9	266°	0.70★
E	4– 9–64	265°	104	L	1963/1964	175°	54–155	12	275°	0.79★★
				R	1963/1964	359°	52–159	6	318°	0.64
F	4– 9–64	265°	118	L	1963/1964	175°	54–155	14	270°	0.20
				R	1963/1964	359°	52–159	9	298°	0.83★★
G	8– 5–68	185°	29	L	12–10–67	83°	73	7	152°	0.71+
				R	11–10–67	265°	71	11	174°	0.93★★
H	9– 5–68	185°	29	L	5–4–68/19–4–68	85°	32	5	184°	0.56
				R	10–4–68/ 1–5–68	267°	30	9	199°	0.89★★
I	13– 5–69	97°	29	L	8–10–68/26–4–69	4°	27	12	88°	0.62★
				R	20–9–68/ 9–5–69	181°	28	11	155°	0.75★★
J	24– 9–70	269°	112	L	18– 8–70	180°	117	6	268°	0.82+
				R	3– 9–70	4°	27	7	303°	0.81★
K	2–10–56	358°	20	L	26– 9–56	268°	23	7	343°	0.68+
				R	30– 9–56	95°	23	11	32°	0.58+
L	14– 8–60	94°	44	L	8– 8–60	45°	22	16	8°	0.60★
				R	8– 8–60	144°	22	15	24°	0.53+
M	22– 8–60	268°	23	L	21– 8–60	175°	10	17	122°	0.86★★
				R	21– 8–60	2°	9	15	46°	0.73★★
N	24– 9–60	92°	10	L	10– 9–60	356°	69	12	360°	0.82★★
				R	10– 9–60	166°	77	9	67°	0.21

[1] Date = day-month-year; Dir. = direction in degrees clockwise from north; Dist. = distance in km.
[2] Symbols refer to the statistical significance (Rayleigh test): ★★ = $P < 0.001$, ★ = $P < 0.01$, + = $P < 0.05$, no symbol = $P > 0.05$.

release in the birds' lives; pigeons from both groups released on each of the 2 days, but each bird only once); (2) 8 August 1960, group A 22 km southwest, group B 22 km northwest; (3) 14 August 1960, both groups 44 km west (= test release L); (4) 21 August 1960, group A 9 km south, group B 10 km north; (5) 22 August 1960, both groups 23 km east (= test release M); (6) 10 September 1960, group A 69 km south, group B 77 km north; (7) 24 September 1960, both groups 10 km west (= test release N). Thus groups A and B were released from the east and the west in common, but alternating with these flights, group A was released from the south and group B from the north. Accordingly, the number of preceding "training flights" increased from one in release L to three in release N, always with a "neutral" flight in between.

In releases A–D and K–N the loft site was at Wilhelmshaven on the north German coast; in releases E and F at Osnabrück about 150 km south of Wilhelmshaven; in releases G and H at Zorneding about 20 km east-southeast of Munich, southern Germany; and in releases I and J at Seewiesen, about 30 km southwest of Munich. The pigeons of the four loft sites were of different racing stocks.

To facilitate an examination of the material as a whole, results published earlier are treated again here. This concerns releases A, B, C, K (Wallraff 1959a), and D, E, F (Wallraff 1967).

The experimental procedure was the same through the years as described earlier (Wallraff 1959a, 1970). It was identical or at least very similar to that described by Alexander and Keeton (1972), except that the sequence of birds within each release did not always alternate precisely between *L* and *R*. There was, instead, sometimes a chance sequence, but never were the whole groups separated in time.

All the releases were conducted under sunny weather conditions with weak or moderate winds.

The following statistical tests designed especially for circular distributions were used: the Rayleigh test and the V test (both for one sample), and the nonparametric two-sample test of Mardia, Watson, and Wheeler (B test). They are all described by Batschelet (1972). When the B test was used, tie values were either arranged symmetrically (in case of odd numbers of equal values), or they were arranged as "unfavorably" as possible, i.e. in the manner that resulted in the highest chance probability, *P*.

RESULTS

The vanishing bearings in each of the releases are shown in Figure 1. Although the diagrams reflect a great diversity, they have one aspect in common: When looking towards home, the bearings of group *L* appear, in the mean, left of those of group *R*. This is true in all of the 14 releases, and this fact alone leads to the conclusion that there is a systematic dependence on the kind of preceding experience. (In one test, L, it may be doubtful whether the bearings can be categorized at all with respect to the former home directions; but this does not affect the conclusiveness of the findings, as the binomial chance probability, one-tailed, for splits of 14:0, 13:0, and 13:1 is $P \leqslant 0.001$.)

Besides this general agreement, the magnitude of the angular differences varies greatly. In the most extreme case, D, the mean vectors point almost exactly to the two preceding home directions and are,

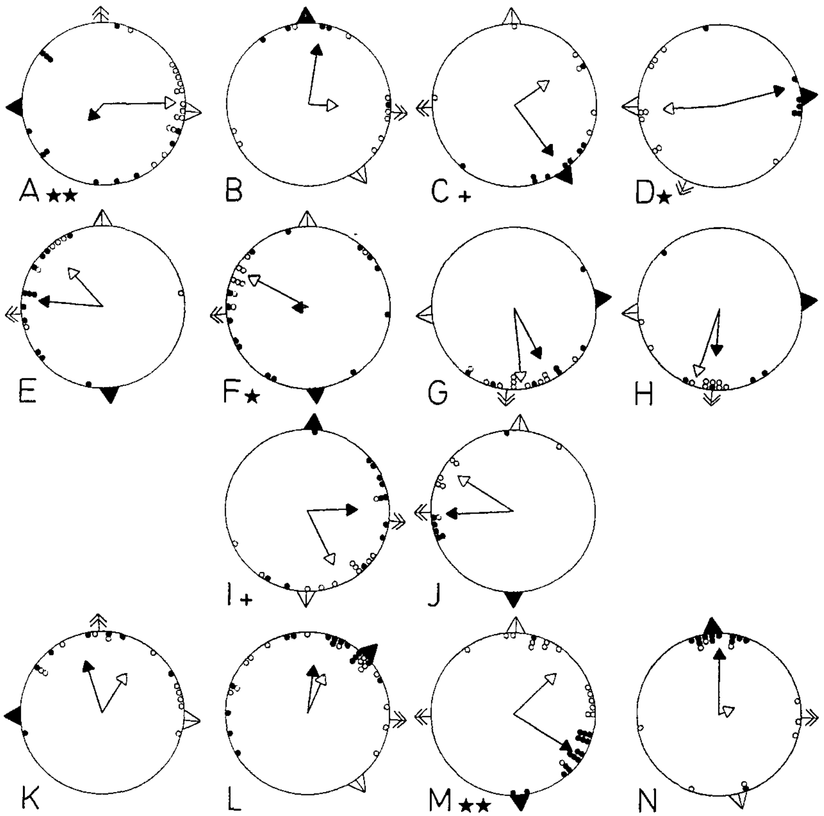

Figure 1. Vanishing bearings of individual pigeons in releases A–N (cf. Table 1). At the periphery of each diagram, the double-headed arrow points to the actual homeward direction, while the other arrowheads indicate the homeward direction of the last preceding flight of group *L* (black) and group *R* (white). Black dots refer to birds of group *L*, white dots to birds of group *R*. The mean vectors calculated from their distribution originate in the center and are characterized by corresponding arrowheads. (The greatest possible length of the mean vectors coincides with the radius of the circles.) The letters are followed by a symbol if the distributions of the two samples differ significantly from each other with $P < 0.001$ (★★), $P < 0.01$ (★), or $P < 0.05$ (+), respectively (B test).

consequently, opposite to each other, while in other cases the difference is very small. Accordingly, the difference between the two groups within the single releases is sometimes significant, and sometimes it is not (see Figure 1). Moreover because of small sample sizes and/or large scatter, some of the samples do not show a statistically significant directional preference (see Table 1). But statistical significance is not a prerequisite for using the data in a second-order analysis.

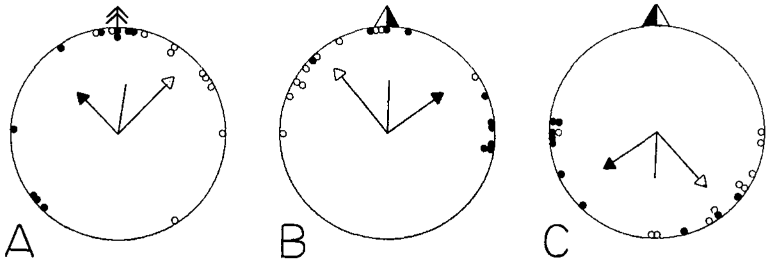

Figure 2. The mean bearings of second-flight pigeons in relation to three reference directions. Each point corresponds to the direction of a mean vector in Figure 1, A–J. The second-order mean vectors shown here are calculated from these points, separately for groups *L* (black) and *R* (white), and for both groups together (without arrowhead). A, reference direction (top) = actual homeward direction; B, reference direction (top) = last preceding homeward direction; C, reference direction (top) = last preceding homeward direction of the compared group (i.e. group *L* in relation to previous home of group *R*, and vice versa).

The results of such an analysis are presented in Figure 2. The 20 mean directions of the 10 releases with second-flight pigeons (Figure 1, A–J) were taken as units (irrespective of the lengths of the vectors) and arranged with respect to three different directions of reference.

Figure 2A shows the deviations from the actual homeward direction. In the mean, group *L* deviates 44 degrees to the left, and group *R* 44 degrees to the right. The probabilities that the samples belong to a uniform distribution are $P < 0.05$ (L) and $P < 0.01$ (R) (Rayleigh test). The difference between them is significant with $P < 0.05$ (B test). The mean vector calculated from all 20 directions together deviates by only 9 degrees from home. With a vector length of 0.472, the overall distribution is clearly different from random ($P < 0.01$, Rayleigh test), and with a homeward component (cf. Wallraff 1967) of +0.467 it is obviously oriented toward home ($P < 0.005$, V test).

Figure 2B shows the same data arranged with the homeward direction in the *previous* release of each group of birds at the top of the diagram. The picture looks rather similar to diagram A. The deviations from the reference direction are 54 (L) and 38 (R) degrees. Note that the signs are interchanged, as is appropriate to the geometrical relationships. The mean vector resulting from all 20 directions deviates by only 2 degrees from the earlier home direction. The distribution is clearly different from uniformity (vector length 0.496, $P < 0.01$), and the "homeward" component of +0.495 ($P < 0.001$) is very similar to that resulting from the distribution in the arrangement of Figure 2A. It follows that the directional choices of the pigeons at departure were determined by the

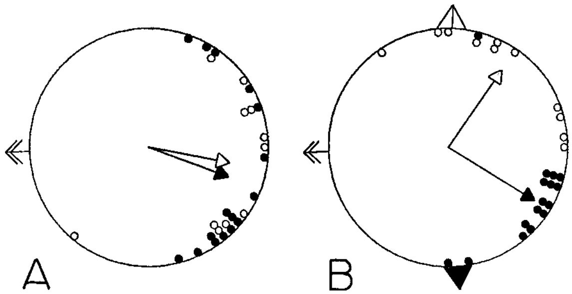

Figure 3. Vanishing bearings of group *L* (black) and *R* (white) at 23 km east of Wilhelmshaven. A, first-flight pigeons, groups *L* and *R* not yet treated differently (13 and 15 July 1960). B, second release of the same individuals at the same place after limited "training" from north (*L*) and south (*R*), respectively (22 August 1960). Symbols as in Figure 1.

relationship of both the former release site and the test release site to the loft. In the mean of the data presented here, the two influences were of equal magnitude.

Figure 2C demonstrates, in contrast to B, that the pigeons' bearings were negatively correlated with the previous homeward direction of the *compared* group of birds released simultaneously. This contrast corroborates the effect of individual experience.

(In Figure 2 only the releases of second-flight pigeons are included as they represent the most homogeneous material. In the releases K–N the birds had completed 2–6 preceding flights, and in the sequence of L–N the same individuals participated with an increasing number of training flights. If these four releases are included in the calculations, the results remain similar to those shown in Figure 2. The homeward component in the test release (+0.387, $P < 0.005$) becomes somewhat smaller, but the component toward previous home (+0.467, $P < 0.001$) remains nearly unchanged. For the eight additional directions alone it is +0.397.)

One release allows a further comparison that throws some light on the effect of experience on a more individual basis. The birds participating in flight M (see Figure 1, Table 1), which was the fifth release in their life, had been released as first-flight pigeons about 6 weeks earlier at the same place 23 km east of Wilhemshaven. In the meantime they had been flown from 22 km northwest (*L*) or southwest (*R*), from 44 km west (*L* and *R*), and from about 10 km north (*L*) or south (*R*). Figure 3 shows the vanishing bearings of the same individuals released for the first and the second times at the same place. (Only those birds are included from which a bearing could be recorded in both releases. Therefore the number of points in Figure 3B is somewhat smaller than that in Figure 1M.) Obviously a separation of the two groups occurred in the second flight that was not evident in the first release, when the birds had not yet been differentially treated. The distributions of all the points together do not differ very much in the two diagrams, and both distributions can be thought of as being normal for this place, at which our pigeons regularly flew away from home (cf. Wallraff 1959b). But within this normal scope, the *L* birds covered the southern and the *R* birds the northern edge of the sample after they had been released previously from north or south, respectively. The difference between the two groups in this second flight is statistically significant ($P < 0.001$, B test).

DISCUSSION

The data presented confirm earlier conclusions that pigeons are affected in their selection of bearings by the directions of previous homing flights. The birds appeared to be deflected towards the side of the homeward direction of their last preceding flight, which was usually their first flight. The magnitude of this deflection varied greatly; the degree to which the birds followed the influence ranged from nearly zero to 100%.

It has not yet been determined which circumstances are responsible for the quantitative differences. Thus answers can be only of a hypothetical nature. I presume that the amount of deflection is mainly dependent on how sure the birds are in their directional choices, based on available navigational parameters. The great variability inherent in the patterns of initial orientation (cf. Wallraff 1959b, 1970) suggests that this surety varies greatly between places as well as in time. On this basis it may be possible to interpret at least some of the diagrams in Figure 1.

In the releases G and H, for instance, the pigeons seemed to have rather good information on the direction they should fly to get home, and therefore they did not rely very much on the directions they had successfully flown earlier. Release L shows that the direction chosen on the basis of the actual situation rather than on earlier experience does not necessarily coincide with the true homeward direction. There are reasons to assume that at this place (44 km west of Wilhelmshaven) the birds regularly had very little doubt on where to go as they strongly preferred northeasterly directions in nearly every release (cf. Wallraff 1959b, Figure 8). In other cases some interplay between different "forces" may occur. At a place 20 km south of Wilhelmshaven, inexperienced or minimally experienced birds normally exhibited a fairly strong tendency to vanish towards the east (cf. Wallraff 1959a, 1960).

In release A, this tendency seemed to be intensified in group *R* by the preceding home flight from the west, resulting in a strong accumulation of bearings in the east. In group *L* of this release, however, the original eastward tendency may have been opposed by a somewhat stronger tendency towards west, induced by the previous home flight from the east, and the resulting conflict may have caused the great scatter. At the place 23 km east of the loft mentioned above in connection with Figure 3, the Wilhelmshaven pigeons showed generally two preferred directions at departure (cf. Wallraff 1959b, Figures 8, 22, and 23); the main peak of the headings was in the east-southeast, and a smaller peak pointed northeast. In the releases at this place shown here (C and M), the two groups with different directional experience were contrastingly distributed about these two generally preferred directions. At the locality 160 km north-northeast of Wilhelmshaven, the normal tendency towards southeast shown by first-flight pigeons (cf. Wallraff 1970, Figure 15) seems to have had so weak an influence that the birds based their directional choices purely on the courses they had successfully flown earlier (Figure 1D; cf. also Wallraff 1967, Figure 7).

These interpretations are based on the assumption that pigeons, when in doubt where to go, simply give preference to the compass direction that led towards home in an earlier flight. Because of the simple geometrical relationships apparent in the data, it seems obvious to me that an effect of this kind exists. It might be, however, that the navigational process itself is also affected. The experience gained in earlier homing flights could influence the manner in which the birds determine their flight directions from the available environmental cues. In other words, the effect of experience might not only result in a compass tendency's being superimposed on directional tendencies originating from other sources, but it might also influence the way in which the parameters composing the birds' "map" are processed. If the experience comes from only one preceding flight or from only a few flights, its effect on the navigational process could be assumed to be dependent on the areas the birds have covered during their previous movements. Thus birds with different directional experience might utilize somewhat different "maps." This could result in different individual orientation behavior that cannot be explained on the basis of the geometrical relationships between the homeward directions in a sequence of releases.

It cannot be decided positively whether this second possible kind of an experience effect is realized in the data presented here. Perhaps the behavior of group *L* in release F as compared with release E could be understood in this way (cf. also Alexander and Keeton 1972, Figure

4C). Most likely to fall into this category are cases in which the mean directions of group *L* and *R* deviate significantly from each other but, with respect to the earlier homeward directions, with an opposed sign. Only one case of this kind is known (Alexander and Keeton, Figure 2F), and so the question of whether the navigational process in a stricter sense (i.e., the "map" component) is affected by asymmetrical directional experience cannot be answered definitely at present. It is at least probable, however, that the pigeons' ability to determine the relation between their position and the loft site increases with increasing *general* experience (Wallraff 1959a; Schmidt-Koenig 1963, 1966; Wallraff and Graue 1973).

The results shown above coincide with those presented by Wallraff (1959a, 1967) and Graue (1965). They do not coincide so well with those of Alexander and Keeton (1972), but they are not in direct contradiction with them as the assumption that the differences between the results are merely quantitative in nature cannot be refuted. Though Alexander and Keeton could not prove an effect of directional experience statistically, they still obtained more results in favor than against the expectations, as they themselves admitted. (The proportion was 6:3, or if a somewhat modified evaluation is applied, 8:3.)

An attempt to make the findings of Alexandar and Keeton more comparable to those presented here results in some differences in the treatment of their data: (a) Series V is omitted as the birds were very experienced and as in the north and south tests groups A and B were released on different days. (b) Test I-2 consists of two, and test II-1 consists of three releases on different days, and thus I am reckoning with five instead of two releases. (c) Test III-west is included as a distinction between more or less northerly or southerly distributions is still possible. (d) Test IV-1 is included as the question of one-sample significance is not a necessary precondition for including the mean direction in a second-order analysis. The modified treatment leads to a total of 11 releases from which 8 are in agreement with the expectations. Though it cannot be excluded that the split of 8:3 is due to chance ($P = 0.113$), a meaningful coincidence with the expectations rather than total independence is nonetheless suggested.

It should be mentioned that series V is not excluded because it disagrees with the tendency seen in the other series. In only one of the four tests composing it is the sign of the difference clearly opposite to that expected. It should also be mentioned that test I-2 (which includes one of the three releases with results against expectation) was conducted after a reversal of the training directions, and it cannot be excluded that the effect of the first training pattern was still stronger than that of the later one. And, finally, it should be mentioned that the only two releases with second-flight pigeons (series IV), which are the releases most comparable with my data, fit quite well with the results shown in Figure 1 of this paper. Unfortunately, however, the first releases of these birds were not from opposite directions, and in the test release the homeward direction was not between the earlier ones. Thus the results could not be expected as clear-cut as they might have been otherwise.

So far, pigeons of six different loft sites originating from different strains have been examined (Graue 1965, Alexander and Keeton 1972, this paper), and in all cases at least the same tendency, in accordance with the theoretical expectations based on the geometry of earlier releases, was observed. (This leads to a "third-order split" of 6:0, with a binomial probability $P = 0.016$.) Thus in contrast to Alexander and Keeton, I conclude that this kind of an experience effect is a rather general phenomenon in pigeon homing. As the degree of its manifestation varies between nearly zero and 100% (see above), one cannot expect significant results in each single release or even in each set of only a few releases. A variety of factors may affect the amount of deflections, as for instance the loft site and the release site, the strain of the pigeons, and the level of their general experience. It might well be that the pigeons of the Cornell University loft used by Alexander and Keeton are less sensitive to influences caused by asymmetric experience than the birds used by Graue in Ohio and by me in Germany. This seems especially probable if the hypothesis is true that the magnitude of the experience effect is dependent on the "sureness" of the navigational deductions of the birds, as the Cornell pigeons are, in general, much better homeward-oriented than Graue's and my birds (cf. Keeton 1970, Graue 1970, Wallraff 1959b, 1970).

For this study, releases were selected that allow comparisons between groups of pigeons with opposed directions of homing experience. From these one can expect the clearest results, but it should be emphasized that the release of different groups at the same time and place is not an inevitable precondition for an analysis of an effect of directional experience. Diagrams such as those shown in Figures 2A and 2B can also be derived from one-sample releases. This offers the possibility of including much more material and therewith the chance of finding correlations between the experience effect and such factors as site of release, number of the birds' earlier flights, divergence angle of successive homeward directions, and length of time between successive releases. As yet only tentative discussions of these aspects would be possible.

Acknowledgments

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Summary

Fourteen test releases were conducted in which pigeons with different directional experience participated. In group *L*, the homeward

direction in the last preceding release was 90 ± 45 degrees to the left of the homeward direction in the test release, whereas in group *R* it was 90 ± 45 degrees to the right. In 10 of these tests the birds had completed only one preceding homing flight, which was the first release in their life. In all cases the sign of the mean angular difference between the bearings of the two groups was as expected on the assumption that the birds have a tendency to deviate from the common mean in the direction that led them homeward in their last preceding flight. (In one test it is difficult to decide whether the results can be categorized in this sense. Omitting it still results in a split of 13:0.) The magnitude of the deflections varied between nearly zero and 100%. Some aspects of the effect are discussed. It seems to be a rather general phenomenon in pigeon homing, though the degree of its expression varies greatly.

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