

Homing Behavior of Pigeons Not Disturbed by Application of an Olfactory Stimulus

William T. Keeton and A. Irene Brown

Section of Neurobiology and Behavior, Langmuir Laboratory, Cornell University, Ithaca, New York 14853, USA

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Summary. In a second attempt to repeat recently published experiments that appear to support an hypothesis that olfactory cues play an important role in pigeon navigation, we have conducted 15 experiments in which α -pinene in vaseline was applied to the birds' beak and nostrils prior to release, a procedure reported by Benvenuti *et al.* (1973) to cause a decrement in homing performance. Our results show no consistent difference between the experimental and control birds in any of the three parameters (initial orientation, rapidity of orientation, homing speed) measured by Benvenuti *et al.*

Introduction

In 1972 Floriano Papi and his colleagues at Pisa proposed that olfactory cues play an important role in pigeon homing, providing at least some of the information comprising the so-called "map" component in the orientation process (Papi *et al.*, 1972). These investigators have since published a long series of papers providing experimental data in support of their hypothesis.

Impressed with the consistency of the results of Papi's group, we have begun a series of experiments designed to repeat theirs in order to see if their olfactory model appears to hold for the orientational behavior of our own birds. Our first attempt was to repeat the experiments of Papi *et al.* (1973) in which cues (presumably olfactory) detected during the initial portion of the outward journey appeared to influence the birds' bearings upon release at a test site, but our results (Keeton, 1974) did not agree with those of the Italian workers; we did not find such an effect. We here report a second attempt, this time to repeat the experiments of Benvenuti *et al.* (1973) in which strongly odorous substances painted on or near the birds' nostrils were reported to cause a decrement in homing performance.

Methods

Our 15 experiments were modeled after certain of those of Benvenuti *et al.* (1973). In 9 of their 10 experiments they applied strongly odorous organic substances, mixed with vaseline, to the

beak and nostrils of the experimental pigeons, and plain vaseline to the beak and nostrils of the controls; in one of their experiments the substances were applied to cotton flocks taped to the beak just in front of the nostrils. We chose to follow the former procedure, i.e. we painted the material directly onto the beak and nostrils. In all of their experiments, Benvenuti and his colleagues applied the substances at the test site immediately before the release of each bird. We followed this procedure in 12 of our experiments, but in the other 3 (our Series IV) we applied the substances at the loft just prior to beginning the journey to the test site, with the thought that more dramatic results might be obtained if the substances could provide confusing or masking stimuli both on the outward journey and at the release site.

In various of their experiments the Italian workers used three different organic materials as the test substance: a mixture of extracts of parts of a variety of plants; olive oil; and α -pinene. We used α -pinene in all of our experiments, mixing it with vaseline in the ratio of 10 ml/15 g as indicated by Benvenuti *et al.* (1973). Plain vaseline was applied to the control birds.

We used 6 different release sites, as follows: Weedsport, New York, 73.5 km, home bearing 173°. Castor Hill Fire Tower, New York, 143.3 km, home bearing 200°. Rome, Pennsylvania, 60.7 km, home bearing 353°. Orwell, Pennsylvania, 65.5 km, home bearing 348°. South Towanda, Pennsylvania, 79.5 km, home bearing 2°. Eagles Mere, Pennsylvania, 117.2 km, home bearing 7°.

The pigeons used by Benvenuti *et al.* ranged in age from 5 to 17 months at the start of their experiments. All but those used in the one experiment with cotton flocks had had numerous previous homing flights, including ones from roughly the same direction (and often from comparable distances), though not the exact same sites, as the experimental release sites. In our own case, we used pigeons of a variety of ages and previous experience, as follows:

Series I. Birds Familiar-to-Site

Experiment 1. Weedsport, 22 and 24 October 1973. Old birds (2 or more years old); extensive previous experience, including a flight from the test site the previous month.

Experiment 2. Weedsport, 25 October 1973. Young birds (5-6 months); considerable previous experience from all directions, including a flight from the test site the previous month.

Series II. Yearlings New-to-Site

Experiment 3. Rome, 21 May 1974. During the previous year the birds had flown from various distances up to 24 km from all directions and 120 km W. As yearlings, they had flown up to 32 km from all directions.

Experiment 4. Eagles Mere, 5 June 1974. The birds were those used in experiment 3; they had been given a flock release from Rome between the two tests.

Experiment 5. Rome, 3 June 1974. During the previous year the birds had had flock releases up to 32 km E and W, 24 km S, and 64 km N, plus a single-toss release from 73 km N. As yearlings, they had had flock tosses from 32 km E and W, and both flock and single tosses from 24 km S.

Experiment 6. Eagles Mere, 5 June 1974. The same birds as in experiment 5.

Experiment 7. Eagles Mere, 14 May 1975. The birds were a mixture of those previously used in experiments 10, 11, 13, and 14.

Experiment 8. Castor Hill, 1 July 1975. The birds had not been flown the previous year. As yearlings they had had flock releases up to 32 km E, S, and W, and 40 km N, plus a single-toss release from 64 km N.

Series III. Young Birds New-to-Site

Experiment 9. Weedsport, 25 October 1973. The birds had had flock releases up to 32 km from all directions, plus a single-toss release from 72 km W.

Experiment 10. Weedsport, 23 September 1974. The birds had had flock releases up to 24 km N, E, and W and up to 16 km S, plus single-toss releases from 16 km N and E.

Experiment 11. Weedsport, 27 September 1974. The birds had had the same experience as those in experiment 10.

Experiment 12. South Towanda, 26 September 1974. The birds had had the same experience as those in experiment 10.

Series IV. α -Pinene Applied at Loft: Birds New-to-Site

Experiment 13. Orwell, 4 October 1974. Mostly the same birds as in experiment 10, but with a few birds of similar age and experience added.

Experiment 14. Weedsport, 22 October 1974. Mostly the same birds as in experiment 12, but with a few birds of similar age and experience added.

Experiment 15. Eagles Mere, 9 May 1975. The same birds as in Experiment 14.

The birds were released singly from the hand (alternating treatments), and were observed with 10×50 binoculars until they vanished from sight. The interval from release to vanish was timed with a stopwatch. Homing times were recorded by an observer at the loft. The mean bearing for each treatment was calculated by vector analysis, and the distribution of the bearings was evaluated by calculation of the uniform probability (P) under the Rayleigh test.

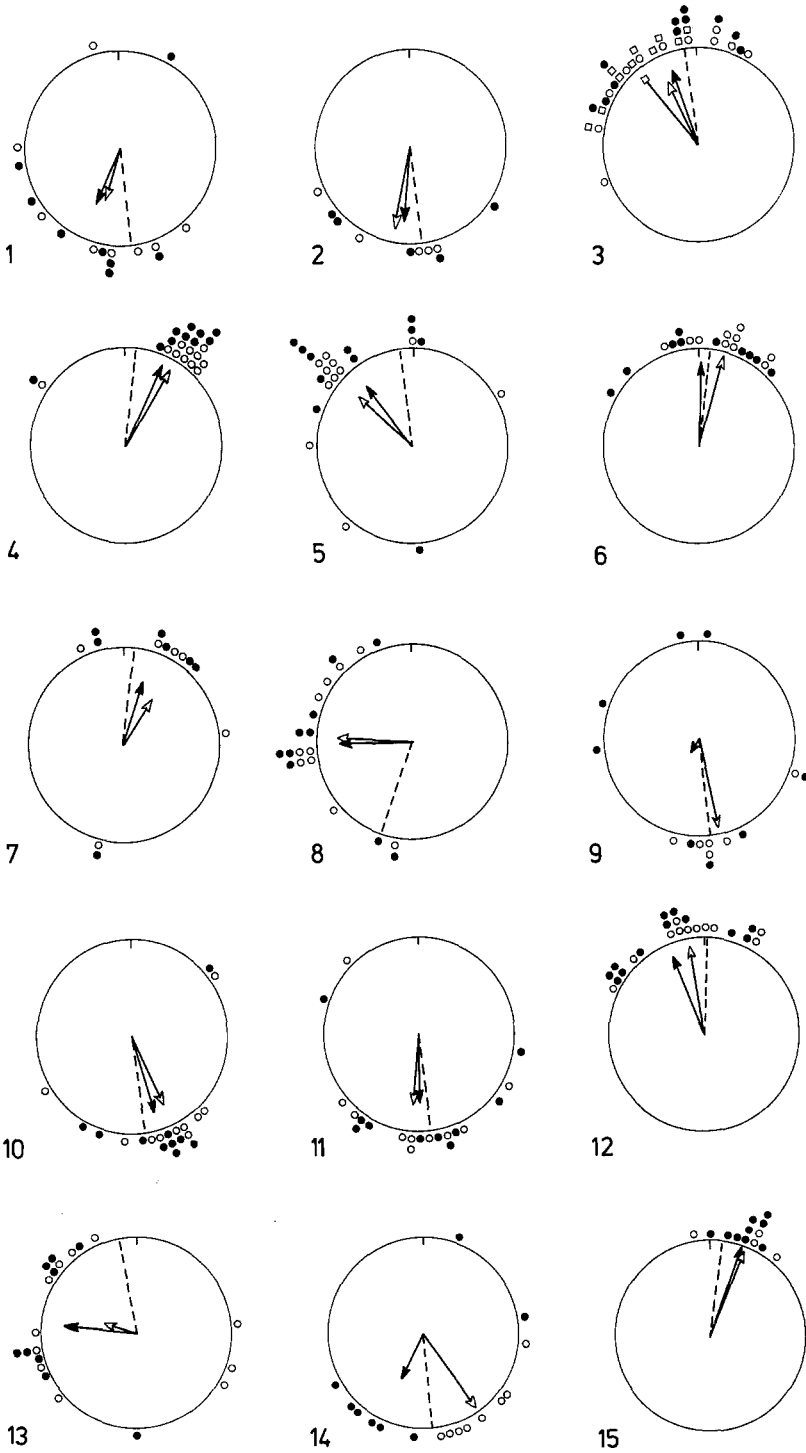
Results

The vanishing bearings obtained in the 15 experiments are shown in Figs. 1–15. Bearings of control birds are indicated by open circular symbols and bearings of experimental birds by solid symbols (in experiment 3, a second control group without vaseline was used; their bearings are indicated by open squares). The respective mean vectors are distinguished by open and solid arrow heads; the length of each vector (r) is proportional to the tightness of clumping of the bearings. The home direction is shown by a dashed line and geographic north by a small line at the top of the circle.

Table 1 gives numerical data for each treatment in each experiment. It can be seen that the bearings were significantly ($P\leq 0.05$) nonrandom in all but five cases: the controls in experiments 1, 7, and 13, and the birds with α -pinene in experiments 9 and 14. Thus the experimental birds departed randomly no more often than did the controls.

In the majority of the experiments, the mean vectors of the two treatments were remarkably similar in both bearing and vector length (see Figs. 1–8, 10–12, 15). Amongst the experiments where both treatments were nonrandom (and hence could be compared under the Watson and Williams F test; Batschelet, 1965), there was no case in which the mean bearing of the birds with α -pinene differed statistically from that of the controls. However, in experiment 14—one of the experiments in which the birds with α -pinene were not significantly oriented (though the southwesterly preference of the majority of the birds might well have reached significance if the sample had been larger)—the distributions of the two sets of bearings differed significantly ($P=0.001$) under the Watson U^2 test (Burr, 1964).

In the absence of a significant difference between the bearings of the two treatments in most of the individual experiments, we can ask whether a second-order analysis reveals a significant pattern of small differences running through the 15 experiments. Benvenuti *et al.* (1973) used the statistic u of the V test



Figs. 1-15. Vanishing bearings for experiments 1-15

Table 1. Results of the experiments

Ex- peri- ment ^a	Home direc- tion	Dis- tance (km)	Birds re- leased ^b	Mean bear- ing	Mean vector length (<i>r</i>)	<i>P</i>	Mean vanish- ing in- terval (min)	Returns same day and (later)	Mean speed of day birds (km/hr)
<i>Series I. Birds Familiar-to-site</i>									
1C	173°	73.5	10 (8)	195°	0.5620	0.076	11.8	10	41.8
E			11 (8)	204°	0.6307	0.036	6.2	9 (2)	49.3
2C	173°	73.5	6 (5)	191°	0.8655	<0.025	4.7	3 (2)	27.6
E			7 (5)	185°	0.7819	<0.05	6.7	4 (1)	38.7
<i>Series II. Yearlings New-to-site</i>									
3C	353°	60.7	12 (11)	336°	0.7511	<0.001	4.6	8 (3)	14.3
CC			11 (10)	322°	0.9193	<0.001	4.7	8 (3)	28.2
E			15 (11)	341°	0.8434	<0.001	3.8	9 (6)	26.7
4C	7°	117.2	11	32°	0.9057	<0.001	3.2	5 (6)	41.4
E			10	26°	0.9064	<0.001	3.0	5 (3)	35.4
5C	353°	60.7	12 (11)	312°	0.7323	0.001	5.8	11 (1)	17.2
E			11	322°	0.7459	<0.001	4.2	11	30.4
6C	7°	117.2	11 (10)	16°	0.9526	<0.001	3.4	3 (2)	34.7
E			11 (10)	2°	0.8428	<0.001	3.2	0 (1)	—
7C	7°	117.2	7 (6)	34°	0.5278	0.193	3.5	2 (3)	27.3
E			8 (7)	18°	0.6413	0.050	5.8	3 (3)	30.1
8C	200°	143.3	10	273°	0.7846	<0.001	4.1	3 (3)	21.6
E			11 (10)	269°	0.7503	0.002	6.5	0 (8)	—
<i>Series III. Young Birds New-to-site</i>									
9C	173°	73.5	6	168°	0.8971	0.003	6.5	2 (4)	19.6
E			8	213°	0.1503	0.843	7.0	0 (4)	—
10C	173°	73.5	11 (10)	156°	0.7630	0.001	7.3	9 (0)	23.0
E			11 (10)	164°	0.8029	<0.001	6.2	8 (2)	25.0
11C	173°	73.5	11 (10)	186°	0.7096	0.004	5.5	7 (3)	32.0
E			10	180°	0.6869	0.006	4.5	3 (5)	25.9
12C	2°	79.5	11	350°	0.8954	<0.001	3.5	5 (4)	22.8
E			12	337°	0.8615	<0.001	3.7	10 (1)	21.7
<i>Series IV. α-Pinene Applied at Loft, Birds New-to-site</i>									
13C	348°	65.5	12 (11)	285°	0.3362	0.295	6.0	7 (4)	29.9
E			11 (9)	275°	0.7605	0.003	5.2	6 (5)	27.4
14C	173°	73.5	11 (8)	143°	0.9184	<0.001	5.1	2 (8)	39.3
E			11 (8)	207°	0.5119	0.122	9.7	0 (8)	—
15C	7°	117.2	7 (4)	21°	0.9495	<0.025	7.4	2 (4)	24.2
E			11 (9)	19°	0.9891	<0.001	5.3	3 (7)	34.4

^a C=controls, CC=controls without vaseline, E=experimental birds with α-pinene.

^b When bearings were not obtained for all birds released, the number of bearings is given (in parentheses).

in such an analysis, and found that in all 10 of their experiments the control birds had a higher value. We use instead the homeward component h [$h=r \cdot \cos(\alpha-\beta)$, where r is the length of the mean vector, α is the mean direction, and β is the home direction], which is independent of sample size and hence

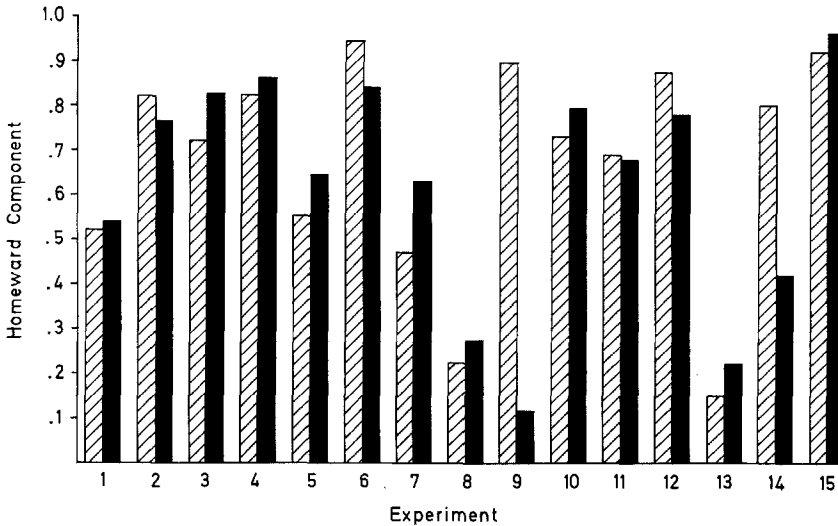


Fig. 16. Histogram comparing the homeward component of control birds (cross-hatched) and birds treated with α -pinene (solid black). In 6 of the experiments the control birds had the larger homeward component, and in 9 of the experiments the experimental birds had the larger homeward component

more appropriate for direct graphical comparisons¹. We show the homeward components in Fig. 16. As can be seen, the value for the control birds is greater in 6 experiments and the value for the experimental birds is greater in 9. In short, in more than half the cases it was actually the experimentals that had the larger homeward component. There is clearly no pattern of consistently better homeward orientation by the control pigeons.

If we single out the three experiments (experiments 9, 13, and 14) in which the mean vectors of the two treatments differed most in direction or scatter or both, we find that the controls performed better in two (Figs. 9, 14) and the experimentals in one (Fig. 13).

It is of interest that in experiment 8 the release site was Castor Hill, a location at which Cornell pigeons regularly exhibit a strong clockwise bias (Keeton, 1973). The normal bias was apparent in the bearings of the birds tested with α -pinene (Fig. 8), hence the treatment had not interfered with whatever map cues cause the bias at that site.

Benvenuti *et al.* (1973) reported that their control birds departed significantly faster from the release sites than did the experimental birds. In none of our

¹ The test statistic $u [u = (2/n^{\frac{1}{2}} \cdot n \cdot h)$ is a function not only of the birds' performance, as measured by the homeward component h , but also of sample size. Thus if two samples of 8 and 12 bearings both had a homeward component of 0.7 (i.e. the two groups of birds oriented equally well), then their respective u values would be 2.8 and 3.4. Comparing these values in a histogram would give the impression that the birds of the second group had performed better, whereas in fact the difference would be due solely to the experimenter's use of more birds. However, in the case of Benvenuti *et al.* (1973; Fig. 5), if the u values are changed to the corresponding h values, the overall result remains the same (i.e. the controls have the higher value in each of their experiments).

experiments was the difference between the vanishing intervals of the two treatments significant at the 0.05 level (Mann-Whitney U test). Indeed, in 9 of the 15 experiments it was actually the experimental birds that had the shorter mean vanishing interval. When the data from all experiments were pooled and analyzed by the matched-pairs sign test (comparing each control bird with the experimental bird released nearest it in time) as done by Benvenuti *et al.*, we got 128 pairs (omitting ties), in 68 of which the control bird vanished in the shorter time; this result is not significantly different from random ($P=0.27$, one-tailed test).

Finally, Benvenuti *et al.* (1973) report that their control birds showed significantly better homing performance than their experimental birds. We found no consistent difference in our experiments. In 10 of the 15 experiments, more control birds returned home on the day of release and in 5 more experimentals returned (one-tailed binomial probability=0.151). Of the 11 experiments in which there were day birds from both treatments, the mean speed of those birds was greater for the controls in only 4 experiments, whereas it was greater for the α -pinene birds in 7 ($P=0.89$, one-tailed). The total percentage of birds homing was greater in the controls in 6 experiments and greater in the α -pinene birds in 7 ($P=0.71$, one-tailed) (there were ties in two experiments). Pooling data from all experiments in a matched-pairs sign test gives 136 pairs (omitting ties), in 70 of which the controls homed faster, a result not significantly different from random ($P=0.40$, one-tailed).

Discussion

Unlike Benvenuti *et al.* (1973), we found no evidence that α -pinene influences vanishing intervals or homing speeds. Therefore the vanishing bearings provide the principal point on which different interpretations might rest. But as we have shown, there was no consistent difference in this parameter in our experiments, and indeed in most cases the mean vectors of the experimental and control pigeons were remarkably similar.

Only if one focuses on experiments 9 and 14 might one find any support for the idea that application of α -pinene can produce a decrement in orientation. In short, one must single out two experiments from a total of 15, and even then the strongest statement that could be made is that α -pinene may interfere with accurate initial orientation in a very few unpredictable cases. The counter argument, that α -pinene may sometimes aid orientation (based on experiment 13 and on the fact that the experimental birds had the larger homeward component in more than half the experiments), would have almost as strong experimental support! We are unwilling to accept either conclusion; in our view, the evidence does not convincingly reveal any difference between the two treatments.

In our opinion, the evidence put forward by Benvenuti *et al.* (1973) that α -pinene influences initial orientation is not much more convincing than our own. The Italian investigators used α -pinene in five of their ten experiments. Though the control birds exhibited the greater homeward component in all

five cases, the difference between the bearings of the two treatments was statistically significant in only one of the five (their experiment 7).

In summary, we are unconvinced that application of α -pinene to the nostrils of our pigeons significantly influences the birds' homing performance in any of the three parameters measured (initial bearings, vanishing intervals, homing speeds).

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