# Orientation by Pigeons Deprived
# of Olfaction by Nasal Tubes

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**Summary.** In an effort to avoid the trauma and other nonolfactory effects produced by surgical sectioning of pigeons' olfactory nerves, and to avoid the interference with breathing produced by nostril plugs, a way of making pigeons anosmic by inserting plastic tubes in their nostrils was developed. A total of 16 experimental releases were conducted from unfamiliar sites to compare the homing behavior of birds wearing a tube in each nostril with controls wearing a tube in only one nostril. In five short-distance releases (less than 25 km), no convincing differences in initial orientation, vanishing intervals, or homing success were observed. In eleven releases from longer distances (more than 76 km), the experimental birds were random in three cases and the controls were random in two. In no case were the differences in the distributions of the bearings of experimental and control birds statistically significant, nor were there ever significant differences in vanishing intervals. However, experimental birds had much poorer homing success from these long-distance releases. It is concluded, in view of the anosmic pigeons' good orientation at distant unfamiliar sites, that olfaction is not necessary for homeward orientation and hence that it cannot be the basis of the birds' navigational map. Poor homing success from long distances is probably a consequence of the physical irritation and interference with breathing unfortunately produced by the nasal tubes.

## Introduction

Papi et al. (1972) have proposed that olfactory cues constitute the basis of the navigational map hypothesized by Kramer (1953) for homing pigeons. During the last five years, these investigators have performed a variety of experiments designed to test their olfactory model; their results have been consistently positive. By contrast, our attempts to repeat some of these experiments have mostly failed (Keeton, 1974; Keeton and Brown, 1976).

Only in experiments utilizing bilateral olfactory nerve sectioning have we (Hermayer and Keeton, ms) seen some of the same effects reported by Papi et al. (1971; see also Benvenuti et al., 1973). But since the surgically induced deficit in both our experiments and those conducted by Papi's group was much greater in homing success than in initial orientation, we have not been convinced that these experiments truly demonstrate interference with navigation per se; the results could be due to reduced motivation to keep flying as a consequence of some physical distress experienced by the birds in flight (accelerated breathing through denervated nasal passages might well "feel" strange). Indeed, it is well established that olfactory nerve sectioning can lead to a variety of changes in behavior patterns that do not involve olfaction itself (e.g., Hutton et al., 1974, in tests with visual — *not olfactory* — cues, found faster learning of two-way shock avoidance by pigeons with sectioned olfactory nerves than by control pigeons).

In view of our doubts about nerve sectioning as a method for producing anosmia, we devised an alternative procedure — the insertion of flexible plastic tubes in the pigeons' nostrils. The birds can breathe through these tubes, but the inhaled air does not contact the olfactory mucosa. We here report the results of 16 homing experiments conducted with pigeons wearing these tubes.

## Methods

We constructed the nasal tubes from #605 Genflex tubing (G.C. Electronics Corp., Rockford, Illinois), which has an external diameter of 2.4 mm and a luminal diameter of 1.4 mm. The first version of the tubes (used in experiments 1–4) was approximately 20 mm long (Fig. 1A); left and right tubes differed slightly in length (Fig. 1 B). They had a bend (produced by softening over an alcohol flame) of approximately 90° near the inner end and were flared beyond the bend into a funnel shape. These tubes were inserted through the choanal opening and pushed forward until their outer ends emerged from the nostrils. Each tube was held in place by a single surgical stitch (silk) through the wall of the tube (outer end) and the dorsal wall of the nostril. In order to block entry of air around the tube, the space around its outer end was sealed with silicone glue. A later version of the tubes (used in experiments 5–16) was much simpler and faster to insert, and caused less bleeding and trauma to the birds. Tubes of this sort lacked the terminal funnel, hence they could be inserted through the external nares. Each tube was fastened in place by a silver clip (McKenzie Brain Clips, #B4222, Dittmar and Penn, Philadelphia, Pennsylvania). No sealant was used, as in laboratory tests of olfactory responsiveness this was found to be unnecessary.

The tubes formed an air passage between the external nares and the epiglottal region, but prevented contact between the air and the olfactory epithelium. Birds wearing a tube in each nostril were tested for responsiveness in a special olfactory test chamber, using our standard cardiac response method described in detail elsewhere (Kreithen and Keeton, 1974). Normal birds, or birds with a tube in only one nostril, showed a marked cardiac response (increased rate of heart beat) when turpentine vapor was added to an air stream flowing past the head (the vapor pulses lasted 10 s). Such birds could easily detect pulses consisting of 20% saturated turpentine vapor (at 25 °C) and 80% filtered air. By contrast, birds with tubes (of either version) in both nostrils did not respond to pulses of 80% saturated vapor and 20% air; there were some behavioral responses to pulses of 100% saturated turpentine vapor, but these appeared to be due to irritation of the eyes and/or the lungs. (More details of our olfactory testing of pigeons using cardiac conditioning will be published elsewhere.)

On the evening before each release, experimental birds (E) were fitted with nasal tubes bilaterally; control birds (C) were fitted with a single tube — in the right nostril in half the birds and in
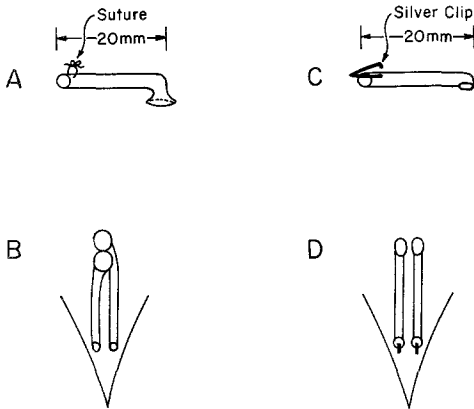
**Fig. 1 A–D.** Details of the two types of nasal tubes used in the experiments. **A** Lateral view of a tube of the early type. **B** Schematic ventral view of type-1 tubes in position in the nasal passages (the bird's beak points toward the bottom of the page); one tube is slightly longer than the other and is bent both laterad and ventrad, so that its funnel opening is positioned behind that of the other tube. **C** Lateral view of a tube of the later type. **D** Schematic ventral view of type-2 tubes in position; the two tubes have exactly the same dimensions, and their openings are side by side

the left nostril in the other half. Experimental and control birds were drawn from the same population; i.e., they lived in the same loft, were the same age, and had been given identical training.

All the experimental releases were conducted at sites where the birds had not previously been released (9 different sites were used). Moreover, all sites were at a greater distance than any in that direction from which the birds had previously flown. The 9 groups of birds used, and their longest flights prior to the start of testing were:

Group 1. Young birds (i.e., hatched the same year as the testing and less than 7 months old). Trained up to 8 km in all four cardinal compass directions. Used in experiments 1–5, 7, 10, and 15.

Group 2. Young birds. Trained up to 24 km in all four directions. Used in experiments 7, 10, and 15 (together with Group 1 birds).

Group 3. Young birds. Flown from 66 km N, 33 km E, 19 km S, and 25 km W. Used in experiment 11.

Group 4. Young birds. Trained up to 26 km N, 37 km SE, and 18 km S; not trained from E or W. Used in experiments 8 and 9.

Group 5. Yearlings. Birds with varying experience, but most flown from 73 or 143 km N, 27 km E, 40 or 66 km S, and no more than 8 km W. Used in experiment 6.

Group 6. Yearlings. With varying experience, but most flown from 73 or 143 km N, 27 km E, 40 km S, and 70 km W. Used in experiment 12.

Group 7. Yearlings. Flown from 66 km N, 33 km E, 49 or 65 km S, and 32 km W. Used in experiment 16.

Group 8. Yearlings. Flown from 66 or 73 km N, 16 km E, 37 km SE, 18 km S, and 16 km W. Flown from 27 and 40 km N on the two days immediately before testing. Used in experiment 13.

Group 9. Yearlings. Flown from 26 km N, 16 km E, 37 km SE, 40 km S, and 16 km W. Flown from 25 and 40 km S on the two days immediately before testing. Used in experiment 14.

The dates of the experiments (all in 1975 unless otherwise indicated) were as follows: 1, 13 Aug.; 2, 21 Aug.; 3, 19 Aug.; 4, 22 Aug.; 5, 8 Oct.; 6, 18 Nov.; 7, 23 Oct.; 8, 20 Nov.; 9, 20 Nov.; 10, 28 Oct.; 11, 6 Nov.; 12, 18 Nov.; 13, 30 Apr 76; 14, 30 Apr. 76; 15, 5 Nov.; 16, 5 Dec.

In the experiments, birds were released singly from the hand, alternating experimental and control birds; in six of the experiments some unmanipulated birds – designated CC – were

also released. The birds were observed with $10 \times 50$ binoculars until they vanished from sight, and their vanishing bearings were recorded to the nearest 5 degrees. 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. The bearings of the two treatments in each experimental release were compared under Watson's $U^2$ test. The vanishing intervals and homing times were compared under the Mann-Whitney $U$ test.

In the figures showing vanishing bearings, each symbol on the periphery of the large circle represents the bearing of one bird. Bearings of control birds are indicated by open symbols and bearings of experimental birds by solid black symbols; the respective mean vectors are distinguished by open or solid arrowheads. In a few cases, bearings of CC birds (i.e. birds wearing no nasal tube) are shown as open squares with diagonal lines through them. A dashed line from the center of the large circle to the periphery indicates the home direction, and a small line at the top of the circle locates geographic north.

In the captions, $n$ is the number of birds released, followed by the number of bearings (in parentheses); $mvb$ is the mean vanishing bearing; $r$ is the length of the mean vector; $p$ is the uniform probability under the Rayleigh test; $mvi$ is the mean vanishing interval, in minutes; *returns* is the number of birds that successfully returned home the day of release, followed by the number that returned later (in parentheses); and $mht$ is the mean homing time of day birds, in hours. In each case, the first-given value is for C birds and the second value is for E birds; when CC birds were used, their value is given third.

## Results

### Short-Distance Releases (Less Than 25 km)

The first two experimental releases, utilizing Group 1 birds, were from a site 19.1 km E of the loft (home direction, 288°). In both releases both treatments were well oriented homeward, and there was no significant difference between them (Fig. 2). Indeed, in experiment 1 the mean directions of the two treatments were nearly identical (274°) and the vector lengths differed by only 0.016. There were no significant (i.e., $P \leq 0.05$) differences between vanishing intervals, though in test 1 the experimental birds departed quicker at $P = 0.086$. There were no significant differences in homing times. A total of 4 out of 22 experimental birds and 2 out of 21 controls were lost; this very small difference was the only respect in which the performance of the experimentals might be deemed appreciably poorer than that of the controls.

The next two releases (experiments 3 and 4) were from a site 17.9 km west of the loft (home direction 91°). Experiment 3 had been planned to utilize the same birds used in experiment 1, but by accident 4 of the experimental and 3 of the control birds were in fact experiencing tubes for the first time. Mean bearings for birds in their first tube release ($E_1$ and $C_1$ birds) are plotted separately in Figure 3A from those of birds on their second tube release ($E_2$ and $C_2$), even though this makes the sample sizes too small for statistical evaluation; we considered it appropriate to make this separation because, as can be seen from Figure 3A, the orientation of the $E_1$ birds seemed clearly different from that of the $E_2$ birds. Both the $E_1$ and the $C_2$ birds were oriented in the direction usual for this site, namely slightly counterclockwise from home. By contrast, the $E_2$ birds appeared to be going more to the northwest. Some
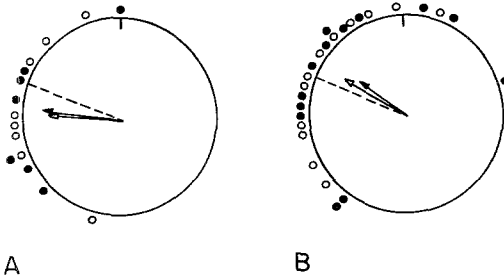
**Fig. 2A and B.** Vanishing bearings for two releases from 19.1 km East. **A** Experiment 1: $n=9(8)$, 9(7); $mvb=274.4°$, 274.6°; $r=0.765$, 0.781; $p=0.005$, 0.008; $mvi=5.9$, 4.6; $returns=7(2)$, 5(1); $mht=0.8$, 0.7. **B** Experiment 2; $n=12(12)$, 13(13); $mvb=299°$, 305°; $r=0.740$, 0.582; $p<0.001$, 0.010; $mvi=4.1$, 4.6; $returns=10(0)$, 12(0); $mht=1.1$, 1.2
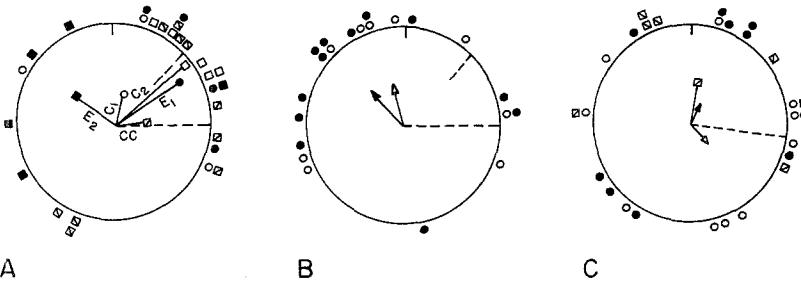


**Fig. 3A–C.** Vanishing bearings for three short-distance releases from the West. **A** Experiment 3: $n=3(3)$ for $C_1$, 5(5) for $C_2$, 4(4) for $E_1$, 6(5) for $E_2$, 10(10) for CC; $mvb=17°$, 48°, 55°, 305°, 85°; $r=0.362$, 0.948, 0.820, 0.522, 0.361; $p=$sample size too small to calculate for $C_1$, 0.004, 0.058, 0.270, 0.279; $mvi=8.3$, 3.2, 6.3, 4.4, 5.0; $returns=2(0)$, 5, 4, 5(1), 10; $mht=1.2$, 3.8, 2.4, 1.5, 1.0. **B** Experiment 4: $n=10(9)$, 12(12); $mvb=345°$, 318°; $r=0.405$, 0.485; $p=0.235$, 0.056; $mvi=5.3$, 4.9; $returns=7(1)$, 6(1); $mht=1.5$, 1.4. **C** Experiment 5: $n=13(10)$, 13(10), 8(7); $mvb=135°$, 22°, 9°; $r=0.270$, 0.250, 0.479; $p=0.495$, 0.546, 0.206; $mvi=14.2$, 10.7, 7.2; $returns=11(1)$, 11(0), 7(1); $mht=1.8$, 1.3, 2.1. The short dashed line at 45° in **A** and **B** indicates the mean of means for many previous releases of moderately experienced pigeons new to the site; this, rather than the home direction, would ordinarily be the predicted bearing for an experiment with such birds

unmanipulated pigeons (CC birds), released at the same time, were not quite significantly different from random, though their mean was in the proper direction. There were no significant differences between E and C birds in vanishing intervals or homing times, whether the two treatments were subdivided or kept intact, but both the E birds ($P<0.01$) and the C birds ($P<0.06$) had slower homing times than the unmanipulated birds.

Experiment 4 utilized pigeons that had been flown in experiment 2. The bearings (Fig. 3B) of neither the E nor the C birds were significantly different from random, though those of the E birds approached significance ($P=0.056$). Again there were no significant differences between the two treatments in either vanishing intervals or homing times. Taking experiments 4 and 5 together, 3 out of 18 control birds were lost, and 5 out of 22 experimentals.
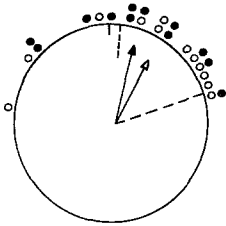
**Fig. 4.** Vanishing bearings for experiment 6 from 70.2 km West, $n=12(12)$, $12(12)$; $mvb=30°$, $16°$; $r=0.740$, $0.830$; $p<0.001$, $<0.001$; $mvi=4.3$, $5.8$; $returns=7(4)$, $3(3)$; $mht=3.2$, $3.0$. The mean of means for previous releases of comparably trained pigeons (short dashed line) is at $4°$

The last of this series of short-distance releases (experiment 5) was from a site (near Mecklenburg, N.Y.) 24.7 km W of the loft (home bearing, 95°). In addition to E and C birds, some unmanipulated CC birds were used. The bearings of all three treatments were random (Fig. 3C). There were no significant differences between any of the treatments in either vanishing intervals or homing times. One C bird and 2 E birds were lost; all CC birds returned.

*Releases from Longer Distances (More Than 65 km)*

Experiment 6 was from a site (near Campbell, N.Y.) 70.2 km W of the loft (home bearing, 72°). The pigeons used (Group 5) had previously been released no more than 8 km W, hence this site should not have been familiar to them. The bearings of both treatments were well oriented in the north-northeasterly direction usual for this site (Fig. 4), and the difference between them was not significant, nor were the vanishing intervals significantly different. Though the homing times of the birds that returned the day of release were not different, there clearly was a difference in homing success – 7 out of 12 control birds returned the day or release and only 1 was lost, whereas only 3 out of 12 experimentals returned on the day and 6 were lost.

Experiments 7, 8, and 9 were from the N, the first two from a site (near Auburn, N.Y.; home bearing, 170°) 66.2 km distant and the third (near Weedsport, N.Y.; home bearing 173°) 73.5 km. The pigeons used had previously been released no more than 26 km N. In 7 and 8, the bearings of both treatments were well oriented (Figs. 5A and 5B) and the differences between them were not significant, nor did either differ significantly from the bearings of CC birds released at the same time. The vanishing intervals of the C and E birds did not differ significantly from each other in either experiment, but in experiment 7 the vanishing intervals of the CC birds were longer than those of the C and E birds at $P<0.05$ and $P<0.10$ respectively. Both homing times and homing success were comparable for C and E birds.

Experiment 9 differed from 7 and 8 in that the bearings of the E birds were not statistically oriented, whereas those of the C birds were (Fig. 5C). However, the two distributions were not significantly different. The two treat-
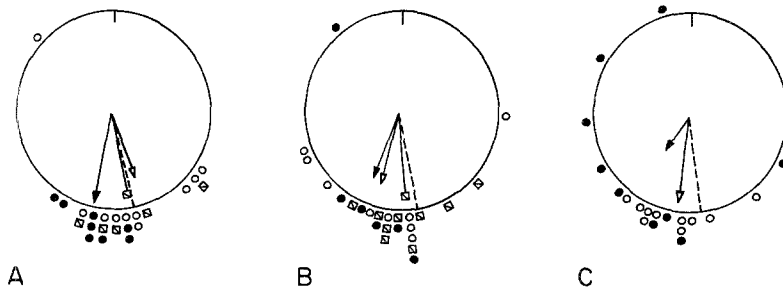
**Fig. 5A–C.** Vanishing bearings for three experiments from 66.2 or 73.5 km North. **A** Experiment 7: $n = 11(10)$, 8(8), 7(5); $mvb = 166°$, 191°, 171°; $r = 0.734, 0.972, 0.924$; $p = 0.002, <0.001, 0.006$; $mvi = 6.2$, 6.1, 10.5; $returns = 5(6), 3(5), 4(3)$; $mht = 2.5, 2.3, 4.7$. **B** Experiment 8: $n = 12(9), 11(6), 10(9)$; $mvb = 194°$, 202°, 174°; $r = 0.736, 0.717, 0.934$; $p = 0.004, 0.038, <0.001$; $mvi = 5.1, 8.6, 5.3$; $returns = 2(2), 2(1)$, 5(3); $mht = 2.2, 3.2, 2.2$. **C** Experiment 9: $n = 12(10), 12(10)$; $mvb = 190°$, 216°; $r = 0.928, 0.432$; $p < 0.001, 0.156$; $mvi = 5.0, 8.1$; $Returns = 2(5), 2(0)$; $mht = 1.7, 3.0$
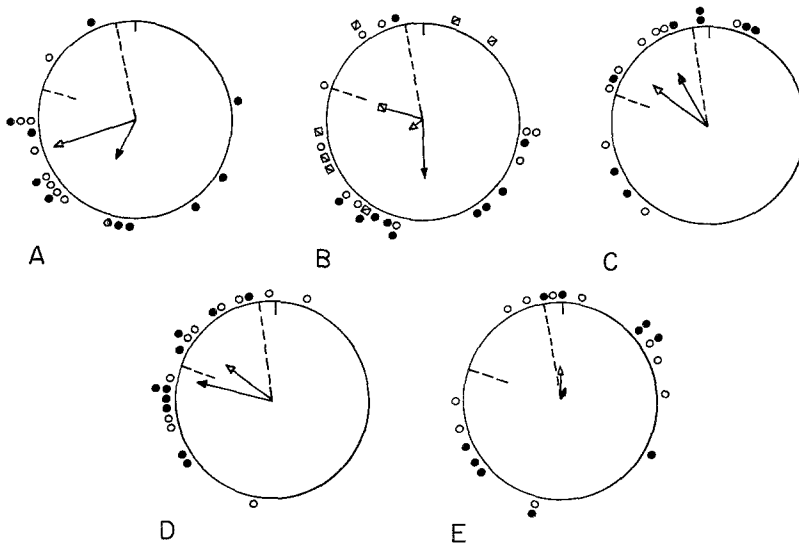


**Fig. 6A–E.** Vanishing bearings for five experiments from 65.5 km South. **A** Experiment 10: $n = 10(8)$, 12(11); $mvb = 254°$, 207°; $r = 0.898, 0.454$; $p < 0.001, 0.102$; $mvi = 8.8, 7.4$; $returns = 1(4), 0(2)$; $mht = 1.3, —$. **B** Experiment 11: $n = 13(10), 14(10), 8(7)$; $mvb = 237°$, 179°, 286°; $r = 0.196, 0.577, 0.459$; $p = 0.691, 0.031, 0.237$; $mvi = 6.9, 10.6, 7.6$; $returns = 4(5), 0(4), 2(6)$; $mht = 2.3, —, 1.7$. **C** Experiment 12: $n = 11(8), 12(8)$; $mvb = 306°$, 331°; $r = 0.730, 0.615$; $p = 0.009, 0.043$; $mvi = 4.4, 8.5$; $returns = 4(3), 1(2)$; $mht = 2.4, 1.5$. **D** Experiment 13: $n = 11(10), 10(10)$; $mvb = 305°$, 283°; $r = 0.654, 0.843$; $p = 0.010, <0.001$; $mvi = 7.3, 8.0$; $returns = 6(5), 4(3)$; $mht = 4.1, 4.3$. **E** Experiment 14: $n = 11(10)$, 10(10); $mvb = 357°$, 12°; $r = 0.365, 0.089$; $p = 0.269, 0.928$; $mvi = 6.1, 8.8$; $returns = 9(1), 5(0)$; $mht = 2.8, 3.4$. The mean of means for previous releases of comparably trained pigeons (short dashed line) is at 289°
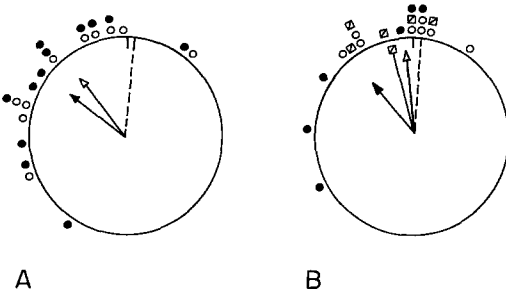
A                          B

**Fig. 7A and B.** Vanishing bearings for two experiments from 79.5 and 113.1 km South. **A** Experiment 15: $n=11(10), 12(12)$; $mvb=319°, 306°$; $r=0.759, 0.732$; $p=0.001, <0.001$; $mvi=4.6, 4.8$; $returns=4(0), 2(4)$; $mht=2.8, 3.4$. **B** Experiment 16: $n=10(8), 12(6), 6(5)$; $mvb=355°, 320°, 347°$; $r=0.923, 0.704, 0.956$; $p<0.001, 0.044, 0.003$; $mvi=3.1, 4.3, 0.6$; $returns=7(1), 2(3), 2(0)$; $mht=2.1, 2.0, 1.7$

ments did not differ significantly in vanishing intervals, and both had only two birds home on the day of release. However more controls returned later, so that more experimentals were lost — 10 of 12 as contrasted with 5 of 12 for the controls.

Experiments 10–14 were all conducted from a release site (near Orwell, Pennsylvania; home bearing, 348°) 65.5 km S of the loft, where vanishing bearings usually show a pronounced counterclockwise bias. The results of these five tests were exceedingly inconsistent (Fig. 6). In experiment 10, the controls were oriented and the experimentals were random (Fig. 6A). In experiment 11, the situation was nearly reversed — the controls were random and the experimentals were oriented, but in a southerly direction (such southerly orientation is sometimes seen in normal pigeons at this site) (Fig. 6B). In experiment 12, both treatments were well oriented in the northwesterly direction usual for this site (Fig. 6C). In experiment 13, both treatments were again oriented (Fig. 6D). And finally, in experiment 14, both treatments were random (Fig. 6E). In none of the five experiments were the distributions of the C and E bearings significantly different. However, in experiment 11, the distribution of CC bearings differed from that of the E bearings at $P<0.026$. In no case was there a significant difference in vanishing intervals. In only one respect was there a clear pattern in the results of these five tests — in all five tests more control birds than experimentals returned home the day of release and in all five more experimental birds were lost.

The last two experiments were conducted from even farther S — experiment 15 from a site (near South Towanda, Pennsylvania; home bearing, 2°) 79.5 km S, and experiment 16 from a site (near LaPorte, Pennsylvania; home bearing 3°) 113.1 km S. In each experiment the bearings of both the C and the E pigeons were oriented (Fig. 7), and in neither case did they differ significantly from each other. In neither experiment did the C and E birds differ significantly in vanishing intervals, but in experiment 16 both groups took significantly longer to vanish than did CC birds ($P=0.02$ for C birds and $P=0.004$ for

E birds; two-tailed tests). In both experiments more C birds returned home the day of release.


## Discussion

The five short-distance releases, taken as a whole, revealed no convincing differences between anosmic birds and birds that could still smell. The two treatments oriented almost equally as well in the two releases from the east (experiments 1 and 2), and almost equally as poorly in the three releases from the west (experiments 3–5). Vanishing intervals and homing speeds were equivalent. Only in numbers of birds lost — 6 out of 52 controls and 11 out of 57 experimentals — might there have been some difference.

Thinking that the absence of any pronounced differences between the C and E birds in these experiments might possibly have been due to recognition of familiar landmarks (even though all three release sites were at least 10 km beyond any previous release of the birds), we decided to conduct all later releases from longer distances, so that the possibility of landmark recognition would be lessened. The six release sites (1 west, 2 north, and 3 south) used in these later experiments were all at least 65 km from the loft. Moreover, they were either 25.5 km (experiments 12 and 14) or more than 40 km (experiments 6–11, 13, most of 15, 16) beyond any previous release of the birds (in experiment 15, 3 of the C birds and 3 of the E birds had once been released 14 km from the test site).

In seven of the eleven longer-distance experiments, the E birds were significantly oriented in roughly the predicted direction; in one experiment (11) the E birds were oriented but not in the predicted direction; and in the remaining three experiments (9, 10 and 14) the E birds departed randomly. The control birds had random bearings in two experiments (11 and 14). In no case was the difference between the distributions of the experimental and control bearings statistically significant. Thus, although the E birds did not usually orient quite as well as the C birds (the E mean vector was shorter than the C mean vector in 7 of the 11 experiments), they certainly exhibited repeatedly an ability to orient in an appropriate direction at distant unfamiliar sites in the complete absence of olfactory cues. Moreover, since the vanishing intervals of the E birds were never significantly longer than those of the controls, it would seem that orientation without olfaction is not appreciably more difficult than orientation with olfaction.

We call special attention to experiments 13 and 14, which were designed to examine the possibility that special directional training might aid the orientation of anosmic pigeons at distant unfamiliar sites. On the two days immediately preceding the tests, the birds used in experiment 13 (Group 8) were flown from 27 and 40 km N, and the birds used in experiment 14 (Group 9) were flown from 25 and 40 km S. If, in the test releases, the anosmic birds had a tendency to fly the same direction they had flown on the previous two days, then we would have expected the pigeons in experiment 14 (which had become accustomed to flying N) to be better oriented than the pigeons in experiment 13

(which had become accustomed to flying S). The actual results were contrary to this expectation – the birds in experiment 13 were much the better oriented (compare Figs. 6 D and 6 E). We conclude, therefore, that the anosmic pigeons showed no tendency merely to fly in an accustomed direction, and that when they oriented homeward at distant sites they were navigating in an approximately normal manner, despite the absence of olfactory cues.

In one respect there was a clear and impressive difference between the E and C pigeons in the longer-distance releases – many fewer E birds actually made it home (only 54 of 125, as compared with 87 of 124 controls). Is this evidence that the birds required olfactory cues for successful navigation, despite the fact that they could orient accurately initially? We think not. Despite our hopes that the nasal tubes would cause little trauma to the birds as compared with nerve sections (Papi et al., 1971; Benvenuti et al., 1973), and interfere minimally with breathing as compared with plugs inserted in the nostrils (Papi et al., 1972; Snyder and Cheney, 1975), the technique was a partial failure in both respects. The tubes caused irritation and quite evident discomfort to the birds, and they often became plugged with mucus, thus partially or even completely obstructing air flow. We therefore do not find it surprising that the orientation behavior of the E birds was often slightly inferior to that of the controls, nor do we find it surprising that many of the birds that vanished initially toward home did not complete the journey from the distant sites. We strongly suspect that the combination of the physical discomfort and the difficulty of breathing led to diminished motivation to fly and hence to the birds' landing when only part way home. If they did not return the day of release, the chances of their tubes becoming completely plugged would have greatly increased, thus leading to few later returns. By contrast, most E birds successfully returned from the five shorter-distance releases on the day of release, presumably because the necessary flying time was short enough that the problem of stress and the resulting diminished motivation did not become severe. We hope in the future to evaluate our explanation for the poor homing success from long-distance releases by using an airplane to track pigeons wearing nasal tubes.

In summary, in view of the accurate orientation by anosmic birds in most of our experiments, we cannot agree that olfaction is the basis of our pigeons' navigational map. Olfaction may possibly be one of the many redundant sources of cues sometimes used by pigeons in orienting (as indeed such cues appear to be used by Papi's birds), but we conclude that they are not a necessary part of the pigeons' navigational system.

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