J. comp. Physiol. 94, 187—193 (1974)

Olfactory Navigation of Pigeons: The Effect of Treatment with Odorous Air Currents*

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Received May 13, 1974

Summary. From fledging time, two groups of homing pigeons were protected for most of the time from wind exposure. Instead, they were subjected to artificial odorous winds. One of the two groups was subjected to an odorous wind of olive oil from the S and an odorous wind of a solvents' mixture ("synthetic turpentine") from the N. The other group underwent the opposite treatment (odorous wind of olive oil from the N and odorous wind of synthetic turpentine from the S). The birds of the first group, released from two points 21.0 and 26.5 km W of the aviary flew in a northerly direction when olive oil was applied to their nostrils and in a southerly direction when synthetic turpentine was applied. Under the same conditions, the birds of the second group flew in the opposite directions. These results support the olfaction hypothesis of pigeon navigation (Papi *et al.*, 1972).

Introduction

Recent experiments on homing pigeons deprived of olfactory perception (Papi *et al.*, 1971, 1972) gave rise to an olfaction hypothesis of pigeon navigation, which has been supported by a set of further experiments (Papi *et al.*, 1973a; Benvenuti *et al.*, 1973a, b). According to this hypothesis, there exist natural odorous substances, which in different areas give rise to a specific prevailing odour. During the first months of life, pigeons learn to recognize the odour prevailing in the loft area as well as "foreign" odours carried by the winds. Moreover, they associate these different "foreign" odours with the direction from which they come, thus gaining information about odours prevailing in the surrounding areas. When released far from the loft, the birds establish the home direction, provided that the prevailing odour of the release point area has already been perceived at the loft as one of the "foreign" odours. The home direction is then opposite to the direction from which that odour was usually sensed in the loft, and the birds can assume the deduced direction by means of the sun compass or of another compass orientation mechanism.

The olfaction hypothesis has been tested by preventing young pigeons from smelling in open air, i.e. when exposed to the winds. The treatment proved to affect the initial orientation, as the birds were not homeward oriented in the test releases (Papi *et al.*, 1973a). In the present paper we report the results of further research carried out in order to test the olfaction hypothesis. Young pigeons were exposed as little as possible to natural winds and subjected instead to artificial odorous winds sent from specific directions. The birds were then released far from the loft after applying to their nostrils the same odorous substances as

* Supported by the Consiglio Nazionale delle Ricerche.

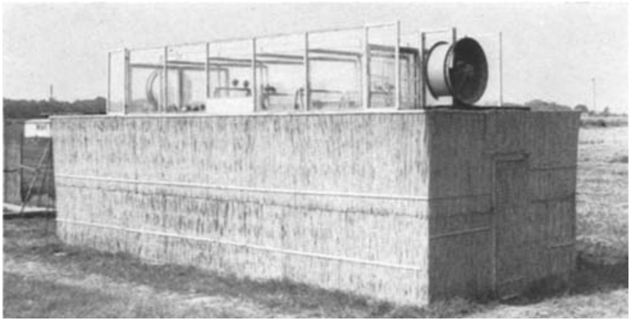

Fig. 1. Aviary with corridors above. The fans are functioning

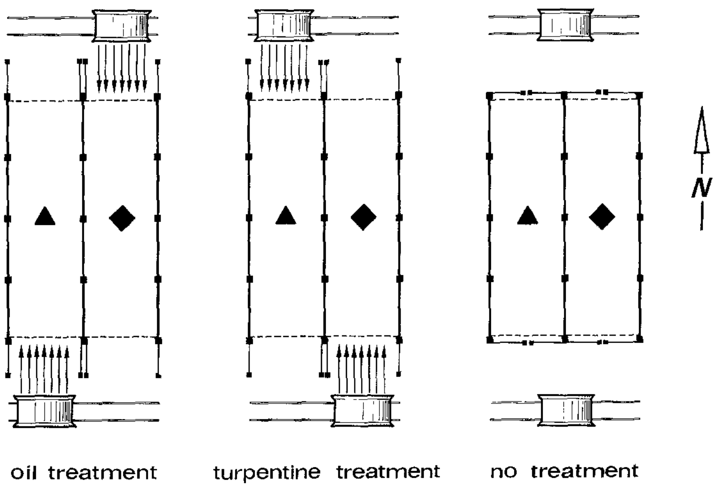

Fig. 2. Diagram of the treatments illustrated on the plan of the corridors. The symbols (triangles and diamonds) indicate the corridors occupied by the corresponding groups of pigeons

in the artificial winds. According to the olfaction hypothesis the pigeons should fly in the direction opposite to that from which they were accustomed to perceiving the odour now applied to their nostrils.

Methods

I. Outline of the Procedure

From fledging time two groups of pigeons were kept in an aviary fenced with plastic and bamboo material, with the birds allowed access to a glass corridor placed on the roof of the aviary (Fig. 1). Each of the two groups of pigeons occupied half of the aviary and each had its own corridor. Since the aviary was oriented with the major axis in a N-S direction, one group of pigeons, which we will call "triangles", occupied the W half of the aviary and corridor, and the other group, the "diamonds", the E half of the aviary and corridor. For treatment, all of the pigeons were attracted into the corridors with food and the passages to the aviary were closed. The doors at the ends of the corridors were then opened and two ventilators were turned on, so that each group would be exposed to the same odour for the same interval of time from opposite directions. Two types of treatment were used: odorous wind with olive oil (or, more precisely, the volatile parts of olive oil) and odorous wind with a mixture of solvents ("synthetic turpentine", see below). The triangles were treated with olive oil odour from the S and with synthetic turpentine from the N, the diamonds with olive oil from the N and with synthetic turpentine from the S (Fig. 2). For 43 days (June 19th—July 31st, 1973) the birds underwent 12 treatments with olive oil, 38 hrs in all, and 13 treatments with synthetic turpentine, 40 hrs and 30 min in all. Two release experiments were then carried out on August 6th and 7th at a release site 21 km E of the loft. The birds that returned were subjected for 8 days (August 9th to 16th) to 5 treatments with olive oil for a total of 15 hrs, and 4 treatments with synthetic turpentine for a total of 14 hrs, after which two further release experiments were performed on August 18th and 20th at a release point 26.5 km E of the loft.

II. Data on the Aviary and the Air Currents

The aviary, 4.00 m wide × 9.00 m long and 2.80 m high, was set up on the property of the Istituto di Zoocolture at S. Piero a Grado near Pisa. The roof consisted on wooden boards on top of which the glass corridors were constructed. Each corridor was 1.25 m wide × 6.00 m long and 1.30 m high. The vertical walls were of glass, while those at the two extremities were also closed on the inside by a wire-netting so that the glass wall could be opened to allow for air passage during treatment. Above, the corridors were closed by a wire-netting at 1.00 m from the floor. On the floor of each corridor there were two holes that permitted passage from the aviary to the corridors. In addition each corridor had access to the outside by means of an opening with movable vertical bars. These bars were regulated so that the birds could either go in and out or go only into the corridors. These openings were usually closed by a board as shown in Fig. 1, at the bottom of the outer wall of the corridor.

The fans were 80 cm in diameter, and were mounted on a track that allowed them to be moved in order to send air into either corridor. When the fans were not being used they remained in the center. The velocity of the air currents created by the fans and measured along the axis of the fan was 7–8 m/sec for the entire length of the corridor. At 15 cm from the floor, the wind velocity when measured in different points, varied from 7 to 13 m/sec.

The olive oil used was of a particularly aromatic quality. The mixture of solvents called "Acqua ragia tre gemme" was a commercial product of the Sprint Company, Florence. It is a synthetic turpentine containing toluene (approx. 60%), terpene hydrocarbons (approx. 5%) as well as saturated hydrocarbons. This mixture does not contain more than 1% α-pinene. The very intense odour of this mixture is slightly different from that of pure toluene. The substances were brushed onto strips of cloth stretched over a wooden frame that was attached to the end of the corridor in front of the fan during treatment. In addition, a Petri dish with either olive oil or synthetic turpentine, renewed every hour, was placed on the floor in front of the ventilator.

III. Treatment of the Birds

The stock of 61 pigeons used in these experiments was bought from the breeders in the Valle Padana at the time of fledging. They arrived at S. Piero on April 27th, 1973, and were all kept in an aviary fenced with plastic material and located near the experimental aviary. On June 6th they were divided into two groups (30 triangles and 31 diamonds) and transferred into the experimental aviary. They were allowed access to the corridors beginning

June 9th. The birds were kept slightly starved and trained to come at the sound of a whistle that was blown whenever they were given food. Thus, the pigeons would be called into the corridors or inside and to same extent could be recalled to the aviary after their spontaneous flights.

The alternation of the odorous wind treatment with olive oil and that with turpentine was at random. The duration of the treatment varied from 2 to 5 hrs (usually 3 hrs or 3 hrs and 30 min). In most cases, only one treatment was given per day, sometimes two. The treatments were not performed or were suspended under the following atmospheric conditions: sun not visible, southern or northern winds, winds from other directions with a velocity of more than 4–5 m/sec. During the treatment, the pigeons usually remained in the half of the corridor farthest from the fan, most of them facing the fan.

Flights outside the aviary were permitted on only ten occasions. On four different days in July the pigeons were attracted out of the corridors with food and left free to fly within the surrounding area. On other occasions between July 26th and August 5th the following training releases were made: 200 m E, 200 m N, 250 m S, 500 m W, 500 m E, 1500 m W of the loft. These releases allowed the birds to become accustomed to being captured and remaining closed in the baskets. During transportation for the last two training releases the birds became familiar with the special containers used for transportation to the test release sites. On all of these occasions the sky was prevailingly clear, with light winds mainly from the W.

During these free flights seven pigeons flew away and did not return to the aviary. Three other pigeons that had remained outside of the aviary for more than three consecutive days were excluded from the experiments, whereas those that had stayed out for shorter periods of time were included. Thus 24 triangles and 27 diamonds in all were available for the test releases.

Particular caution was taken to transport the birds to the release sites in such a way that they would not be able to perceive the odours present either in the areas crossed or at the test release site until the time of release. In fact, it has recently been demonstrated (Papi *et al.*, 1973b) that initial orientation is influenced by sensory inputs occurring during the outward journey which may be of an odorous nature. For this reason each bird was closed in a metal container (32 cm $\times$ 18 cm and 22 cm high) which was airtight. A tank of compressed air provided each container with fresh air. The odorous substance was applied to each pigeons as soon as it was removed from the container, and then it was immediately released. The olive oil was applied directly onto the beak and the nostrils. In the experiment of August 7th a mixture, which contained equal parts of synthetic turpentine and pure vaseline, was thinly spread on the birds' beak and nostrils with a little brush. In the experiment of August 18th we added the synthetic turpentine to cotton flocks applied to the beak as described by Benvenuti *et al.* (1973b).

The pigeons were tossed singly, alternating one triangle with one diamond. They were observed with 10 $\times$ 40 binoculars until they disappeared.

IV. Statistical Methods

Bearings were tested for randomness by the Rayleigh test (Batschelet, 1965). Vanishing times and homing performances were compared by the Mann-Whitney *U* test (Siegel, 1956).

Results

Four test releases were carried out:

1. August 6th. From Fornacette, home distance 21.0 km, home direction 280°. Clear sky, wind 3–4 m/sec from E. Olive oil was applied to all of the birds. The first half of the triangles was released (12) as well as the first half of the diamonds (14). Ten vanishing points of triangles and 13 vanishing points of diamonds were recorded (Fig. 3A and B, open symbols).

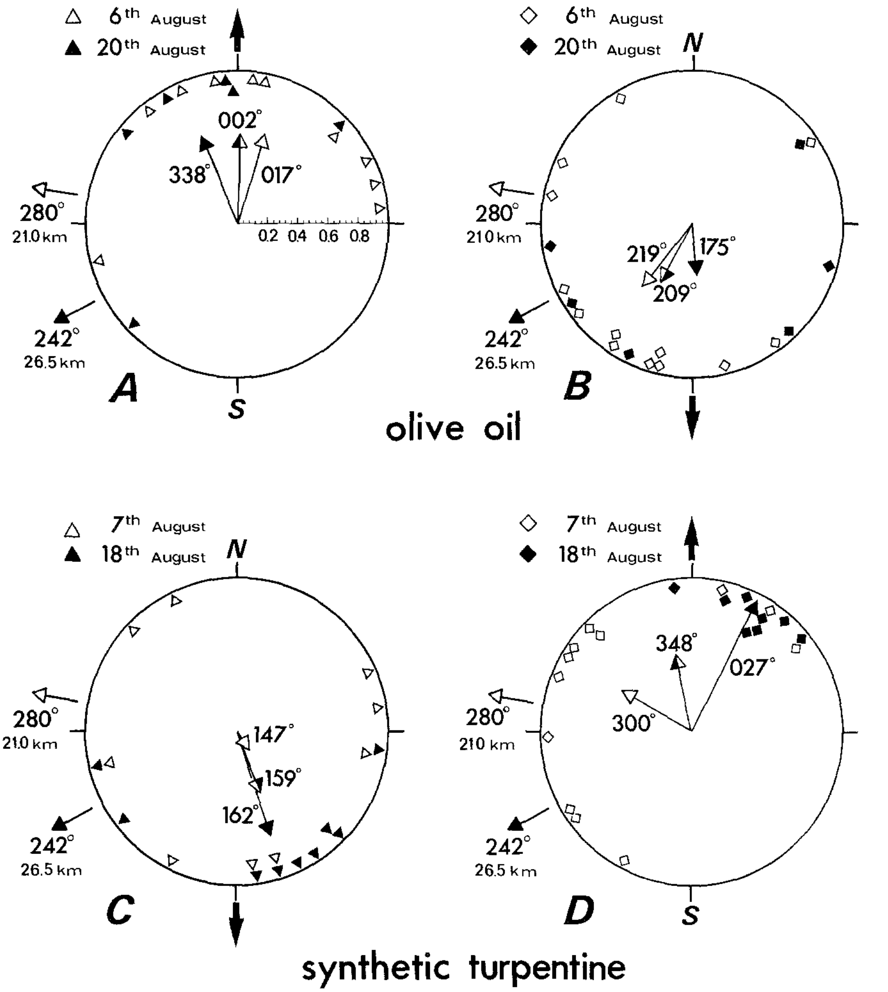

Fig. 3. Initial orientation in test releases. Each symbol on the periphery of the circle indicates the vanishing bearing of one bird. In each diagram the vanishing bearings from two localities are reported. The outer arrows, near W, indicate the homesite, direction and distance of which are given; the large outer arrow (in N or S) indicates the predicted direction. The mean vectors corresponding to open symbols, to filled symbols and to the pooled distribution of both are indicated inside the circle (arrow with open, filled and half-filled head respectively). The length of the vectors can be read with the scale indicated in the first diagram. For other explanations, see text

In this and in the successive test releases, the number of vanishing bearings recorded was less than the namber of pigeons released because some of the birds either disappeared very near the release point behind vegetation or other objects or perched in the surroundings.

2. August 7th. From the same release point. Clear sky, haze, the wind initially from E (1–2 m/sec), turns to NW (2 m/sec) then to SW (5 m/sec) and finally to W (5 m/sec). Turpentine was applied to all of the birds. The second

half of the triangles were released (12) as well as the second half of the diamonds (13). Nine vanishing points of triangles and 12 vanishing points of diamonds were recorded (Fig. 3C and D, open symbols).

3. August 18th. From a release point near Bientina. Clear sky, haze, no wind. Home distance 26.5 km, home direction 242°. Turpentine was applied to all of the birds. All of the birds that had returned from the first experimental flight were released again (10 triangles and 13 diamonds). Nine vanishing points of triangles and 8 vanishing points of diamonds were recorded (Fig. 3C and D, filled symbols).

4. August 20th. From the same release point of the third experiment. Clear sky, haze, no wind. Olive oil was applied to all of the birds. Those that had returned from the second experimental flight were again released (10 triangles and 9 diamonds). Six vanishing points of triangles and 6 vanishing points of diamonds were recorded (Fig. 3A and B, filled symbols).

In the diagrams of Fig. 3, the directions are presented into the four groups corresponding to: A) all the triangles with oil application, B) all the diamonds with oil, C) all the triangles with turpentine, D) all the diamonds with turpentine. The mean vectors corresponding to the pooled distributions (arrows with half-filled head inside the circles) deflected no more than 29° from the expected direction and were always nearer to the predicted direction than to the home direction. The combined distributions always differed from random (Rayleigh test, $p < 0.01$ for A and D, $p < 0.05$ for B and C).

The mean vectors relative to the eight sets of bearings (white arrows and black arrows inside the circles) were always closer to the predicted directions than to the home direction, except in the case of the diamonds on August 7th. In three cases, however, (triangles of August 7th and 20th, diamonds of August 20th) the distribution of vanishing points did not differ from a random distribution (Rayleigh test, $p > 0.05$).

A comparison of the vanishing times did not reveal significant differences between the triangles and diamonds in any of the test releases. Nor were there any significant differences in the homing performances. A subdivision of the birds, according to those that homed the same day, those that returned later, and those lost, produced the following data: on the 1st release, triangles 5, 5, 2; diamonds 9, 4, 1. On the 2nd release, triangles 5, 5, 2; diamonds 7, 0, 4. The homing times of the birds that returned the same day ranged from 39 min to more than 10 hrs. The homing times of the 3rd and 4th release were not recorded. On the 3rd release, 3 triangles and 1 diamond did not return, on the 4th, 1 triangle and 1 diamond.

Discussion

The results show that treatment with odorous air currents and applications of the same odours at the time of release influence the initial orientation in a predictable way. The birds, when released with an odorous substance applied to their nostrils, show the tendency to fly in a direction opposite to that from which they were accustomed to perceiving the same odour when subjected to wind treatments in the aviary. It must be emphasized that: 1) this tendency persists even in the second release from a new release point, 2) pigeons of the same group, released from the same point, prefer opposite directions according to the substance applied to the nostrils, 3) pigeons of both groups, when released from the same point and with the same substance applied to their nostrils, tend to fly in opposite directions.

Since most of the pigeons, in spite of the erroneous olfactory information, succeeded in returning to the loft, the problem arises as to how they managed to find the home site. This problem has been discussed by Papi *et al.* (1973a) in relation to the return of pigeons that were prevented from associating the odours carried by the winds with the direction from which they came. It was proposed that the birds sought the familiar smell of the loft area by means of a trial and error mechanism. This explanation could be valid in our case, although other mechanisms may not be excluded, including, in particular, an optical search for the loft based on landmarks. In our case the optical search would be facilitated by the short distance between the homesite and the release point. The results of recent experiments on pigeons subjected to an alteration of the learning process in the loft (Baldaccini *et al.*, 1974) also indicate that the visual search for known landmarks should be considered as a substitute homing mechanism.

The results of the present experiments confirm the existence of an olfactory navigation mechanism, and, moreover, support the hypothesis that pigeons, by smelling the winds, inform themselves on the odours prevalent in the surrounding areas.

We would like to thank Prof. G. Berti for analysis of the solvents' mixture and for many useful suggestions. We are grateful to Dr. J.D. Coulter for correcting the English text.

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