

Pigeon Navigation: Charcoal Filter Removes Relevant Information from Environmental Air

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Summary. Homing pigeons were displaced and kept until they were released in airtight containers ventilated with environmental air that could be passed through: (a) a filter made of fiberglass paper retaining large portions of the solid and liquid aerosol particles, (b) an additional filter consisting of activated charcoal, or (c) no filter (controls). Before its release, each bird was taken out of the container, and its olfactory epithelium was immediately anesthetized by lidocaine (Xylocaine). Thus, neither experimental nor controls were able to smell while their initial orientation behavior was being observed.

The controls' initial bearings were better home-ward-oriented than those of pigeons ventilated with charcoal-filtered air in 14 of 17 releases conducted in Italy and Germany, at distances of 24–155 km. In the final analysis, the bearings of the charcoal-filter birds did not show any relation to the direction toward home, whereas those of the controls did. Pigeons ventilated with air that had passed through only the paper filter did not behave noticeably differently from control pigeons.

It is concluded that the material bases of olfactory navigation in pigeons are substances dispersed in the atmosphere, most probably in a molecular state.

Introduction

During the last decade, Papi and other investigators (Papi et al. 1972, 1980; Papi 1976; Wallraff 1980b, c) accumulated a growing body of evidence that homing pigeons require an intact olfactory apparatus for their returns from unfamiliar distant sites. It has been concluded that the reduced performances of anosmic pigeons reflect specific deficits of their navigational mechanism and not solely some general

preconditions for homing such as motivation or alertness. This conclusion implies that the pigeons deduce relevant information from particular substances dispersed in the atmosphere. Additional support of this idea can be derived from outward-journey detour experiments with and without olfactory stimulation (Papi et al. 1978a) and from experiments in which wind directions at the loft site were reversed (Ioalé et al. 1978; Ioalé 1980). No attempt has been made, however, to verify the inference directly by removing related substances from the environmental air. An attempt of that sort appears necessary as a first step toward the eventual identification of the substances involved.

The time of transport to and the stay at the release site was considered the best-suited phase of a homing experiment for exposing the pigeons to appropriately filtered environmental air. We decided to use this phase, although it had been shown that the pigeons normally do not need information gathered during passive displacement for their subsequent return from distant sites (Wallraff 1980a). It had also been shown, however, that it is sometimes possible to modify their behavior immediately after release by varying olfactory conditions during transportation by means of detours or by preventing the birds from smelling environmental odors (Papi et al. 1973, 1978a; Wallraff et al. 1981). That means that pigeons do not generally ignore the conditions during displacement. The degree by which these conditions affect initial orientation, however, is highly variable and probably depends on the local and temporal availability of relevant navigational cues (Wallraff 1980a; Wallraff et al. 1980). Thus, actual olfactory information available during the first minutes of flight may or may not supersede preceding false information or perceptual deficit. To become independent of this variable and to ensure that the pigeons can only make use of memorized olfactory information they had

gathered under the well-controlled experimental conditions in advance of the take-off, we released not only the experimentals, but also the majority of the controls under local anesthesia of their olfactory epithelium (cf. Schmidt-Koenig and Phillips 1978).

Two types of filters were used: one retained only the aerosol, i.e., solid and liquid particles floating in the atmosphere; the other also absorbed molecules in the gas phase.

Materials and Methods

Containers and Filters

The pigeons were transported in airtight wooden containers (external 128 × 53 cm, 29 cm high) covered with a removable Plexiglas plate and an additional narrow-meshed plastic lattice (Fig. 1). Each container consisted of two parts; the bird chamber was 75 cm long, 50 cm wide, and 24 cm high. At one end was a round opening for air supply, 19 cm in diameter, which could be closed with a filter. Through a small opening in the other narrow end (diam. 4 cm), air could be exhausted by a vacuum cleaner mounted in the second chamber with its outlet through the end opposite to the air entrance. Incoming and outgoing air had to pass through adequately perforated plates distributing the airstream over the whole width of the bird chamber. This chamber was cross-divided into two parts by wirenet. In one side two round openings (diam. 13 cm), that could be firmly closed allowed the transfer of single pigeons by hand.

Over the whole width of the air-entrance opening, a filter could be mounted that was held by PVC rings and stabilized by wire lattices. A fiberglass filter (Schleicher & Schüll, No. 8) was used to remove aerosol particles (treatment FX; see below for code to treatment types). For the retention of both aerosol and gaseous substances (type FFX), a similar filter paper (Schleicher & Schüll No. 3387) was used with similar retention rate, but lower air resistance. In addition, a Plexiglas cylinder was used that was densely filled with granular (1.5 mm) activated charcoal (Merck 2514). The cylinder was 19 cm in diam. and 26 cm in length (internal). At its front end (entrance), it was closed with a highly porous fiber-fleece filter. If a container was used for control pigeons (types CX and CC), however, no filter(s) were used. Instead, a solid PVC plate was mounted that was perforated with 14 holes 5 mm in diam., which caused air resistance similar to that of the filters.

If a container was firmly closed, filter(s) or control plate mounted, and the vacuum cleaner in operation, a low pressure of about 4–6 mb existed in the bird chamber. The flow rate of the air was about 150 l/min. Thus, if the airstream had been completely homogeneous (which was certainly not the case), the air in the chamber would have been exchanged in about 40 s (avg. air velocity about 2 cm/s).

The spectra of aerosol contents in containers equipped with the two types of filters, as well as in a control container, were determined under natural atmospheric conditions.¹ The density of particles (number per size-class and vol. of air), with diameters ranging from 0.04 to 2 μm, was reduced in both filter containers to a rate of 5%–15% of that measured in the control container. The retention rate of the fiberglass filter alone was about 95% for particles less than 0.4 μm and 85%–90% for the larger sizes. Since

the smaller particles occur more frequently in the atmosphere by several orders of magnitude, the filter retained within the range of measurement about 95% of the number of particles floating in the atmosphere (yet only about 85%–90% of their volume).

Local Anesthesia

Before release, most of the pigeons' olfactory epithelia were anesthetized by applying commercial Xylocaine Spray (Astra Chemicals) into each nostril. A single puff per side was given with its dose somewhat reduced against the normal volume. (This simple application differs from that described by Schmidt-Koenig and Phillips (1978) who sprayed through the choanal opening.) The anesthetic effect was examined by laboratory experiments that included the two possible variables that are unavoidable in the field: (a) the applied doses of Xylocaine may differ with varying volumes per spray pulse as well as the exact location of the spray cannula within the nostril; (b) the responsiveness may differ among individual pigeons. In order to include both variables, the increase of heart rate in response to an olfactory stimulus was measured in 22 pigeons, one series of tests in one session per individual. The birds were not conditioned; no electric shock was applied; only spontaneous responses to olfactory stimuli were recorded. The experimental set-up was generally like that described by others (e.g., Wenzel 1967): the pigeon was fixed in a holder, kept in a dark box, and exposed to an airstream (5 l/min) that could be loaded with odorous substances. In the tests described here, the complete airstream was saturated with amylacetate for a duration of 20 s. The heart rate before, during, and after this phase was recorded.

About 30 min after the beginning of each session and after two stimulation tests, Xylocaine was applied to the nostrils, and at 10-min intervals the bird's reaction to amylacetate was tested. Pigeons that did not show a clear reaction in the first two control tests (those whose heart rate did not increase by at least 20 beats/min in both tests) were discarded. This led to a reduction of our sample from 22 to 17. The response curves of this sample of birds for selected time intervals from the Xylocaine application are shown in Fig. 2A–F. It is obvious that 10 min after application there is no response at all. After 20 and 40 min, few birds start to react again, and after 80 min, some reaction can be observed in about half of the birds. Variability (also intraindividual) remains very high, however, and never comes back to the low level of the two control tests at the beginning (Fig. 2G). Yet it should be stressed in this context that some damping in the reaction is to be expected anyhow and can, in fact, be observed in untreated pigeons, too, since the procedure does not include any reinforcement. A steady-state level of response was reached about 1.5 h after Xylocaine application. As the olfactory stimulus was very strong, one may assume that responses to lower concentrations were obviated in all pigeons, for at least 30–60 min.

In the field experiments, the pigeons were commonly released within 5–20 min after Xylocaine application. Thus, we can be quite sure that the initial orientation was not noticeably influenced by current smelling of environmental odors.

Types of Experimental Treatment

Five types of experimental treatment were used, which are designated by abbreviations:

CC: Control-control pigeons. From loft site to individual release kept in container with undisturbed natural air. Release without particular treatment, i.e., without local anesthesia.

CX: Control pigeons treated with Xylocaine. Kept in container with undisturbed natural air. Prior to release each pigeon was treated with Xylocaine Spray as described above.

FX: Filter pigeons treated with Xylocaine. Kept in container

1 Measurements were conducted by D. Paffrath, Institut für Physik der Atmosphäre, Deutsche Versuchsanstalt für Luft- und Raumfahrt (DFVLR), D-8031 Oberpfaffenhofen

ventilated with natural air passed through fiberglass filter. Xylocaine treatment as in CX birds.

FFX: Filter-filter pigeons treated with Xylocaine. Kept in container ventilated with natural air passed through charcoal filter plus fiberglass filter. Xylocaine treatment as in CX birds.

BAX: Bottled-air pigeons treated with Xylocaine. Kept in container ventilated with bottled air (8–15 l/min). Xylocaine treatment as in CX birds. (Vacuum cleaner is switched off; air comes from a compressed-air cylinder through the otherwise closed entrance opening of the container.)

General Procedures

The pigeons were divided into three or four groups, which were composed as similarly as possible with respect to age and preceding homing experience, and at random with respect to other qualities. In repeated releases of the same birds, treatment type per group varied from release to release.

The BAX pigeons were transported inside of the van. In all other cases, the containers were placed on top of the van with the air-entrance openings in the forward direction and open to undisturbed air (Fig. 1). The pigeons had an open view to the sky, which was limited by the plastic lattice to an area about 35°–45° above the horizon. Exhausters were in permanent operation for several minutes before departure at the loft site until about 10–40 min after arrival at the release site. After about 10–15 min of

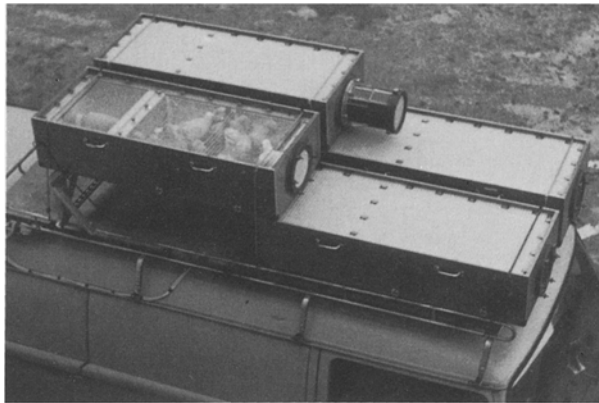
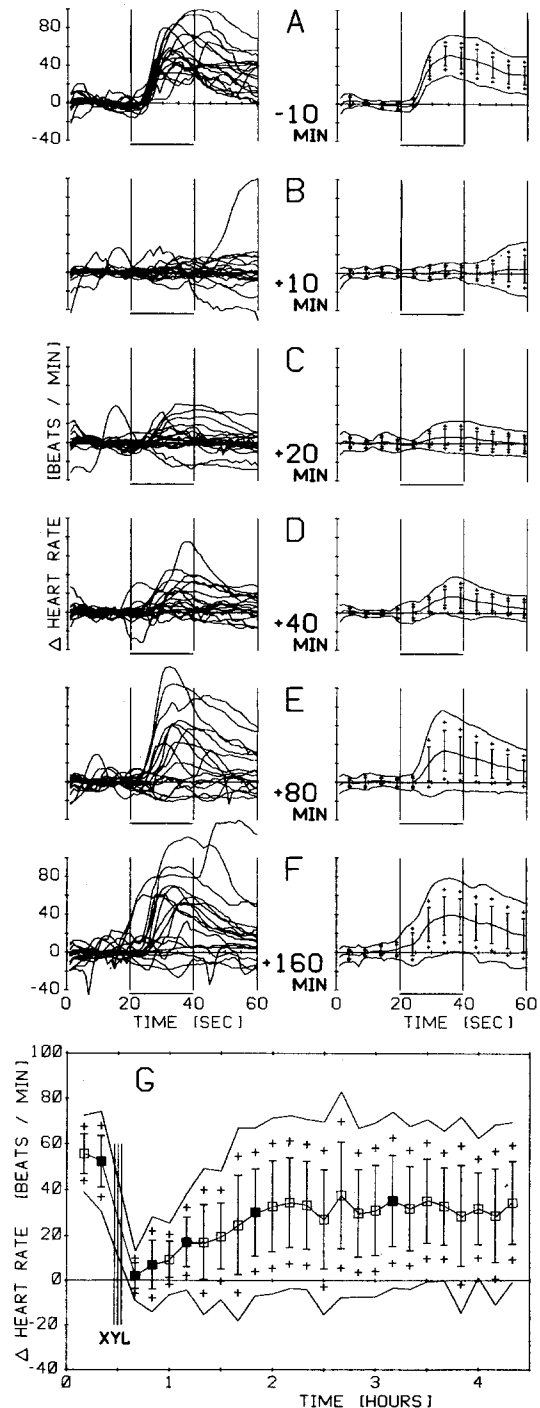


Fig. 1. Four experimental containers placed on top of the van used for transportation. The lattice cover of one of the containers is removed. The upper two containers are equipped with filters (at the back: FFX, at the front: FX), the lower two with control plates. Further explanation is in the text

Fig. 2A–G. Effect of Xylocaine application on heart-rate responses to amylocetate. **A–F** Response curves of 17 pigeons (left: individual, right: means) at different time intervals before (**A**) and after (**B–F**) application of Xylocaine. Abscissa: Time from 20 s before until 20 s after stimulus application. Amylocetate was added to the breathing air during seconds 20–40. Ordinate: heart rate (beats/min), difference from avg. during prestimulus time (s 1–20). In the right-hand diagrams \pm standard deviation curves are drawn as well as 95% and 99% confidence intervals of the means (vertical bars and crosses). **G** Mean heart-rate increases in response to amylocetate during the whole duration of the 17 experiments. The ordinate marks the difference in heart rate between s 36–40 and s 16–20 (i.e., before and at the end of stimulus application). XYL marks the time of Xylocaine application. Means of tests illustrated in **A–F** are drawn as filled squares. Standard deviation and confidence intervals are as in **A–F**

interruption for placing the containers in an appropriate manner on the ground, ventilation was again in effect for about 10–20 min before the first pigeon was taken out for release. Depending on the distance of displacement, pigeons were exposed to the container airstream prior to release for 100–260 min. The pigeon released last was exposed for about 1–3 h longer (about 2–6 h, including the time without active ventilation).

During release, the exhausters were in operation in a rotating manner so that one or two of them were active at the same time. Individual pigeons were taken out while the respective vacuum cleaner was switched off. Appropriate precautions and handling



ensured that only minimal air exchange could take place during this transfer. If the bird did not belong to the CC group, it was treated with Xylocaine immediately after removal. Then it was kept in a small crate until the preceding bird was tossed in the air and had left the observer's range of sight. Time between Xylocaine application and release was 5 min as a minimum, in most cases shorter than 10 min, and only exceeded 20 min as an exception (depending on the vanishing interval of the preceding bird). The releasing procedure itself and the field-glass observation were as usual (e.g., Wallraff 1980a, b). Pigeons were released alternately, by twos, from different containers.

The same filters (fiberglass paper and charcoal filling) were used for three releases at most and thereafter renewed. The time of return to the loft was not recorded so that the data available are restricted to initial orientation.

Pigeons and Releases

Nine releases were conducted in Italy, with pigeons housed in a loft near Pisa, and eight releases took place in Germany, with pigeons from a loft near Würzburg. In both countries, we made two series of experiments with different birds. The releases within each series took place in a number sequence; the pigeons were not used in any other manner between these releases.

Series A. Releases 1–5, Italy, were conducted with young pigeons (age 4–5 months) with little experience. In the first two releases, the birds were completely inexperienced in homing and had only made some free flights at the loft site. From release 3 on, the pigeons returned from releases 1 and 2 were used together. The dates, homeward directions, distances, and treatment types used were as follows:

- Release 1) 2 August 1980, 168°, 30 km, CC, CX, FFX, BAX
- Release 2) 3 August 1980, 314°, 24 km, CC, CX, FFX, BAX
- Release 3) 6 August 1980, 241°, 31 km, CX, FX, FFX
- Release 4) 9 August 1980, 333°, 36 km, CC, CX, FX, FFX
- Release 5) 11 August 1980, 160°, 42 km, CC, CX, FX, FFX

Series B. Releases 6–9, Italy, contained experienced, older pigeons. The birds were 2–7 (mostly 3–5) years old and had returned earlier many times from various directions and distances. Most of the pigeons were last used in November 1979 for a series of short-distance releases from eastern directions. The dates, homeward directions, distances, and treatment types were as follows:

- Release 6) 5 August 1980, 160°, 42 km, CX, FX, FFX
- Release 7) 7 August 1980, 333°, 36 km, CX, FX, FFX
- Release 8) 10 August 1980, 326°, 105 km, CX, FX, FFX
- Release 9) 12 August 1980, 193°, 132 km, CX, FX, FFX

Series C. Releases 10–13, Germany, were conducted with young pigeons (age 4–8 months) of little experience. Releases 10 and 11 were made with second-flight pigeons that had their first flight from about 7.5 or 30 km NW or SW (release 10) and from about 7.5 or 30 km NE or SE (release 11). In releases 12 and 13, returners from both the preceding releases were consolidated. In order to replace lost birds, in the last release we included 20 second-flight pigeons that had returned from 180 km NW or SE. The dates, homeward directions, distances, and treatment types were:

- Release 10) 18 September 1980, 270°, 60 km, CC, CX, FX, FFX
- Release 11) 19 September 1980, 092°, 56 km, CC, CX, FX, FFX
- Release 12) 21 October 1980, 360°, 59 km, CC, CX, FX, FFX
- Release 13) 28 October 1980, 180°, 60 km, CC, CX, FX, FFX

Series D. Releases 14–17, Germany, contained experienced older pigeons. The birds were 1–5 years old and had returned several or many times from various directions and distances, most of them

up to at least 180 km. None had been released at any of the release sites used in this study. The last preceding release was from 60 km north. In order to replace lost birds, in the last release we included 10 young, third-flight pigeons returned from release 13 and belonging to the 20 replacement birds of series C. The dates, homeward directions, distances, and treatment types were:

- Release 14) 16 August 1980, 181°, 155 km, CC, CX, FX, FFX
- Release 15) 5 September 1980, 357°, 150 km, CC, CX, FX, FFX
- Release 16) 20 September 1980, 090°, 153 km, CX, FX, FFX
- Release 17) 1 November 1980, 270°, 147 km, CX, FX, FFX

All releases were made while the sun was visible or at least localizable. The winds were weak or moderate (maximum about 15 km/h) except during release 17, which was conducted with a rather strong wind (approx. 20–30 km/h near ground level) coming from the east (approx. 80°) and at a low temperature (approx. 5°C).

Data Analysis

From the pigeons' bearings at the takeoff, mean vectors were calculated consisting of direction $\bar{\alpha}_N$ (0° = north) or $\bar{\alpha}_H$ (0° = home) and length \bar{a} (ranging between 0 and 1). The mean homeward component is $\bar{c}_H = \cos \bar{\alpha}_H \times \bar{a}$. Data from two or more releases are either simply pooled (with 0° = home) or combined according to the rules of pseudopooling (Wallraff 1979, Appendix B) with reduced n ($N_{\text{red}} = n$ of smallest sample multiplied by number of samples) as the actual number of units.

The statistical significance in circular distributions was tested by means of the Rayleigh test, the V test, the Watson $U_{n,m}^2$ test (Batschelet 1965, 1972), and the Wilcoxon-Mann-Whitney U test or t test as adapted to circular distributions ('adapted U test,' 'adapted t test;' Wallraff 1979, Appendix A). For noncircular distributions, common tests were used as described in related textbooks.

Results

Initial Bearings

All the vanishing bearings of the individual releases are documented in the circular diagrams of Figs. 3–6. The figures also explicitly show the most relevant parameter for a comparison between experimental groups, the homeward component \bar{c}_H .

Details of the single releases with their great variability will not be considered (see Discussion), but the material will be evaluated in various ways as a whole. Only releases 1 and 2 will be inspected separately in advance.

In these two experiments, the charcoal-filter group (FFX) was compared with controls ventilated with natural air (CX and CC), on the one hand, and with birds ventilated with bottled air (BAX), on the other. It is obvious that the FFX pigeons behaved in the same way as those completely isolated from environmental odors and quite differently from both types of controls (Fig. 3, releases 1 and 2). It remains an open question as to why both groups, BAX and FFX, preferred directions nearly opposite to home; yet the perfect coincidence between the two types induced us to replace the 'negative controls' BAX in

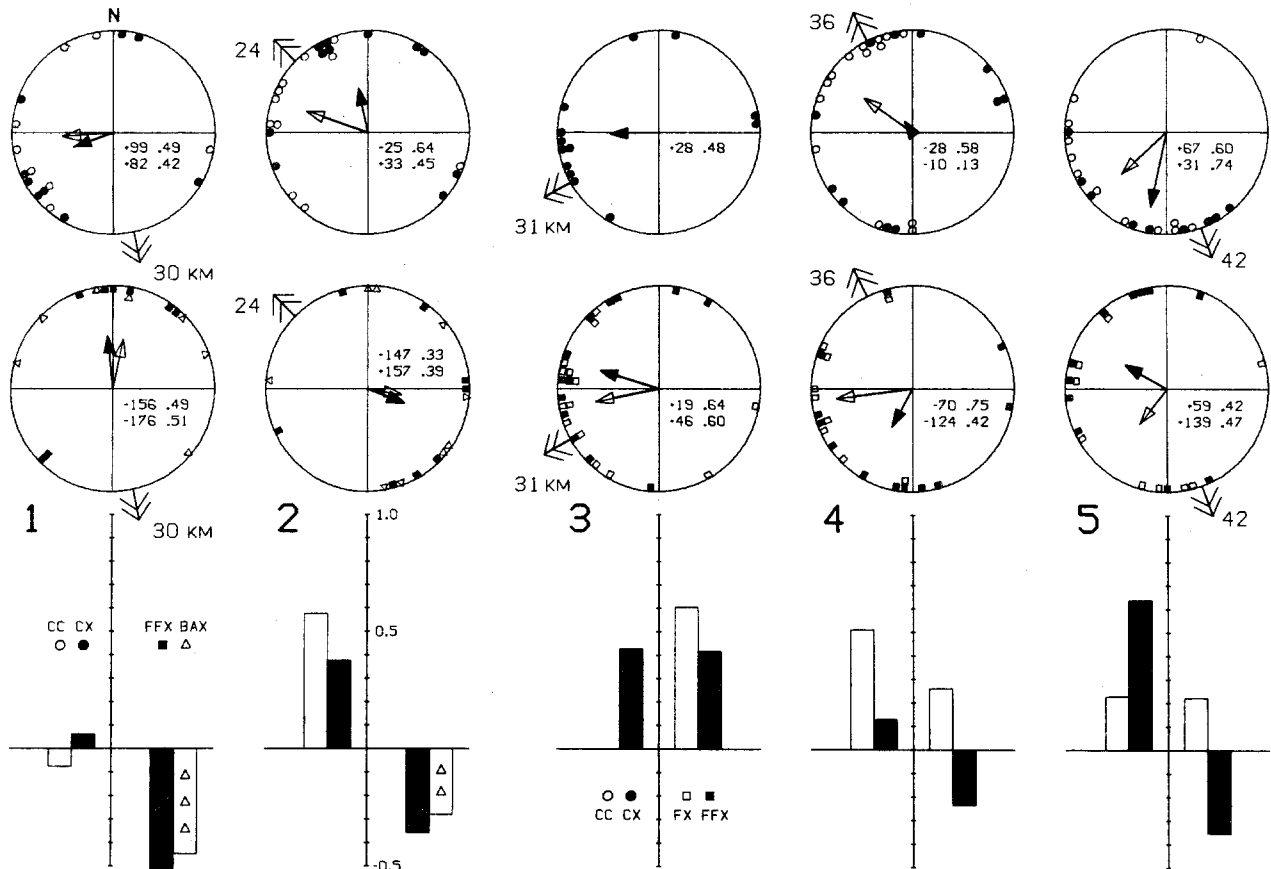


Fig. 3. Series A (releases 1-5, numbers indicated), little experienced young pigeons in Italy, initial orientation. Circular diagrams: Each symbol on the periphery represents the vanishing bearing of one bird. Resulting mean vectors are given as arrows ($\bar{a}=1$ equals radius) and as numbers ($\bar{\alpha}_H, \bar{a}$) within the circles (sequence: 'white,' 'black' sample). Homeward directions (double-headed arrows) and distances (numbers) are indicated. Upper row, controls (CC open, CX filled circles), lower row, experimentals (FX open, FFX filled squares, BAX open triangles). Histograms: corresponding homeward components, \bar{c}_H (from left to right: CC, CX, FX, FFX, BAX)

the further releases by a second experimental group, FX.

Charcoal-Filter Birds (FFX) vs Xylocaine-Treated Controls (CX)

The mean homeward component of the charcoal-filter birds, FFX, is lower than that of the Xylocaine-treated controls, CX, in 14 of 17 releases ($P=0.006$; sign test). In the CX birds, \bar{c}_H is positive (i.e., the mean direction deviates less than 90° from home) in 14 releases (82%), and in the FFX birds, in only 7 releases (41%). The means of 17 means are $\bar{c}_H=+0.266$ (CX) and -0.039 (FFX). The differences between pairs of \bar{c}_H (per release) are significant with $P<0.005$ (Wilcoxon signed-rank test, one-tailed).

Level and significance of homeward orientation can be best assessed by combining the corresponding releases from opposite directions. For this purpose release 3, which has no counterpart, has to be

omitted and some deviations from geometrical symmetry in Italy have to be overlooked. Table 1 shows the combined homeward components. In seven of eight pairs of releases in CX \bar{c}_H is positive, but this is true in only three pairs in FFX. In all eight pairs, the value of FFX is lower than that of CX ($P=0.004$; sign test). The significant homeward orientation of CX pigeons is evident in Italy as well as in Germany and in young birds of little experience as well as in well-experienced older birds. Although the overall mean is not very high, with $\bar{c}_H=+0.256$, there is no doubt that initial orientation of the CX pigeons includes, on average, a significant homeward pointing component. Not a trace of such a component can be seen in the FFX results.

If we omit the general level of homeward directedness and look only for a relative comparison between the two kinds of treatment, we may directly pool the initial bearings with respect to their deviation from home without producing noteworthy bias. This is because the number of bearings of CX

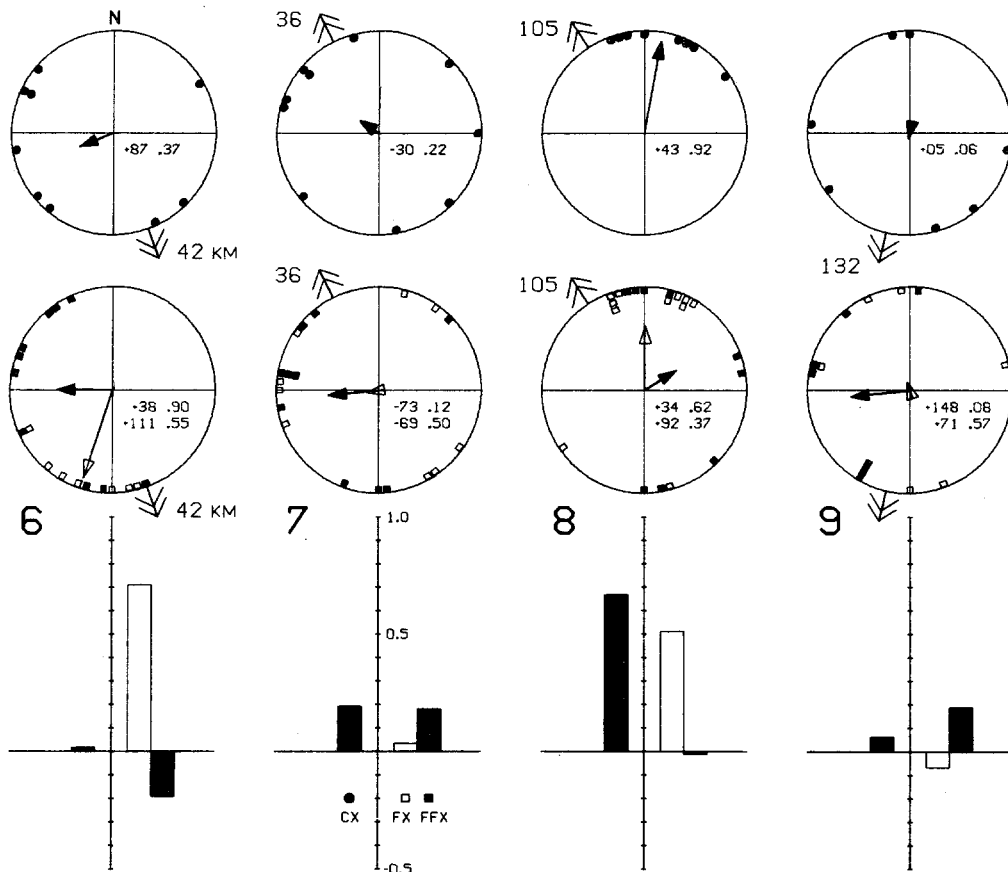


Fig. 4. Series B (releases 6-9), experienced older pigeons in Italy. For explanation see Fig. 3

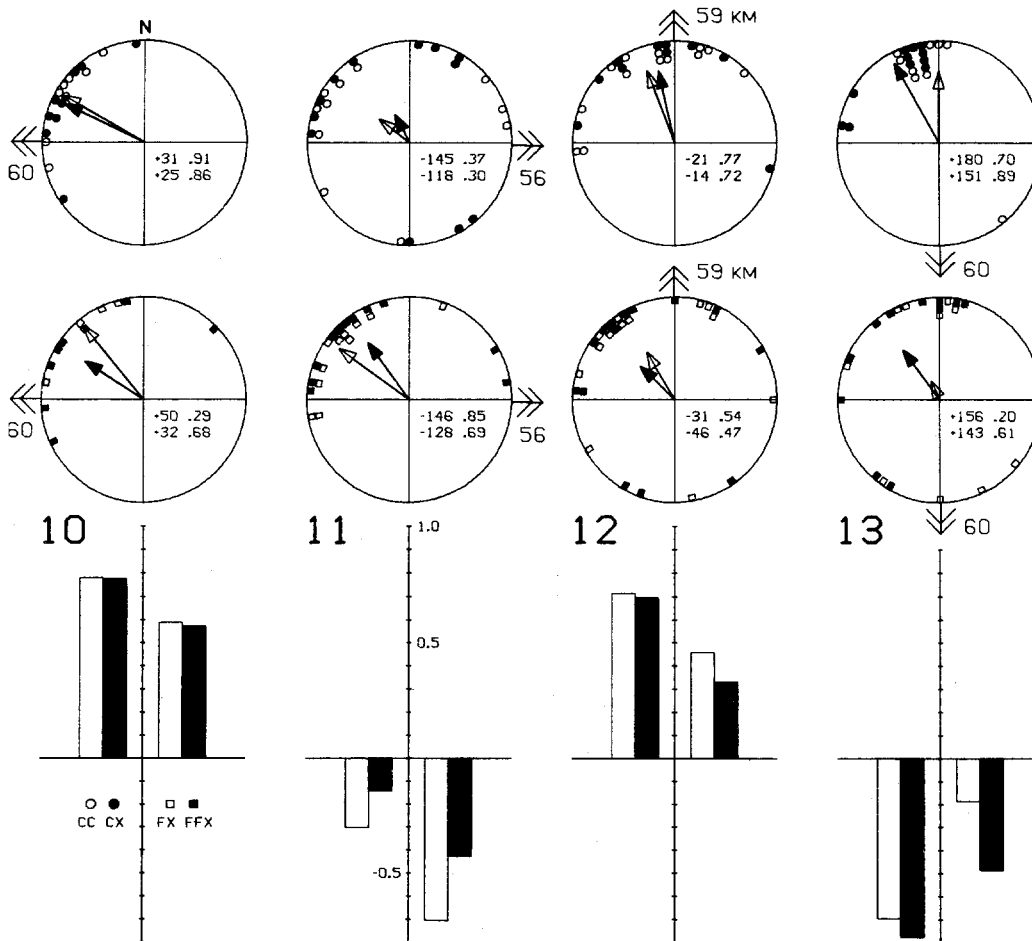


Fig. 5. Series C (releases 10-13), little experienced young pigeons in Germany. For explanation see Fig. 3

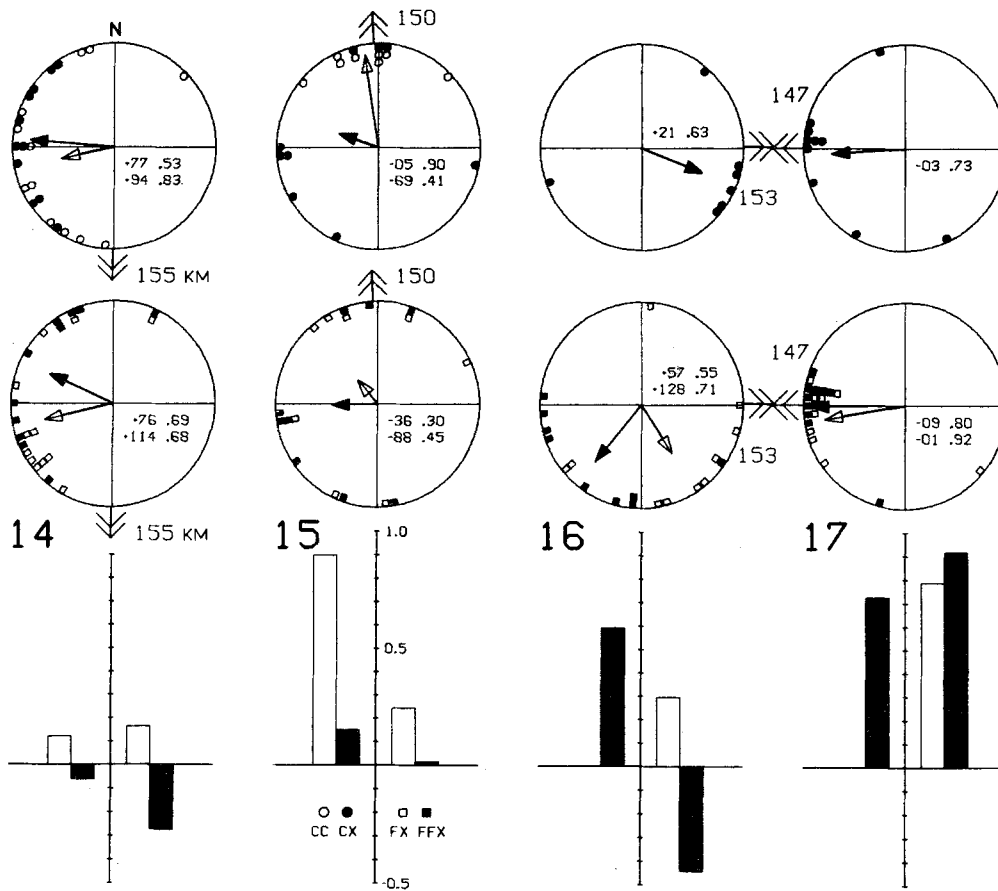


Fig. 6. Series D (releases 14-17), experienced older pigeons in Germany. For explanation see Fig. 3

Table 1. Mean homeward components of vanishing bearings in corresponding pairs of releases from opposite directions and in higher-order groups of releases. All birds Xylocaine-treated, CX controls, FX paper filter, FFX charcoal+paper filter

Series	Release	CX		FX		FFX	
		N_{red}	\bar{c}_H	N_{red}	\bar{c}_H	N_{red}	\bar{c}_H
A	1+ 2	18	+0.218	—	—	16	-0.434
	4+ 5	18	+0.382*	18	+0.240	22	-0.294
B	6+ 7	18	+0.105	14	+0.372*	20	-0.006
	8+ 9	14	+0.365*	12	+0.222	14	+0.089
C	10+11	18	+0.317*	10	-0.058	14	+0.073
	12+13	20	-0.041	20	+0.137	22	-0.079
D	14+15	18	+0.044	16	+0.204	18	-0.131
	16+17	14	+0.658***	20	+0.542***	18	+0.239
A, 4 releases (young)		36	+0.300**	—	—	32	-0.364
B, 4 releases (old)		28	+0.235*	24	+0.297*	28	+0.042
C, 4 releases (young)		36	+0.138	20	+0.040	28	-0.003
D, 4 releases (old)		28	+0.351**	32	+0.373**	36	+0.054
A+B, 8 releases (Italy)		56	+0.268**	(36)	(+0.278**) ^a	56	-0.161
C+D, 8 releases (Germany)		56	+0.245**	40	+0.206*	56	+0.026
A+C, 8 releases (young)		72	+0.219**	(30)	(+0.106) ^a	56	-0.184
B+D, 8 releases (old)		56	+0.293***	48	+0.335***	56	+0.048
Total (16 releases)		112	+0.256****	(70)	(+0.237**) ^a	112	-0.068

Data of 2, 4, 8, and 16 samples, respectively, are combined by means of pseudopooling. Significance levels are given according to the *V* test: **** $P < 0.0001$; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; no symbol $P > 0.05$

^a 6 and 14 releases, respectively

Table 2. Mean compass directions of vanishing bearings in combined symmetrical releases (CX, FX, FFX: see Table 1)

Series	CX		FX		FFX	
	$\bar{\alpha}_N$	\bar{a}_N	$\bar{\alpha}_N$	\bar{a}_N	$\bar{\alpha}_N$	\bar{a}_N
A + B, 8 releases (Italy)	294°	0.151	(247°	0.259) ^a	281°	0.207
C + D, 8 releases (Germany)	306°	0.441****	294°	0.411***	289°	0.544****
Total (16 releases)	303°	0.295****	(280°	0.320****) ^a	287°	0.375****

Releases are combined by means of pseudopooling. For N_{red} see corresponding lines in Table 1. Significance levels (Rayleigh test) are given as in Table 1

^a 6 and 14 releases, respectively

and FFX per release are comparable so that unequal representation of different releases and asymmetry of site distribution affect both types of treatment in a similar way (cf. Wallraff 1979, Appendix B). The overall homeward component of the 17 releases pooled is $\bar{c}_H = +0.247$ (CX; $\bar{\alpha}_H = +36^\circ$, $\bar{a} = 0.305$, $n = 166$; $P < 0.0001$, Rayleigh test and V test) and $\bar{c}_H = -0.031$ (FFX; $\bar{\alpha}_H = +108^\circ$, $\bar{a} = 0.102$, $n = 171$; $P > 0.1$, Rayleigh test and V test). The difference between the pooled distributions is statistically significant with $P < 0.001$ (Watson $U_{n,m}^2$ test with respect to general difference, adapted U test with respect to deviation from home) and with $P < 0.01$ (adapted U test with respect to scatter).

For the pooled data shown in Fig. 7 (excluding releases 1 and 2), the results are $\bar{c}_H = +0.246$ (CX; $\bar{\alpha}_H = +33^\circ$, $\bar{a} = 0.292$, $n = 145$; $P < 0.0001$, Rayleigh test and V test) and $\bar{c}_H = +0.005$ (FFX; $\bar{\alpha}_H = +87^\circ$, $\bar{a} = 0.100$, $n = 154$; $P > 0.1$). The distributions are significantly different from each other with $P < 0.005$ (adapted U test, homeward orientation as well as scatter).

Some difference between the initial bearings of CX and FFX can be observed even less than 1 min after release. The ratio of \bar{c}_H being lower or higher in FFX than in CX is 11:6 after 20 s and 13:4 after 40 s of flight. From pooled 40-s bearings of 17 releases, the results are $\bar{c}_H = +0.186$ (CX; $\bar{\alpha}_H = +33^\circ$, $\bar{a} = 0.222$, $n = 188$; $P < 0.001$, Rayleigh test and V test) and $\bar{c}_H = -0.019$ (FFX; $\bar{\alpha}_H = +104^\circ$, $\bar{a} = 0.082$, $n = 191$; $P > 0.1$). The distributions are significantly different from each other with $P < 0.005$ (adapted U test, homeward components).

If the vanishing bearings are inspected not with respect to their homeward orientation, but to a possible preference for a certain compass direction, it becomes evident that the FFX birds are not completely disoriented. On average, FFX as well as CX pigeons preferred directions around WNW, with FFX more pronounced than CX and in Germany more pronounced than in Italy (Table 2).

Paper-Filter Birds (FX) vs Xylocaine-Treated Controls (CX)

The mean homeward component of the single-filter (fiberglass) birds, FX, is lower than that of the CX controls in 8 of the 15 releases in which this type was used (releases 3–17). In both groups, \bar{c}_H is positive in 12 (80%) of 15 experiments. The means of 15 means are $\bar{c}_H = +0.272$ (CX) and $+0.261$ (FX). Thus, the values are comparable.

In both groups, \bar{c}_H is positive in six of seven corresponding pairs of releases, and the value of FX is lower than that of CX in four of seven pairs (Table 1). No drastic differences occur in the numerical values of symmetrical releases (Table 1), and the overall means of the means of 14 releases are $\bar{c}_H = +0.261$ (CX) and $+0.237$ (FX). The result of simple pooling is shown in Fig. 7, and the respective means of FX (15 releases) are $\bar{c}_H = +0.271$, $\bar{\alpha}_H = +16^\circ$, $\bar{a} = 0.282$ ($n = 145$; $P < 0.0001$, Rayleigh test and V test) (CX: $\bar{c}_H = +0.246$, see previous section).

Thus, there is no noteworthy difference indicated between CX and FX results, and this concerns not only homeward orientation, but also the preferred compass direction (Table 2).

Charcoal-Filter Birds (FFX) vs Paper-Filter Birds (FX)

The mean homeward component of the filter-filter (charcoal) pigeons, FFX, is lower than that of the single-filter pigeons, FX, in 11 of 15 releases in which both types were used ($P = 0.059$; sign test). The means of 15 means are $\bar{c}_H = +0.261$ (FX) and $+0.013$ (FFX). The differences between pairs of \bar{c}_H (per release) are significant with $P < 0.02$ (Wilcoxon signed rank test, one-tailed). For further comparisons see Table 1. The pooled distributions (Fig. 7) are significantly different from each other with $P < 0.01$ (adapted U test, homeward orientation as well as scatter).

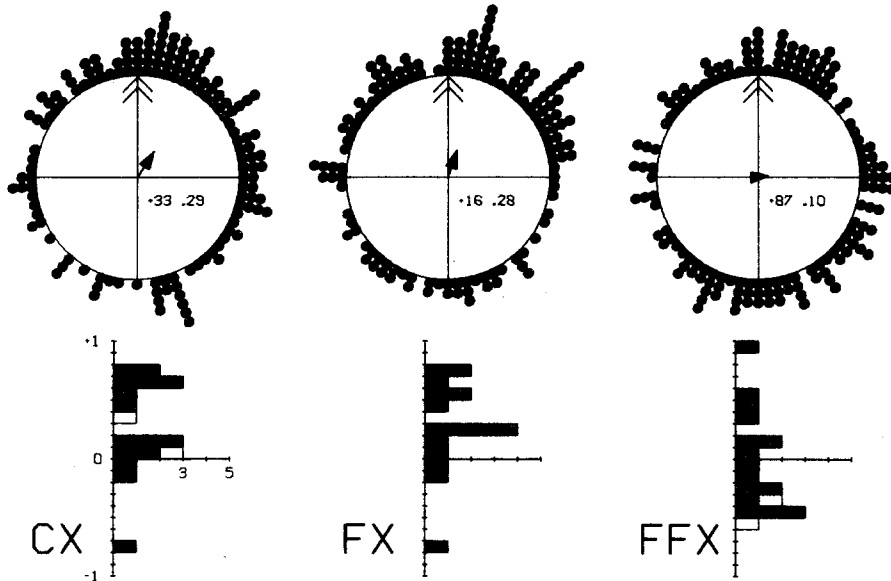


Fig. 7. Vanishing bearings of releases 3-17 pooled with homeward direction upward. Histograms show distributions of mean homeward components, \bar{c}_H , per release (in CX and FFX means of releases 1 and 2 are added as white rectangles)

Compass preferences are somewhat more pronounced in FFX than in FX. The means of the means of 14 symmetrical releases are $\bar{\alpha}_N=280^\circ$, $\bar{a}_N=0.320$ (FX; $N_{\text{red}}=70$) and $\bar{\alpha}_N=283^\circ$, $\bar{a}_N=0.442$ (FFX; $N_{\text{red}}=98$) (see also Table 2).

Controls with and without Local Anesthesia (CX vs CC)

Only the Xylocaine-treated controls, CX, are directly comparable with the filter types. It may be interesting, however, to ascertain to what extent this experimentally manipulated control type differs from completely untreated control-controls, CC. The latter type was used in only 10 of 17 releases (see Figs. 3-6). The mean homeward component of CX is lower than that of CC in 7 of these 10 releases. Means of means are $\bar{c}_H=+0.275$ (CC; $N_{\text{red}}=80$) and $+0.184$ (CX; $N_{\text{red}}=90$). Simple pooling leads to $\bar{c}_H=+0.275$ (CC; $n=107$) and $+0.158$ (CX; $n=102$). The difference between the distributions is not statistically significant ($P=0.07$; adapted U test with respect to home), yet it suggests the conclusion that there is some effect from the Xylocaine treatment. As releases 4 and 15 demonstrate, the effect in some cases can be very drastic. (In these two releases the difference in homeward orientation is statistically significant under the adapted U test with $P<0.05$ and $P<0.01$.)

Vanishing Intervals

The time between release and vanishing from sight is not noticeably different in Xylocaine-treated controls and in filter types. Arithmetic means of 17 medians (per release) are 2.70 (CX) and 2.71 (FFX). The median of the vanishing intervals is larger in FFX than in CX in 9 of 17 releases.

Some difference is indicated, however, between Xylocaine-treatment and no treatment. The respective median is larger in CX than in CC in 7 of 10 releases in which both of these two types were used. The arithmetic means of the 10 medians are 2.25 min (CC) and 2.62 min (CX), and the differences are significant with $P<0.05$ (Wilcoxon signed-rank test, one-tailed).

Discussion

Comments on the Data

The differences between the summarizing diagrams (Fig. 7) are not very impressive, since even the controls (CX) appear rather weakly homeward oriented. Although this homeward orientation is statistically highly significant and although statistical significance of the differences is also sufficient, one may ask why the controls do not stand out more clearly against the charcoal-filter birds (FFX). In our opi-

nion, two circumstances are mainly responsible for this outcome:

(1) *General Peculiarities of Initial Orientation.* If the initial bearings of normal untreated pigeons at symmetrical release sites are combined, their average homeward directedness often appears rather low, especially in inexperienced or little experienced birds (e.g., Wallraff 1967, Fig. 1; 1978, Table 1). Thus, the average level of homeward orientation in the experiments shown here is not exceptional. In particular, the results obtained with the little experienced pigeons in Germany (series C, Fig. 5) have to be seen against the background of very poor homeward orientation of normal first-flight pigeons released at the same four sites (unpublished data). (We nevertheless used these sites because of the higher risk of bird losses at longer distances and the ensuing risk of an unfinished series.)

Most cases of weak homeward directedness, especially in the German series, are in some way connected with the preference of the pigeons for a particular compass direction ('preferred compass direction or PCD'; Wallraff 1967, 1978, 1980b). Since the PCD persists in anosmic pigeons (Wallraff 1978, 1980b), it is to be expected that the difference between controls and charcoal-filter pigeons decreases as the PCD component dominance over the homeward component increases even in the controls. This is obviously the case in series C (Fig. 5) and also in some other releases. Small differences should also be expected in cases in which the PCD (Table 2) coincides more or less with the direction toward home like in releases 3 and 17. (In the last-mentioned release, strong tailwinds (see p. 70) certainly contributed to the extremely uniform westward tendency.)

Those releases are most conclusive, therefore, in which the Xylocaine-treated controls (CX) are significantly homeward oriented ($P < 0.05$, V test), but in which their bearings do not include at the same time a significant PCD component (pointing toward 294° and 306° , respectively; see Table 2). These preconditions are met in releases 2, 5, 8, and 16. In these four cases, the charcoal-filter birds (FFX) behaved fundamentally differently from the CX pigeons; differences are statistically significant in each individual release ($P < 0.01$ in releases 5, 8, and 16; $P < 0.05$ in release 2; adapted U test). Means of the four mean homeward components are $\bar{c}_H = +0.568$ (CX) and -0.290 (FFX). Differences between pooled distributions are highly significant ($P < 0.0001$; adapted U test or t test; simple pooling or pseudopooling). As the four releases are selected only with regard to the behavior of the controls and not with

regard to related differences from experimentals, no unjustified feedback exists from the effect to be proved to the process of data selection. Thus, in the most conclusive experiments, the effect of air filtration is very drastic.

No inverted selection of releases, based on FFX data, can be made, since FFX data meeting the above preconditions do not exist. In the only four experiments in which the FFX bearings are non-randomly oriented toward home, they are as well or even better PCD-oriented (releases 3, 10, 12, and 17). Even in these rather inconclusive releases, CX is somewhat better than FFX (CX: $\bar{c}_H = +0.655$; FFX: $\bar{c}_H = +0.559$).

(2) *Effect of Local Anesthesia.* Although the overall directional difference between Xylocaine-treated controls (CX) and untreated control-controls (CC) is not statistically significant, it appears probable that the nonexistence of current olfactory information reduces, on average, the orientational performance of pigeons immediately after release, even if the birds could smell the environmental air in advance of the takeoff (see also increased vanishing times). If we extrapolate the CC/CX relation based on only 10 releases (p. 75) to the grand total, the mean homeward component of the controls would have to be increased from $+0.26$ (CX, Table 1) to about $+0.35$. This value would agree with many other data on pigeon homing from symmetrical sites, in particular in a mixed sample consisting of little and highly experienced birds (cf. Wallraff 1978, Table 1).

If we take the above-mentioned concomitant circumstances into account, it is not surprising that the effect of air filtration in the pooled data does not come out more clearly. It equals in magnitude, by the way, the effect of making pigeons definitely anosmic (cf. Wallraff 1980b, c). What differs from the anosmia data is not the difference between controls and experimentals, but the general level of homeward orientation in both of them. It remains unknown whether there exists a particular reason for this difference in the levels of performance. At the moment, we will not discuss speculative interpretations.

Attention should also be given to the first two releases (Fig. 3) in which not only 'positive' controls ventilated with undisturbed natural air were used, but also 'negative' controls ventilated with bottled air (BAX) that were definitely isolated from potential olfactory cues. The fact that the bearings of the charcoal-filter pigeons (FFX) not only differed from those of both sorts of 'positive' controls, but also perfectly coincided with those of the 'negative' controls, demonstrates that charcoal-filtered natural air

obviously does not contain more useful information than completely environment-independent air coming from a compressed-air cylinder.

Conclusions

Our experiments strongly suggest that pigeons can be deprived of stimuli necessary for homeward orientation not only by interruption of their olfactory input ducts (by means of nerve sections, plugging of nostrils, etc.; e.g., Papi et al. 1972, 1980; Wallraff 1980b), but also by elimination of related substances from the air they breath. Thus, the findings reported here fit perfectly with earlier results and all together leave little doubt that homing pigeons, when displaced to unknown areas, are able to extract information on their position in relation to home from substances dispersed in the atmosphere. As it is possible to remove the sources of information by adequate filtration of the environmental air, their material nature as physicochemical substances appears established.

The initial step toward an eventual identification of the substances involved is already done: The aerosol seems to be of no or of little importance in this context. Elimination of solid and liquid particles floating in the atmosphere, as far as it was achieved by the filter papers used in type FX, had no recognizable effect on homeward orientation. In contrast, filters made of activated charcoal had an effect, so we may conclude that substances used for navigation are dispersed in the atmosphere most probably in a molecular state. Related molecules, on the other hand, cannot be indefinitely small; otherwise, they would not have been retained by charcoal.

Since the pigeons themselves – their receptors, their CNS, their breathing – remained untreated during the critical phase of experimentation, it is hardly conceivable that any nonspecific general circumstances were responsible for the different orientation performances of control and experimental birds. Therefore, our findings add to earlier evidence indicating that olfaction acts as an integral constituent of the navigational system and not merely as some motivational agent (Papi et al. 1978b; Wallraff 1980b).

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