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Pigeon homing: Different effects of olfactory deprivation in different countries

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Summary. This study compares the orientation of untreated pigeons and pigeons subjected to olfactory deprivation at two lofts near Pisa, Italy, at a loft at Ithaca, New York, USA, and at a loft at Frankfurt a.M., FRG. The experimental birds were rendered anosmic by nasal plugs until Gingicain, a local anaesthetic, was applied shortly before release. The Italian and American control pigeons appeared to orient towards home equally well, while the control pigeons in Germany frequently preferred directions that deviated significantly from the home direction. The effect of olfactory deprivation was small in the USA and in Germany; it was significantly larger in Italy, indicating that Italian pigeons depend on olfactory information to a much greater extent. These findings suggest that there are important regional differences in the strategies and cues pigeons use to navigate. The varied roles of olfactory information, and the reasons for these differences are discussed.

Introduction

The orientation system of pigeons has been a field of intense research during the last three decades. Yet so far, the problem of how the birds, after passive displacement into unknown territory, determine their home direction, is still an open question. Several factors have been discussed; possibly, they interact to form a multimodal, redundant system (cf. Able 1980; Keeton 1980; Schmidt-Koenig 1987).

The olfactory hypothesis that suggests that odors are of great importance (for summary, see Papi 1982, 1986; Wallraff 1983) is one of the most controversial attempts to explain the pigeons' homing ability. Experiments in Italy by Papi and his coworkers and by Wallraff (for summary, see Papi 1976, 1982, 1986; Papi et al. 1984; Wallraff 1980a, in press) indicate that olfactory information plays the most important role. Attempts to replicate these findings, however, often yielded different results: in North America and in the Tübingen area, FRG, the observed effects were much smaller, in many cases negligible (for summary, see Keeton 1980; Schmidt-Koenig 1980, 1987).

Most authors, faced with this clear discrepancy, concluded that Italian pigeons rely to a much greater extent on olfactory information than pigeons in other parts of the world (e.g. Keeton and Brown's discussion in Papi et al. 1978; Keeton 1980; Schmidt-Koenig 1980; Walcott and Lednor 1983). Papi (1982) and Wallraff (1983), however, did not accept this interpretation: "My conclusion is that olfaction is a necessary component of pigeon navigation in all countries. The idea that Italian pigeons depend to a greater extent on olfactory cues ... was not confirmed by experimental results. The sole difference from country to country probably concerns the degree of homeward directedness and of homing success, with the Italian birds often performing better..." (Papi 1982, p. 154).

In view of this, and of methodological differences that might have added to the inconsistency of results, a comparative study using identical methods at various lofts seemed highly desirable. Here we report the first results of such a study comparing the normal orientation and the effect of olfactory deprivation in Italy, in upstate New York, USA, and at a loft in Frankfurt a.M., FRG.

Methods

1. Test sites and test birds

For the Italian part of the study, we used pigeons from two lofts in the Pisa area: Montefoscoli (43°33′ N, 10°45′ E) in the hilly region south of the Arno valley, and Arnino (43°39′N, 10°18′ E) at the mouth of the river Arno, 2 km from the Tyrrhenian coast. The Montefoscoli birds were 4–5 months old, and the Arnino birds about 3 months old at the time of the experiments. They had been given eight previous flock releases from ca. 6 km and ca. 18 km in the cardinal compass directions.

Twelve releases were performed in Italy, six with birds from each loft. All pigeons were new to the test sites; they had never been released before at that particular locality or in its immediate vicinity. Montefoscoli birds were released at four symmetrically distributed sites at ca. 40 km, and then at two sites ca. 20 km located opposite each other; vector addition of the home directions yields a resultant vector of 190°, with a length of 0.02. The length of this vector is a measure of the asymmetry of sites; it would be 0 if the sites were ideally symmetric and 1.0 if they were all in the same direction. The Arnino birds were first released at four sites ca. 20 km from their loft, with the sea in the west preventing ideal symmetry of the release sites used, and then at two sites 40 km north and 55 km south of the loft, with the home directions opposite each other. Altogether, the home directions of the sites used for Arnino birds result in a vector of 267°, 0.17. (For more detailed information, see W. Wiltschko et al. 1986.)

The American part of the study was performed with pigeons from the Cornell Pigeon Loft near Ithaca, New York (42°26′ N, 76°26′ W). The birds were about $2^1/_2$ months old when the tests began; they had been given 28 flock releases up to ca. 15 km in the cardinal compass directions. As release sites, we selected four symmetrically distributed locations at ca. 20 km, four at 32 km, and two sets of four at 60–65 km (Table 1); the 16 home directions, when added, yield a vector of 6°, 0.01. As in Italy, all birds were new to the test sites.

The German part of the study was performed with pigeons from the loft in Frankfurt a.M. (50°08′ N, 8°40′ E). The birds had been trained in 32 releases up to 20 km in the cardinal compass directions and were ca. 3 months old at the beginning of the test series. As test sites, we used five sets of four sites, two at 40 km and one each at 60 km, 80 km, and 120 km. Their exact positions are described by R. Wiltschko and Wiltschko (1985a); the resultant vector from the 20 home directions is 129°, 0.005. Here, too, the birds were unfamiliar with the sites.

2. *Experimental treatment*

The methods of depriving the test birds of olfactory information have been described in detail by W. Wiltschko et al. (1986), so we give here only a short summary, emphasizing that the procedure was in every way comparable in the three countries.

The experimental birds were transported to the release site with their nostrils plugged with cotton which was covered with vaseline mixed with citrus odor. The plugs were held in place by adhesive tape tightly covering the upper mandible. Immediately before release, the plugs were removed and the birds were made anosmic by spraying the local anesthetic Gingicain (Hoechst AG, active substance Tetracain) through the nostrils into the nasal cavities. After allowing at least 1 min for the drug to become effective, the pigeon was set free to fly.

In the USA and in FRG, the controls wore a band of adhesive tape leaving the nostrils open during displacement. Prior to being released, they were treated with a spray that contained only Frigen, the propelant, but not the active substance of Gingicain. Similar controls were also released in 4 of the 12 Italian tests; in the other 8 releases, we used completely untreated controls. Tests in which both types of controls were released together never suggested any differences between the two groups (W. Wiltschko et al. 1986, 1987a).

The pigeons were released singly, alternating anosmic birds and controls, and watched by one or two observers using 10 × 40 binoculars until they vanished from sight. Their vanishing bearings were recorded with a compass to the nearest 1° (Italy) or 5° (USA and FRG). The release was continued until the desired number of bearings for each group – 10 in Italy and at the farthest quartets of sites in the USA and in FRG, otherwise 12 – had been obtained. The vanishing intervals were recorded with a stop watch, and the homing times of the returnees were recorded by an observer at the home lofts.

3. *Data analysis and statistical treatment*

We used the methods of circular statistics described by Batschelet (1981)

3.1. Critical parameters and pooling the data. For each sample, the following parameters were determined: the direction α_m and lengths r_m of the mean vector, the deviation of the mean direction from the home direction, Δh, the homeward component h, with $h = r_m \cdot \cos \Delta h$, the median vanishing interval, the median homing speed (medians were calculated instead of means as these data are not normally distributed) and the return rate as a percentage.

For comparison and correlation purposes, we also calculated for the controls d_{home} which represents the distance of the tip of the control vector from the home point (the point in the home direction on the periphery of the circle with radius 1), as

$$d_{\text{home}} = \sqrt{(r_c \cdot \sin \Delta h_c)^2 + (1\text{-}r_c \cdot \cos \Delta h_c)^2}.$$

The Rayleigh test was used to test the mean vector for directional preference. In case of significance, Δh was compared with the 95% confidence interval to find out whether the mean direction differed significantly from the home direction. In this way we distinguish between three types of samples according to their initial orientation: (i) non-significant samples, (ii) significant samples whose mean is significantly different from the home direction thus showing a 'release site bias' (see Keeton 1973), and (iii) significant samples whose confidence interval included the home direction. In the latter case, the mean direction cannot be discriminated from the home direction, and for simplicity these releases are referred to as being 'homeward oriented'. We have to keep in mind, however, that the statistical methods at present only indicate when the mean direction is significantly different from home and not the opposite case; thus, not finding a bias does not necessarily mean that preferred direction and home direction are identical.

The mean vectors of the controls for each test series were pooled with respect to home. The center of distribution was determined and tested with the Hotelling test for directional preference. Likewise, the vectors were pooled and tested with respect to geographic north. Because of the symmetrical location of the release sites, the homeward tendencies cancel each other, and any tendency to fly in a 'preferred compass direction' should become evident. The mean vectors of the experimentals were analysed in the same fashion.

3.2. Testing for an effect of olfactory deprivation. To assess the effect of olfactory deprivation in the individual releases, the data of experimentals and controls were compared in the following way. To look for differences in preferred direction, the Watson-Williams test was used. If the vector lengths were below 0.65 and this test could not be applied, we used the Mardia test, which indicates differences in distribution without indicating whether they involve different directional preferences or different variances. To look for differences in scatter, the Mann-Whitney U test was applied to the deviations of the individual bearings from their mean direction. The vanishing intervals and the homing times were compared using the Mann-Whitney *U* test.

In a second-order statistic, we compared the distributions of the mean vectors of anosmic birds and controls using Mardia's two-sample test for bivariate samples. The parameters (r_m etc.) of the releases of each series were compared using the non-parametric Wilcoxon test for matched pairs of data in order to find what parameters were significantly affected in each country.

3.3. Comparison between the three countries. To find out whether the homeward directedness and homing performance differed between the three countries, parameters of the control samples were compared using the Mann-Whitney *U* test.

In order to compare the effect of olfactory treatment in the three countries, we needed a measure that reflected changes in direction as well as changes in variances. So we calculated d_c, the distance between the tips of the mean vectors of experimentals and controls, as

$$d_c=\sqrt{(r_c\cdot\sin\alpha_c-r_E\cdot\sin\alpha_E)^2+(r_c\cdot\cos\alpha_c-r_E\cdot\cos\alpha_E)^2}.$$

Thus, to compare the effect on initial orientation, the values of d_c obtained in Italy, the USA and FRG were tested against each other using the Mann-Whitney *U* test. Likewise, we compared ΔC, the angular differences between experimentals and controls, and the differences induced by the treatment in the other parameters.

Results

The results obtained in Italy have been published by W. Wiltschko et al. (1986); those obtained in Germany by W. Wiltschko et al. (1987a). Both these papers contain detailed lists giving the original data for each individual release. A corresponding list of the data obtained in New York, USA, is given in Table 1. In the following sections, we will present the data pooled in a way that facilitates comparison.

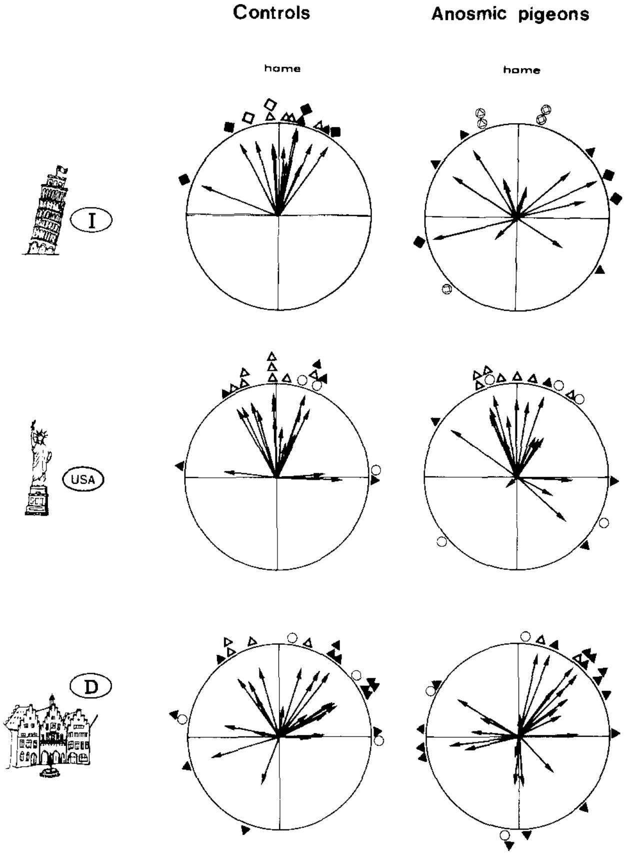

Fig. 1. Orientation of controls and anosmic pigeons near Pisa, Italy (upper diagrams; *triangles*, Montefoscoli birds; *diamonds*, Arnino birds), in Ithaca, New York, USA (*middle diagrams*) and in Frankfurt a.M., Germany, pooled with respect to home. The *arrows* represent the mean vectors of single releases; the *symbols* at the periphery of the circle mark the mean direction and indicate type of release: *open circles*, non-significant; *open triangles and diamonds*, 'homeward oriented' *solid triangles and diamonds*, significant bias. For numerical values, see Table 2

1. The orientation behavior of controls

All three series are significant ($P<0.01$ at least, Hotelling test) when pooled with respect to home (Fig. 1, Table 2). Yet some striking differences are evident (Table 3). The proportion of 'homeward oriented' samples (in the sense that their mean direction is not significantly different from the home direction) in FRG (20%) is lower than in Italy or the USA, where 50% of the samples are 'homeward oriented'. In FRG, 'release site biases' are typical, i.e. in 60% of the releases the birds prefer a direction that is significantly different from the home direction. Not only the percentage, but also the size of the biases is greater: the median value in FRG, 62°, is twice as large as the corresponding values from Italy and New York, 30° and 31° respectively ($P<0.01$, Mann-Whitney *U* test). Hence parameters like the distance of the vector tip from the home point, d_{home}, and the homeward component *h* in the Germany data differ significantly from those obtained in Italy and the USA, while those of the latter two series are not different from each other (Table 3).

Table 3 also compares the homing performance (here, only the 12 German releases up to 60 km are considered, see Schmidt-Koenig 1970). The differences are less impressive. The fastest homing speed was recorded in the USA; it was slightly slower in Italy. The German pigeons have the lowest median homing speed; it differs significantly from that of the American, but not from that of the Italian birds. This particular group of German birds, though, appeared to be especially slow compared to German birds in other series (see R. Wiltschko and Wiltschko 1985a). The return rate is equal in all three countries.

Table 1. Data from the American releases

	Date	Home direction		Pigeons released (bearings)	Mean vector		Δh	ΔC	Med. van. int.	Homed day 1 (later)	Median homing time
		distance	Tr.		α_m	r_m					
R_1	17. 7. 85	236°	C	15 (12)	234°	0.82***	− 2°		5:02	12 (3)	2:11^a
		20.4 km	AO	15 (12)	220°	0.43	−16°	−14°**^{s}	4:50	13 (2)	1:17^a
	17. 7. 85	288°	C	13 (12)	309°	0.75***	−21°		5:30	13	0:46
		19.1 km	AO	14 (12)	297°	0.82***	+ 9°	−12°	6:43	14	0:56
	18. 7. 85	47°	C	15 (12)	16°	0.85***	−31°*		6:39	15	0:32
		17.5 km	AO	13 (12)	23°	0.71**	−24°	+ 7°	6:02	13	0:29
	16. 7. 85	103°	C	13 (12)	195°	0.71**	−92°*		6:16	13	0:55
		22.9 km	AO	15 (12)	196°	0.65**	+93°*	+ 1°	7:21	15	0:51
R_2	23. 7. 85	163°	C	13 (12)	161°	0.64**	− 2°		4:56	13	0:42
		32.3 km	AO	12 (12)	203°	0.49	+40°	+42°	4:15	12	1:04
	21. 7. 85	269°	C	12 (12)	290°	0.95***	−21°*		3:33	12	0:49
		33.5 km	AO	14 (12)	287°	0.93***	+18°*	− 3°	4:10	14	0:57
	23. 7. 85	349°	C	14 (12)	332°	0.75***	−17°		5:30	14	1:40^a
		30.9 km	AO	13 (12)	332°	0.93***	−17°	0°	5:48	12 (1)	1:56^a
	22. 7. 85	91°	C	19 (12)	107°	0.39	+16°		5:32	18 (−)	0:56
		33.9 km	AO	15 (12)	320°	0.17	−131°	−147°	5:22	15	1:16**
R_3	28. 7. 85	170°	C	14 (12)	197°	0.81***	+27°		4:51	14	1:44
		66.2 km	AO	15 (12)	204°	0.53*	+34°	+ 7°	5:15	11 (1)	2:17
	30. 7. 85	254°	C	15 (12)	279°	0.47	+25°		3:29	14 (−)	2:23
		73.5 km	AO	15 (12)	279°	0.49	+25°	0°	5:05***	8 (2)	5:29**
	29. 7. 85	348°	C	13 (12)	346°	0.90***	− 2°		5:15	12 (1)	1:30
		65.5 km	AO	12 (12)	338°	0.67**	−10°	− 8°	5:51	8 (3)	4:35**
	27. 7. 85	72°	C	16 (12)	53°	0.88***	−19°		3:57	15 (1)	1:59
		70.2 km	AO	14 (12)	49°	0.81***	−23°	− 4°	4:18	6 (5)	8:00***
R_4	10. 8. 85	223°	C	10 (10)	309°	0.54	+86°		5:11	8 (1)	1:50
		62.3 km	AO	12 (10)	356°	0.73**	+133°*	+47°	6:10	8 (3)	7:22**
	12. 8. 85	281°	C	10 (10)	288°	0.56*	+ 7°		9:00	9 (1)	2:16
		62.3 km	AO	13 (10)	281°	0.83***	0°	− 7°	9:36	10 (−)	4:56**
	9. 8. 85	46°	C	12 (10)	20°	0.87***	−26°		3:46	12	2:13
		56.6 km	AO	11 (10)	350°	0.87***	−56°*	−30°	6:30*	7 (2)	3:08*
	8. 8. 85	102°	C	11 (10)	19°	0.59*	−83°*		6:08	11	2:08
		66.3 km	AO	12 (10)	344°	0.46	−118°	+35°	5:16	11 (1)	2:00

Tr. = treatment; C = control; AO = anosmic pigeons; α_m, r_m = direction and lengths of the mean vector; asterisks at r_m indicate significance by the Rayleigh test; Δh = deviation of the mean direction from the home direction; asterisks indicate that the mean is significantly different from the home direction (95% confidence interval), i.e. the sample shows a 'bias'; ΔC = angular difference between anosmic pigeons and controls; the asterisks and *s* indicate a significant difference in scatter (Mann-Whitney *U* test); 'Med. van. int.' = median vanishing interval in min:s. The median homing times are given in h:min, 'a' indicates that the release was performed in the afternoon which seems to result in prolonged homing times; asterisks indicate significant differences between anosmic pigeons and controls (Mann-Whitney *U* test). Significance levels: * $P<0.05$, ** $P<0.01$, *** $P<0.001$

Any attempt to compare the 'homeward directedness' of the three series seems problematic because it is not clear by what criteria it is to be assessed. Considering the portion of homeward oriented samples and parameters like d_{home}, Δh and h, the Italian and American pigeons appear equally well oriented: Italy and the USA have the same high percentage of homeward oriented samples; release site biases, when they occur, are mostly rather small. The orientation in FRG, on the other hand, with numerous and large release site biases, appears to result in presumably less direct, but equally successful, homing flights.

Altogether, our data do not support the assumption that Italian birds generally perform better than pigeons in other regions; the Italian birds used in this study, at least, were not better oriented and did not home faster than the American pigeons from the Cornell loft at Ithaca, New York, USA.

Finally, the initial orientation of the pigeons

Table 2. Mean vectors of Italian, American, and German pigeons

	Tr.	N	Orientation pooled with respect to					
			Home		Significant difference	North		Significant difference
			α_h	r_h		α_N	r_N	
Italy, all releases	C	12	0°	0.72***	***			
	AO	12	3°	0.25				
Montefoscoli loft	C	6	12°	0.74**	**	153°	0.07	–
	AO	6	−11°	0.37		96°	0.43	
Arnino loft	C	6	−11°	0.73**	**	240°	0.48	–
	AO	6	36°	0.16		235°	0.45	
Ithaca, New York, USA	C	16	5°	0.58***	–	321°	0.24	–
	AO	16	2°	0.42**		314°	0.34*	
Frankfurt a.M., FRG	C	20	19°	0.36**	–	295°	0.20	–
	AO	20	30°	0.24		269°	0.13	

Tr = treatment, C = control, AO = anosmic pigeons. α_h, r_h and α_N, r_N indicate the center of distribution of the mean vectors pooled with respect to home and the North respectively. Asterisks at r_h and r_N indicate that the series is significantly different from random by the Hotelling tests; asterisks in the column 'significant difference' indicate differences between anosmic pigeons and controls by Mardia's two-sample test for bivariate samples. Significance levels as in Table 1

Table 3. Orientation behavior of control pigeons. Parameters differing significantly from those in the other two regions are given in bold print. Significant differences by the Mann-Whitney U test, significance levels as in Table 1

	Montefoscoli, Arnino, Italy (I)	Ithaca, NY, USA	Frankfurt a.M., FRG (D)	Comparison: significant difference		
				I/USA	I/D	USA/D
Number of						
releases	12	16	20			
sign. mean vectors	12 = 100%	13 = 81%	16 = 80%			
"homeward oriented" samples	6 = 50%	8 = 50%	4 = 20%			
samples with a sign. bias	6 = 50%	5 = 31%	12 = 60%			
Median size of bias:	30°	31°	**62°**	–	**	**
Median value of						
distance d_{home}	0.37	0.44	**0.64**	–	**	*
deviation from home Δh	16°	21°	**56°**	–	***	**
vector length r_m	**0.86**	0.75	0.69	*	*	–
home component h	+0.75	+0.71	**+0.36**	–	***	**
vanishing interval (s)	256	**313**	270	*	–	*
homing speed (km/h)	29.9	32.0	22.3	–	–	**
return rate	100%	100%	97%	–	–	–

was tested for a 'preferred compass direction', a directional tendency Wallraff (1978) believes to exist in pigeons of all lofts. No such tendency emerged in any of the countries (Table 2). The relatively long vector of the Arnino pigeons in Italy appears to be caused by the strong asymmetry of the test sites used.

2. *The effect of olfactory deprivation*

The mean vectors of the anosmic pigeons (Fig. 1, right) and their centers of distribution (Table 2) clearly indicate that the effect of anosmia in Italy is greater than in the other two regions, because only in Italy did olfactory deprivation induce a significant change in the distribution of vectors ($P < 0.001$, all 12 releases; $P < 0.01$, Arnino and Montefoscoli loft separately, Mardia's two-sample test for bivariate samples).

Figure 2 shows the vectors of the anosmic samples pooled with respect to the mean of the controls; significant changes in *direction* are marked by asterisks. In Italy, the initial orientation of anosmic pigeons and controls is significantly different in 10 of the 12 releases. Two distinct types of effect can be distinguished (see W. Wiltschko et al. 1986): (i) pronounced increases in scatter leading to disorientation, and (ii) pronounced changes in

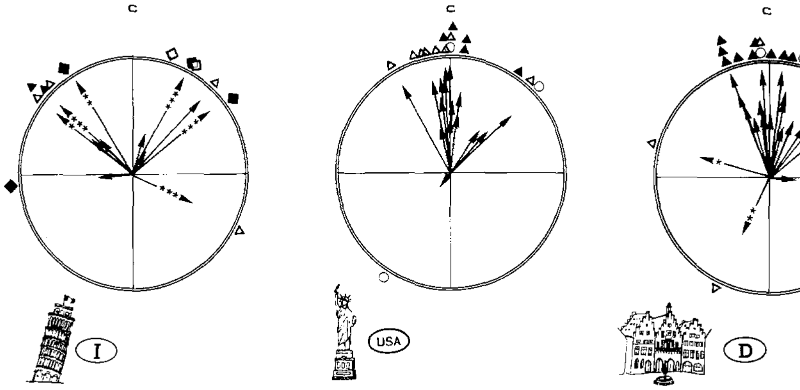

Fig. 2. Vectors of the anosmic pigeons plotted relative to the mean of the controls in the same release to illustrate the induced differences. The symbols at the periphery of the circle mark the mean directions and indicate to which type the respective *control* sample belongs (symbols as in Fig. 1). Vectors whose direction deviates significantly from the control direction are marked with *asterisks*. * $P<0.05$, ** $P<0.01$, *** $P<0.001$. *Left:* data from Italy: $n=12$, $\alpha=-6°$, $r=0.39$, $P<0.05$. *Middle:* data from USA: $n=16$, $\alpha=+1°$, $r=0.60$, $P<0.01$. *Right:* data from Germany, $n=20$, $\alpha=+6°$, $r=0.52$, $P<0.001$ (Hotelling test)

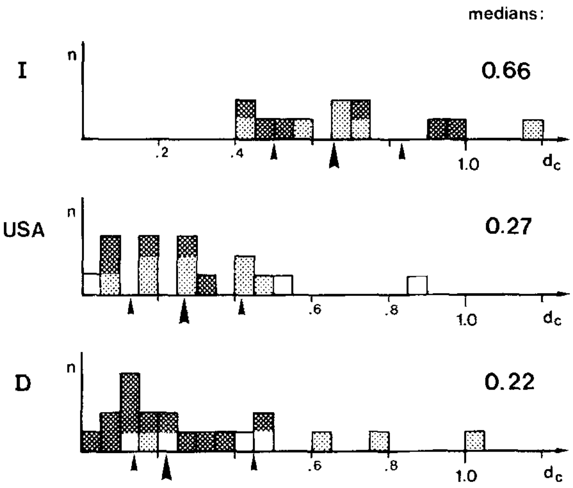

Fig. 3. Frequency distribution of d_c, the distance between the tips of the mean vectors of controls and anosmic pigeons. The *large arrows* mark the median value given numerically at the right side, *smaller arrows* mark the 1st and 3rd quartiles. The *shading* indicates to which type of the control sample belongs: *open*, non-significant; *light*, 'homeward oriented', and *dark*, significant 'bias'

direction with little scatter (Fig. 2, left). In the USA, a significant effect on initial orientation is found only once; it is an increase in scatter. Generally, the overall effect seems to be a slight change in direction together with a slight increase in scatter; some releases appear to be totally unaffected. In FRG, the effect appears to be rather inconsistent (comp. W. Wiltschko et al. 1987a). Most releases were more or less unaffected; four times we found a significant difference in scatter that did not show a consistent trend. Yet in 3 of the 20 releases a significant change in direction led to a marked increase in the deviation from home (Figs. 1 and 2, right).

To allow an assessment of the induced differences in initial orientation, Fig. 3 gives the frequency distribution of d_c, the distance between the tips of the mean vectors of experimentals and controls. At 0.66, d_c in Italy is significantly larger than in the USA and FRG, 0.27 and 0.22 respectively ($P<0.001$, Mann-Whitney U test).

Table 4 shows how olfactory deprivation affected the various parameters by giving the median values and the distribution of the induced differences. In Italy, all parameters except the return rate were significantly affected; the anosmic pigeons had shorter vector lengths and large deviations from the controls, which resulted in shorter homeward components, longer vanishing intervals, and slower homing speeds. Numerically, the differences were markedly larger than in the USA, where four parameters were affected, and in FRG, where only two were affected. If we compare the changes in initial orientation and homing performance (Table 4, last columns) we do not find a significant difference between the USA and FRG. In Italy, however, olfactory deprivation was more effective than in the two other regions, which leads to the conclusion that Italian birds rely much more on olfactory information.

To find out whether the size of the effect is greater when the birds are better homeward oriented, we compared differences in d_c between tests with 'homeward oriented' controls and tests in which the controls showed biases. In Italy, they were equal (median values 0.66 and 0.65); in the USA d_c in samples with biases was slightly smaller (median 0.17 compared to 0.27). In FRG, this trend was even more pronounced: median d_c is 0.17 when the controls show a bias, but 0.70 when they are 'homeward oriented' ($P<0.05$, Mann-

Table 4. The effect of olfactory deprivation. Asterisks at the medians indicate that the parameter in question was significantly affected (Wilcoxon test, matched pairs of data). The distribution of the induced differences is indicated: how often the change was to 'better' orientation in the sense of smaller deviation from home, longer mean vectors and homeward components, shorter vanishing interval, faster homing speed, and higher return rate of the controls (under 'C'), of the anosmic pigeons (under 'AO') or no change at all (under '0'). Differences in the amount of change were compared with the Mann-Whitney U test; significance levels as in Table 1. Data differing significantly from the other two regions are given in bold print

	Lofts in Italy (I)				Ithaca, NY, USA				Frankfurt, FRG (D)				Comparison: Significant difference		
	Median	Distrib.			Median	Distrib.			Median	Distrib.			I/USA	I/D	USA/D
		C	0	AO		C	0	AO		C	0	AO			
Median value of distance d_C	**0.66**				0.27				0.22				***	***	–
Changes induced in															
direction	**46°****	9	0	3	8°*	9	1	6	18°*	13	0	7	**	**	–
vector length r_m	−0.16*	8	0	4	−0.07	10	2	4	−0.02	10	2	8	–	*	–
home component h	−**0.36*****	12	0	0	−0.16*	11	1	4	−0.09	12	0	8	**	**	–
vanishing interval (s)	+24*	8	0	4	+30*	11	0	5	+11	12	1	7	–	–	–
homing speed (km/h)	−**22.5****	11	0	1	−8.3**	12	0	4	−8.3**	15	1	4	*	*	–
return rate	−4%	6	4	2	0%	6	9	1	0%	9	5	6	–	–	–

Whitney U test, Fig. 3). Correlation of d_c with d_{home} of the controls, however, was never significant (coefficients of correlation: −0.34, +0.23 and −0.31, respectively). Thus the assumption that the effect of olfactory deprivation is correlated with the degree of homeward directedness is not generally true; such a tendency is suggested, if at all, only for the German data.

Last we examine whether the anosmic pigeons show a tendency to fly in a 'preferred compass direction', as Papi (1982) and Wallraff (1982, 1983) have reported (data in Table 2, right). The only group that shows a significant ($P < 0.05$, Hotelling test) tendency to fly in a particular geographic direction are the anosmic pigeons in the USA that, ironically, at the same time show a more pronounced tendency to fly toward home ($P < 0.01$). Nowhere did olfactory deprivation significantly affect the data when pooled with respect to north ($P \gg 0.05$, Mardia's two sample test). Thus the behavior of the anosmic pigeons cannot be explained by a preferred compass direction.

Discussion

There were slight differences in age and experience of the test birds. The former appear irrelevant since all birds were trained, experienced pigeons (see R. Wiltschko and Wiltschko 1985b). The fact that the Italian pigeons had far fewer training releases than either the American or the German birds might be more important. Yet their treatment was very similar to the normal procedure of treating pigeons at Papi's loft, so that this might help to make our data comparable with the results obtained by Papi and his coworkers in their numerous studies (cf. Papi 1982, 1986).

In contrast to many other studies on olfactory navigation, we used a reversible method which made pigeons only temporarily anosmic. We do not know how great the degree of anosmia really was, but as the procedure and the circumstances of its application were the same, it was equal in the three countries. The effect, however, varied greatly. As different sensory thresholds appear highly improbable, we believe that differences in the evaluation and status of olfactory information explain these differences in effect.

1. The different roles of olfactory information

Our data, showing that the pigeons in the USA are equally well homeward oriented, but far less affected by olfactory deprivation than the Italian birds, do not support Papi's (1982) and Wallraff's (1983) hypothesis that odors are the only source of information producing good orientation. Instead they suggest that there are important regional differences in the strategies and cues pigeons use.

What are the orientation processes in the three countries as shown in our data? The deviation from the home direction might indirectly tell us something of the strategy used. As we pointed out in earlier papers (see W. Wiltschko and R. Wiltschko 1982, for a detailed discussion), release site biases might indicate the use of local 'map' information as opposed to information about the direction of displacement obtained during the outward journey; the biases are assumed to stem from irregularities in the distribution of the local 'map' factors. In case of the homeward oriented samples, however, the strategy is less clear, as these samples might just as well arise from the use of outward journey information as from the use of local map information which indicates the home direction correctly. Long vectors mean good agreement between the birds of one group and might indicate that the navigational information is clear and unequivocal; short vanishing intervals suggest that it is easily obtained.

In view of this, we might speculate on the factors and strategies used, especially with regard to the role of olfactory orientation. In Italy, the navigational information appears clear and easily obtained, the small biases suggesting a fairly regular, predictable distribution of the map factors. Olfactory deprivation generally had a large effect, independent of whether the pigeons were homeward oriented or showed a bias. This would indicate olfactory map factors (see Papi et al. 1972); they and possible olfactory information obtained during the outward journey (see Baldaccini et al. 1982) appear to be predominantly used by the Italian birds. Here the Italian part of our study is in excellent agreement with the results of former studies by Papi and his colleagues in Italy (for review, see Papi 1976, 1982, 1986; Papi et al. 1984).

Yet interestingly, even in Italy, disorientation, which might be expected if a crucial factor was removed, was observed in only five of the tests at 20 km distance. In the other seven releases (six of them at 40 km) the vectors of the anosmic pigeons were fairly long, but the birds showed a large deviation from the direction chosen by the controls as well as from the home direction (see W. Wiltschko et al. 1986). In these cases, the experimental birds' behavior was presumably controlled by non-olfactory factors. A tendency to fly in a 'preferred compass direction' was not indicated by our data. Possibly the birds changed to normally unused alternative cues that were available only at greater distances and indicated a 'false' home direction.

In the USA, the shorter vectors and the longer vanishing intervals of the controls suggest that the navigational information is less easily obtained than in Italy; homing, however, is fastest there. The high percentage of 'homeward oriented' samples and the small biases indicate that the map factors show only small deviations from a regular course.

These map factors, however, appear to be largely non-olfactory. The small effects of the treatment suggest that odors play a role only as a redundant factor which, if unavailable, is hardly missed. Here our findings are similar to earlier results of Keeton and his collegues who studied the effects of various olfactory treatments at the same loft in Ithaca, New York (Keeton 1974; Keeton and Brown 1976; Keeton et al. 1977; Papi et al. 1978; Hermayer and Keeton 1979; cf. Keeton 1980).

In FRG, pigeons make their decision as fast as in Italy, but they do not agree as well, which might indicate individual differences between birds in the interpretation of navigational information. The numerous and large biases suggest that the birds normally used local map factors. These factors appear to be rather irregularly distributed, and they are clearly non-olfactory, as anosmic birds always oriented like their controls when these showed a bias. Yet in three releases where the controls were 'homeward oriented', possibly using information obtained during the outward journey, we found large deviations that were comparable to those observed in Italy (Fig. 3, below; see W. Wiltschko et al. 1987a). This seems to suggest that olfactory information provides information during displacement, which, however, is used only occasionally at some sites.

Altogether, our data on initial orientation indicate a rather varied role of olfactory information. It is a highly important factor in a 'map' as well as during the outward journey in Italy, it seems to be a frequently used factor of minor importance in New York, USA, and appears to be only occasionally used during the outward journey by pigeons in Frankfurt, FRG.

The reduction of homing speed is the most consistent effect of olfactory deprivation. The reasons for this are not easy to understand, because its occurrence is not correlated with the amount of change in initial orientation (see W. Wiltschko et al. 1987a; Table 1). In Italy, this effect is also markedly greater than in the USA and in FRG where it is not always observed.

2. *Possible reasons for regional differences*

Olfactory information is by no means the only factor where regional differences have been reported. There are also differences in navigational strategy. While pigeons in FRG normally cease to use outward-journey information when they have become older and more experienced and are no longer affected by manipulations during displacement (Wallraff 1980b; R. Wiltschko and Wiltschko 1985b), such manipulations – magnetic as well as olfactory – continue to affect the orientation behavior of experienced pigeons in Italy (e.g. Wallraff et al. 1980; Baldaccini et al. 1982; Benvenuti et al. 1982; Papi et al. 1984).

Likewise, the role of magnetic cues is not equal in all regions. Walcott (1986, in press), for example, reported that pigeons from a loft in Massachusetts were disoriented at a strong magnetic anomaly, while pigeons from the loft in Ithaca, New York, were not. Treatment with alternating magnetic fields prior to the release that greatly affected the initial orientation in Italy (Papi et al. 1983) was found to have only a negligible effect or none at all in American and Southern German pigeons (Benvenuti, in litt.; Papi et al. 1987).

This leads to the question of why these differences occur. Three possible causes must be considered: (1) genetic differences, (2) regional differences in the availability and suitability of potential orientation cues and (3) differences induced by early experience, i.e. by the various techniques of raising and training pigeons.

Studies exchanging eggs and young birds and comparing the orientation of pigeons of different origin have not so far indicated any great genetic differences (Kiepenheuer et al. 1979; Foa et al. 1984). Differences in the type of navigational factors used, however, have not been systematically studied.

Regional differences in the availability and the regularity of potential navigational factors must be expected to be important. As experienced pigeons make use of learned orientation mechanisms and acquire the knowledge of 'map' factors by experience (Wallraff 1974; Papi 1976; W. Wiltschko and Wiltschko 1978), their 'maps' need not be identical in all parts of the world. Considering the variety of their sensory input (see e.g. Kreithen 1978), we might expect pigeons to select from the available factors those which provide the most suitable and most reliable information in their home region.

The various ways of raising and maintaining pigeons might also modify the orientation system, as they might increase the birds' responsiveness to certain factors and induce a lasting preference. Preliminary tests suggest indeed that early experience exerts a crucial influence on the development of the orientation system and the selection of navigational cues (W. Wiltschko et al. 1987b).

3. *Conclusion*

Any comparison of orientation and homing performance must remain tentative as long as it is based only on relatively small samples, like this one. The orientation behavior may vary greatly between sites (see Grüter et al. 1982; R. Wiltschko and Wiltschko 1985c), and it is not clear how well the behavior at a given release site reflects the general picture in that region. Yet the data that are available clearly indicate a fundamental difference in the role of olfactory information at the three lofts.

In view of this, we can no longer expect the navigation system of all pigeons to be identical. A learned system depending on individual experience favors flexibility; it can easily be modified according to the local situation in the pigeon's home region. The navigational system can thus be perfectly adapted to the bird's individual needs and make optimal use of all available cues.

For the experimentor, however, it means that there is no *universal* answer to the question of how pigeons navigate. We will only be able to describe how the orientation system will develop in a certain situation, and we will have to try to learn more about these developmental processes and the factors affecting them.

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