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ARE AMERICAN HOMING PIGEONS GENETICALLY DIFFERENT FROM ITALIAN ONES?

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Summary

The variable results of experiments on anosmic Cornell pigeons, compared with the consistent effect of olfactory deprivation observed in pigeons in Italy, has sometimes been explained by supposing that pigeons in the two countries belong to different genetic strains.

This hypothesis was tested by performing experiments with the progeny of Cornell pigeons transported to Italy as eggs and placed in the nests of Italian foster parents. The homing behaviour of the American birds raised in Italy was compared with that of Italian pigeons hatched and raised in the same loft.

The results of the experiments show that both the American and the Italian pigeons are severely affected by olfactory deprivation in releases at unfamiliar sites, in contrast to the homeward-oriented control groups of both strains. We conclude that there is no major genetic difference in homing mechanism between Cornell and Italian pigeons.

The results of experiments performed in Italy and in the USA have shown that different rearing and training procedures do not induce the development of maps based on different cues. Therefore, the reported differences between the results obtained in the USA and those obtained in Italy may be due to regional differences in the availability of navigational cues.

Introduction

The homing mechanism of pigeons has been extensively investigated in the last 20 years. When the interpretations of various researchers are considered, the present status of our knowledge can be summarized as follows. (1) Olfactory cues play an irreplaceable role for Italian pigeons released at unfamiliar locations (references in Papi, 1986). (2) The Italian results have been confirmed by a long series of experiments performed by Wallraff (references in Wallraff, 1986*a*) with

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pigeons housed in two Bavarian (W. Germany) lofts. (3) According to Wiltschko *et al.* (1987*a*), the total dependence of Frankfurt (W. Germany) birds on olfactory information is revealed when the birds are raised in conditions of limited training experience and optimal exposure to wind-borne cues. In addition, the pigeons may also use non-olfactory information whose nature has not been identified. (4) Cornell (USA) pigeons have produced variable results, ranging from a negligible effect of olfactory deprivation found by Wiltschko *et al.* (1987*b*) to a significant impairment of homing behaviour reported by Benvenuti and Brown (1989) (see also Papi *et al.* 1978).

Hypotheses explaining the variability of results obtained in different laboratories include the possible effects of different rearing and training procedures, the possible effect of using different genetic stocks of birds, and the possibility that regional differences may have an influence on the navigational cues available to pigeons (see Benvenuti *et al.* 1989).

Recent Cornell experiments performed by Benvenuti and Brown (1989) tested the rearing and training hypothesis by comparing the behaviour of two groups of American anosmic birds, one raised in normal Cornell style, which included some pre-test training, and the other in the 'Italian style' with no pre-test training but which offers pigeons more exposure to environmental factors around the loft. Regardless of their rearing and training, all the anosmic birds were disoriented and had poorer homing than their controls.

In this paper we report the results of a series of tests that compare the homing behaviour of Italian pigeons with that of Cornell pigeons raised in Italy.

Materials and methods

The pigeons

The American pigeons used in our experiments were derived from 90 Cornell pigeon eggs that were transported to the Pisa loft in 1987. The hand-carried eggs, cushioned in layers of foam rubber inside a lady's cosmetic case, were transported at ambient temperature by plane and car from Ithaca (NY) to Pisa (Italy). Possible embryonic damage from exposure to X-rays at airports was avoided by having the eggs visually, instead of electronically, inspected. The laying date was marked on each egg and, upon arrival in Pisa (21 h after removal from nests), the eggs were placed under Italian foster parents which had produced eggs at comparable dates. The age of the Cornell eggs ranged from 3 to 17 days. A few of the eggs were rejected by the foster parents and some were infertile. Of the 84 remaining fertile eggs, 71 (84.5 %) hatched successfully. The American fledglings were kept as prisoners in a separate pen and, at the appropriate time, freely bred amongst themselves. The following year the original birds along with some of their early descendents became the progenitors of the 86 'American' birds used in our experiments reported in this paper. The 84 Italian pigeons used in our tests were produced at the same field station by a breeding colony of Italian pigeons belonging to the stock of birds which we normally use in our experiments.

Pre-test experience and test releases

At weaning time, American and Italian fledglings were removed from parental pens, and the groups were integrated in the same loft. This international group enjoyed spontaneous exercise flights and was never subjected to training before it was tested. Tests were conducted when the birds were 3.5–4.5 months old.

Control and experimental birds were transported to the release sites in the same van and were exposed to natural (but not direct) sunlight. Both Italian and American control birds travelled in normal carrying crates without any manipulation. The experimental groups were transported in airtight aluminium containers provided with a transport window and ventilated with air forced through charcoal filters (for references on this method of olfactory deprivation, see Benvenuti and Wallraff, 1985); additionally, the experimentals also had their nostrils plugged with cotton wool and adhesive tape, depriving them of significant olfactory cues *en route*. A few minutes (10 min on average) before an experimental pigeon was released, it was taken from the container, its plugs were removed, and xylocain was sprayed into each nostril. This treatment results in temporary impairment, 60–240 min in duration, of olfactory perception (see Wallraff, 1988).

Test releases were performed at two sites 44 km north and 40 km south of home in good weather conditions (no wind or light wind and sun clearly visible). The birds were released singly, alternating the four treatments: American and Italian unmanipulated control birds (AC and IC, respectively), and American and Italian anosmic experimental birds (AE and IE, respectively). Data were recorded using the standard techniques and procedures (see references in Benvenuti and Wallraff, 1985).

Statistical methods

The distribution of the vanishing bearings of each group of birds in single experiments and in pooled data was tested for randomness using the Rayleigh and the V-test. Comparisons between treatments were made using the Watson U^2-test (see references on the analysis of circular data in Batschelet, 1981). The Mann–Whitney U-test (Siegel, 1956) was used to test for differences between treatments in vanishing and homing intervals (pigeons that homed together were excluded if they belonged to different treatments).

Results

Vanishing time

The flight behaviour of the tossed birds was quite normal and only 12 of 170 birds landed (1 IC, 4 IE, 1 AC, 6 AE). Also the vanishing times were rather short (median times: IC: 2 min 50 s; IE: 3 min 27 s; AC: 3 min 13 s; AE: 3 min 10 s), a significant difference resulting only between IC and IE (pooled data, Mann–Whitney U-test: $P<0.05$).

Initial orientation

Our results (in Table 1) show that the unmanipulated controls, both IC and AC, had better homeward orientation than the respective anosmic experimentals (IE and AE) in most experiments, the only exception being AC *vs* AE in the third test release. This difference between control groups and the respective experimental groups, in single experiments, is significant in three out of eight comparisons (IC *vs* IE in the first and second experiments: Watson U^2-test, $P<0.001$ and $P<0.05$, respectively; AC *vs* AE in the fourth experiment: $P<0.05$). A clearer picture can be obtained by pooling the data with respect to home set to north (Fig. 1 and Table 2). The bearing distributions of both control groups (IC and AC) are homeward-oriented, whereas those of the anosmic experimentals are not different from random. The Watson U^2-test reveals a significant difference between IC and IE ($P<0.001$) and between AC and AE ($P<0.01$). A significant difference is also

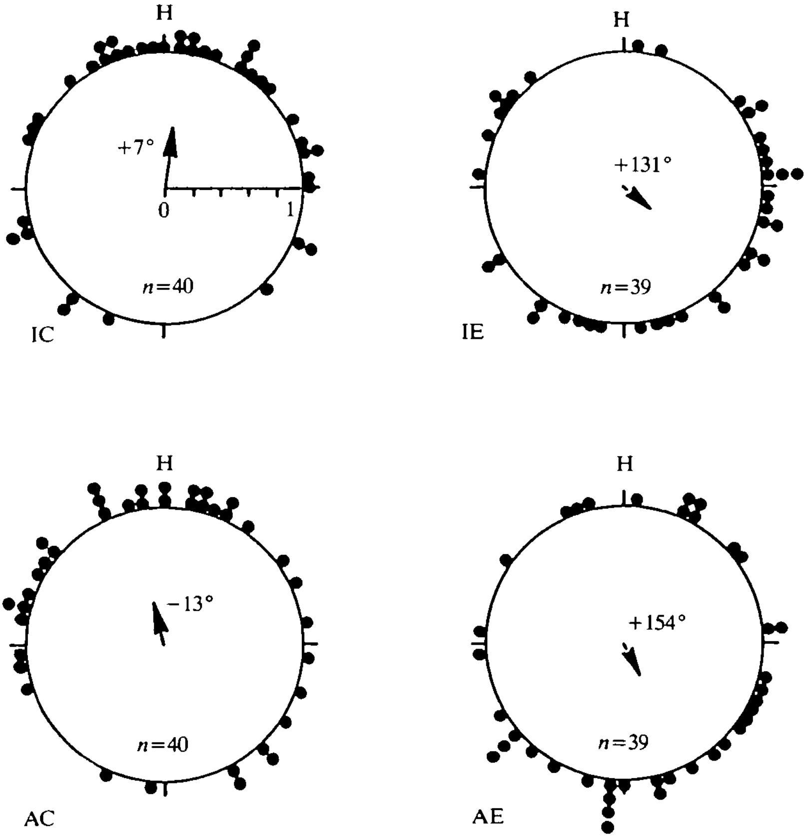

Fig. 1. Vanishing bearings in the experimental series. Four tests have been pooled with the home (H) direction set to north. The symbols in the diagrams represent the vanishing bearings of the pigeons. The arrows within the diagrams are the mean vectors, whose length can be read using the scale in the top left-hand diagram; maximum value=1. IC and AC, Italian and American controls; IE and AE, Italian and American anosmic experimentals.

Table 1. *Results of the experiments*

Date	Home direction and distance (km)	Treatment	*n*(*N*)	**a**	**r**	Dh	Hc	Homing success
1 23 June 1988	161°	IC	10(10)	170°	0.78***	+11°	+0.77***	6–0–1†
	40.4	IE	9(12)	232°	0.34	+71°	+0.11	0–5–6†
		AC	10(10)	187°	0.71**	+26°	+0.63**	6–3–1
		AE	9(12)	258°	0.58*	+97°	−0.07	3–5–3†
2 28 June 1988	334°	IC	10(11)	297°	0.52	−37°	+0.41*	6–3–2
	44.0	IE	10(10)	156°	0.50	−178°	−0.50	1–7–2
		AC	10(10)	288°	0.69**	−46°	+0.48*	5–5–0
		AE	10(11)	168°	0.49	−166°	−0.47	1–6–4
3 5 September 1988	161°	IC	10(10)	233°	0.88***	+72°	+0.27	4–2–3†
	40.4	IE	10(10)	246°	0.80***	+85°	+0.07	3–1–5†
		AC	10(11)	271°	0.56*	+110°	−0.19	5–2–4
		AE	10(12)	237°	0.51	+76°	+0.12	2–2–8
4 6 September 1988	334°	IC	10(10)	281°	0.55*	−53°	+0.34	4–3–3
	44.0	IE	10(11)	202°	0.45	−132°	−0.30	1–4–6
		AC	10(10)	274°	0.75**	−60°	+0.37*	2–3–5
		AE	10(10)	200°	0.66**	−134°	−0.46	0–3–7

n(*N*), number of bearings and of pigeons actually released; **a**, mean direction; r, length of the mean vector; Dh, deviation of the mean direction from the home direction; Hc, homeward component.

Significance by the Rayleigh (**r**) and the *V*-test (Hc) is indicated by asterisks: * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

Homing success: the three figures indicate the number of birds that homed the same day as released, homed one or more days later, or were lost, respectively. Birds that homed together with others have been excluded when they belonged to different treatments. Therefore, the sum of the three figures in some cases, indicated by the symbol †, may not be in agreement with the total number of birds released (*N*).

Table 2. *Pooled results of the experiments*

		Home vector			Compass vector		
Tr	*n*(*N*)	aH	rH	Hc	aN	rN	Homing success
IC	40(41)	+7°	0.45***	+0.45***	239°	0.46***	20–8–9†
IE	39(43)	+131°	0.25	−0.16	214°	0.43***	5–17–19†
AC	40(41)	−13°	0.33*	+0.32**	259°	0.54***	18–13–10
AE	39(45)	+154°	0.25	−0.22	218°	0.46***	6–16–22†

aH and rH, direction and length, respectively, of the mean vector when the bearing distributions are pooled with respect to home set to north (Home vector).

aN and rN, direction and length, respectively, of the mean vector when the bearing distributions are pooled with respect to north (Compass vector).

Other abbreviations as in Table 1.

revealed by comparing IC *vs* AE and AC *vs* IE ($P<0.001$ and $P<0.01$, respectively), whereas there is no significant difference between the bearing distributions of the control groups (IC *vs* AC) or those of the anosmic groups (IE *vs* AE) ($P>0.1$, in both comparisons). Both American and Italian birds (controls and experimentals) show a general tendency to fly westward or southwestward (pooled data, see Table 2); this directional preference is rather common in pigeons raised in the Pisa loft (references on preferred compass direction of pigeons in Wallraff, 1986*b*).

Homing performance

In single experiments, control groups always had a better homing performance than the respective experimental groups (this difference is significant in two cases: IC *vs* IE in the first experiment, and AC *vs* AE in the second experiment; Mann–Whitney *U*-test, $P<0.01$ and $P<0.025$, respectively). In pooled data (Fig. 2) the difference between controls and the respective anosmic groups reaches high levels of statistical significance (IC *vs* IE and AC *vs* AE: Mann–Whitney *U*-test: $P<0.001$ and $P=0.001$, respectively). Comparable levels of statistical significance are obtained by comparing IC *vs* AE and AC *vs* IE, whereas the homing performance of Italian controls is no different from that of American controls ($P>0.1$).

On the whole, Italian controls exhibited homing behaviour superior to that of American controls – a difference that is suggestive, though not significant – in terms of both initial orientation and homing performance.

Discussion

As regards the homing behaviour of the Italian pigeons, our experiments confirm the dependence of the homing mechanism on olfactory information. Contrary to what has been found in other similar experiments performed in Italy

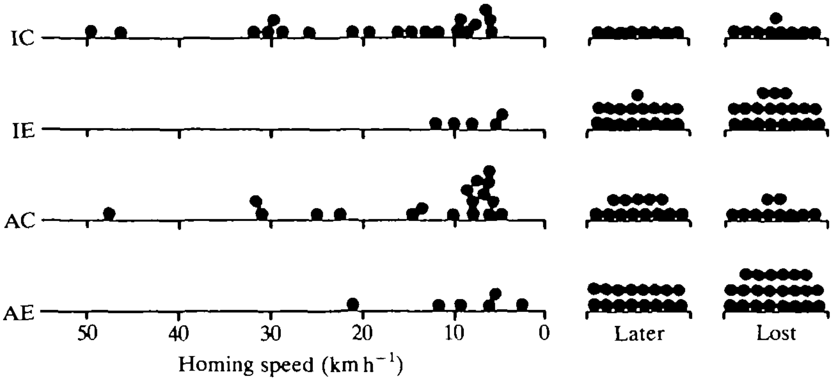

Fig. 2. Homing performance data of the experimental series (pooled results). Symbols are listed according to the homing performance of the birds. For pigeons that homed the same day as they were released, the homing speed is given. Later, birds that homed on days after the day of release; lost, birds that were lost. Other abbreviations as in Fig. 1.

(see Benvenuti *et al.* 1989), in the present case the anosmic birds showed no trace of residual homeward orientation. This can be attributed to the methods of olfactory deprivation during passive displacement, in which nasal plugs and filtered air were combined. This method, certainly more effective than the nasal plugs alone (see Wallraff, 1988), totally prevented the experimental birds from smelling significant cues during transportation to and at the release site. The related effect on homing behaviour cannot be attributed to a non-specific disturbance caused by the treatment, as testified by the normal flight behaviour (normal vanishing time and no significant tendency to land). Moreover, in another experiment in which the same methodology was used, one of us (AG) has verified that the anosmic birds were homeward-oriented in releases at familiar sites, where odorous cues can be replaced by non-olfactory information (Benvenuti and Fiaschi, 1983). It could also be suggested that the anaesthetic used to deprive the released birds of olfactory perception caused a non-specific impairment of homing behaviour. It is plausible that temporary anaesthesia of the olfactory mucosae had effects on the general behaviour of the birds; these non-specific effects, however, are negligible or, in any case, not strong enough to challenge our interpretation of the results. It is worth recalling that in previous experiments (Benvenuti and Wallraff, 1985; Kiepenheuer, 1985) birds subjected to xylocain treatment oriented homewards or in the direction opposite to the home direction, according to the olfactory information they had smelled prior to the release.

The homing behaviour of Cornell pigeons raised in Italy was in every respect similar to that of the Italian birds: in contrast to the controls, the anosmic pigeons were, on the whole, totally incapable of correct homeward orientation and showed impaired homing performance. No trace of residual homeward tendency (exhibited by Cornell pigeons in the USA, see Benvenuti and Brown, 1989, for references) was revealed in the anosmic experimental birds, which showed a stereotyped tendency to fly southwestward, the same directional preference as the Italian pigeons housed in the Pisa loft. Thus, there is no apparent genetic difference between the Cornell and the Italian strains with regard to the mechanisms of navigation. Since the non-olfactory homing mechanism supposed to account for the residual homeward tendency of anosmic Cornell birds (found in experiments performed in the USA) cannot be due to special training and raising procedures (see Benvenuti and Brown, 1989; Benvenuti *et al.* 1989), we can assume that it is based on the use of cues which are not available in the Italian environment.

It may be worth considering, however, that the American control birds were somewhat inferior to the Italian control birds, both in terms of initial homeward orientation and in terms of homing performance. This difference is not significant and may be due to change. However, it could imply that Italian birds are better suited to use the olfactory cues present in the Italian environment. It would not be surprising that pigeons have developed a specialized genetic ability to exploit the cues which prevail in the area where they and their ancestors were selected (it is plausible that olfactory cues in Italy are different from those prevailing in New York State). This implies a genetic difference between the Cornell and the Italian stocks, which does not affect the nature of the homing mechanism, but rather the ability to exploit those cues prevailing in the geographical region where the pigeons have been selected. To corroborate this suggestion we address the reader to the experiments performed by Kiepenheuer *et al.* (1979) with German pigeons raised in Italy and *vice versa*. On the whole, the results show that, in both countries, the homing behaviour of the local birds parallels that of the foreign stock; however, both in Italy and in Germany, foreign pigeons exhibited slightly poorer homing behaviour than the local stock.

A genetic difference between the Italian and German (Bavarian) stock was found by Benvenuti and Ioalè (1988); in this case, however, the reported difference is not caused by navigational ability, which has been proved to be based on olfactory information in both countries, but by the effect of an altered magnetic field on the initial orientation.

In conclusion, our experiments confirm the irreplaceable role of olfactory information in the homing process of Italian pigeons and show that there is no substantial genetic difference between the Italian and Cornell stocks as far as the nature of the homing mechanisms is concerned. The reported differences between the results obtained in Italy and in the USA, regarding the homing behaviour of anosmic pigeons, may be due to regional differences in the availability of olfactory and non-olfactory cues.

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