HOMING PIGEONS USE OLFACTORY CUES FOR NAVIGATION IN ENGLAND

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Summary

Although the use of olfactory cues in pigeon navigation is well established, the generality of olfactory navigation remains uncertain because of apparent variability in results gained by different researchers in different regions. We report the results of the first experiments investigating the effect of anosmia on homing pigeons reared in a previously uninvestigated region, southern England. In series 1, experienced birds showed little effect of anosmia induced with zinc sulphate at unfamiliar sites 30 km and 39 km from the loft, but treated birds were significantly poorer than controls at homing from an unfamiliar site 66 km distant (and in pooled results). In series 2, naive (untrained) birds, both control and zinc-sulphate-treated, showed poor homing abilities and initial orientation from sites 25 km, 36 km and 39 km from the loft. Nevertheless, in pooled results, controls showed significantly better homeward orientation than anosmic birds and were significantly more likely to home on the day of release. The most likely explanation for our results is that pigeons are able to use olfactory navigation in southern England, but that for some reason the olfactory map is relatively weak.

Key words: pigeon, *Columba livia*, homing, navigation, anosmia, olfactory cues.

Introduction

For over 40 years, the homing pigeon (*Columba livia*) has proved a valuable model for investigating how birds navigate in unknown areas, yet many mysteries still remain. More than 25 years ago, Papi and co-workers advanced the hypothesis, based mainly on experimental evidence gathered in Italy, that pigeons navigate from unknown areas by reference to an olfactory map (Papi *et al.* 1972; Papi, 1982, 1986, 1991). A large number of experiments performed in Bavaria confirmed the Italian findings that pigeons may rely on olfactory navigation (Wallraff, 1983, 1990), but left unresolved the question of how general the mechanism might be. Some experiments have supported the idea that olfactory navigation is a general mechanism, for example in Switzerland (Fiaschi and Wagner, 1976), Utah (Snyder and Cheney, 1975), Georgia (Bingman and Benvenuti, 1998), Ohio (Bingman and Mackie, 1992) and New York (Benvenuti and Brown, 1989). In other cases, conflicting results have been obtained (Germany: Hartwick *et al.* 1977; Schmidt-Koenig and Phillips, 1978; Wiltschko and Wiltschko, 1987; Wiltschko *et al.* 1987*a,b*; New York: Keeton and Brown, 1976; Keeton *et al.* 1977; Wiltschko *et al.* 1987*b*). In addition, different authors provide different interpretations of both positive and negative tests of the olfactory hypothesis, and even today a lively debate continues (Able, 1996; Wallraff, 1996; Wiltschko, 1996). Here, we report the results of two series of experiments that attempt to add to our understanding of the generality of olfactory navigation by testing the olfactory hypothesis in a new region. These are the first experiments of this kind to be conducted in England. In the first series of experiments, pigeons with considerable training experience were released at three novel sites ranging from 30 to 66 km from the loft. In the second series of experiments, entirely untrained pigeons were released at three sites ranging from 25 to 39 km from the loft.

Materials and methods

Releases with experienced birds

In September 1995, three displacement experiments were conducted from the Oxford University Field Laboratory lofts at Wytham, Oxford. Subjects were homing pigeons *Columba livia*, some bred at these lofts and some bought at 4 weeks post-hatch from local breeders. The birds ranged in age from yearling to 3 years. They were of mixed background experience, but all had undergone releases at sites 10–15 km from the home loft and in several different directions. None had been released at or near the experimental release sites. Shortly before the experiments were conducted, all birds received three additional training releases at sites up to 36 km southwest of the home loft. Between 1 and 3 days prior to experimentation, birds were

assigned to control or anosmic groups (balancing for age), and then treated to a 5 ml irrigation of the nostrils using a syringe of 4 % ZnSO$_4$·7H$_2$O solution (w/v) (experimentals) to induce temporary anosmia or of bird Ringer's solution (controls); for details on the treatment methods, see Benvenuti *et al.* (1992). Birds were marked with visually distinctive coloured leg-tapes and transported to each release site in open metal cages in the back of a van with the windows open. At the release site, after an acclimatisation period of at least 20 min, birds were tossed singly and followed with 10×40 binoculars in the usual fashion until they vanished. Vanishing bearings and times were recorded. Releases were only conducted when the sun was visible to the human eye and when the wind speed was less than 7 m s^{-1}. Arrival times at the loft were recorded by an additional observer. Different birds were used in the first (Quainton) and second (Paxford) releases. In the third release (Haresfield), out of 18 control birds, six had returned from Quainton, five had returned from Paxford and seven had not previously been used; the experimental group consisted of five birds returned from Quainton, five returned from Paxford and four previously unused pigeons. Further details on the number of birds tested in each experiment and the release sites are given in Table 1.

Releases with naive birds

In September 1996, three further displacement experiments were conducted with untrained pigeons that had either been bred at the Wytham loft or purchased from local breeders. All birds were of a similar age (hatched March–June 1996) and were allowed open access to the outside most days and constant access to an external flight chamber. Birds were given no training releases, but were otherwise treated in the same way as those released in 1995. On the first two critical releases (from Whichenden and Bishopstone), different birds were used. In the third test (Paxford), the control group consisted of seven naive birds and five birds previously used as controls in the first (three pigeons) and second (two pigeons) experiments; the experimental group included eight naive birds and five subjects previously used as controls in the first (three pigeons) and second (two pigeons) experiments. Further details of the experiments are given in Table 1. The third release took place over 2 days because of deteriorating weather on the first day.

Statistics

Initial orientation distributions were tested for randomness using the Rayleigh and the *V*-tests; comparisons between two distributions were made by means of the Watson U^2-test (Batschelet, 1981). Difference in vanishing times and homing performance between the treatments were tested using the Mann–Whitney *U*-test or Fisher's exact test (Siegel, 1956).

Results

Neither vanishing times nor vanishing bearings were recorded for those birds that disappeared from the sight of the experimenter because they flew behind trees at a short distance.

Table 1. *Summary of experimental protocol and results*

Test	Date and site	Distance (km)	Home direction (degrees)	Treatment	n	N	α (degrees)	r	Homeward component	Pooled data Treatment	n	α (degrees)	r	Homeward component
First series (experienced pigeons)														
R1	21/9/95	30	256	C	11	12	065	0.57	−0.56					
	Quainton			E	12	12	006	0.39	−0.13					
R2 .	23/9/95 Paxford	39	137	C	10	12	204	0.30	+0.12	C	26	113	0.16	−0.06
				E	8	13	157	0.13	+0.12	E	21	104	0.19	−0.04
R3 .	29/9/95 Haresfield	66	099	C	14	18	091	0.47†**	+0.46					
				E	6	14	013	0.57	+0.04					
Second series (inexperienced pigeons)														
R1	9/9/96 Whichenden	25	263	C	8	12	182	0.76††	+0.12					
				E	8	12	073	0.34	−0.33					
R2	10/9/96 Bishopstone	36	046	C	7	12	041	0.47**	+0.47	C	20	327	0.37*	+0.31
				E	8	11	238	0.17	−0.17	E	19	158	0.28	−0.26
R3	17/4/96 Paxford	39	137	C	9	12	211	0.58†	+0.16					
				E	6	13	238	0.72†	−0.14					

n, number of vanishing bearings recorded; N, number of birds released; α, mean vector direction; r, mean vector length; C, controls; E, zinc-sulphate treated pigeons.

The distributions are tested for randomness by means of both the Rayleigh and the *V*-tests (the level of significance is indicated by asterisks and daggers respectively); ** $P<0.01$; * $P<0.05$; †† $P<0.01$; † $P<0.05$.

Releases with experienced birds

Details of the release site distances and directions, numbers of birds released, vanishing bearings recorded and the results of circular statistical tests on bearing distributions are given in Table 1 for each of the three sites separately and for the pooled results of all three releases after removing data from the second release of any birds used twice.

Four control birds landed after being tossed: one pigeon landed in each of the two first releases, and two birds landed during the third experiment. One experimental pigeon landed in the second test and four in the third test. The control and the anosmic groups never displayed significantly different vanishing times (median values; Quainton, controls: 160 s experimentals: 250 s; Paxford, controls: 390 s experimentals: 340 s; Haresfield, controls: 270 s experimentals 457 s).

The initial orientation of the control pigeons was significantly different from random in only one case, for the release from Haresfield (66 km from the loft, see Table 1), and home direction was within the 95 % confidence interval of the bearing distribution, although their initial distribution was still not significantly different from that of the anosmic birds (Watson U^2-test). Experimental distributions were never significantly different from random. When results were pooled to include birds released at each of the three sites (but excluding birds released from Haresfield that had previously been released from either Quainton or Paxford), neither the control nor the experimental group was significantly oriented (Fig. 1A). When homing performance was assessed by ranking homing speeds, controls generally tended to be better at homing than experimentals from all three sites (Figs 2, 3A), but were significantly so from the farthest release site (Haresfield, see Table 1) (Mann–Whitney test: $U=61$; $N_1=18$; $N_2=14$; $P<0.01$) and in the pooled data from all three sites (Mann–Whitney test: $U=294$; $N_1=31$; $N_2=29$; $P<0.02$).

Releases with naive birds

Details of the release site distances and directions, numbers of birds released, vanishing bearings recorded and the results of circular statistical tests on bearing distributions are given in Table 1 for each of the three sites separately and for the pooled results of all three releases after removing data from the second release of any birds used twice.

Two controls landed after being released during the first test and three during the second test. Five experimental birds landed during the experiments: two birds in the first test, one in the second and two in the third.

The control pigeons vanished significantly faster than the anosmic birds only in the first release (Mann–Whitney U-test, $P<0.05$) (median values; Whichenden, controls: 180 s experimentals: 384 s; Bishopstone, controls: 411 s experimentals: 434 s; Paxford, controls: 225 s experimentals: 182 s).

Control birds showed significantly oriented vanishing bearings in all three releases, but only in the third release from Paxford was the home direction included in the 99 % confidence limits. Experimental birds were significantly

oriented only in the third release from Paxford, but at all release sites showed a negative homeward component. In the pooled results (excluding any birds released for a second time), controls were significantly oriented (Table 1; Fig. 1B) and the home direction was within the 95 % confidence limits of the distribution. Pooled experimentals (Table 1; Fig. 1B) were randomly scattered, and their distribution was significantly different from that of controls (Watson U^2-test, $P<0.05$).

Homing performances were generally very poor, with many birds failing to return home at all (Figs 2, 3B). When homing performance was assessed by ranking homing speeds, with birds arriving on each day after release tied, there were no significant differences between control and experimental groups. However, because of the unusually poor homing performance in these releases, leading to large numbers of ties in the analysis, we used an alternative method for assessing performance by comparing the number of birds returning on the day of release *versus* those arriving later (perhaps indicating a random search strategy) or not at all. In the first release from Whichenden, controls were significantly more likely than experimentals to home on the day of release (Fisher's exact test: $P=0.037$). In the second and third releases from Bishopstone and Quainton, the differences were not
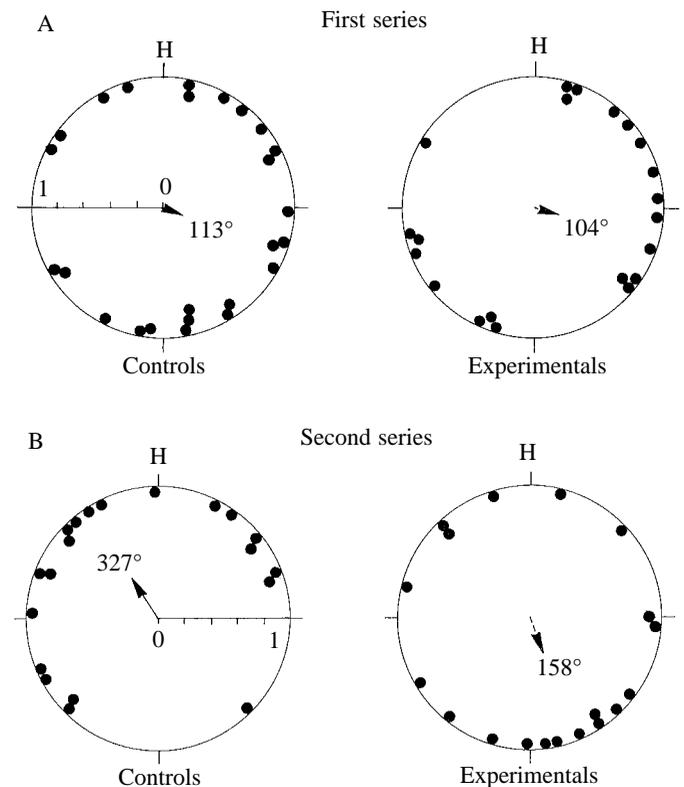

Fig. 1. Initial orientation diagrams for pooled results with home set to 360°. Data from birds released for the second time are not represented in the diagrams or included in the statistics. (A) First series. Pooled initial orientation of experienced pigeons (1995). (B) Second series. Pooled initial orientation of inexperienced pigeons (1996).
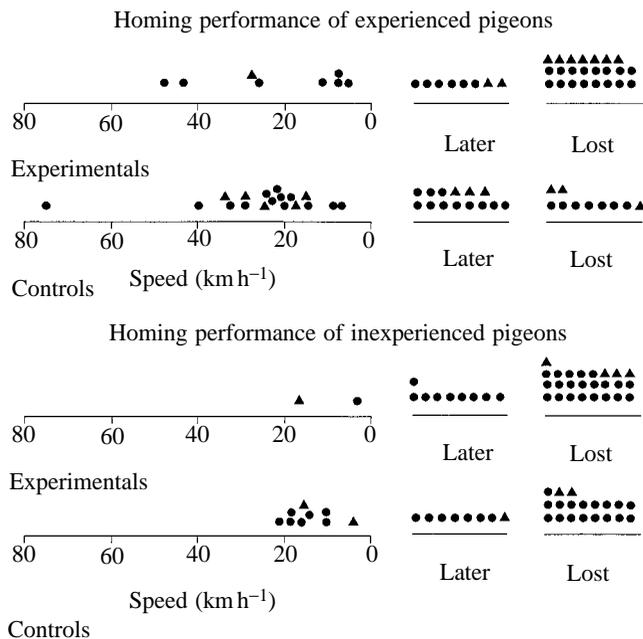
Homing performance of experienced pigeons

80 60 40 20 0   Later   Lost

Experimentals

80 60 40 20 0   Later   Lost

Controls   Speed (km h⁻¹)

Homing performance of inexperienced pigeons

80 60 40 20 0   Later   Lost

Experimentals

80 60 40 20 0   Later   Lost

Speed (km h⁻¹)

Controls

Fig. 2. Homing performance of experienced pigeons (pooled results of the first series) and inexperienced pigeons (pooled results of the second series). Although data from the second release of birds released more than once were not included in the pooled statistical tests, they are included in this figure for comparison (circles represent pigeons in their first test; triangles represent pigeons in their second release).

significant. In the pooled results, excluding data from any bird released for the second time, controls were again significantly more likely to home on the day of release than were experimentals (Fisher's exact test: $P=0.027$).

Discussion

The aim of our experiments was to determine whether deprivation of olfactory cues affects the homing abilities of pigeons in southern England, but we start by discussing some striking features of the general performance of our untreated control birds.

Our results with control pigeons show that, despite their fame as unfailing navigators, homing pigeons can perform poorly in orientation and homing. Pigeon racers obtain high levels of homing performance, by contrast, even in England because they give the pigeons directional training and generally race them from the training direction. In the first series of experiments, we used trained pigeons of mixed age and experience and we observed a poor initial orientation of the control group, which were significantly homeward-oriented only when released from the farthest site. In accord with the observations of Matthews (1953) for English pigeons, the homing performance of our trained control pigeons was always quite good and much better than that of our inexperienced controls used in the second series of experiments. The latter group showed a generally better initial homeward orientation than the experienced group of

pigeons, but their losses following the releases from sites further than 30 km from the loft were striking.

The generally poor initial orientation of our controls may genuinely reflect poor orientational ability. The irrigation of the control pigeons with bird Ringer's solution could conceivably have slightly impaired their ability to smell (perhaps by stimulating the production of mucous) and thus impaired their ability to home. However, Benvenuti and Gagliardo (1996) found that similarly treated controls were not significantly poorer at orienting than untreated birds, making this explanation unlikely. The poor homing performance of the yearling inexperienced control pigeons, used in the second series of releases, could indicate that pigeons have difficulty in acquiring a navigational map within a few months in southern England, perhaps because the climate is unsuitable. Certainly, consistent differences in orientational and homing ability in pigeons released by different research groups in different regions have been noted before. For example, pigeons raised in Italy seem to be the most efficient at orienting and homing compared with pigeons of the same level of experience reared in other regions (for references, see Kiepenheuer et al. 1979; Foà et al. 1982, 1984). The results of comparative experiments seem to have excluded a major involvement of genetic differences among stocks, but instead indicate a dependence of the orientational accuracy on climatic and environmental conditions (Kiepenheuer et al. 1979; Foà et al. 1982, 1984). Moreover, when the influence of possible genetic differences between Italian and American pigeons on olfactory navigation was explicitly tested (by testing American stock in Italy under an Italian protocol), no navigational differences were found (Benvenuti et al. 1990).

Nevertheless, despite this poor performance and the noise generated by the difficulty of obtaining distant vanishing bearings in the cluttered landscape of southern England (Braithwaite and Guilford, 1991), it is clear that the temporary anosmia induced by zinc-sulphate treatment does affect homing when birds are released from unknown sites within an unfamiliar area (see also Wallraff and Neumann, 1989). Moreover, while the control pigeons were homeward-oriented in two single releases and in the pooled results of the second series of experiments, the anosmic birds never displayed a homeward orientation. In similar experiments also using $ZnSO_4$ to induce anosmia at familiar sites, Schmidt and Schlund (1993) found that both anosmic and control pigeons were well oriented at short distance sites (9–24 km), while anosmic pigeons were disoriented at longer distance sites (54–70 km). At unfamiliar sites (Schlund, 1992), anosmic pigeons were disoriented at short-distance release sites and oriented (but not towards home) at longer-distance sites. Interestingly, at the latter sites, controls were also disoriented, suggesting that the lack of homeward orientation seen in the experienced control birds in our study is not unusual.

The results obtained were generally influenced by the experience of the birds and by the distance of the release site from home. Homing performances of anosmic birds were better in our releases of experienced birds (1995) than in our releases of untrained birds (1996), and were better at closer than at more
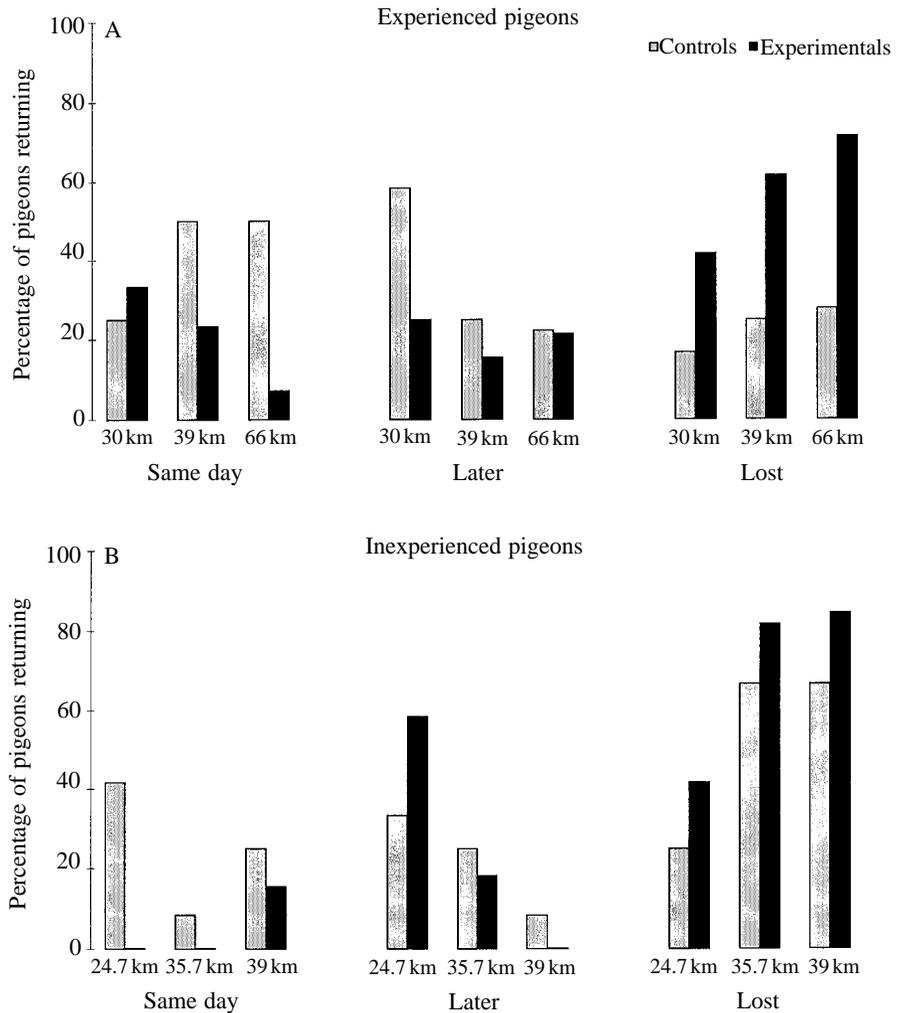
Fig. 3. Percentage of subjects returning on the same day of the experiment, returning later or failing to return from each site separately. Birds released twice are also included. (A) First series (experienced pigeons; 1995). (B) Second series (inexperienced pigeons; 1996).

distant sites, at least in the releases of experienced birds. One explanation is that those anosmic birds that did eventually return may have encountered their familiar area whilst searching or flying randomly after release in the absence of navigational information, and that this was more likely in trained than in untrained birds. These findings are consistent with previous studies showing that the homing performances of anosmic birds are inversely related to the distance of the release site from the loft and directly related to general homing experience (Benvenuti *et al.* 1992; Wallraff and Neumann, 1989).

From all the methods capable of inducing anosmia, we chose to irrigate the olfactory mucosa with a zinc sulphate solution. This method has been shown not to induce systemic effects, such as changes in cardiac responses to auditory or visual stimuli (Schlund, 1992), and to be efficient and easy to use (Wallraff, 1988; Benvenuti *et al.* 1992; Schmidt and Schlund, 1993). We carried out no deliberate releases from familiar sites to control for non-specific impairments in homing caused by the anosmia treatment, since previous studies have demonstrated that zinc-sulphate-treated birds are not detectably affected in the familiar area, or in unfamiliar areas if only treated in one nostril and allowed olfactory input to the

contralateral olfactory mucosa (Benvenuti *et al.* 1992; Benvenuti and Gagliardo, 1996).

We therefore conclude that our results show that English pigeons make use of olfactory cues to navigate in unfamiliar areas, as appears to be the case for birds in other countries. Our results also suggest that navigational abilities, for some reason, are relatively poor at our lofts, although we have yet to determine whether this is due to inherent differences in the conditions allowing navigation (e.g. the stability of the atmosphere) or to differences in stock, rearing and keeping conditions.

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