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THE IMPORTANCE OF ATMOSPHERIC ODOURS FOR THE HOMING PERFORMANCE OF PIGEONS IN THE SONORAN DESERT OF THE SOUTHWESTERN UNITED STATES

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Summary

The importance of atmospheric odours for homing pigeon navigation in a desert environment was tested using birds from two lofts located in the Sonoran desert near Tucson, Arizona, USA. When released from a familiar training site, experienced control pigeons and pigeons given intranasal injections of zinc sulphate to produce anosmia both displayed good homeward orientation and homed rapidly. When released from two unfamiliar locations, in contrast, the controls continued to display good homing performance while the zinc-sulphate-treated pigeons homed poorly. Significant differences in vanishing bearings, homing time and homing success were recorded. When a group of control and a group of zinc-sulphate-treated inexperienced pigeons were released from two unfamiliar locations, both groups homed poorly. Nonetheless, the controls still outperformed the zinc-sulphate-treated birds, the most notable result being a significant difference in homing success. Taken together, these results highlight the importance of atmospheric odours for the operation of the navigational map of the homing pigeon in a desert environment and, together with previous experiments, demonstrate that the role of atmospheric odours in homing does not seem to vary in any salient way with ambient climatic conditions.

Key words: *Columba livia*, pigeon, navigational map, olfactory map, spatial cognition, olfaction, anosmia.

Introduction

The ability of homing pigeons to return home from unfamiliar locations distant from the home loft is generally explained as being the result of a two-step navigational process consisting of independent map and compass (orientation) mechanisms (Kramer, 1952; Wallraff, 1990). The sensory basis of the compass step has been well described. Homing pigeons generally rely on the sun as their primary compass, the so-called sun compass, but they can also rely on the earth's magnetic field when the sun is obscured by clouds or is otherwise not visible (Kramer, 1953; Wiltschko and Wiltschko, 1988). It is also worth noting that the independence of the sun and geomagnetic compass mechanisms has recently been brought into question (Wiltschko *et al.* 1994). In contrast, research into the sensory basis of the navigational map has had a long history of confusion and contradictory results and interpretations (Gould, 1982; Wallraff, 1990; Able, 1996). However, it has now been convincingly shown that pigeons use the distribution of atmospheric odours as an important source of positional information (for reviews, see Papi, 1990; Wallraff, 1990).

Despite the general consensus that atmospheric odours are an important source of navigational information (Able, 1996), a persistent question continues to be how general a phenomenon olfactory navigation is. For example, Wiltschko *et al.* (1987*b*) have reported that olfaction is less important for navigational map operation in some regions of Germany and the United States than in Italy, while Wiltschko *et al.* (1987*a*) have reported that the kind of experience a pigeon has had can influence whether atmospheric odours are important for the navigational map. Although other researchers (Benvenuti and Brown, 1989; Benvenuti *et al.* 1990) have obtained results that contradict the claims of Wiltschko *et al.* (1987*a*,*b*), their work continues to be very influential. Additionally, Waldvogel (1987) proposed a model describing the atmospheric conditions under which odours could be a reliable source of spatial information. The important point of his model is that atmospheric conditions may not be universally well suited for 'olfactory navigation', thus lending theoretical support to the results of Wiltschko *et al.* (1987*a*,*b*).

To test the generality of olfactory navigation across a diversity of climatic conditions, we have previously examined the effects of zinc-sulphate-administered anosmia on homing performance in a number of climatically distinct regions including Mediterranean Pisa, Italy (Benvenuti *et al.* 1992), Great Lakes, Ohio, USA (Budzynski *et al.* 1998) and the hot and humid southeastern United States (coastal Georgia; Bingman and Benvenuti, 1996). Schlund (1992) has performed similar work near the Black Forest of Germany. It is striking that, despite the considerable differences in climate found in these areas, homing performance impairments following zinc-sulphate-induced anosmia were found in each of the locations. These findings therefore suggest that a navigational map based at least in part on olfaction is indeed a global feature of pigeon homing ability. However, before overgeneralizing, we felt it would be appropriate to test pigeons in one other distinct environment: a dry desert. To do this, we examined the homing performance of pigeons subjected to zinc-sulphate-induced anosmia in the arid desert of the United States near Tucson, Arizona.

Materials and methods

Experimental animals and treatment

Two groups of experimental pigeons were used. One group of 25 pigeons was considered experienced. They were approximately 7 months old at the time of testing and were part of the racing team of a local racing hobbyist. The loft was located on a hill in a residential neighbourhood in the Sonoran desert surrounding Tucson, Arizona. The birds had previous experience of approximately 100 km to the northwest and up to 300 km to the east of home. Prior to the first experimental release, all pigeons were given five training releases (two as a group, two as groups of three pigeons and one when the birds were released singly) from a location (familiar site) 63 km east of the home loft. One day prior to the first experimental release from the familiar training site, 13 pigeons were given an intranasal injection of zinc sulphate heptahydrate dissolved in distilled water. Zinc sulphate alters or destroys the olfactory mucosa, effectively rendering pigeons anosmic until regeneration takes places (Benvenuti *et al.* 1992; Schlund, 1992). Zinc sulphate administration is generally considered to be an anosmic procedure with few, if any, side effects (Benvenuti and Gagliardo, 1996). A 4 % solution (2 ml) was injected into each choana, and the solution was allowed to flow out of the nostrils. This solution reliably blocks the ability of pigeons to perceive odours (Benvenuti *et al.* 1992). Therefore, we did not perform tests of olfactory ability on each bird prior to the experimental releases. The remaining 12 controls were subjected to a sham treatment: they were injected with avian Ringer's solution into each choana.

The birds were first given an experimental release from the familiar training site, where a functional navigational map is unnecessary for successful homing because of the accumulated experience with the release site and the route home (Hartwick *et al.* 1977). Therefore, no homing deficit was expected in the zinc-sulphate-treated group. This release served as a control for possible non-specific effects (e.g. loss of motivation or flying ability) of the zinc sulphate treatment. Eleven controls and 13 experimentals were released (the remaining control was released but no data were taken to keep recorded vanishing bearings of the two groups equal). Two days after the experimental release from the familiar site, 11 controls and 11 experimentals participated in the first experimental release from an unfamiliar site, 57 km south of the loft. After this release, the remaining birds in the control group and zinc-sulphate-treated group were each given an additional injection of 1 ml per choana of either 4 % zinc sulphate or avian Ringer's solution. In addition, because of the loss of four zinc-sulphate-treated pigeons from the first unfamiliar release site, one control bird was recruited into the experimental group and given a full dose of 4 % zinc sulphate in each nostril. Two days later, the 10 control and 10 experimental pigeons were released from a second unfamiliar site located 69 km north of the loft.

The 30 pigeons of the second group were inexperienced and were approximately 4 months old at the time of testing. They lived in another loft located in the shallow valley of a residential community approximately 5 km away from the loft of the experienced pigeons. They were allowed to fly freely around the loft, had no racing experience and were given four training releases as a group from approximately 10 km in the cardinal directions prior to the first experimental release. No familiar site training was given. One day prior to the experimental release, 10 pigeons were given a zinc sulphate injection and 10 pigeons were given an avian Ringer's solution injection, as described above. The first experimental release took place from an unfamiliar location 50 km northwest of home. Because of losses, for the second experimental release the 11 zinc-sulphate-treated birds consisted of four zinc-sulphate-treated birds that had returned from the first release, six birds that had not participated in the first release and one bird that was recruited from the controls that had returned from the first release (the last seven birds were given full doses of 4 % zinc sulphate the day before the second experimental release). The controls consisted of seven birds that had returned from the first release and four birds that had not participated in the first release (the last four birds were given a full dose of avian Ringer's solution the day before release). The second experimental release took place from an unfamiliar site approximately 40 km southwest of the loft.

Experimental release procedures

Standard procedures were followed during the experimental releases. Releases took place on sunny days with little or light winds. Pigeons were transported in open crates in the back of a pick-up truck. The birds were released singly, alternating between treatment groups, and followed with binoculars until they disappeared from view. Vanishing bearings and vanishing times were recorded using a compass and stopwatch, respectively. Arrival times were recorded by an observer stationed at the loft.

Data analysis

Statistical analysis of the vanishing bearing data was performed using a Rayleigh test and *V*-test (Batschelet, 1981). Between-group comparisons of vanishing bearings were performed using a Watson U^2-test, homing times using a Mann–Whitney *U*-test and homing success using a χ^2-test or a Fisher test (Siegel, 1956), depending on sample size. For the homing time analysis, birds that returned in groups consisting of both control and experimental pigeons were excluded from the analysis.

Results

Data summarising the homing performance of the pigeons are contained in Table 1 and Figs 1, 2.

Experienced pigeons

Vanishing bearings

From the familiar training site, both the control and the experimental birds were very well oriented in the homeward direction and no between-group differences were found (Fig. 1A; Table 1). In contrast, from the first unfamiliar site, the control birds continued to be well homeward-oriented, whereas the zinc-sulphate-treated birds displayed randomly dispersed vanishing bearings, and the two distributions differed significantly from each other (Fig. 1B; Table 1). From the second unfamiliar release site, controls continued to be well oriented, but the homeward component of the mean vector was small, albeit positive, indicating at best only weak homeward orientation. However, the vanishing bearings of the zinc-sulphate-treated birds continued to be randomly dispersed and again a between-group difference was found (Fig. 1C; Table 1).

Homing times

From the familiar training site, both groups displayed median homing times of approximately 55 min (Fig. 2A). No between-group difference was found. In contrast, from both unfamiliar release sites, controls displayed median homing times of approximately 90 min, while zinc-sulphate-treated birds were significantly slower (Fig. 2B,C). Indeed, a median homing time for the zinc-sulphate-treated birds could not be calculated because no more than half the birds returned home on the day of the release for either experimental release.

Homing success

From the familiar training site, no birds were lost. However, during the course of the two releases from the unfamiliar sites, none of the 12 control birds used was lost, while nine of the 14 pigeons that were part of the zinc-sulphate-treated group for

Table 1. *Results of the experimental series*

Date	Hdr (degrees)	Hds (km)	Tr	*n*(*N*)	α (degrees)	**r**	Hc	U^2	Hp	*U*
Experienced birds: familiar site										
Dec. 5	297	63	C	10(11)	280	0.99***	+0.95***	NS	10.0.0.[a]	NS
			E	10(13)	274	0.99***	+0.92***		12.0.0.[a]	
Experienced birds: unfamiliar sites										
Dec. 7	14	57	C	9(11)	48	0.96***	+0.80**	*	10.0.0.[a]	***
			E	11(11)	63	0.09	+0.06		5.1.4.[a]	
Dec. 11	165	69	C	8(10)	82	0.85**	+0.10	**	10.0.0.	***
			E	8(10)	269	0.26	–0.07		4.1.5.	
Inexperienced birds: unfamiliar sites										
Dec. 6	135	50	C	8(10)	66	0.27	+0.10	***	3.5.2.	NS
			E	9(10)	254	0.71**	–0.35		2.3.5.	
Dec. 8	50	40	C	9(11)	356	0.31	+0.19	NS	7.4.0.	**
			E	10(11)	182	0.16	–0.11		2.2.7.	

Hdr, Hds, the home direction and distance, respectively; Tr, bird treatment; *n*(*N*), the number of vanishing bearings and the number of birds actually released; α direction and **r** length of the mean vector; Hc, homeward component; U^2, level of statistical significance of the Watson U^2-test; Hp, homing performance: the three values separated by points indicate the number of birds that homed on the day of release, the number of birds that homed later and the number of birds lost, respectively; C, control; E, experimental.

In some cases (a), the number of birds in the Hp column does not correspond to the number of birds actually released. This is because birds belonging to different treatments that homed together were not included in the Hp analysis.

U, homing time difference level of statistical significance with the Mann–Whitney *U*-test.

Levels of statistical significance for the Rayleigh (**r** column), *V* (Hc column), U^2 and Mann–Whitney *U* (*U* column) tests are given as asterisks: *P<0.05; **P<0.01; ***P<0.001; NS, not significant.

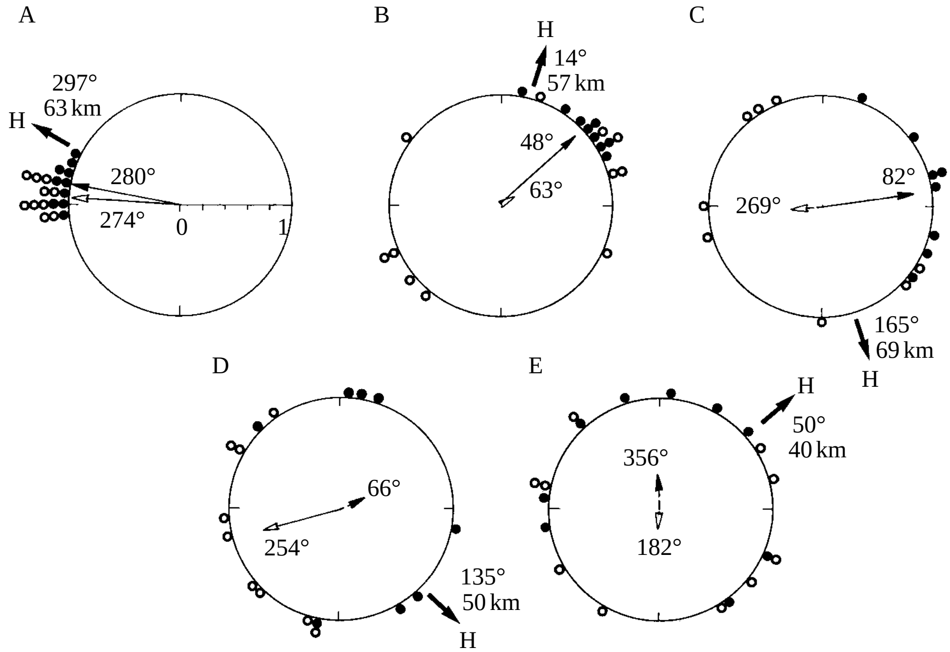

Fig. 1. Vanishing bearings of control (filled dots) and zinc-sulphate-treated (open dots) pigeons. (A) Experienced pigeons from the familiar training site; (B,C) experienced pigeons from the first (B) and second (C) unfamiliar release sites; (D,E) inexperienced pigeons from the first (D) and second (E) unfamiliar release sites. Each dot represents the vanishing bearing of one bird. Arrows in each circle represent the mean vectors for each group (filled arrowheads, controls; open arrowheads, zinc-sulphate-treated). The length of an arrow corresponds to the mean vector length, which can be read using the scale in A (solid lines, $P<0.05$; dashed lines, $P>0.05$, see Table 1). Arrows outside each diagram and the associated numbers identify the distance to and direction of home (H). North is at the top of each diagram.

at least one release were lost. Zinc-sulphate-treated birds were significantly more likely to get lost (Fisher exact test, $P<0.01$).

Taken together, the data from the experienced birds demonstrate a dramatic effect of zinc-sulphate-mediated anosmia on homing performance when the pigeons were released from unfamiliar sites where they would need to use their navigational map to home successfully.

Inexperienced pigeons

Vanishing bearings

From the first unfamiliar release site, controls were not oriented, whereas the zinc-sulphate-treated birds were well oriented but in a direction away from home, and a significant between-group difference was found (Fig. 1D; Table 1). From the second unfamiliar release site, neither group was oriented and no between-group difference was found (Fig. 1E; Table 1). Generally, the vanishing bearing data of the inexperienced controls were poor, but it is worth noting that for both releases the controls had a mean vanishing bearing vector with a positive homeward component, while the experimentals had a mean vanishing bearing vector with a negative component (Table 1).

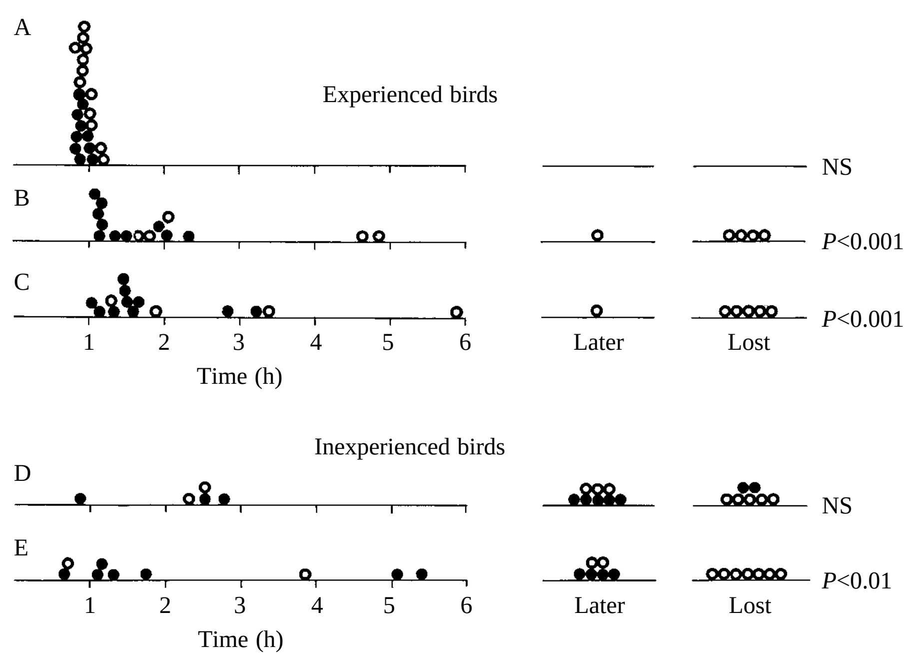

Fig. 2. Homing times of control (filled dots) and zinc-sulphate-treated (open dots) pigeons. (A) Experienced pigeons from the familiar training site, (B) experienced pigeons from the first unfamiliar release site, (C) experienced pigeons from the second unfamiliar release site, (D) inexperienced pigeons from the first unfamiliar release site and (E) inexperienced pigeons from the second unfamiliar release site. Each dot represents the homing time for one bird. Note that pigeons that returned with a bird from the other treatment group were excluded from the analysis.

Homing times

From the first unfamiliar release site, less than half the birds from both groups returned home on the day of release and, therefore, no median homing time could be computed nor was a between-group difference found (Fig. 2D). From the second unfamiliar release site, controls had a median homing time of approximately 5 h while, again, no median homing time could be computed for the zinc-sulphate-treated birds. However, for this release, a significant difference between treatments in homing time was found (Fig. 2E).

Homing success

Two of 10 controls and five of the 10 experimentals failed to return from the first release. For the second release, all controls returned, while seven of 11 experimentals did not. Of the 14 pigeons that served as a control for at least one release, two failed to return as a control. In contrast, of the 17 pigeons that served as a zinc-sulphate-treated bird for at least one release, 12 failed to return when treated with zinc sulphate. Zinc-sulphate-treated birds were significantly less likely to return home (χ^2=7.69, P<0.01).

Although the homing performance of the inexperienced pigeons was clearly inferior to that of the experienced birds described above, zinc sulphate administration was again found to negatively impact homing performance, particularly homing success.

Discussion

The data clearly demonstrate that zinc-sulphate-mediated anosmia, like other anosmic treatments (see Papi, 1990; Wallraff, 1990, for reviews), dramatically impairs the homing performance of experienced pigeons and, to a similar relative extent (see below), that of inexperienced pigeons. Consistent with results obtained in Italy (Benvenuti *et al.* 1992), the southeastern United States (Bingman and Benvenuti, 1996), the Great Lakes of the United States (Budzynski *et al.* 1998) and Germany (Schlund, 1992), pigeons of the Sonoran desert in the area of Tucson, Arizona, USA, seem also to rely on atmospheric odours as an important source of the spatial information necessary for the operation of their navigational map. Collectively, the data stand in strong support of the hypothesis that the perception of atmospheric odours plays a universally important role in the navigational map of homing pigeons. It is worth pointing out that during this study pigeons were regularly released in relative humidities of 10–15 %. The dry air of Arizona contrasts strikingly with the humidity of Georgia, where relative humidities of 60 % and more were present during the releases of Bingman and Benvenuti (1996). This difference in humidity must certainly affect the distribution of odours in the atmosphere but, nonetheless, under both humidity conditions anosmia produced notable homing performance deficits only when pigeons were released from distant, unfamiliar locations.

Our experimental design relied on a deprivation procedure to examine the importance of atmospheric odours for navigation. As such, it suffers from the major criticism of any deprivation study, i.e. were the observed effects a consequence of an impairment in the navigational map or of a non-specific impairment in another attribute, such as motivation or flying ability? We wish to make two points in response to this criticism. First, the excellent performance of the zinc-sulphate-treated experienced birds when released from the familiar release site, a similar distance away from the home loft compared with the unfamiliar release sites, convincingly demonstrates that zinc sulphate administration has no dramatic effect on either motivation or flying ability (for a fuller discussion of this issue, see Benvenuti and Gagliardo, 1996). Second, a number of more elegant, non-deprivation studies have already shown that the perception of atmospheric odours plays a critical role in homing in the areas where these experiments took place (see Papi, 1990; Wallraff, 1990, for reviews). Therefore, we operated under the reasonable assumption that, under some conditions, atmospheric odours are important for homing and used the more expedient, but nonetheless reliable, deprivation procedure to determine whether odours are similarly important in the desert environment of Arizona.

Notable in the present study was the interesting difference in homing performance and the effects of zinc sulphate treatment between the experienced and inexperienced pigeons. The performance of the experienced control pigeons was outstanding, and between-group differences were found in every measure of homing performance. In contrast, the performance of the inexperienced control pigeons was poor, and a reliable between-group difference was only found in the crudest measure of homing performance, i.e. homing success. Given the poor homing performance of the inexperienced controls, it is not surprising that between-group differences were less reliably observed. Indeed, the performance of the inexperienced controls was very reminiscent of that of the control pigeons studied in the southeastern United States (Bingman and Benvenuti, 1996). Both in Arizona and in the southeastern United States, the inexperienced controls were only given free-flight experience and a few training releases from not more than 10 km from home before the experimental releases began. This minimal training experience was obviously not sufficient to allow these birds to learn a robust navigational map and, as a result, made the detection of between-group differences difficult. This observation emphasises the importance of good control homing performance for detecting the effects of experimental treatments.

In any event, the data presented here add further support to the hypothesis that atmospheric odours are a critical source of environmental information necessary for the operation of the homing pigeon navigational map, and the importance of atmospheric odours does not seem to vary as consequence of ambient climatic conditions.

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