

RESEARCH ARTICLE

Pigeon navigation: exposure to environmental odours prior to release is sufficient for homeward orientation, but not for homing

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ABSTRACT

The role of environmental olfactory information in pigeon navigation has been extensively studied by analysing vanishing bearing distributions and homing performances of homing pigeons subjected to manipulation of their olfactory perception and/or the olfactory information they were exposed to during transportation and at the release site. However, their behaviour during the homing flight remains undocumented. In this experiment we report the analysis of tracks of birds made anosmic at the release site by washing their olfactory mucosa with zinc sulfate. We thus can assess the role of local odours at the release site as well as the role of environmental odours perceived on the way, far from the release site. We observed that pigeons transported and kept at the release site in purified air and made anosmic at the release site were unable to orient towards home and were impaired at homing. By contrast, pigeons allowed to smell environmental odours during transportation and at the release site, although made anosmic prior to release, displayed unimpaired homeward orientation, but nevertheless showed impaired homing performance. These results are consistent with the view that local odours at the release site are critical for determining the direction of displacement (olfactory map) and suggest that pigeons consult the olfactory map also during their homing flight in order to be able to find their way home.

KEY WORDS: Olfaction, Homing pigeon, Navigation, GPS tracking

INTRODUCTION

Since Papi et al. (1971) showed that anosmic homing pigeons were dramatically impaired at homing, a large body of evidence has supported the role of olfactory cues in navigation (summarised in Wallraff, 2005; Gagliardo, 2013). The olfactory navigation hypothesis predicts that pigeons are able to associate environmental odours carried by the winds with the directions from which they blow at the home area. Once at the release site, pigeons may be able to determine the direction of displacement simply by recognising the prevalent local odours and recalling from which direction these arrived at the home loft. Although recent tracking studies on wild birds supported the critical role of olfactory information in avian navigation (Gagliardo et al., 2013; Pollonara et al., 2015; Wikelski et al., 2015), evidence supporting olfactory navigation in homing pigeons comes almost exclusively from traditional experiments in which vanishing bearings and homing

performance were recorded. In fact, the only exception is a tracking study (Gagliardo et al., 2011b) reporting that pigeons made temporarily anosmic by anaesthetising their olfactory mucosa displayed impaired navigational abilities, unless they had been allowed to smell local environmental odours during transportation and at the release site prior to the release. Because the effect of the anaesthetic gradually ceases about 1 h after its administration, the behaviour of pigeons challenged to find their way home without exploiting the olfactory information perceived at further distances from the release site remains undocumented.

An important advancement for such studies is the use of GPS/GSM loggers that now allow us to obtain information on the spatial behaviour of the birds that are unable to home (Gagliardo et al., 2014). Thus, we can now study the behaviour of pigeons made anosmic in the long term using zinc sulfate treatment of their olfactory mucosa. In the current experiment, we report the behaviour of pigeons made anosmic at the release site and investigate the role of olfactory information perceived both during transportation and at the release site, and those perceived also along the flight path at greater distances from the release site.

MATERIALS AND METHODS

Bird treatment and release site details

One hundred and forty-eight inexperienced homing pigeons (*Columba livia* Gmelin 1789) of both sexes, hatched in the year of the test at the Arnino field station (latitude, 43°39'26" N; longitude, 10°18'14" E), Pisa, Italy, were used in the study. The pigeons were raised as free flyers and were kept and manipulated according to Italian law on animal welfare (permit numbers 8630/2011 and 893/2015-PR). Twenty days prior to experimental release, all the birds were equipped with a PVC dummy weight, similar in dimension and weight to the GPS data logger they would be carrying, in order to accustom them to flying with a load. The dummy was attached to the pigeons' back by means of a Velcro strip glued on the feathers, which had been trimmed. To track the released pigeons, we used Fleetronic GSM GPS loggers (www.fleetronic.net; weight 25 g; sampling rate 1 fix every minute), so that data could be obtained in cases where the bird did not home. The positional fixes stored by a GPS data logger include latitude, longitude, flight speed, and time of recording.

In each release, three groups of pigeons subjected to three different treatments were tested. The birds were randomly assigned to the three experimental groups in the following way: all the pigeons to be released were placed in a single crate and then placed one by one in each of three cages, alternating the cage each time. Control pigeons (C) were transported in a crate to the release site and released without further manipulation after at least 40 min from the arrival at the release site. The zinc sulfate-treated control pigeons (ZnC) were transported to the release site in an airtight container ventilated with environmental air by an aspirator, so that they could

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perceive environmental odours during transportation. Upon arrival at the release site, these birds were allowed to smell the environmental air at the release site for at least 1 h before being made anosmic. The birds were released at least 2 h after the anosmia treatment, which consisted of washing their olfactory mucosa with a 4% zinc sulfate solution (Guilford et al., 1998). The pigeons were taken out of the airtight container at least 30 min before being released. The zinc sulfate-treated pigeons transported in purified air (ZnPA) were displaced in airtight containers ventilated by air filtered through an active charcoal filter, in order to prevent their exposure to environmental air both during transportation and at the release site. Once at the release site, the birds were made anosmic with zinc sulfate nasal washing. These birds were then taken out of the airtight container at least 30 min before being released. The release took place at least 2 h after the zinc sulfate treatment.

In each release, five pigeons for each experimental group were released (except for one release at Bolgheri, in which four control and four ZnPA birds were released). The six release sites were located in five different directions from the home loft and at distances ranging from 49 to 61 km (details on the release sites are reported in Table 1). For each direction, two releases were performed at the same release site, except for releases from East, which were performed in two sites at different distances from the same direction (Empoli and Montespertoli). The sample size tested for each direction was chosen on the basis of similar studies on homing pigeons (see Gagliardo, 2013). However, since the Arnio field station is located about 5 km from the Tyrrhenian coast, the release sites could not be balanced in all compass directions. Each pigeon was released singly. The releases took place under sunny conditions, with no or light wind.

Quantitative analyses and statistical procedures

The orientation of each bird was analysed both for the whole track recorded and for the initial portion of the track (first 10 km

of flight path). In the latter analysis, the tracks for which the initial portion was totally or partially missing because of equipment malfunction were excluded from the analysis according to a pre-established criterion. For each track, we calculated the individual mean vector averaging the directions taken by the bird while moving from one point to the next at a speed higher than 5 km h⁻¹. The initial fixes of the track closer than 1 km radius from the release site were excluded from the analysis. The mean vector distributions of the three groups of birds were tested for randomness with the one-sample Hotelling test (Batschelet, 1981), both for each release site and by pooling the results from all releases after having standardised the home direction to 360 deg. The same analysis was applied to the first 10 km of route flown by the birds in order to analyse their initial orientation. Comparisons on the orientation performances of the three groups were made on the whole track data, by applying the two-sample Hotelling test (Batschelet, 1981).

In GPS studies where pigeons needed to be recaptured at home in order to download the data, it is usual to analyse the efficiency index of the tracks, which is calculated as the ratio between the track length and the beeline distance between the release site and home. When the track is not complete, the linear distance from the end of the track to the loft is added to the track length (Gagliardo et al., 2011a). However, the efficiency index (EI) is not a useful measure when the flight path of birds unable to reach the home loft is documented, for instance using GPS GSM loggers. We therefore used a parameter, named the homing efficiency index (HEI), which takes into account whether a bird approaches or gets away from home during its flight. The HEI is defined as:

$$HEI = \frac{a}{l} \cdot \frac{(b-c)}{b}, \quad (1)$$

where a is the beeline between the release site and the last fix recorded, l is the track length (as in Gagliardo et al., 2011a,b), b is

Table 1. Data for the three experimental groups of pigeons released from different sites

Group	n (N)	r	α (deg)	Ht	95% CI (deg)	n_{10}	r_{10}	α_{10} (deg)	Ht ₁₀	95% CI (deg)
Bolgheri, 336 deg, 53 km										
C	8 (9)	0.50	333	*	305–338	8	0.61	327	*	308–344
ZnC	10 (10)	0.32	329	**	192–337	10	0.51	315	**	266–330
ZnPA	9 (9)	0.18	323	n.s.	–	9	0.22	281	*	203–328
Saline di Volterra, 309 deg, 50.5 km										
C	8 (10)	0.38	305	*	228–332	8	0.31	293	n.s.	–
ZnC	9 (10)	0.27	287	*	206–327	9	0.33	264	*	217–320
ZnPA	10 (10)	0.22	264	*	185–320	10	0.28	222	*	182–324
Empoli, 264 deg, 49 km										
C	5 (5)	0.78	265	**	262–270	5	0.79	257	**	201–297
ZnC	5 (5)	0.55	265	*	255–036	4	0.72	229	*	126–288
ZnPA	5 (5)	0.39	259	n.s.	–	5	0.55	240	*	173–337
Montespertoli, 270 deg, 61 km										
C	4 (5)	0.66	278	*	180–307	3	0.64	322	n.s.	–
ZnC	5 (5)	0.50	270	*	204–338	5	0.43	295	n.s.	–
ZnPA	5 (5)	0.21	260	n.s.	–	5	0.38	297	n.s.	–
Aglia, 241 deg, 59.9 km										
C	7 (10)	0.32	241	*	231–003	7	0.38	269	*	141–283
ZnC	8 (10)	0.25	269	*	138–313	7	0.14	262	n.s.	–
ZnPA	10 (10)	0.18	213	n.s.	–	10	0.29	191	*	141–285
Marinella, 152 deg, 51 km										
C	7 (10)	0.17	165	n.s.	–	7	0.29	143	n.s.	–
ZnC	7 (10)	0.32	160	n.s.	–	7	0.20	140	n.s.	–
ZnPA	9 (10)	0.39	152	n.s.	–	9	0.27	145	*	102–268

Home direction and distance is shown for each release site. r and α , mean vector length and directions relative to whole track recorded; N (n), number of tracks analysed (number of birds released); Ht, significance level according to the Hotelling test, * P <0.05, ** P <0.01, n.s., not significant; 95% CI, 95% confidence intervals of the distribution; the five left-hand columns report data relative to the initial portion of the track (first 10 km).

the beeline between the release site and home, and c is the beeline between the last fix recorded and home (all in km). Consequently, if the bird failed to approach home, then $HEI < 0$; if the bird approached home, then $HEI > 0$; and if the bird homed, $HEI = EI$. The HEI values of the three groups were compared with a Kruskal–Wallis test and the Dunn’s test (Zar, 1984) was used for multiple comparisons.

For each track, we counted the number of stops made by the bird along its journey. We compared the number of stops per km of path flown using the Kruskal–Wallis test. Dunn’s test was used for multiple comparisons. In order to assess whether the zinc sulfate treatment had detrimental effects on the general performance of pigeons we conducted an analysis on the behaviour of the three groups in the first 10 km of flight path. The Kruskal–Wallis test was applied to the flight speed (as recorded by the GPS for each fix), to the number of stops performed, and to the total time spent sitting during the stops. For the birds that did not stop, the time spent sitting was therefore zero. The Dunn’s test was applied for multiple comparisons. The few tracks for which the sampling frequency was one fix every 5 min due to the device malfunctioning, or when gaps in the sampling occurred within the considered tract of track, were excluded from the analysis of the stops. Tracks with a 5 min sampling rate were included in the flight speed analysis. We also applied the χ^2 to the number of birds that never stopped and the number of birds that landed at least once in the first 10 km of track.

Differences in homing performances were assessed with the Kruskal–Wallis test applied to the following categories: (1) birds homed on the day of release, for which the homing speed has been computed; (2) birds homed on the day after the release; (3) birds homed later; and (4) lost birds.

RESULTS

All the tracks recorded are represented in Fig. 1 and can be inspected in Movebank (www.movebank.org) at doi:10.5441/001/1.721tr877. The orientation data at each release site, both concerning the whole tracks and the first 10 km of the tracks, are reported in Table 1. Considering the analysis on the whole tracks, both C and ZnC birds were significantly oriented at five out of the six release sites (see Table 1 for Hotelling test results), while the ZnPA birds were significantly oriented only at one site. In all these cases, the birds’ mean direction was not significantly different from the home direction (the home direction was included in the 95% confidence

limits). When considering the first 10 km of track, both C and ZnC birds were significantly oriented at three, and the ZnPA at five out of six release sites; at Bolgheri both ZnC and ZnPA initially oriented in a direction different from the home direction.

From the analysis of the pooled data, when home direction was standardised to 360 deg, mean vector distributions relative to the whole tracks emerged that the three groups of birds displayed mean vector distributions significantly different from random. However, while both C and ZnC pigeons oriented in a direction close to the home direction, the ZnPA birds turned out to be oriented in a direction significantly different from the home direction (Hotelling test $P < 0.001$ for all groups: C, $n=39$, $r=0.43$, $\alpha=001$ deg, 95% CI=356–006 deg; ZnC, $n=44$, $r=0.33$, $\alpha=360$ deg, 95% CI=348–010 deg; ZnPA, $n=48$, $r=0.24$, $\alpha=344$ deg, 95% CI=325–356 deg). The mean vector distribution of C birds was significantly different from that of the ZnPA birds (two-sample Hotelling test, $F=8.147$, $P < 0.001$), but not the ZnC pigeons ($F=1.078$, $P > 0.5$). The comparison between the ZnC and the ZnPA birds did not reach the 5% significance level ($F=3.055$, $P=0.06$). Analysis of the first 10 km of tracks produced results consistent with that performed on the whole tracks (see Fig. 2).

The length of the recorded tracks in the three groups of birds was comparable (median length: C, 81.4 km; ZnC, 79.6 km; ZnPA, 73.9 km; Kruskal–Wallis test, $P=0.6$). However, the Kruskal–Wallis test revealed a statistical difference ($P=0.003$) in the homing efficiency index (HEI, Fig. 3) of the three groups of birds (median HEI: C, 0.48; ZnC, 0.21; ZnPA, 0.05). In particular, the C ($n=39$) birds displayed a greater HEI than the ZnPA ($n=48$) pigeons (Dunn’s test $P < 0.002$) but it was comparable to that exhibited by the ZnC ($n=44$, $P > 0.1$) group. The difference between the ZnC and the ZnPA birds did not reach the significance level ($P > 0.1$). However, it is worth noting that the ZnPA birds had a significantly higher tendency to distance themselves from home than the other two groups, as shown by the comparison of the number of birds (2 in both C and ZnC, and 14 in ZnPA) exhibiting negative HEI in the three groups ($\chi^2=15.216$, $P < 0.001$; ZnPA versus ZnC, $\chi^2=9.687$, $P < 0.005$; ZnPA versus C, $\chi^2=8.284$, $P < 0.25$; C versus ZnC, $\chi^2=0.015$, $P > 0.5$).

The number of stops per km of flown path was significantly different in the three groups [Kruskal–Wallis test, $P < 0.01$; C, median number of stops $\text{km}^{-1}=0.13$ ($n=36$); ZnC, 0.19 ($n=41$);

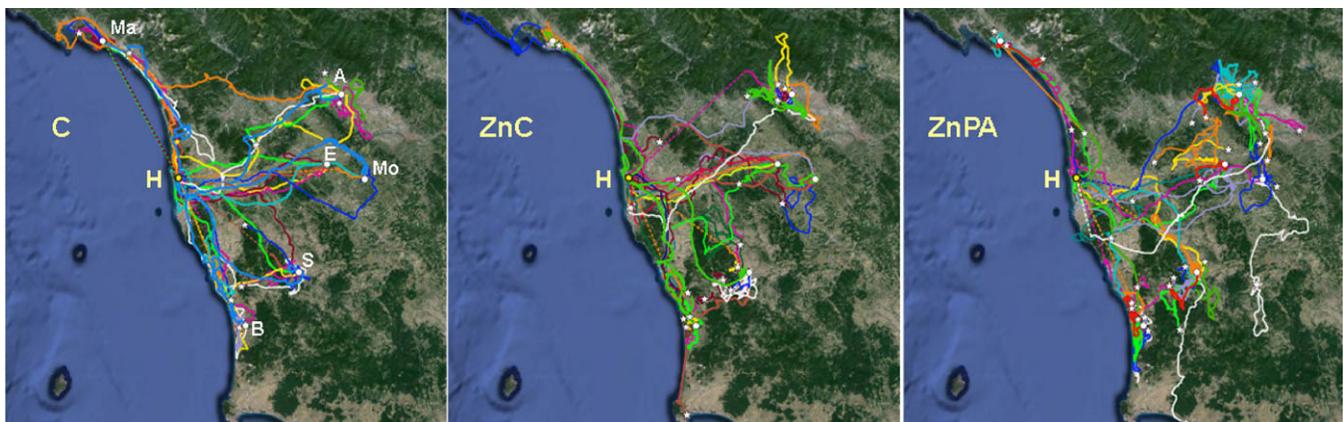


Fig. 1. Tracks of the pigeons released at the six release sites. Different colours indicate individual birds. Release sites and home are indicated by white dots. H, home; Ma, Marinella; A, Agliana; Mo, Montespertoli; E, Empoli; S, Saline di Volterra; B, Bolgheri. White stars indicate the last fix recorded from lost birds. Interrupted tracks of homed birds are linearly connected with dashed lines. C, untreated control birds; ZnC, zinc sulfate-treated control birds exposed to environmental air both during transportation and at the release site; ZnPA, zinc sulfate-treated birds transported and kept at the release site in purified air. Sample sizes are reported in Table 1.

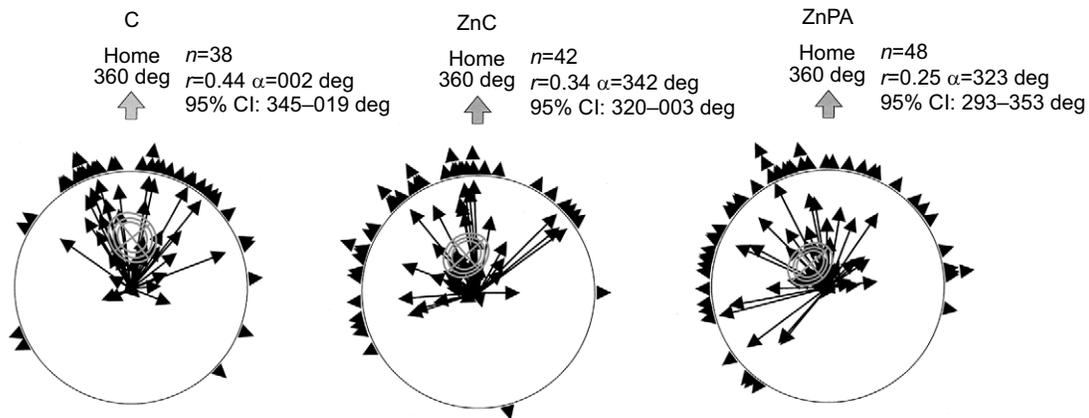


Fig. 2. Initial orientation of the birds in the first 10 km of track. Pooled mean vector distributions of the three groups of pigeons. Each mean vector represents the individual mean bird orientation. The symbols outside the circles represent the orientation of the mean vectors. Confidence interval (CI) ellipses of the second order distributions are reported (Hotelling test, $P < 0.001$ for the three distributions).

ZnPA, 0.19 ($n=45$]), as the C birds performed significantly fewer stops per km of path flown than the other two groups (Dunn's test $P < 0.05$ for both comparisons). However, when the analysis was restricted to the first 10 km of flight path, no significant difference emerged (C, $n=36$; ZnC, $n=42$; ZnPA, $n=45$; Kruskal–Wallis test, $P > 0.2$; the median number of stops was 2 for all three groups). Nevertheless, it is worth noting that 8 out of 36, and 5 out of 42 C and ZnC birds, respectively, never landed during the first 10 km of track, whereas only 1 out of the 45 ZnPA birds did so (comparison of the three groups: $\chi^2=7.949$ $P < 0.025$; C versus ZnC, $\chi^2=1.486$ $P > 0.1$; C versus ZnPA, $\chi^2=8.1$ $P < 0.005$; ZnC versus ZnPA, $\chi^2=3.172$ $P > 0.05$). The comparison of the time spent sitting (Fig. 4) during the first part of the track (10 km) was significantly different according to the Kruskal–Wallis test ($P < 0.05$). The Dunn's test revealed that this difference was due to the longer time spent sitting by the ZnPA compared with the C pigeons (C versus ZnPA, $P < 0.05$; C versus ZnC, and ZnC versus ZnPA, $P > 0.1$). However, while flying, the three groups of birds displayed similar flight speed [Fig. 5; Kruskal–Wallis test, $P > 0.3$; median flight speed: C, 53 km h^{-1} ($n=38$); ZnC, 52 km h^{-1} ($n=42$); ZnPA, 52 km h^{-1} ($n=48$)].

The homing performance of the three groups of birds (Fig. 6) was significantly different according to the Kruskal–Wallis test ($P < 0.001$; C, $n=49$; ZnC, $n=50$; ZnPA, $n=49$). The Dunn's test

revealed that the C birds were significantly faster and more proficient at homing than both the ZnC ($P < 0.02$) and the ZnPA ($P < 0.002$) pigeons. In fact, more than half of the C birds homed on the day after their release, whereas for both ZnC and ZnPA, more than half of the birds were unable to home. It is worth noting that this study was conducted on naïve birds at their first homing experience. This might explain the relatively poor homing speed of the unmanipulated control birds.

DISCUSSION

Traditional experiments, in which vanishing bearing distributions were analysed, suggested that environmental odours perceived during the outward journey and at the release site can provide sufficient information to allow homeward orientation in homing pigeons (Wallraff and Foà, 1981; Benvenuti and Wallraff, 1985; Wallraff et al., 1992). Our analysis conducted on the GPS tracks confirm that homing pigeons exposed to environmental odours during transportation and at the release site displayed unimpaired homeward orientation, even if made anosmic prior release (ZnC birds). These birds turned out to be homeward oriented already at the beginning of their flight (the first 10 km of the track), supporting the critical role of release site odour information for determining the direction of displacement. By contrast, the birds transported and kept at the release site in purified air, and released after having been

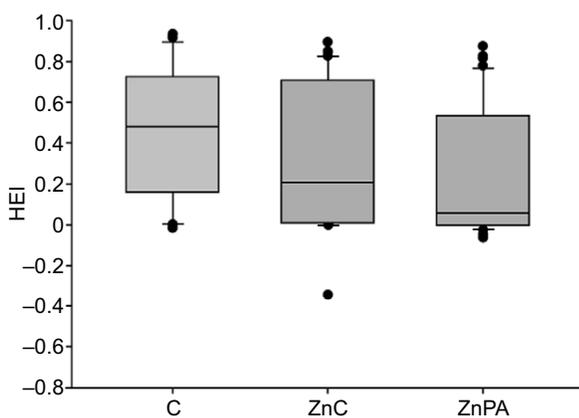


Fig. 3. Homing efficiency index. Box plots report the median HEI values. Second and third quartiles are represented for the three groups of pigeons. See Materials and Methods for details.

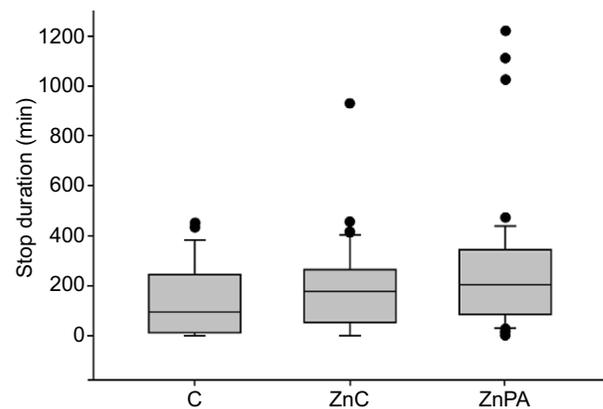


Fig. 4. Time the birds spent landing rather than flying in the first 10 km of path. Box plots show the median values and second and third quartiles for the three groups of birds.

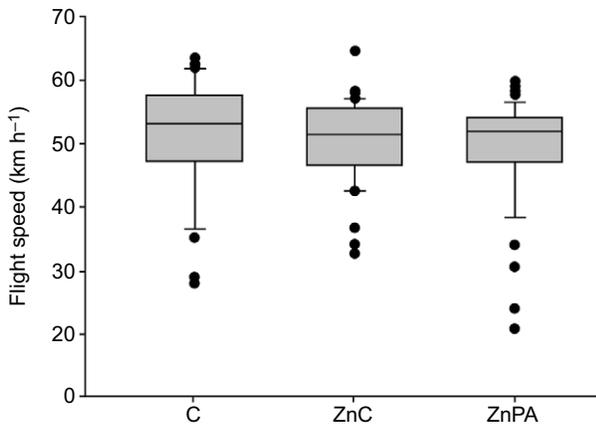


Fig. 5. Median flight speed. Box plots show the median values and second and third quartiles for the three groups of birds.

made anosmic (ZnPA) oriented in a direction significantly different from the home direction, and significantly different from that exhibited by unmanipulated control birds (C). This is consistent with observations of a previous tracking study, in which pigeons were made anosmic prior to release for a short period by treating their olfactory mucosa with a local anaesthetic (Gagliardo et al., 2011a,b).

The novel aspect highlighted by the current study is the behaviour of the pigeons en route, when challenged to find their way home without olfactory information, despite having been exposed to environmental olfactory information before release. The ZnC birds were dramatically impaired in their homing performance, although we showed that they determined the home direction on the basis of the olfactory information perceived prior release. This group performed similar to birds that were not exposed to environmental odours during the experiment (ZnPA). Together, these data suggest that homing pigeons are likely to consult the olfactory map along their way, and that the olfactory information perceived beyond the release site area plays a critical role for a successful homing. This conclusion is consistent with a previous tracking study investigating functional asymmetries in the pigeon olfactory system in a homing task (Gagliardo et al., 2011a). Pigeons released with the right nostril occluded were more likely to stop on their way home and to make longer exploratory flight at the stop sites, compared with pigeons released with the left nostril occluded. This was interpreted to be due to a greater difficulty in consulting the olfactory map en route when the dominant side of the olfactory system was prevented from

receiving olfactory information (right olfactory mucosa/left piriform cortex) (Gagliardo et al., 2005b; Patzke et al., 2011). Consistently, both ZnC and ZnPA birds were more likely to stop along their flight than the C birds. However, this difference did not emerge in the first 10 km of path flown after release. These data suggest that the higher number of stops in the anosmic birds was not due to a non-specific effect of the zinc sulfate treatment performed before release, but instead, a larger number of stops might indicate a greater uncertainty in the navigational decision along the way. Nevertheless, non-significant non-specific effects of the treatment cannot be completely excluded.

Consistent with their homeward orientation, the ZnC pigeons were significantly more likely to display a positive homing efficiency index, indicating a tendency to approach home, even though they were impaired at homing overall. By contrast, the ZnPA birds were significantly more likely to increase their distance from home, as about a third of them displayed a negative homing efficiency index.

According to some authors, olfactory stimuli perceived during transportation and at the release site activate a navigational mechanism based on non-olfactory cues (olfactory activation hypothesis; Jorge et al., 2009, 2010), rather than providing map information, as predicted by the olfactory map hypothesis (Papi, 1989; Wallraff, 2005; Gagliardo, 2013). The olfactory activation hypothesis predicts that olfactory stimuli different to those perceived by the birds at the home area would simply inform the birds that they have been taken away from home, without providing any navigational information. According to the olfactory activation hypothesis, the olfactory activated birds are able to home by relying on a navigational mechanism based on non-olfactory cues (for a debate, see Wallraff, 2014; Phillips and Jorge, 2014; for tracking data not confirming the olfactory activation hypothesis, see Gagliardo et al., 2011a,b). The impaired homing performance of the ZnC birds reported in this experiment is not consistent with the olfactory activation hypothesis. In fact, the ZnC birds, having been exposed to environmental odours during transportation and at the release site, were able to have their navigational system fully activated as demanded by the olfactory activation hypothesis. Consequently, according to the olfactory activation hypothesis, they should have been able to use a navigational mechanism based on non-olfactory cues (magnetic and infrasound, for instance). This is not what we observed here.

One might argue that the anosmia treatment might have affected the pigeons' homing success because of a non-specific effect of the zinc sulfate on the birds. However, this seems very unlikely in the

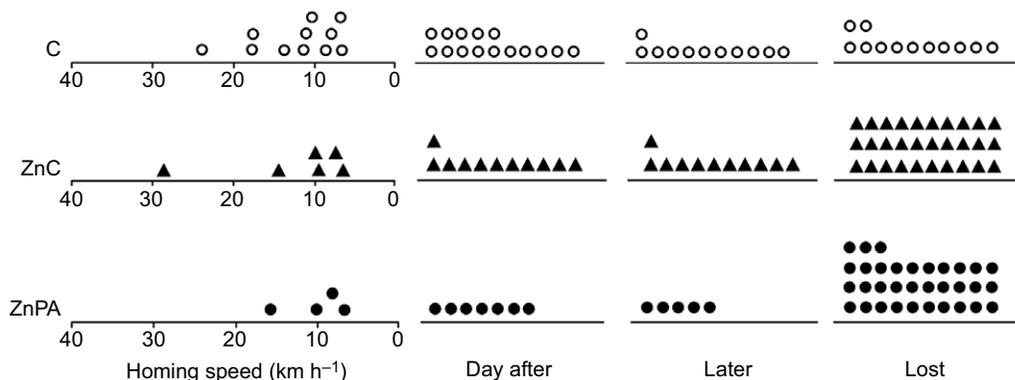


Fig. 6. Homing performance of the three groups of birds. Each symbol represents one pigeon. For the pigeons homed on the day of release, homing speed is reported. Number of pigeons homed 1 day after their release, later than 1 day after release and those lost are indicated on the right.

light of previous evidence. Non-specific effects of zinc sulfate have been tested by Benvenuti and Gagliardo (1996) in an experiment in which unilateral nasal washing was combined with unilateral occlusion of the nostril. When the occluded nostril was ipsilateral to the zinc sulfate washing, the birds displayed unaltered navigational abilities. Zinc sulfate-treated birds released from familiar locations were as good as unmanipulated controls at homing (Benvenuti et al., 1992). It has been also shown that zinc sulfate-treated birds displayed unaltered cognitive abilities in conditioning experiments (Budzynski et al., 1998). When released under clock-shift at familiar locations, anosmic homing pigeons turned out to be more likely to re-orient on the basis of landmarks according to a pilotage strategy, rather than a site-specific compass orientation strategy (Gagliardo et al., 1999, 2005a). The use of pilotage, which requires complex memorisation and recalling of spatial relationships among multiple visual topographical elements, indicates that zinc sulfate treatments do not interfere with the pigeons' cognitive abilities and do not produce general impairment.

For the first time, we show results for anosmic birds treated with zinc sulfate at the release site. This differs from other experiments in which the same treatment occurred at least 1 day before. One might argue that the observed navigational impairment could be due to stress following the treatment, rather than the lack of olfactory information. Interestingly, analysis of the behaviour of the birds during the initial part of their flight (first 10 km of track) highlighted impaired performance of ZnPA, but not ZnC birds compared with the control birds. In fact, among the treated group, only the ZnPA birds were significantly more likely to land and to spend longer time sitting compared with the unmanipulated control pigeons, although no general difference on median number of stops and on flight speed emerged among the three pigeon groups. In addition, it is worth remarking that the ZnC birds oriented towards home within the first 10 km of flight, whereas the ZnPA pigeons oriented in a direction significantly different from the home direction. We therefore suggest that there are no important side effects of the zinc sulfate treatment on the birds, and we conclude that the ZnPA impairment observed in the first part of the flight is consistent with the interpretation that these pigeons completely lack olfactory navigational information.

In conclusion, our tracking study supports the specific role of environmental chemosensory signals in the atmosphere for determining the direction of displacement in homing pigeons and for navigating home from unfamiliar locations. In particular, our tracking data highlight the importance of environmental odours perceived during the homing journey for a successful homing.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

A.G. and M.W. designed this study. A.G. and E.P. performed the tests and the data analysis. A.G. and M.W. wrote the manuscript.

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Data availability

The tracks for each pigeon are available in Movebank (www.movebank.org) at doi:10.5441/001/1.721tr877.

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