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The influence of experience in orientation: GPS tracking of homing pigeons released over the sea after directional training

Gaia Dell'Ariccia*, Giacomo Dell'Omo and Hans-Peter Lipp

Division of Neuroanatomy and Behaviour, Anatomy Institute, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

*Author for correspondence (e-mail: gaia.dellariccia@access.uzh.ch)

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SUMMARY

Flight experience is one of the factors that influences initial orientation of displaced homing pigeons (*Columba livia*). Prior studies showed a systematic dependence of initial orientation on previously flown direction. Using GPS data loggers, this study sought to examine the effect of previous directional training of 40 homing pigeons when they were released over the sea, in the absence of proximal landmarks, in a direction almost perpendicular to that of previous training flights. Our results demonstrated that previous directional training evoked a systematic and predicted deviation from the beeline over the sea that appeared as a compromise between the direction of training and the direction to the loft. Pigeons were able to efficiently correct their flight direction only once over land, where they flew significantly slower and less directly than over the sea.

Key words: *Columba livia*, directional training, experience, GPS tracking, homing pigeon, landmarks, sea.

INTRODUCTION

Individual experience, gained from previous homing flights, is one of the various factors that influences the initial orientation of displaced homing pigeons (*Columba livia*) (Wallraff, 1967). Pigeons benefit from repeated releases from the same site, considerably increasing their homing performance, especially during the first three-to-six releases (Graue, 1965; Wallraff, 2005). Moreover, GPS tracking studies showed that increased familiarity with a release site entails stereotyped routes during homing (Biro et al., 2004), often along longitudinal landmarks roughly pointing home, such as roads and railways (Lipp et al., 2004).

Despite numerous studies on the effects of increased familiarity with an area and the relative increase in homing performance, few experiments have investigated the effects on orientation of repeated releases in the same direction, once the birds are released from new locations. Wallraff (Wallraff, 1974) found that there is a systematic dependence in the vanishing bearings on the direction of previous experience: released pigeons tend to fly in the same direction previously flown, albeit with high individual variation. He hypothesized that the amount and availability of external information for orientation influence the magnitude of the deviation: the more such information is available, the less pigeons rely on previously flown direction. Moreover, he also hypothesized that the navigational process itself could be affected. In other words, the effect of experience might not only result in a directional preference but it could also influence the manner in which the parameters composing the birds' 'map' are processed. According to the 'Map-and-Compass' model (Kramer, 1957), displaced birds first determine their position relative to the home loft based on locally available cues (the map step) and with the aid of olfactory stimuli (Papi, 1991; Wallraff, 2005), they then calculate a homeward course (the compass step) with the aid of the position of the sun (Kramer, 1953) and, presumably, magnetic cues (Wiltschko and Wiltschko, 2003).

The importance of landmarks for orientation is a controversial subject and it remains unclear to which degree they can contribute in the determination and learning of a homeward direction (for a review, see Walcott, 2005); however, numerous studies demonstrated that over familiar territories pigeons follow longitudinal landmarks when available and prefer to fly over areas rich in landmarks (Biro et al., 2004; Lau et al., 2006; Lipp et al., 2004). Moreover, landmarks seem to stabilize the flight direction, even over unknown territories (Lipp et al., 2004).

In this study, we investigated the effect of directional training on orientation of homing pigeons in a context of absence of landmarks. We first trained two groups of pigeons from one of two land release sites located in opposite directions from the loft. We then released these birds individually from a boat at sea, from a point located at an almost perpendicular direction from training flights. Previous experiments have shown that pigeons forced to cross water surfaces chose the shortest way to the coast but also that the general flight direction is not affected once the birds have recognized the home bearing (Wagner, 1972). We selected a release site at sea equidistant from land in all directions over a 100 degree angle bisected by the beeline to the loft. We expected that, if experience gained with directional training entails a biased compass orientation, pigeons will follow the training direction and will reach the coast either to the left or right of the beeline, respectively. Once the coast has been reached, the continuation of flights according to the training direction would indicate a predominant role of directional learning on orientation. On the contrary, a correction to the right homewards direction would indicate the capacity to determine the correct home bearing, gained either during the flight to the coast or from additional terrestrial cues.

MATERIALS AND METHODS

The homing pigeons (*Columba livia* Gmelin 1789) used for this study were all young (approximately six months old) with no previous homing experience. They were located in the facilities of the University of Zurich at Testa di Lepre, Italy, 25 km NW of Rome (12.28 deg.N; 41.93 deg.E). Pigeons of both sexes and with different flying experience inhabited the same loft. Food (a mixture of various cereals, peas, corn and sunflower seeds sold commercially for racing pigeons), grit and water were provided *ad libitum*. All birds were habitually allowed to fly freely outside the loft but none of the experimental pigeons were transported to any other location before the actual experiment.

The entire experiment was carried out between March and July 2006. Forty pigeons in total, both males and females, were equipped with dummies to habituate them to fly and live with the load (22 g, 4–5% of total body mass). The dummy weight was a small piece of PVC, of the same size and mass of the GPS data-logger, which was affixed on their backs with Velcro® strips, following a procedure already described by Biro et al. and Dell'Ariccia et al. (Biro et al., 2002; Dell'Ariccia et al., 2008).

The experiment took place in two stages, due to the availability of GPS loggers. A group of 20 pigeons that had no previous release experience were trained as follows: two flock releases from two sites, 5 km and 10 km distant from the loft, respectively, in the same direction as that of the final release site – Castel Romano (12.44 deg.N; 41.71 deg.E), which was 27 km SE from the loft. From here, pigeons were then released twice as a flock, four times in pairs and six times individually. At the end of this training, every pigeon was released 14 times, always from the same direction with respect to the home loft. During the last two individual releases, we equipped birds with GPS loggers to track their home route. After training, all 20 pigeons were released individually from the sea. The sea release site (11.99 deg.N; 41.77 deg.E) was 30 km SW from the loft and 20 km from the coast at a point between two small promontories, which were at the same distance from the release site – always at 20 km; moreover, the beeline between the sea release site and the loft was perpendicular to the coastline. The angle included between the direction of previous training and the beeline between the sea release site and the loft was 80 deg.

The procedure was then repeated with a new sample of inexperienced pigeons but now from a release site opposite to the first release site. These 20 pigeons had the same age, sex and experience as the first group. They were accustomed to wearing dummies and had received exactly the same training procedure as that of the first group but were released from sites NW from the loft until being released from the final site – Santa Severa (11.98 deg.N; 42.03 deg.E), which was 27 km NW from the loft. Again, after directional training, pigeons were released individually from the sea, from exactly the same site 30 km from the loft. In this case, the angle included between the direction of previous training and the beeline between the sea release site and the loft was 60 deg.

In the last two individual releases from land and in the releases from sea, pigeons were equipped with GPS loggers (www.technosmart.eu): the dummies were replaced by GPS data-loggers just before the release and replaced again on the birds after retrieving the GPS at the loft. The loggers took one positional fix every second and then stored the data. Further technical information can be found in Lipp et al. (Lipp et al., 2004).

All releases took place in sunny conditions for both groups. Birds were released for training with no or light wind; both sea releases took place in days with no wind at all. The total absence of wind was also subsequently verified using the daily ocean wind data by satellite recording that are freely available on the website: http://podaac.jpl.nasa.gov/DATA_PRODUCT/OVW/index.html (Product 109).

During training releases, we lost three pigeons from the NW release site whereas during the sea release, two pigeons got lost – one previously trained from the NW and one from the SE. During the sea release, one GPS logger failed to record and one pigeon returned without his GPS logger; in both cases, the pigeons were previously trained from the NW. Therefore, we finally analyzed 19 tracks of pigeons previously trained from the SE and 14 tracks from the NW.

The raw data were downloaded from the GPS loggers to a computer and analyzed first for possible artefacts and irregularities of recording (program WINTRACK. Freeware D. P. Wolfer at www.dpwolfer.ch/wintrack) (Steiner et al., 2000; Wolfer et al., 2001). The program then extracted the following variables: homing speed (HS: average speed recorded by GPS logger during flight, excluding measures of speed of less than 5 km h^{-1}), flight altitude (ALT), total number (TNrst) and total duration (TTrst) of rests (rests were defined as episodes longer than 5 s with GPS or ground speed less than 5 km h^{-1}), total flying time (TTfly), direction of deviation (DEVlin) and average distance (ADlin) to the beeline between the release site and the loft, and vanishing error (VE: the difference, in degrees, between the vanishing bearing 1 km from the release point and the loft direction).

We also calculated the straightness index (SI) for each track as D/L, in which D is the beeline distance from the starting point to the goal (or the difference between initial and final beeline distance to the loft in case of incomplete tracks) and L is the total path length flown (Benhamou, 2004). This is a scale-independent measure and, considering the high precision of path reconstruction at 1 fix s^{-1}, a reliable estimator of the efficiency of the orientation process.

The variables obtained by WINTRACK and the SI were subsequently statistically analyzed in two different ways: those with a normal distribution (HS, TTfly, DEVlin, ADlin, VE) and those normalized (ALT) were analyzed using the unpaired Student's *t*-test whereas the other parameters that had a non-normal distribution (TNrst, TTrst, SI) were analyzed with the Mann–Whitney *U*-test to compare the effects of different directional training. Normality was tested using the Kolmogorov–Smirnov test.

To investigate possible changes in flight parameters during flight, we cut all tracks at the point where they cross the coastline then compared HS and SI in the path over the sea and over land within each individual flight. To calculate the SI of the segments, we applied the previous formula considering the point of intersection of each track with the coastline as the goal for the sea segments and as the starting point for the land segments. In this way we obtained the real index values for every track segment. We used the paired *t*-test and the Wilcoxon test for HS and SI, respectively.

Analyses were performed using the software package STATISTICA 7™ and with the aid of http://www.physics.csbsju.edu/stats/ (Kirkman, 1996). Plotting of GPS tracks was done with the aid of MapInfo™.

RESULTS

We observed a remarkable difference in the orientation over the sea between homing pigeons from the two different training groups. Results are summarized in Fig. 1, which shows the well-oriented tracks of pigeons during their last training release (Fig. 1A) and the biased orientation in the sea release (Fig. 1B).

Considering sea tracks (Fig. 1B), it appears evident that all pigeons were deeply influenced in their orientation by the direction of previous training: none of the pigeons flew in the opposite direction, and the beeline between the release site and the loft marked an almost complete separation between the groups. However, within both groups there was a certain degree of variability in the amount of deviation from the beeline to the loft.

Most of the pigeons (22 out of 33) crossed the coast over one of the small coastal towns present in this region (Fig. 2). Looking

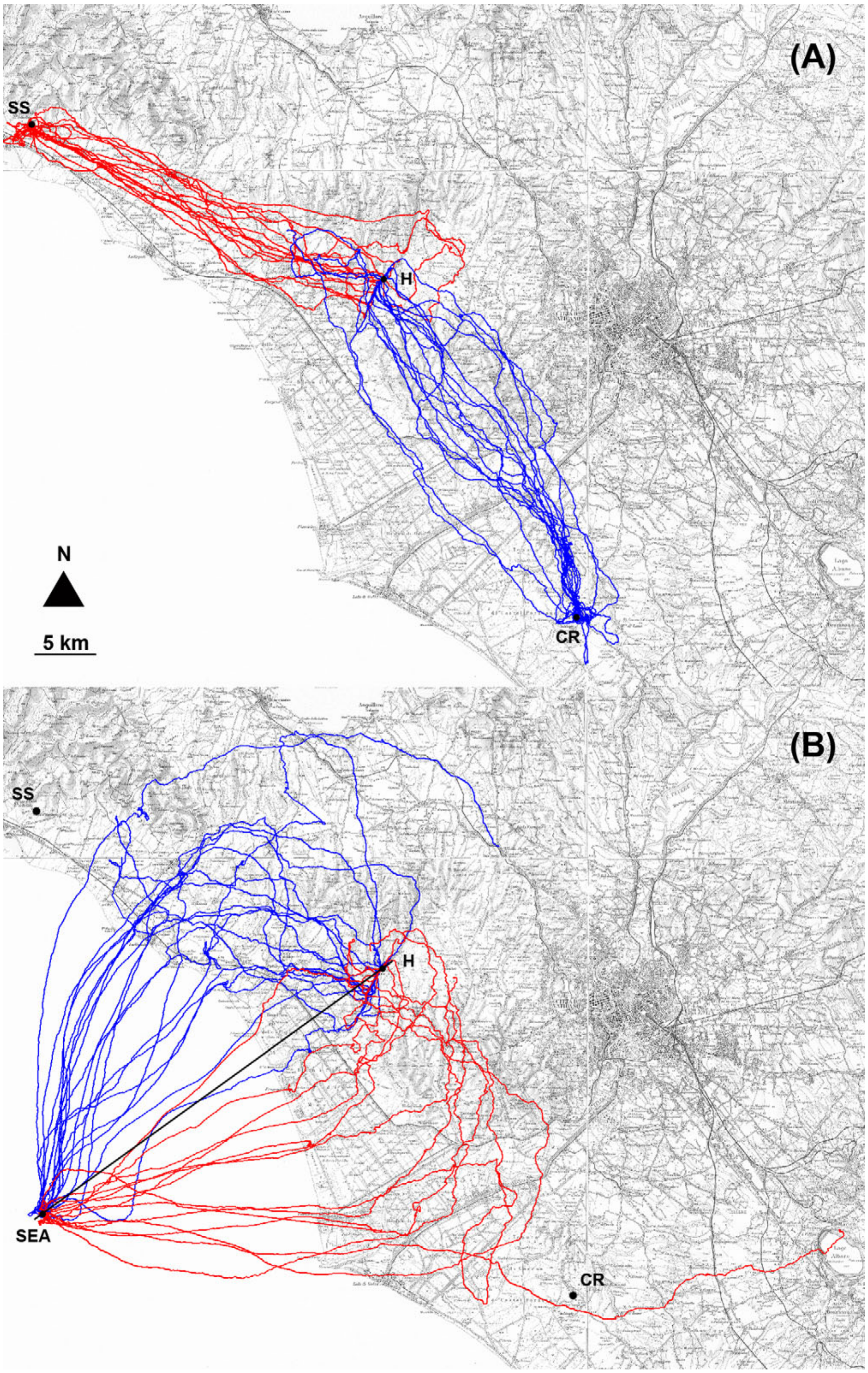

Fig. 1. GPS tracks of homing pigeons (A) during their last training release and (B) during the experimental sea release (SEA). Red tracks: pigeons trained from the release site SS, north-west of the home loft (H). Blue tracks: pigeons trained from the release site CR, south-east of the home loft.

from the sea, towns appear as the most evident and proximate feature of the coastline. This suggests that pigeons could have directed their flight towards conspicuous (even if unknown) points of the coastline.

Once over land, the majority of pigeons (28 out of 33) started to correct their home course and reorient towards the loft, after a variable path length. Some of them changed the home course gradually whereas others changed it abruptly. Only a few pigeons, four in each group, settled down soon after reaching the coast but this appeared not to be linked with the pattern of subsequent reorientation. On the contrary, five pigeons, three previously trained from the SE and two previously trained from the NW, continued to fly in the biased direction, two of them until their GPS batteries became exhausted (they, however, later returned to the loft), the

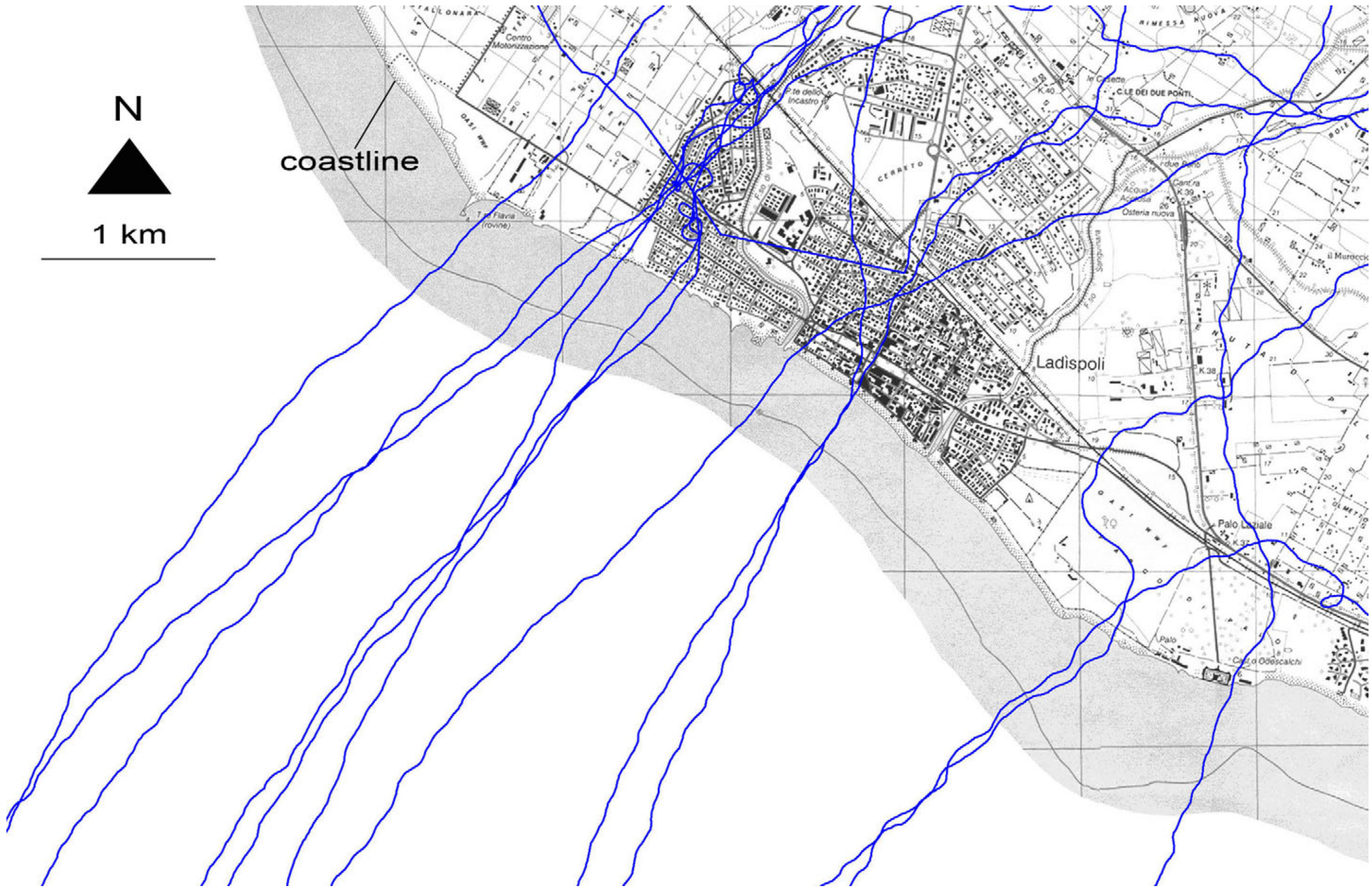

Fig. 2. Detail of Fig. 1B showing eight tracks crossing the coastline in correspondence of the town of Ladispoli and four tracks crossing over countryside and cultivated areas. The high density of conspicuous buildings makes towns the most evident feature of the coastline when looking from the sea.

others continued until the moment when they reversed their biased course.

The difference between the two groups in the average deviation from the beeline from the release site to the loft was highly significant in terms of direction (DEVlin, unpaired *t*-test: t_{31}=7.614, P<0.00001) whereas there was no difference in the magnitude of such deviation (ADlin, unpaired *t*-test: t_{31}=–0.26, P=0.8). Moreover, no other flight parameters were influenced by the difference in previous directional training, indicating that the bias occurred primarily during the initial orientation step (P=0.8 for TTfly; P=0.1 for VE; P=0.5 for HS; P=0.5 for SI; P=0.7 for ALT; P=0.5 for TTrst; P=0.9 for TNrst).

The influence of previous training was also assessed by measuring the average deviation of the path over the sea from the previous training direction. For the group previously trained from the NW it was 23 deg. whereas for the group previously trained from the SE the deviation was 52 deg. This discrepancy is due to the fact that for the NW group, the previous training direction exactly corresponded at sea to the direction to the small promontory to the south on the coast whereas for the SE group, the previous training direction was slightly beyond the promontory to the north. As a consequence, for this group, the coastline limited the deviation from the correct beeline, enhancing the deviation from previous training.

Comparisons of the tracks' segments over the sea with the segments over land showed that when flying over the sea, pigeons had faster and more direct flights than when over land (for HS, *t*-test: t_{31}=–4.42, P=0.0001; for SI, Wilcoxon signed-ranks test: T=–4.94, P<0.0001) (Fig. 3).

DISCUSSION

Our results showed a strong effect of previous directional training on initial orientation of pigeons released at sea. All pigeons had a strong tendency to fly with a bias in the direction from which they had been initially trained, even if there was an individual variability in the magnitude of deviation. Moreover, pigeons started to correct their direction only after reaching the coast, and showed high difference in flight behaviour over sea and over land.

The absence of proximal landmark cues over the sea obliged pigeons to rely primarily on their compass sense. The chosen sea release site was 20 km from the coast and equidistant to the shore for an angle of approximately 100 deg. symmetrically around the beeline from the release site to the loft. Thus, the directions chosen by the pigeons were not biased by simply choosing the shortest way to the coast. It is likely that, when released, pigeons saw the coastline, which probably accounts for the lack of initial flight paths pointing to the open sea. Moreover, the flight paths we recorded towards unknown coastal regions suggest that the birds were barely steering towards coastal landmarks, as highlighted by the fact that the majority of pigeons reached the coast over towns.

The observed flight paths over the sea appeared to reflect an individually variable compass setting between the tendency to

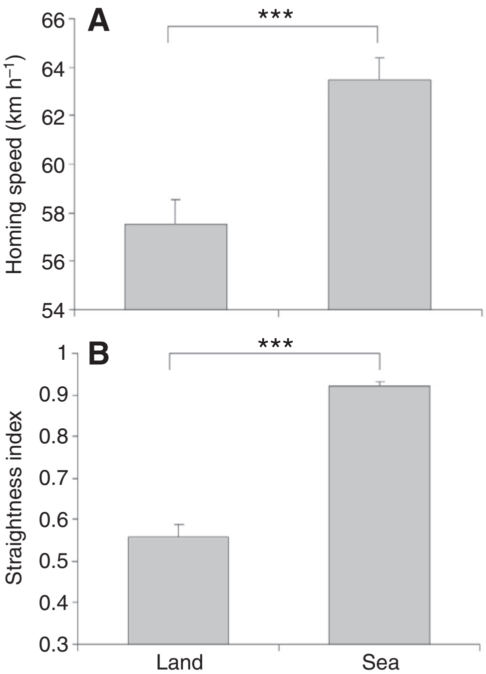

Fig. 3. (A) Average homing speed recorded by GPS and (B) straightness index during flight paths over sea and over land of the same tracks. When over sea, pigeons fly faster and straighter than when flying over land. Bars indicate means and s.e.m. ***P<0.0001.

rapidly approach the shore, the acquired training direction and the true home direction. In extreme cases, the birds either headed home almost perfectly or followed the previous training direction, respectively. On average, however, the flight direction over the sea appeared to reflect a mean between the true home direction and the previous training one. This is more evident in pigeons previously trained from the NW, for which the training direction corresponds to the direction of the small promontory to the south on the coast. Their average direction is exactly the mean between previous training and beeline to the loft.

As strict terrestrial birds, pigeons are neither able to swim nor float, hence they generally avoid flying over water surfaces; when forced to cross them, they choose the shortest way to the coast (Bonadonna et al., 1997; Wagner, 1972). However, on one hand, the choice of the release site (i.e. equidistant from the shore within 100 deg.) ruled out a directional choice based on the shortest distance to the shore. On the other hand, stress associated with flying over water may have led pigeons to reach the coast very rapidly and directly. This is reflected in the significantly higher speed and straightness of flight recorded over sea than over land, and is also supported by the fact that pigeons released at sea circled significantly less around the release point than pigeons released over land, even when from familiar locations (G.D'A., G.D'O. and H-P.L., unpublished data). Thus, the limited corrections of the flight directions over the sea may be related to the aversive component of this environment, giving previous experience a predominant role in the determination of bearings under these conditions.

Pigeons reached land over completely unknown territories, as birds trained in the north reached land south of the loft and *vice versa*. Once they had reached the coast, only a few individuals continued to fly in the direction of previous training whereas most of them (28 out of 33) were able to correct their course more or less gradually. Such changes in flight direction suggest that the acquired directional training was no longer a decisive factor, once they were over land, in homeward orientation.

Wallraff has hypothesized that the less information available for orientation the more pigeons rely on previous flown direction (Wallraff, 1974). From our data it is not possible to conclude whether the terrestrial environment contains more information for a correct orientation or whether pigeons could have already determined the correct loft position over the sea but preferred to first reach the coast rapidly and follow the homeward direction afterwards. Once over land, pigeons appeared attracted by landscape features, thus increasing path tortuosity and decreasing flight speed. Lau and colleagues demonstrated that pigeons are generally attracted by territories with higher densities of edges, which are considered a relevant feature characterizing landscapes (Lau et al., 2006). Over such kind of territories, pigeons' flights show higher levels of entropy, i.e. an increase in directional and orientation changes. Therefore, the attraction by landmarks could distract pigeons from the chosen home direction, inducing them to frequently reorient and gradually redirecting towards the correct home course.

At the same time, some pigeons, in particular those that continued to fly with a bias in the training direction after crossing the coastline, turned abruptly, changing their route by 90 deg. to 180 deg. We can suppose that pigeons inverted their route most probably when the map mechanism gave them the information that the home loft was actually in the opposite direction (Wallraff, 1991).

An alternative explanation could be the existence of a sense of distance, perhaps an odometric memory as found in other species homing (Wittlinger et al., 2006). This sense, possibly acquired with repeated release experience from the same homing distance, may provide pigeons with an indication of the approximate flight distance to the home loft, leading them to reorient once this distance has been covered. In our study, most birds changed their orientation soon after reaching the coast, which was only at a slightly shorter distance from release point than previously experienced homing distance. This makes it impossible at present to discriminate between the two factors that would necessitate more specific experiments, such as releases of pigeons previously trained from different distances. Corrections after an expected flight distance, however, are frequently observed by GPS tracking of highly trained pigeons [for examples, see the flight tracks of the training flights (Fig. 1A), and also tracks in Lipp et al. (Lipp et al., 2004)].

In conclusion, releases over the sea can reveal orientation behaviour of pigeons with particular clarity, as flight paths are less confounded by topographical attractors. Our results indicate that previous flight experience resulted in a conflict between acquired directional experience and setting off the compass direction from an unknown release site, expressed over the sea by the motivation of reaching the shore as fast as possible. Once they had reached the coast, pigeons were able to correct their biased orientation and redirect homewards. Further investigations would be necessary to elucidate the relative role of the various potential mechanisms operating such correction, including the map mechanism, the influence of landmarks or the presence of a sense of distance.

LIST OF ABBREVIATIONS

ADlin	average distance to beeline between release site and loft
ALT	flight altitude
D	beeline distance from starting point to the goal

DEVlin	direction of deviation from the beeline between release site and loft
HS	homing speed
L	total path length flown
SI	straightness index
TNrst	total number of rests
TTfly	total flying time
TTrst	total duration of rests
VE	vanishing error

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