RESEARCH ARTICLE

Olfactory lateralization in homing pigeons: a GPS study on birds released with unilateral olfactory inputs

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SUMMARY

A large body of evidence has shown that pigeons rely on an olfactory-based navigational map when homing from unfamiliar locations. Previous studies on pigeons released with one nostril occluded highlighted an asymmetry in favour of the right nostril, particularly concerning the initial orientation performance of naïve birds. Nevertheless, all pigeons experiencing only unilateral olfactory input showed impaired homing, regardless of the side of the occluded nostril. So far this phenomenon has been documented only by observing the birds' vanishing bearings. In the present work we recorded the flight tracks of pigeons with previous homing experience equipped with a GPS data logger and released from an unfamiliar location with the right or the left nostril occluded. The analysis of the tracks revealed that the flight path of the birds with the right nostril occluded was more tortuous than that of unmanipulated controls. Moreover, the pigeons smelling with the left nostril interrupted their journey significantly more frequently and displayed more exploratory activity than the control birds, e.g. during flights around a stopover site. These data suggest a more important involvement of the right olfactory system in processing the olfactory information needed for the operation of the navigational map.

Key words: homing pigeon, olfaction, navigation, lateralization, GPS tracking.

INTRODUCTION

Since the olfactory navigation hypothesis was first proposed by Floriano Papi (Papi et al., 1971), a large body of evidence supporting the crucial role of olfactory cues in navigation has accumulated (Wallraff, 2005). This hypothesis predicts that pigeons learn the association between the environmental odours carried by the winds with the direction from which they blow (Ioalè et al., 1990), so individuals can build up a map of the region around the home area on the basis of the distribution of olfactory cues (Wallraff and Andreae, 2000). When birds are displaced, the identification of the prevalent local odours provides the pigeons with information about the direction of displacement. Therefore, the released birds are able to orient towards home using a compass mechanism (Keeton, 1971; Schmidt-Koenig, 1961). The strongest evidence in favour of the olfactory navigation hypothesis comes from two main kinds of experimental protocols: (1) the manipulation of the olfactory system in order to prevent odour perception prior to release (Gagliardo et al., 2009; Papi, 1982; Wallraff et al., 1989) and (2) the manipulation of olfactory information, either in terms of odour quality or wind direction at the home loft, aimed at preventing or manipulating map learning (Ioalè et al., 1978; Ioalè et al., 1990; Odetti et al., 2003; Papi et al., 1974; Papi, 1986; Wallraff, 1979). The latter, applied on birds with an intact olfactory system, provided results supporting a specific role of olfactory cues in navigation and contradicting the olfactory activation hypothesis, which attributes to the olfactory stimuli a role in priming a non-olfactory navigational mechanism (Jorge et al., 2009).

Because of the relevance of olfactory stimuli in spatial behaviour on a large scale, homing pigeons represent an excellent animal model for investigating functional asymmetry in the avian olfactory system, although this issue was taken into consideration only recently. The first evidence of functional lateralization in the avian olfactory system was provided in chicks exposed to olfactory stimuli during imprinting (Vallortigara and Andrew, 1994). This study revealed that chicks performed better in a discrimination task between olfactory familiar and unfamiliar rearing objects when the olfactory input was conveyed through the right nostril. An advantage of the right nostril was also reported in relation to the head shaking response, following the presentation of a high concentration of eugenol (Rogers et al., 1998). The first comparison of initial orientation and homing performance from unfamiliar sites in pigeons receiving unilateral olfactory inputs (Benvenuti and Gagliardo, 1996) was done on birds with previous extensive homing experience and it did not highlight any functional asymmetry. A more recent study on naïve pigeons showed a clear advantage in favour of the right nostril (Gagliardo et al., 2007), with regard to their initial orientation. The homing success of the birds with unilateral nostril occlusion was, however, lower than controls, regardless of the side of the treatment.

In order to investigate the behaviour en route of birds receiving a unilateral olfactory input, we performed a homing experiment from an unfamiliar location using birds that were outfitted with GPS data loggers and released with one nostril occluded. So far

the effect of unilateral occlusion of the nostrils on orientation has been documented by recording the vanishing bearings of naïve birds (Gagliardo et al., 2007), whereas in the present work we used pigeons with previous homing experience. In this way we increased the probability of all birds returning with their loggers, although we did not expect any difference between the groups with right and left nostril occlusion (Benvenuti and Gagliardo, 1996).

MATERIALS AND METHODS
General procedure

Thirty-one pigeons (*Columba livia*, Gmelin 1789), approximately 12–18 months of age and hatched at the Arnino field station (43°39′26″N, 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. Individuals had a single previous homing experience as they had been released once from 40 km north or south from home 1 year before the experiment. The experiments took place in July 2008. The pigeons were divided into three experimental groups: unmanipulated control pigeons (C; $N=9$), pigeons released with the right nostril plugged (RNP; $N=9$) and pigeons released with the left nostril plugged (LNP; $N=10$). Twenty days prior to the experimental releases 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 to the feathers, which had been trimmed.

GPS data loggers

We used miniature GPS data loggers (www.technosmart.eu) to record the positional data of flying birds with an accuracy of ~4 m (Steiner et al., 2000; Lipp et al., 2004). For the current study, the GPS data loggers stored one position fix every 10 s. However, in one case (LNP pigeon 520) a device was unable to receive a satellite signal for a short period. During such a recording gap, a straight flight path between interrupted fix points is visualised in the track and that portion was not included in the analysis. The positional fixes stored by the GPS data loggers include latitude, longitude and time of recording. The devices also provide information about altitude, but with insufficient precision to allow a reliable analysis. The tracks for each pigeon for each recorded release were visualised with MapInfo (Dalkeith, UK).

Test releases

The evening before the experimental releases, one nostril of each of the RNP and LNP pigeons was plugged. The plugs were made with a small amount of paste (Xantopren®, Heraues Kulzer, Hanau, Germany), which turns into a solid rubbery plug after insertion into the nostril. The plugs were removed once the pigeons homed. If, during the night, some pigeons had lost the plug, it was replaced early in the morning before displacement to the release site. From our preliminary observations, the pigeons are able to expel the plug within a few days. Therefore, we assume pigeons that did not return to their home loft eventually lost their plug.

All birds were released from Cigoli (43°40′34″N, 10°49′19″E; home direction 267 deg, home distance 41.6 km). Just prior to release, the dummy on the back of each pigeon was replaced with a GPS data logger. Each pigeon was released singly, with at least 30 min between releases. All the experimental releases took place under sunny conditions, with no or light wind.

Quantitative analyses and statistical procedures

All tracks shorter than 15 km were excluded from the analysis. For each pigeon, we considered the following aspects of the flight path in the analysis: track length, stops and tortuosity of the path. Moreover, we analysed the virtual vanishing bearing at 2 km from the release site.

Efficiency index

To compare the length of the homing journey we considered the efficiency index, which we calculated as the ratio between the track length and the beeline distance between the release site and home. When the tracks were not complete we added the linear distance from the end of the track to the loft. The efficiency indices of the experimental groups were compared using the Kruskal–Wallis test. Dunn's test was used for multiple comparisons.

Behaviour at stop sites

We considered a 'stop site' a location where a bird interrupted its flight. A stop site was identified by visually inspecting the track at a high magnification and a pigeon was defined as having left a stop site when it departed the stop site and flew for more than 500 m without coming back. We compared the number of stops relative to the recorded track length using the Kruskal–Wallis test. Dunn's test was used for multiple comparisons.

At stop sites, the birds, besides sitting, also flew over the same area without progressing their journey; therefore, we assumed that a bird was performing exploratory flights when the recorded speed was greater than or equal to 20 km h^{-1}. For each stop performed by each bird, the length of the path flown at a speed of at least 20 km h^{-1} was calculated. When such a path exceeded 500 m we assumed that a bird in that particular stop had performed an exploratory behaviour and we considered that stop as an exploratory stop. It should be noted that movement at a speed of at least 20 km h^{-1} was always preceded and followed by movements at a lower speed (10–18 km h^{-1}) before landing and after taking off. For analysis, we assigned a score to each bird depending on the number of the exploratory stops performed; the scores of the groups were compared using the Kruskal–Wallis test. Dunn's test was used for multiple comparisons.

The percentage of time spent by the three groups of birds at the stop sites relative to the duration of the recorded flight was compared using the Kruskal–Wallis test, and Dunn's test was used for multiple comparisons.

Tortuosity

To perform this analysis we drew concentric circles around the release site with radii increasing by 1 km intervals. The analysis was performed from the ring ranging from 1 to 2 km up to the ring ranging from 29 to 30 km. We considered separately the portions of the tracks included in the ring delimited by two consecutive circles, as reported in Fig. 1. For each portion we considered the direction taken by the bird moving from one point to the next and, therefore, calculated the mean vector. The mean vector length is a suitable parameter for indicating directional stability because it tends to be small when the birds frequently change their direction and tends to be ~1 when they maintain a stable direction. Therefore, we applied a two-way repeated-measures (RM) ANOVA on the mean vector lengths relative to portions of the tracks recorded at increasing distances in order to compare the tortuosity in the flight path of the three experimental groups. The Student–Newman–Keuls (SNK) method was applied for multiple comparisons. This analysis was made after having excluded the portions of the tracks recorded at the stop sites.

Fig. 1. Example of how a track was divided into portions for the analysis of tortuosity. Each portion included the tracts of the path falling within the ring delimited between two successive circles of 1 km increasing radius (left panel). The analysis was performed from the ring ranging from 1 to 2 km up to the ring ranging from 29 to 30 km. In the right panel, a section of the track falling within the first ring is represented. The arrows represent the directions taken by the bird flying from one fix to the next, which have been used to calculate a mean vector.

Virtual vanishing bearings and virtual vanishing and homing times
We recorded the direction of the birds at both 1 and 2 km from the release site, the latter corresponding to the virtual vanishing bearing. The circular distributions were tested for randomness by means of both the Rayleigh and V-tests and compared using the Mardia–Watson–Wheeler test (Batschelet, 1981). In addition, we compared the virtual vanishing times (the time taken by the bird to fly 2 km away from the release site) and the homing times of the three experimental groups using the Kruskal–Wallis test.

RESULTS
One C pigeon and one RNP pigeon returned without a GPS data logger and one LNP pigeon did not home. Four tracks (one C and three LNP) were shorter than 15 km and were excluded from the analysis. Therefore, we obtained seven tracks for C pigeons, six tracks for LNP pigeons and eight tracks for RNP pigeons (see Fig. 2A–F).

Efficiency index
The RNP pigeons tended to display longer tracks and, therefore, a lower efficiency index than the other two groups, although the Kruskal–Wallis test did not reveal a significant difference between the efficiency indices of all of the tracks of each of the three groups of birds (median efficiency indices are 0.680, 0.480 and 0.435 for C, LNP and RNP, respectively).

Stops
The number of stops for each pigeon and the locations of the stops can be observed in Fig. 2A–F. In the same figure, a magnification of a track at a stop site is presented as an example (Fig. 2G). The median number of stops per km was as follows: C, 0.03; RNP, 0.10; and LNP, 0.06. The results of the Kruskal–Wallis test applied to

the number of stops relative to the recorded track length revealed a statistically significant difference ($P<0.05$). In particular, the RNP group stopped significantly more often than the C group (Dunn's test, RNP *vs* C, $P<0.05$). No difference emerged between the LNP group and the other two groups.

As regards the exploratory behaviour at the stop sites, the median scores were as follows: RNP, 3; LNP, 1.5; and C, 0. The Kruskal–Wallis test revealed a significant difference between groups ($P=0.031$). In particular, the RNP pigeons were significantly different from the C pigeons (Dunn's test, $P<0.05$) but not from the LNP pigeons. No difference emerged between the LNP and C groups.

According to the Kruskal–Wallis test, the groups differed in the percentage of time spent at the stop sites relative to the duration of the recorded flight ($P=0.041$). Dunn's test revealed that this value was significantly higher for the RNP group than for the C group ($P<0.05$), but not compared with the LNP pigeons. No difference emerged between the LNP and RNP groups (median percentage of time: C, 34.6%; LNP, 59.5%; and RNP, 76.9%).

Tortuosity
The analysis of the tortuosity applied to sectors of the tracks at increasing distances from the release site showed a significant difference between the three experimental groups (two-way RM ANOVA, $F_{2,18}=5.753$, $P=0.012$). As shown in Fig. 3, the RNP group showed a smaller vector length than both the C (SNK, $P=0.010$) and LNP groups (SNK, $P=0.027$). The analysis revealed a statistically significant difference among the different distances from the release site between groups (two-way RM ANOVA, $F_{28,496}=2.478$, $P<0.001$). In fact, all pigeons, regardless of experimental group, consistently showed a more tortuous path soon after having left the release site (portion of the tracks included in
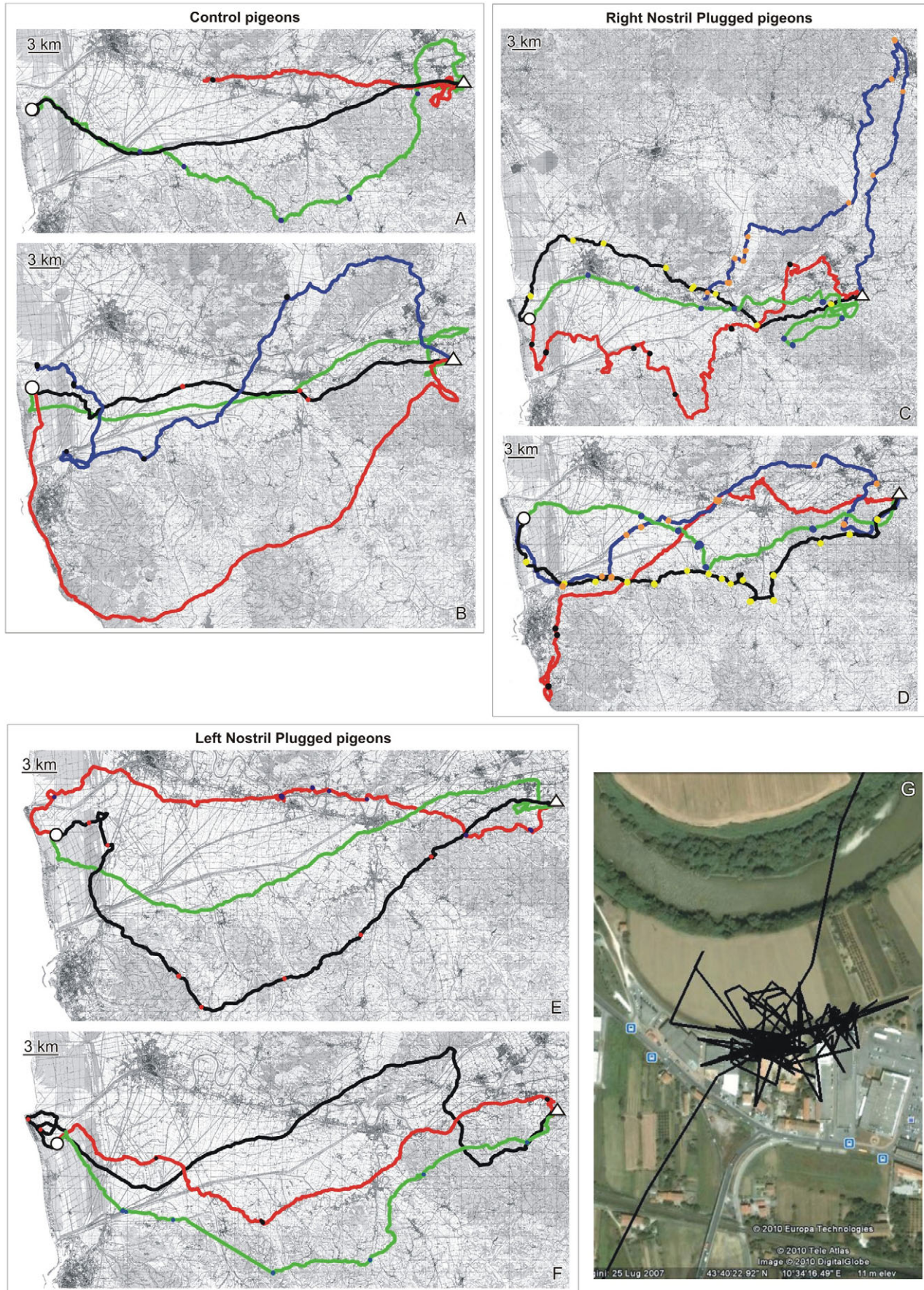
Fig. 2. See next page for legend.

Fig. 2. Tracks of pigeons belonging to the three experimental groups: control, right nostril plugged (RNP) and left nostril plugged (LNP). Open triangle, release site; open circle, home site. The stop sites are marked with a different colour for each track. Individual pigeons and date of release are indicated as follows. (A) Tracks of control pigeons: red, #872, 09/07/2008; black, #551, 16/07/2008; green, #787, 09/07/2008. (B) Tracks of control pigeons: red, #757, 16/07/2008; black, #812, 15/07/2008; blue, #798, 15/07/2008; green, #181, 15/07/2008. (C) Tracks of RNP pigeons: red, #530, 15/07/2008; black, #856, 09/07/2008; blue, #748, 09/07/2008; green, #141, 11/07/2008. (D) Tracks of RNP pigeons: red, #867, 09/07/2008; black, #750, 16/07/2008; blue, #888, 11/07/2008; green, #577, 16/07/2008. (E) Tracks of LNP pigeons: red, #766, 12/07/2008; black, #850, 16/07/2008; green, #174, 09/07/2008. (F) Tracks of LNP pigeons: red, #537, 09/07/2008; black, #859, 11/07/2008; green, #520, 16/07/2008. (G) Example of movements of a pigeon around a stop site.

the 3–4 km sector) than at greater distances (SNK, $P<0.05$). There was no significant interaction between treatment and distance from the release site (two-way RM ANOVA, $F_{56,496}=0.678$, $P=0.964$).

Virtual vanishing bearings and virtual vanishing and homing times

The three groups of pigeons were significantly oriented at both 1 km (Rayleigh test: C, $P<0.001$; LNP, $P<0.005$; RNP, $P<0.02$) and 2 km (Rayleigh test: C, $P<0.002$; LNP, $P<0.02$; RNP, $P<0.01$) from the release site. The mean vector length, mean vector direction and the homeward component are as follows, respectively, for each group of birds: 1 km from the release site, C, 0.95, 265 deg and +0.95; LNP, 0.85, 247 deg and +0.80; and RNP, 0.71, 243 deg and +0.65; 2 km from the release site, C, 0.93, 262 deg and +0.92; LNP, 0.84, 243 deg and +0.77; and RNP, 0.77, 243 deg and +0.70. The Mardia–Watson–Wheeler test did not reveal any significant difference in orientation between the groups ($P>0.5$) at either 1 or 2 km from the release site.

The virtual vanishing times (relative to 2 km distance) of the three groups were not significantly different according to the Kruskal–Wallis test ($P>0.1$; median vanishing times: C, 2 min 24 s; LNP, 3 min 52 s; RNP, 2 min 55 s).

The three experimental groups did not differ in their homing times according to the Kruskal–Wallis test ($P>0.05$), although the RNP group tended to take a longer time to home (median homing times: C, 3 h 12 min; LNP, 4 h 2 min; and RNP, 7 h 40 min).

DISCUSSION

The analysis of the homing flight path of experienced pigeons receiving a unilateral olfactory input highlighted some of the effects of the right nostril occlusion, which remained undetected when observing only the initial orientation of the birds at vanishing. Consistent with a previous report on the orientation performance of experienced unilaterally anosmic pigeons (Benvenuti and Gagliardo, 1996), no functional asymmetry emerged in the virtual vanishing bearing, i.e. the direction of the birds at 2 km from the release site.

In contrast, the analysis of the tracks revealed that the occlusion of the right nostril apparently affected the behaviour of the birds *en route*. The birds receiving the olfactory input only from the left nostril interrupted their journey more often than both those receiving input from the right olfactory mucosa only and those receiving bilateral olfactory inputs. Therefore, the delayed movement behaviour of the RNP pigeons cannot be explained with an effect of the nasal plug *per se*, but is instead consistent with the interpretation that the treatment specifically affects the right olfactory system. An inspection of the behaviour of the birds at their stop sites revealed that the pigeons did not simply interrupt their homing flight for resting, but also performed some flight activity around the stop site, which might represent an exploratory behaviour for sampling navigational cues. This hypothesis should be testable in the future using data loggers recording even higher-definition GPS data, allowing for a test of directional bias within flights around a stop site. Interestingly, the RNP pigeons exhibited such exploring activity more often compared with the control pigeons, which might suggest that birds have difficulty gathering and processing olfactory cues received with the left olfactory mucosa. Nevertheless, the main behavioural difference between the LNP and RNP birds emerged in the tortuosity of the flight path. In fact, the group released after occlusion of the right nostril displayed a more tortuous flight path than both the un-manipulated control pigeons and the birds smelling with the right nostril. On the whole, the behaviour of the RNP pigeons suggested a specific role of the right nostril in processing olfactory information useful for the operation phase of the navigational map. This might be due to an advantage of the right nostril/olfactory bulb in perceiving and/or discriminating the local environmental odours, although this functional dominance is not accompanied by a higher immediate-early gene ZENK expression
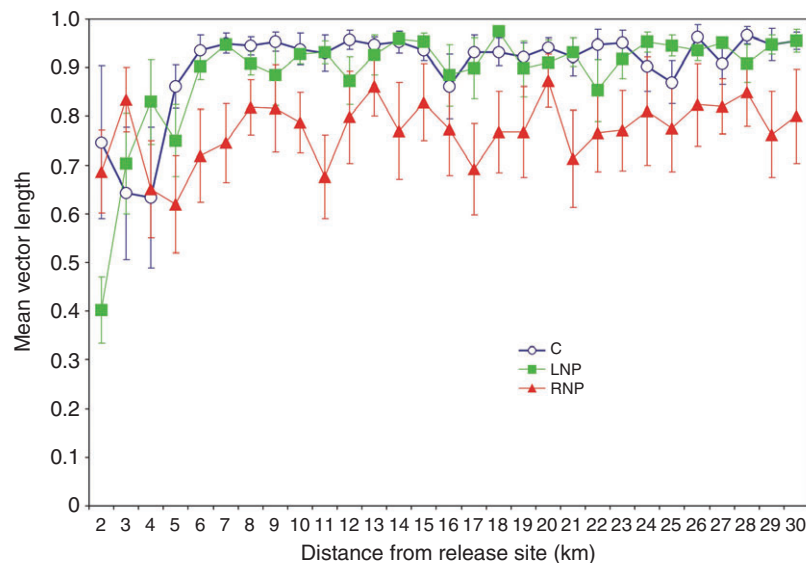

Fig. 3. Mean vector lengths relative to the portion(s) of the track falling within each ring as shown in Fig. 1, and calculated on the directions taken by the birds moving from one fix to the next. The mean vector length is taken as a measure of the tortuosity of the path.

in the right olfactory bulb in comparison with the left one (Patzke et al., 2010).

Our findings are consistent with the reported asymmetry in favour of the right nostril observed in chicks discriminating between familiar and unfamiliar olfactory rearing objects (Vallortigara and Andrew, 1994) or responding with head shaking to a high concentration of eugenol (Rogers et al., 1998). Interestingly, a lateralization in favour of the right nostril has also been demonstrated in humans, particularly in evaluating odour intensity (Thuerauf et al., 2008) and in olfactory detection and discrimination (Kobal et al., 2000; Zatorre and Jones-Gotman, 1990).

According to anatomical studies on homing pigeons, the olfactory bulbs project mainly to the piriform cortex through both ipsilateral and contralateral fibres, although the latter are less numerous (Bingman et al., 1994; Reiner and Karten, 1985). A specific role of the piriform cortex in pigeon navigation is supported by lesion experiments, which have shown a navigational impairment in the piriform-cortex-ablated pigeons (Papi and Casini, 1990). The same was observed in ZENK activation experiments, which showed an activation of the piriform cortex following displacement to an unfamiliar location (Patzke et al., 2010). Release experiments on pigeons subjected to unilateral piriform cortex ablation showed that both the left and right portions of the piriform cortex are involved in the homing process from unfamiliar sites, but that the left piriform cortex plays a dominant role. In fact, although the birds with ablation to the left piriform cortex were randomly scattered after release, the pigeons with lesion to the right piriform cortex displayed an unimpaired initial orientation (Gagliardo et al., 2005a). It is worth noting that the pattern of the scattering is reversed when occluding one nostril. In fact, a similar impairment in initial orientation occurs in birds released either after ablation of the left piriform cortex or after occlusion of the right nostril (Gagliardo et al., 2007).

Despite the fact that the contralateral contribution of projections from the receptor to the central processing areas (as the piriform cortex) in the olfactory system of birds is low, whereas in the visual system all fibres of the optic nerve cross over completely (Güntürkün, 1997), interestingly, we observed a similar pattern of functional asymmetry, i.e. an advantage of the right receptor and a dominance of the left hemisphere in processing the sensory inputs (Gagliardo et al., 2001; Gagliardo et al., 2005b; Prior, 2006). This suggests a possible involvement of other brain structures and neural connections in olfactory-guided navigation other than the (mainly) ipsilateral projection between the olfactory bulb and the piriform cortex.

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