

## Navigational abilities of adult and experienced homing pigeons deprived of olfactory or trigeminally mediated magnetic information

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### SUMMARY

**Anatomical evidence and conditioning experiments have suggested that magnetoreceptors innervated by the ophthalmic branch of the trigeminal nerve are located in the upper beak of homing pigeons. Following these findings it has been proposed that the trigeminally-mediated magnetoreceptors are able to detect magnetic field intensity, which might be useful for a position finding mechanism for pigeons homing from unfamiliar locations. Recent data have shown that, in inexperienced pigeons, section of the ophthalmic branch of the trigeminal nerve does not impair navigational abilities. Similarly, no impairment was observed if the trigeminal section was performed on young pigeons, before they have had the opportunity to learn a navigational map. By contrast, section of the olfactory nerve either in adult inexperienced pigeons or in young birds before map learning, disrupted their homing performance. Nevertheless, because a magnetic map mechanism requires training flights for learning the magnetic gradient of the territory around the loft, the question remains as to whether the navigational performance of adult experienced pigeons can be affected by lack of magnetic information. To answer this question we extensively group-trained adult pigeons and then surgically deprived them of either olfactory or trigeminally mediated magnetic information, prior to testing their navigational abilities. The birds deprived of trigeminally mediated magnetic information displayed similar navigational abilities as intact control pigeons, whereas the olfactory-deprived pigeons were dramatically impaired in homing. Our data show that even in trained adult pigeons, olfactory cues are needed for homing from unfamiliar locations and that the lack of magnetic information does not affect navigational abilities of experienced adult homing pigeons.**

Key words: homing pigeons, magnetic map, olfactory map, navigation.

### INTRODUCTION

About forty years ago a turning point in the research on pigeon navigation occurred when it was shown that pigeons made anosmic (unable to perceive smells) were impaired in homing from unfamiliar areas (Papi et al., 1971). Since then many experiments conducted in different countries by different researchers have replicated these findings and accumulated evidence in favour of the critical role of olfactory cues in pigeon navigation over unfamiliar areas [see Wallraff (Wallraff, 2005) for an extensive review]. Nevertheless, some authors have never questioned the idea that successful homing relies on a magnetic map learned by experiencing the magnetic gradients of the area flown over during training or exploratory homing flights (Gould, 1998; Gould 2004; Walker, 1998; Walker, 1999). The results of several different kinds of studies have been interpreted by some authors as evidence in favour of the existence of a position finding mechanism based on magnetic information. One such kind of study proposed the presence of magnetite particles innervated by the ophthalmic branch of the trigeminal nerve in the upper beak of the pigeons (Fleissner et al., 2003; Williams and Wild, 2001); another was a laboratory demonstration that putative upper beak magnetoreceptors are functionally involved in sensing differences in magnetic field intensity (Mora et al., 2004); and yet another found an effect of magnetic pulse treatments on the initial orientation of pigeons and migratory passerines (Beason 2005; Wiltschko et al., 2006). The characteristic of the proposed magnetic map is that it should be learned during previous homing or migratory flights by allowing the birds to experience the magnetic gradient(s)

of a region (Walker, 1998; Wiltschko et al., 1987; Wiltschko et al., 2006) and the magnetic intensity values of the area flown over are thought to be sensed through a putative trigeminally mediated magnetoreceptor.

In fact, experiments using homing pigeons subjected to bilateral section of either the ophthalmic branch of the trigeminal nerve or the olfactory nerve failed to confirm the existence of a magnetic map, by showing that the magnetically deprived pigeons oriented and homed as well as the controls. In addition, further evidence was added to the already long list of findings of dramatic disruption of the navigational performance of anosmic pigeons. These results were obtained either by performing the nerve sections on adult pigeons with no homing experience prior the test (Gagliardo et al., 2006) or by testing intensively trained pigeons subjected to sensory deprivation when young, before map learning could have occurred (Gagliardo et al., 2008).

Here we report the results of a further experimental protocol designed to assess whether the trigeminally mediated magnetic information is necessary for a position-finding mechanism, that is, nerve sections on adult pigeons with homing experience followed by release from unfamiliar locations.

### MATERIALS AND METHODS

#### Training procedures

All the 99 pigeons (*Columba livia* L.) used in the experiments were bred and hatched at the Arnino Field Station near Pisa (latitude 43°39'26"N, longitude 10°18'14"E; magnetic parameters during the

experiment: magnetic intensity 46.59  $\mu\text{T}$ , magnetic inclination 59°49'). The birds were bred and kept according to the Italian laws on animal welfare.

At about 30–35 days after hatching they were released from the loft and allowed to fly freely around the home area. About 60 days later all the pigeons started a program of training flights consisting of 22 group releases. The birds were trained from sites located in different directions and at progressively increasing distances up to 10 km from the home loft. The difference between the magnetic parameters of the last three training sites and the home loft were as follows: from the northern site  $-0.04 \mu\text{T}$  (magnetic intensity) and  $-0^\circ 05'$  (magnetic inclination); from the eastern site  $-0.02 \mu\text{T}$  and  $-0^\circ 01'$ ; from the southern site  $+0.02 \mu\text{T}$  and  $+0^\circ 06'$ . On the days on which the pigeons were not trained, they were encouraged out of the loft to fly freely around the home loft area. The maximum distance to which the birds were trained was the same, and the number of releases was similar to that reported in previous experiments aimed at testing the development of magnetic navigation in dependence of training procedures (Benvenuti et al., 1990; Gagliardo et al., 2008; Wiltschko et al., 1987; Wiltschko et al., 1989).

At the end of the training program the pigeons were randomly assigned to three experimental groups as follows: (1) anosmic (ON;  $N=33$ ): the birds underwent bilateral section of the olfactory nerves; (2) magnetically deprived (V1;  $N=34$ ): the birds underwent bilateral section of the ophthalmic branch of the trigeminal nerve; (3) intact control (C;  $N=32$ ): the birds were unmanipulated. The experimental procedure was approved by the Ethical Committee for Experimentation on Animals of the University of Pisa (C.A.S.A.).

At least 10 days after the surgery four experimental releases were performed. The release sites were at medium (50–60 km) or longer distance (75–100 km) from home (see Tables 1 and 2 for details). Each pigeon took part in only one release.

### Surgery

The surgical procedures were similar to those used in previous studies (Gagliardo et al., 2006; Gagliardo et al., 2008; Mora et al., 2004) and were performed by the same person (Wild). Each pigeon was anaesthetised with an intramuscular injection of 20% chloral hydrate ( $2 \text{ ml kg}^{-1}$  body mass) and fixed in a stereotaxic device with ear and beak bars. A burr hole was drilled through the cancellous bone of the rostral skull in the midline to expose the pair of adjacent olfactory nerves. These were sectioned midway between the olfactory bulb and the point at which the nerves begin to diverge

to pass to the olfactory epithelium, that is, proximal to the point at which V1 crosses over the olfactory nerve and olfactory epithelium. On each side, V1 was sectioned within the orbit in two places, one immediately before the nerve exited the front wall of the orbit and another proximal to the superior oblique muscle. A piece of nerve 2–3 mm in length was then extracted. To prevent any regrowth and thus VI reclaiming access to the beak, a drop of surgical cyanoacrylate glue was applied to the foramen through which VI normally exits the front wall of the orbit.

### General procedure and statistics

All the experimental releases took place in sunny conditions with no or light wind. During the releases, the birds were released singly, alternating between treatments. Each bird's flight was observed until it vanished from view, using  $10 \times 40$  binoculars; then, after 2–3 min, the next bird was released, and so on. A record of the azimuth of the vanishing bearing, as well as the vanishing time, was recorded and an observer at the home loft recorded the arrival of each pigeon on the day of the release, so that homing times could be calculated.

For each vanishing bearing distribution, we calculated a mean vector and homeward component; the homeward component ranged from  $-1.0$  to  $+1.0$  and gives an indication of the strength of homeward orientation. The vanishing bearing distributions were tested for randomness by means of both Rayleigh and V-tests (Batschelet, 1981). Comparisons between three or four distributions were made with nonparametric analysis of variance (Kruskal–Wallis). This was done for both the angular difference ( $0$ – $180$  deg.) between the vanishing bearing of each subject and the mean direction of its group, to test for group differences in dispersion, and the angular difference ( $0$ – $180$  deg.) between the vanishing bearing of each subject and the home direction, to test for group differences in orientation (Wallraff, 1979). When the Kruskal–Wallis test identified significant overall group differences, we performed multiple comparisons with the Dunn's test (Dunn, 1964). Vanishing times and homing performance were compared by means of the Kruskal–Wallis analysis of variance and Dunn's test. When two or more pigeons homed together, they were not represented in the diagrams and were excluded from the statistical analysis of homing performances.

## RESULTS

### Medium distance releases

Both the C and the V1 pigeons were significantly oriented at the two release sites (Bolgheri and Marinella) (see Table 1 for the

Table 1. Medium distance releases

Release site	Group	<i>N</i>	<i>n</i>	$\alpha$	<i>r</i>	hc	vt	hs
Bolgheri 336° 54.8 km 05/09/2008 (+0.12 $\mu\text{T}$ , +0°26')	C	8	8	301 deg.	0.94***	+0.77***	2'43"	10.2
	V1	9	9	313 deg.	0.89***	+0.82***	2'35"	8.6
	ON	8	8	194 deg.	0.56	-0.44	4'39"	Lost
Marinella 154° 57.3 km 04/09/2008 (-0.12 $\mu\text{T}$ , -0°23')	C	8	8	211 deg.	0.83**	+0.45*	3'09"	Day after/later
	V1	8	8	194 deg.	0.79**	+0.61**	4'17"	Day after/later
	ON	8	8	295 deg.	0.69*	-0.54	3'48"	Lost
Pooled results (home direction set to 360 deg.)	C	16	16	008 deg.	0.62**	+0.61***	3'01"	5.3/day after
	V1	17	17	004 deg.	0.72***	+0.72***	3'27"	Day after
	ON	16	16	174 deg.	0.49*	-0.49	3'57"	Lost

Release site: name of the release site, home direction, distance, date of the experiment and the difference in the magnetic intensity and inclination (in brackets; values according to the International Geomagnetic Reference Field) with respect to home are indicated.

Group: C, intact control pigeons; V1, pigeons with section of the ophthalmic branch of the trigeminal nerve; ON, pigeons with section of the olfactory nerves. *N*, birds released; *n*, birds for which the initial orientation was recorded;  $\alpha$ , mean vector direction; *r*, mean vector length; hc, homeward component; vt, median vanishing time; hs, median homing speed expressed in  $\text{km h}^{-1}$  (day after; pigeons that homed on the day after the release; later: pigeons that homed later than the day after the release; lost: pigeons that never returned home).

The asterisks in the *r* and hc columns indicate the results of the Rayleigh and V-tests, respectively: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ .

Rayleigh test and V-test results). The distribution of the ON birds was not different from random at Bolgheri, according to both the Rayleigh and V-tests. At Marinella the ON birds were significantly oriented according to the Rayleigh test, but their mean vector direction was oriented in the opposite quadrant with respect to home. At both release sites the distributions of the three experimental groups did not differ in dispersion (Kruskal–Wallis  $P>0.1$ ), but were significantly different in orientation (Kruskal–Wallis,  $P<0.005$  and  $P<0.0005$  for Marinella and Bolgheri, respectively). At both release sites this difference was due to the behaviour of the anosmic pigeons, which oriented differently from both the other two experimental groups (Dunn’s test, Marinella ON vs C  $P<0.01$ ; ON vs V1  $P<0.001$ ; Bolgheri ON vs C  $P<0.005$ , ON vs V1  $P<0.001$ ).

Because different groups of pigeons were tested, we were able to pool the data collected at the two release sites according to their deviation from the home directions and by setting the home direction to North (Table 1, Fig. 1). The pooled distributions of groups C and V1 were significantly different from uniform according to both the Rayleigh and V-test (see Table 1) and their vectors were homeward directed (see the confidence limits given in Fig. 1). By contrast, the pooled distribution of the ON birds was significantly different from uniform according to the Rayleigh test, but not according to the V-test (see Table 1), which takes into account the expected direction. In fact the ON pigeons mean vector was directed opposite to the home direction (see the confidence limits given in Fig. 1). The three pooled vanishing distributions were not statistically different in dispersion (Kruskal–Wallis,  $P>0.1$ ), but they were significantly different in orientation (Kruskal–Wallis,  $P<0.001$ ). In

particular, the ON group oriented differently from both the V1 and C pigeons (Dunn’s test  $P<0.001$  in both comparisons).

The homing performance of the three experimental groups released from Bolgheri was consistent with their initial orientation (Kruskal–Wallis  $P<0.001$ ; see also Table 1). None of the ON pigeons homed from Bolgheri, whereas all but one of the C pigeons, returned home to Arnino (Dunn’s test ON vs C and ON vs V1  $P<0.001$ ; C vs V1  $P>0.1$ ). From Marinella the control birds were poorer at homing than those tested from the same site in other experiments (Gagliardo et al., 2008; Ioalè et al., 2008); however, more than half of the ON pigeons were lost, but most of the C and V1 homed successfully. The Kruskal–Wallis test did not reveal any statistical difference in the homing performance of the three experimental groups.

Considering the pooled data of the two experiments, the Kruskal–Wallis test applied to the homing performance revealed a statistical difference among groups ( $P<0.00025$ ) and multiple comparisons indicated that the ON pigeons were significantly poorer at homing than both the C and V1 pigeons (Dunn’s test,  $P<0.001$  in all comparisons). The V1 group’s homing performance was very similar to that of control pigeons.

The median values of vanishing times are reported in Table 1. According to the Kruskal–Wallis test, the three experimental groups were significantly different in their vanishing times when released from Bolgheri ( $P<0.01$ ) and the ON pigeons tended to be slower than the other two groups (Dunn’s test, Bolgheri ON vs V1,  $P<0.02$ ; ON vs C  $P<0.05$ ). No difference in the vanishing time of the three groups was observed at Marinella.

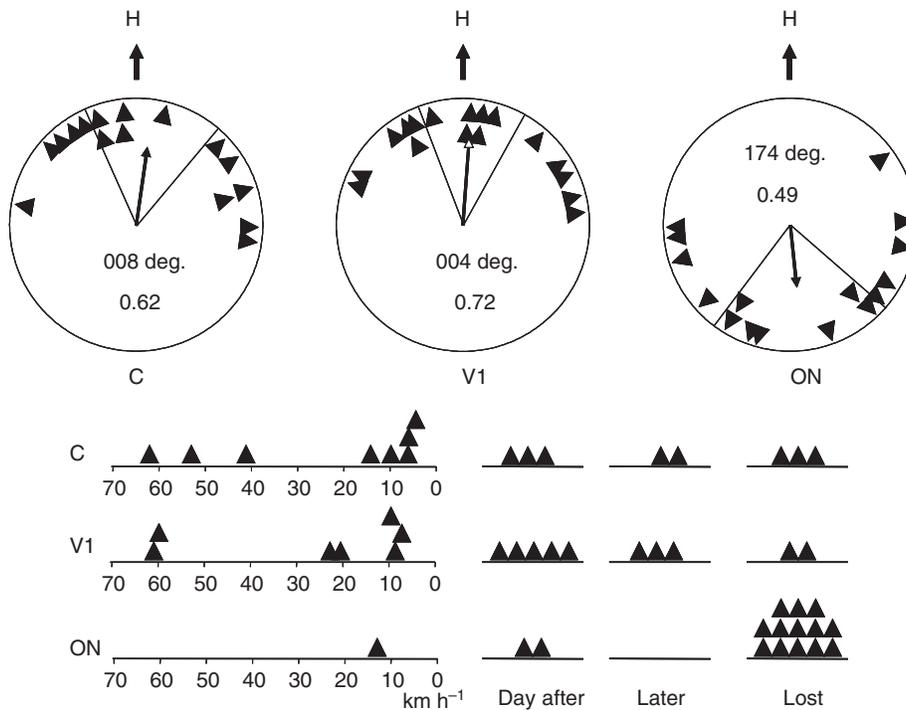


Fig. 1. Releases from medium distances. (Top) Pooled data relative to the initial orientation and homing performance recorded at Bolgheri and Marinella. Circular diagrams showing the initial orientation of the pigeons: each symbol on the periphery of each circle identifies the vanishing bearing of one bird. C: intact control pigeons; V1: pigeons subjected to the sectioning of the ophthalmic branch of the trigeminal nerve; ON: pigeons subjected to the sectioning of the olfactory nerves. The home direction is set at 360 deg. Arrows inside each circle represent the mean vector of each group, whose direction and length is reported. The inner lines delimit the 95% confidence limits. (Bottom) Pooled homing performance: Each symbol identifies the performance of one pigeon. Symbols and abbreviations as in Fig. 1.  $\text{km h}^{-1}$ : mean homing speed of the birds that homed on the day of the release; one day: pigeons that homed on the day after the release; later: pigeons that homed later than the day after the release; lost: pigeons that never returned home. Pigeons that homed together are not included in the diagrams.

Table 2. Long distance releases

Release site	Group	N	n	$\alpha$	r	hc	vt	hs
Filattiera 157° 79.3 km 02/09/2008 (+0.20 $\mu$ T, +0°39')	C	8	7	183 deg.	0.85**	+0.76**	7'14"	Later
	V1	8	8	184 deg.	0.83**	+0.82***	3'25"	Later/lost
	ON	7	7	275 deg.	0.70*	-0.33	5'31"	Lost
Il Lupo 326° 105.3 km 03/09/2008 (+0.21 $\mu$ T, +0°47')	C	8	8	340 deg.	0.44	+0.43*	4'33"	Day after
	V1	9	9	312 deg.	0.64*	+0.62**	3'40"	Day after
	ON	9	7	205 deg.	0.30	-0.15	5'01"	Lost
Pooled results (home direction set to 360 deg.)	C	16	15	021 deg.	0.63**	+0.59***	5'34"	Later
	V1	17	17	008 deg.	0.68***	+0.72***	3'40"	Day after/later
	ON	16	14	143 deg.	0.30	-0.24	5'05"	Lost

Release site: name of the release site, home direction, distance, date of the experiment and the difference in the magnetic intensity and inclination (in brackets; values according to the International Geomagnetic Reference Field) with respect to home are indicated.

Group: C, intact control pigeons; V1, pigeons with section of the ophthalmic branch of the trigeminal nerve; ON, pigeons with section of the olfactory nerves. N, birds released; n, birds for which the initial orientation was recorded;  $\alpha$ , mean vector direction; r: mean vector length; hc, homeward component; vt, median vanishing time; hs, median homing speed expressed in km h<sup>-1</sup> (day after: pigeons that homed on the day after the release; later: pigeons that homed later than the day after the release; lost: pigeons that never returned home).

The asterisks in the r and hc columns indicate the results of the Rayleigh and V-tests, respectively. \*\*\*P<0.001, \*\*P<0.01, \*P<0.05.

By pooling the data from the two releases a statistical difference in vanishing times emerged (Kruskal–Wallis test, P<0.05); nevertheless the Dunn’s test did not reveal any statistical difference among the groups.

**Long distance releases**

The C pigeons were significantly oriented with both Rayleigh and V-test at Filattiera, but according to only the V-test at Il Lupo, whereas the V1 birds were significantly oriented according to both statistical tests at both release sites (see Table 2 for the Rayleigh test and V-test results). Similarly to what happened at Marinella (release from north, medium distance), at Filattiera the ON birds were significantly oriented according to the Rayleigh test, but their mean vector direction was not oriented homeward (see the homeward component value in Table 2). At both release sites the anosmic birds headed west, possibly attracted by the nearby river Magra valley. In fact it has often been observed that prominent landscape features can attract or repel flying pigeons (Ioalè et al., 1994; Wagner, 1972), and can exert a critical influence, especially

on anosmic birds that are impaired in navigation. At Il Lupo the distribution of the ON birds was not different from random, according to both the Rayleigh and V-tests. At both release sites the distributions of the three experimental groups did not differ either in dispersion or in orientation (Kruskal–Wallis P>0.1). As in the medium distance releases, different pigeons were used so as to allow data pooling (Table 2, Fig. 2). The pooled distributions of groups C and V1 were significantly different from uniform according to both the Rayleigh and V-test (see Table 2) and their vectors were homeward directed (see the confidence limits given in Fig. 2). By contrast, the pooled distribution of the ON birds was not significantly different from random according to both the Rayleigh test and the V-test (see Table 2). The three pooled vanishing distributions were not statistically different in dispersion (Kruskal–Wallis, P>0.1), but they were significantly different in orientation (Kruskal–Wallis, P<0.001) in that the ON group oriented differently from both the V1 and C pigeons (Dunn’s test P<0.002 in both comparisons).

The homing performance of the three experimental groups released from Filattiera were on the whole quite poor and no

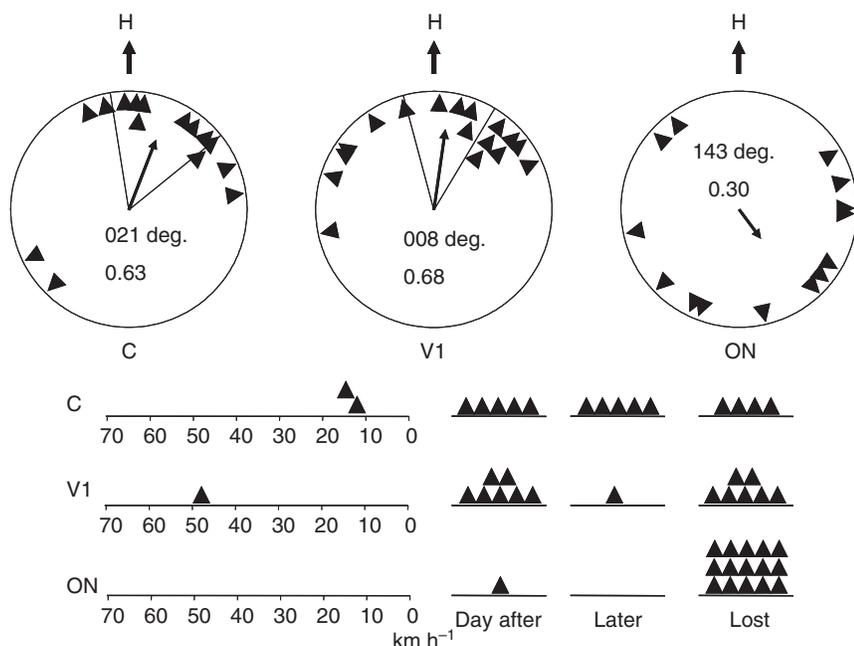


Fig. 2. Releases from longer distances. Initial orientation and homing performances relative to the releases from Il Lupo and Filattiera. Other explanations as in Fig. 1.

difference was revealed by a statistical comparison (Kruskal–Wallis  $P > 0.1$ ), although a higher number of ON pigeons were lost, compared with the other two groups. From Il Lupo, the Kruskal–Wallis test revealed a statistical difference in the homing performance of the three experimental groups ( $P < 0.005$ ). None of the ON pigeons homed from this release site and the statistical comparison confirmed that this group was poorer in homing than the other two experimental groups (Dunn's test ON vs C and ON vs V1  $P < 0.001$ ; C vs V1  $P > 0.1$ ).

Considering the pooled data of the two experiments, the Kruskal–Wallis test applied to the homing performance revealed a statistical difference among groups ( $P < 0.002$ ) and multiple comparisons indicated that the ON pigeons were significantly poorer at homing than both the C and V1 pigeons (Dunn's test,  $P < 0.001$  in both comparisons), whereas no difference was observed between the C and the V1 pigeons.

The median values of vanishing times are reported in Table 2. According to the Kruskal–Wallis test, the three experimental groups were significantly different in their vanishing times when released from Filattiera ( $P < 0.05$ ). In particular the V1 pigeons were faster than both the C and the ON pigeons (Dunn's test,  $P < 0.001$  in both comparisons). No difference in the vanishing time of the three groups was observed at Il Lupo. By pooling the data from the two releases a statistical difference in vanishing times emerged (Kruskal–Wallis test,  $P < 0.05$ ); according to the Dunn's test the V1 pigeon vanishing times were significantly faster than those of the control birds.

## DISCUSSION

Our results clearly show that pigeons subjected to section of the ophthalmic branch of the trigeminal nerve oriented and homed no differently from the intact birds, whereas the olfactory nerve section produced a severe impairment in navigation. This clear-cut result does not support the existence of a magnetic map useful for a position finding mechanism. In fact, we have shown that magnetically deprived pigeons, through section of the ophthalmic branch of the trigeminal nerve, displayed homing performances similar to those of un-manipulated controls. It is worth noting that in our study the use of an alternative map mechanism (for example a non-trigeminal-mediated geomagnetic map) did not emerge, as the navigational performance of olfactory-deprived pigeons were totally disrupted.

The description of a putative magnetoreceptor in the upper beak (Fleissner et al., 2003; Williams and Wild, 2001) and the subsequent demonstration that the integrity of the ophthalmic branch of the trigeminal nerve is necessary for the discrimination of magnetic stimuli in an operant conditioning context (Mora et al., 2004) has led to the assumption that the trigeminally mediated magnetoreceptor could detect magnetic information useful for a true navigation task (Wiltschko et al., 2006). Nevertheless, this assumption was actually not based on experimental evidence, and failed to be confirmed by experiments conducted in the field. Pigeons' navigational performance from unfamiliar sites was unaffected by section of the ophthalmic branch of the trigeminal nerve, regardless of their previous homing experience as shown in: (1) inexperienced birds sectioned when adult (Gagliardo et al., 2006), (2) birds sectioned when young before map learning and then extensively trained (Gagliardo et al., 2008), (3) extensively trained and sectioned birds after map learning (present work).

Our results confirm the critical role of olfactory information in pigeons' navigation and do not support the idea that a redundancy of cues is used in a 'true navigation' task, that is, one involving the ability to find the way to a known location without relying on

familiar landmarks (Griffin, 1952). It is worth noting that, when released from unfamiliar locations, the navigational performance of anosmic pigeons is always disrupted, regardless of the training protocol to which the birds are subjected (Gagliardo et al., 2006; Gagliardo et al., 2008). The lack of olfactory information, therefore, does not appear to be compensated by the use of geomagnetic information in a navigational map mechanism. This evidence is in contrast to the existence of a multicue system often postulated by several authors for navigation over unfamiliar areas (Ganzhorn, 1992; Keeton, 1974; Walcott, 2005; Wiltschko et al., 1987).

More than ten years ago Able (Able, 1994) stated that 'the evidence that pigeons use magnetic cues as part of their map is almost entirely indirect'. Nowadays the situation has not changed, as the only experimental work aimed directly at testing the existence in homing pigeons of a position finding mechanism based on magnetic stimuli, provided negative results (Gagliardo et al., 2006; Gagliardo et al., 2008). On the contrary, several experiments showed that pigeons use a geomagnetic compass (Ioalè, 1984; Ioalè, 2000; Keeton, 1971; Visalberghi and Alleva, 1979; Wallcott and Green, 1974). Although it is a common opinion that geomagnetic compass orientation is mediated by the cryptochromes of the retina (Ritz et al., 2000; Wiltschko and Wiltschko, 2005), a possible involvement of the trigeminal system in determining a magnetic directional reference has not been experimentally excluded so far.

The present work has shown, once again, that whatever the experience of the pigeons might be, magnetic stimuli are unnecessary for navigation from unfamiliar locations and that olfactory cues are the only cues used when knowledge of the landscape cannot provide topographical reference for localizing the home loft. The function of the putative magnetoreceptor in ecologically relevant behaviours thus remains mysterious.

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