

Navigational abilities of homing pigeons deprived of olfactory or trigeminally mediated magnetic information when young

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SUMMARY

Anatomical evidence and conditioning experiments have recently suggested that magnetoreceptors are located in the upper beak of homing pigeons, where they are innervated by the ophthalmic branch of the trigeminal nerve. These findings have raised the issue of whether the trigeminally mediated magnetoreception is involved in the navigational mechanisms of homing pigeons. Recent data have shown that, in inexperienced pigeons, section of the ophthalmic branch of the trigeminal nerve does not impair navigational abilities, whereas the navigational performance of inexperienced pigeons is disrupted after section of the olfactory nerve. Nevertheless, the issue of whether the stimuli available during development of the navigational mechanism can influence the types of cues used in determining the direction of displacement remains unresolved. To address this issue, we surgically deprived young pigeons of either olfactory or trigeminally mediated magnetic information, and then later tested their navigational abilities subsequent to an intensive training flight program of up to 10 km in different directions. The birds deprived of trigeminally mediated magnetic information when young developed navigational abilities at the same level as intact control pigeons, whereas the olfactory deprived pigeons displayed randomly scattered initial orientation and poor homing performance. Our data show that olfactory cues are needed for the development of navigational abilities from unfamiliar locations and that the lack of magnetic information does not affect the development of homing abilities.

Key words: homing pigeon, magnetic map, olfaction, trigeminal nerve.

INTRODUCTION

The nature of the cues used by homing pigeons to deduce positional information [*'map step'* in Kramer's view (Kramer, 1953)] has been the subject of lively debate for more than 30 years. Since the olfactory navigation hypothesis was first proposed by Papi and colleagues (Papi et al., 1971), a large body of evidence has accumulated in favour of the crucial role of olfactory cues in pigeon navigation over unfamiliar areas (Wallraff, 2005). Nevertheless, from time to time, speculations as to the existence of a magnetic map are raised in contrast to the olfactory navigation hypothesis (Gould, 1998; Gould, 2004; Walker, 1999; Walker, 1998).

The discovery of iron (possibly magnetite) particles innervated by the ophthalmic branch of the trigeminal nerve, located in the upper beak of the birds (Fleissner et al., 2003; Williams and Wild, 2001) and functionally involved in magnetoreception (Mora et al., 2004), constituted the most recent challenge to the olfactory navigation hypothesis. As much of the experimental evidence in favour of the olfactory navigation hypothesis was achieved by releasing birds made anosmic with different manipulations involving parts of the upper beak (nostrils, olfactory mucosa) (Benvenuti et al., 1998; Bingman et al., 1998; Guilford et al., 1998; Wallraff, 1988; Wallraff, 2005; Wallraff et al., 1989), Mora and colleagues (Mora et al., 2004) suggested that the observed navigational impairment following anosmia might have actually been due to accidental damage of the nearby putative magnetic receptor. A recent paper (Gagliardo et al., 2006) overcame this objection to the olfactory navigation hypothesis, by showing that inexperienced homing pigeons with a proximal section of the olfactory nerve that did not

involve the beak were unable to navigate, whereas birds subjected to section of the ophthalmic branch of the trigeminal nerve displayed unimpaired orientation and homing performance from unfamiliar locations. However, the issue of whether trigeminally mediated magnetoreception is involved in the pigeon navigation system is still unresolved, if one considers the idea proposed by some authors (Walcott, 2005; Wiltschko et al., 1987) that the conditions under which they are raised can determine the nature of the cues used for navigation. According to this view, pigeons rely on a multi-cue system to deduce positional information and the conditions under which they are raised have a major impact on the ontogenesis of the map, as they determine the type of stimuli used for navigation. If this is the case, pigeons fully exposed to olfactory information during development, but deprived of magnetic stimuli useful for development of the navigational map, should rely on olfactory navigation when released from unfamiliar locations. Alternatively, pigeons raised without access to olfactory information would not be able to develop an olfactory map, but should be able to navigate on the basis of magnetic stimuli, providing they are subjected to training flights in order for them to learn the magnetic gradient of the region around the loft. A widespread idea is that the magnetic stimuli useful for deducing positional information are sensed through the trigeminally mediated magnetoreceptor in the upper beak (Beason, 2005; Beason and Semm, 1996; Wiltschko and Wiltschko, 2005). Therefore, pigeons subjected to sectioning of the ophthalmic branch of the trigeminal nerve should not be able to acquire magnetic information useful for navigation. In the present paper we compared the orientation and homing performance of pigeons subjected to

group training flights while being raised without either olfactory or magnetic information.

MATERIALS AND METHODS

Training procedures

All pigeons 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 μ T, magnetic inclination 59°49'). The birds were bred and kept according to the Italian laws on animal welfare. At the time of fledging (30–35 days after hatching), before they had developed navigational abilities, the pigeons were randomly assigned to three experimental groups as follows: (1) anosmic (ON, $N=47$), the birds underwent bilateral section of the olfactory nerves; (2) magnetically deprived (V1, $N=44$), the birds underwent bilateral section of the ophthalmic branch of the trigeminal nerve; (3) intact control (C, $N=50$), 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.).

Fifteen days after the operation, all the pigeons from the three experimental groups started a program of training flights in groups consisting of birds from all three treatment groups: in this way, the birds with a possible navigational impairment had the opportunity of developing the homing experience, and therefore learning the environmental cues available, by following the intact control pigeons. There were 22 of these training flights, which lasted until the experimental releases from unfamiliar locations. 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 are as follows: from the northern site -0.04μ T (magnetic intensity) and $-0^{\circ}05'$ (magnetic inclination); from the eastern site -0.02μ T and $-0^{\circ}01'$; from the southern site $+0.02 \mu$ 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 (Benvenuti et al., 1990; Wiltschko et al., 1989; Wiltschko et al., 1987).

At the end of the training program, two series of experimental releases were performed with all the returned birds (ON, $N=40$; V1, $N=40$; C, $N=44$). The sites of the first series of releases were located at about 50–60 km from home, whereas the sites of the second series of releases were located further afield (see Tables 1 and 2 for details). Each pigeon took part in only one release from the first series and, if it returned, in a single release from the second series.

Surgery

The surgical procedures [approved by the Ethical Committee for Experimentation on Animals of the University of Pisa (C.A.S.A.)] were similar to those used in previous studies (Gagliardo et al., 2006; Mora et al., 2004) and were performed by the same person (M.W.). However, because of the need to discourage regrowth of sectioned nerves over a period of several months, the surgery was more extensive. Each pigeon was anaesthetized with an intramuscular injection of 20% chloral hydrate (2 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, i.e. proximal to the point at which V1 crosses over the olfactory nerve and

olfactory epithelium. This surgery was the same as that previously performed (Gagliardo et al., 2006), but in order to try and prevent regrowth in the present experiments the cut ends of the nerves were peeled back and a drop of dental cement was placed between and over them. Bleeding was stopped with Gelfoam. 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 re-grown V1 reclaiming access to the beak, a drop of surgical cyanoacrylate glue was applied to the foramen through which V1 normally exits the front wall of the orbit.

As the operation occurred long before the experimental tests, it was necessary to check the nerves for possible regeneration. Therefore, on completion of the experimental releases, all the ON pigeons that had homed singly (11) and 16 randomly chosen birds with a sectioned V1 were sacrificed by injecting a lethal dose of chloral hydrate and the nerves were visually inspected under a microscope. The birds showing re-grown nerves were excluded from the analysis.

General procedure and statistics

All the experimental releases took place in sunny conditions with no or light wind, with the exception of the day of the release from Filattiera, when there was a sudden worsening of the weather conditions in the home loft area and all the birds tended to stop because of the rain. During the releases, the birds were released singly, alternating between treatments. The flight of each bird 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 ranges 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 carried out for both the absolute angular difference (0 – 180°) between the vanishing bearing of each subject and the mean direction of its group, to test for group differences in dispersion, and for the angular difference (0 – 180°) 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 using 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 relative to homing performances.

RESULTS

In none of the 16 birds initially subjected to a section of V1 and later checked for re-growth was there any evidence that the nerves had regained access to the beak. In fact, only a proximal stump of the nerve was visible in most cases. By contrast, in all the ON birds that homed alone (11), at least one of the paired nerves had re-grown either under or over the dental cement. Therefore, the

Table 1. Series 1 data

Release site	Group	<i>N</i>	<i>n</i>	α	<i>r</i>	<i>hc</i>	<i>t_v</i>	<i>s_h</i>
Bolgheri 336° 54.8 km 08/08/2007 (+0.12 μ T, +0°26')	C	15	15	319	0.88***	+0.85***	2'37"	27.9
	V1	14	14	330	0.91***	+0.90***	2'07"	43.5
	ON	11	10	305	0.64*	+0.55*	4'21"	Lost
Agliaiana 242° 59.6 km 10/08/2007 (-0.13 μ T, -0°18')	C	15	13	254	0.79***	+0.77***	4'28"	7.4
	V1	13	13	255	0.75***	+0.73***	3'58"	5.5
	ON	11	10	342	0.29	-0.10	6'47"	Lost
Marinella 154° 57.3 km 11/08/2007 (-0.12 μ T, -0°23')	C	14	13	188	0.71***	+0.59***	3'51"	28.1
	V1	13	13	187	0.64***	+0.54**	4'00"	11.3
	ON	8	7	334	0.44	-0.44	5'00"	Later
Pooled results	C	44	41	006	0.75***	+0.74***	3'18"	24.8
	V1	40	40	010	0.74***	+0.73***	3'23"	10.8
	ON	30	27	055	0.09	+0.13	5'11"	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 parentheses; 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*, number of birds released; *n*, number of birds for which the initial orientation was recorded; α , mean vector direction expressed in degrees; *r*, mean vector length; *hc*, homeward component; *t_v*, median vanishing time expressed in minutes and seconds; *s_h*, median homing speed expressed in km h⁻¹ (1 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). The asterisks in the *r* and *hc* columns indicate the results of the Rayleigh and V test, respectively. ****P*<0.001; ***P*<0.01; **P*<0.05.

orientation and homing data from these birds were excluded from the analysis.

Series 1

The results of the three tests are reported in Table 1. Both the C and the V1 pigeons were significantly oriented at the three release sites (Bolgheri, Agliana and Marinella) (see Table 1 for the Rayleigh test and V test results). By contrast, the distributions of the ON birds were different from random in only one of the three releases (Bolgheri), according to both the Rayleigh and V tests.

Although the ON pigeons tended to be more scattered in their initial orientation than did the C and the V1 groups, the vanishing bearing distributions of the three experimental groups were not statistically different in dispersion (Kruskal-Wallis, *P*>0.05). When angular distances were tested, the Kruskal-Wallis test revealed a difference in the orientation between the three experimental groups only at Agliana (*P*<0.05), the ON birds orienting differently from both C and V1 pigeons (Dunn's test, *P*<0.05 in both comparisons).

Because different groups of pigeons were tested, we were able to pool the data collected at the three release sites according to their

deviation from the home directions and by setting the home direction to North (Table 1 and Fig. 1). The pooled distributions of groups C and V1 were significantly different from uniform, according to both the Rayleigh and V tests (see Table 1), and their vectors were homeward directed (see the confidence limits represented in Fig. 1). By contrast, the pooled distribution of the ON birds was randomly scattered according to both the Rayleigh and V tests. The three pooled vanishing distributions were statistically different in dispersion (Kruskal-Wallis, *P*<0.002), but not in orientation. Multiple comparisons indicated that the ON birds were significantly more scattered than both the V1 and the C (Dunn's test: *P*<0.01 in both comparisons).

The homing performance of the three experimental groups was consistent with their initial orientation (see Table 1 and Fig. 2). The ON pigeons were dramatically impaired in homing. By contrast, most of the C and V1 pigeons homed successfully. The Kruskal-Wallis revealed significant difference in the homing performance in all the releases of Series 1 (Kruskal-Wallis, *P*<0.002 at Bolgheri; *P*<0.001 at Agliana and *P*<0.05 at Marinella), the ON pigeons being significantly poorer than the other two experimental groups (Dunn's

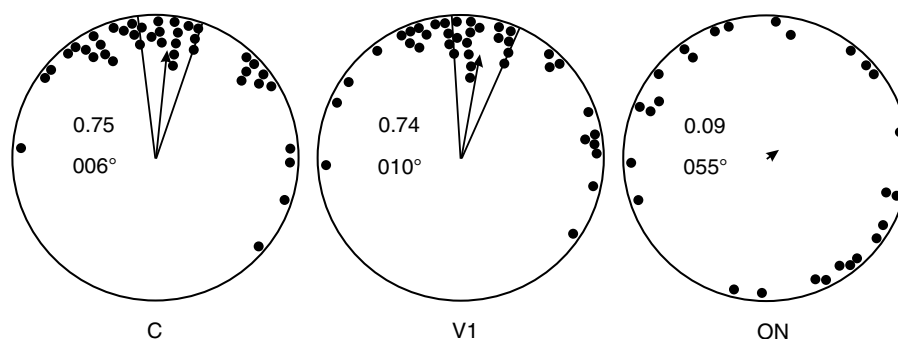


Fig. 1. Series 1. Pooled data relative to the initial orientation recorded at Bolgheri, Agliana and Marinella. Circular diagrams showing the initial orientation of the pigeons; each symbol on the periphery of each circle identifies the vanishing bearing of one bird. C, intact control pigeons; V1, pigeons subjected to the section of the ophthalmic branch of the trigeminal nerve; ON, pigeons subjected to the section of the olfactory nerves. The home direction is set at 360°. Arrows inside each circle represent the mean vector of each group, the length and direction of which are reported. The inner lines delimitate the 95% confidence limits.

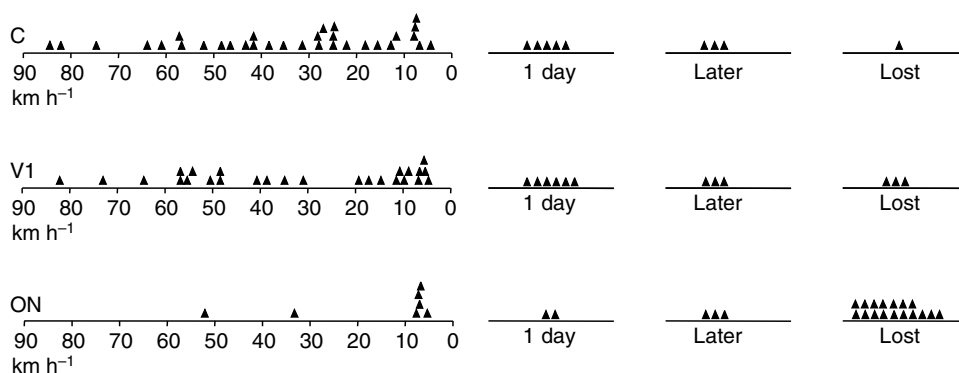


Fig. 2. Series 1. Pooled homing performance from Marinella, Agliana and Bolgheri. Each symbol identifies the performance of one pigeon. C, intact control pigeons; V1, pigeons subjected to the section of the ophthalmic branch of the trigeminal nerve; ON, pigeons subjected to the section of the olfactory nerves; km h^{-1} , mean homing speed of the birds that homed on the day of the release; 1 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.

test, $P < 0.005$ at Bolgheri; $P < 0.001$ at Agliana and $P < 0.05$ at Marinella).

Considering the pooled data of the three experiments, the Kruskal-Wallis test applied to the homing performance revealed a statistical difference among groups ($P < 0.001$) 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 homing performance of the V1 group 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 both Bolgheri ($P < 0.001$) and Agliana ($P < 0.05$), the ON pigeons tending to vanish slower than the other two groups (Dunn's test, Bolgheri ON versus V1, $P < 0.001$; ON versus C $P < 0.02$; Agliana ON versus V1 $P < 0.05$).

The three experimental groups displayed a statistical difference in their pooled vanishing times (Kruskal-Wallis test, $P < 0.001$) and multiple comparisons showed that ON pigeons were significantly slower than both the other groups (Dunn's test, ON versus C, $P < 0.005$; ON versus V1, $P < 0.001$).

Series 2

All the pigeons that homed in the releases of Series 1 took part in the releases of Series 2. The results are reported in Table 2 and

Figs 3, 4. The behavior of the experimental groups released at further distances was consistent with that observed in the releases at medium distances (Series 1). Control (intact) and V1-sectioned pigeons were always significantly oriented (see Table 2 for Rayleigh and V test results). The single release distributions of the ON pigeons were not statistically tested, owing to the small sample size; however, in two out of three releases, they displayed a negative homeward component (see Table 2). The comparisons between the groups revealed statistically significant differences in orientation only at Il Lupo (Kruskal-Wallis $P < 0.02$): the ON pigeons orienting differently from the other two groups (Dunn's test $P < 0.02$, in both comparisons). For the single releases, no differences in dispersion between the groups were revealed by the Kruskal-Wallis test.

The pooled initial orientation distributions of the ON pigeons were not different from random, whereas those of the C and V1 groups were significantly homeward oriented (see the Rayleigh and the V test results in Table 2 and the confidence limits represented in Fig. 3). On the whole, the ON pigeons were significantly more scattered than the other two groups (Kruskal-Wallis $P < 0.002$; Dunn's test ON versus C $P < 0.02$; ON versus V1 $P < 0.001$), although there was no significant difference in orientation.

The ON pigeons displayed significantly poorer homing performance when compared with the other two experimental groups in two releases (Kruskal-Wallis test, Torre a Castello $P < 0.02$; Il Lupo $P < 0.01$). The Dunn's test revealed that the ON birds were

Table 2. Series 2 data

Release site	Group	N	n	α	r	hc	t_v	s_h
Torre a Castello 292° 106.5 km 16/08/2007 (+0.03 μT , +0°17')	C	15	13	299	0.94***	+0.93***	2'41"	12.6
	V1	12	11	292	0.96***	+0.96***	2'32"	14.1
	ON	4	4	333	0.77	+0.58	4'47"	Lost
Il Lupo 326° 105.3 km 17/08/2007 (+0.21 μT , +0°47')	C	15	12	327	0.79***	+0.79***	2'52"	1 day
	V1	12	12	326	0.89***	+0.87***	2'42"	8.9
	ON	4	4	211	0.52	-0.22	3'26"	Lost
Filattiera 157° 79.3 km 23/08/2007 (-0.20 μT , -0°39')	C	14	11	183	0.83***	+0.74***	4'25"	1 day
	V1	12	11	172	0.84***	+0.75***	3'57"	1 day
	ON	4	3	296	0.77	-0.58	4'19"	Lost
Pooled results	C	44	36	011	0.84***	+0.83***	2'55"	1 day
	V1	36	34	005	0.88***	+0.88***	2'57"	9.2
	ON	12	11	101	0.15	-0.03	3'26"	Lost

See Table 1 for explanations and definitions.

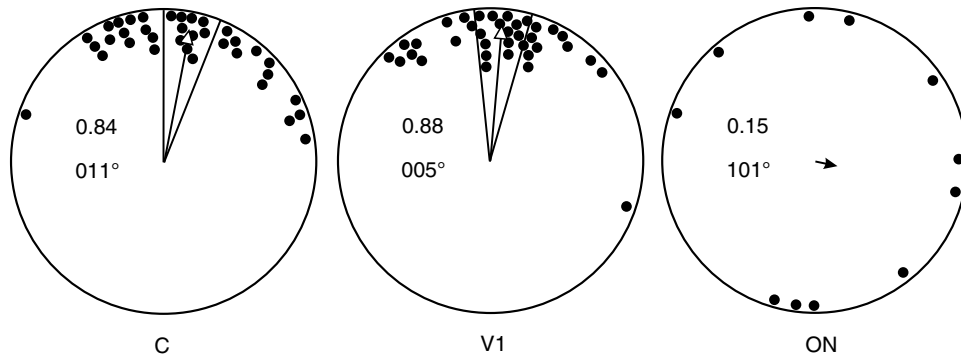


Fig. 3. Series 2. Initial orientation relative to the releases from Torre a Castello, Il Lupo and Filattiera. See Fig. 1 for further details.

significantly poorer in homing than the V1 birds at both sites, and significantly poorer than the C pigeons at Il Lupo. The analysis of the pooled homing performance showed that the ON pigeons were significantly poorer than both the other experimental groups (Kruskall-Wallis $P < 0.001$; Dunn's test $P < 0.001$ in both comparisons).

No between-group differences in vanishing times were found either in the single releases or in the pooled data (Kruskall-Wallis $P > 0.5$).

DISCUSSION

Our results clearly show that pigeons raised with section of the olfactory nerves and exposed to geomagnetic information during the numerous training flights are dramatically impaired in navigation. By contrast, pigeons deprived of trigeminally mediated magnetic information during map development, displayed orientation and homing performance in all ways similar to those of the intact control pigeons. Therefore, these results fail to support the existence of a multi-cue system of navigation, consistent with results reported in previous papers (Benvenuti et al., 1990; Ioalè et al., 2008; Papi et al., 1989). Moreover, our results contradict the idea that the exposure to stimuli of different natures can determine the type of the cues that constitute the physical basis of the navigational map.

It is worth noting that all the ON pigeons that homed from the greater-distance release sites and were checked for regrowth of their olfactory nerves but showed evidence of nerve re-growth, strengthening the idea that olfactory cues are necessary for homing from unfamiliar locations. By contrast, intact trigeminal nerves are

neither sufficient nor necessary for either the development of navigational abilities or the operation (Gagliardo et al., 2006) of the navigational map mechanism.

The homing performances of the three groups of pigeons were consistent whether released from medium (50–60 km) or longer distances (80–110 km): only a few intact and trigeminally sectioned pigeons were lost and most of the ON pigeons were not able to home in both series of tests. In addition, the initial orientation performance was stable within an experimental group at both distances. Therefore, the greater difference in the magnetic gradient between the release and home sites that might have been perceived by the ON pigeons when released at further distances, did not provide them with useful navigational information.

Thus far, the only direct test of the involvement of the trigeminal nerve (V1) in mediating magnetic information have been in a laboratory testing (operant) situation in which pigeons were trained to discriminate the presence *versus* the absence of a magnetic anomaly in a tunnel (Mora et al., 2004). Section of V1, but not of the olfactory nerve, completely abolished the discrimination. However, the only two experiments (Gagliardo et al., 2006) (and the present work) conducted in the field to assess the navigation abilities of pigeons with section of V1 have failed to support the idea that the perception of magnetic stimuli is required for homing from unfamiliar locations under clear skies. Therefore, all the experimental evidence yielded so far contradicts the hypothesis that trigeminally mediated magnetoreception is involved in the navigational map mechanism in homing pigeons. However, the possibility that this structure is involved in the magnetic compass mechanism persists and remains to be assessed.

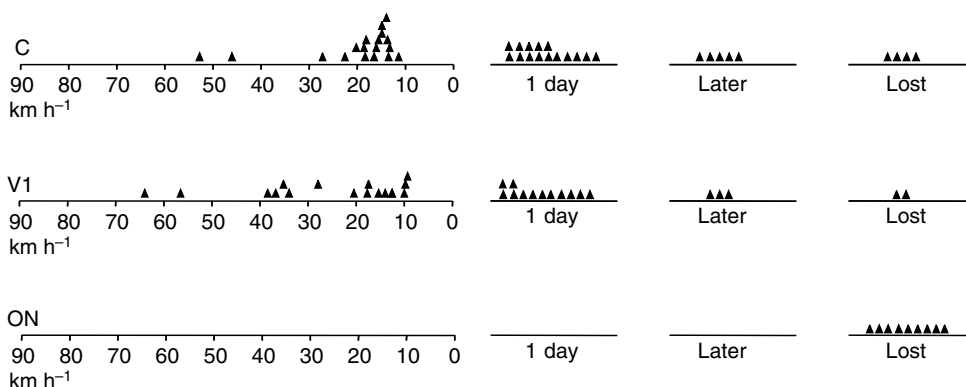


Fig. 4. Series 2. Homing performance relative to the releases from Torre a Castello, Il Lupo and Filattiera. See Fig. 2 for further details.

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