THE ROYAL SOCIETY

Relevance of visual cues for orientation at familiar sites by homing pigeons: an experiment in a circular arena

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Whether pigeons use visual landmarks for orientation from familiar locations has been a subject of debate. By recording the directional choices of both anosmic and control pigeons while exiting from a circular arena we were able to assess the relevance of olfactory and visual cues for orientation from familiar sites. When the birds could see the surroundings, both anosmic and control pigeons were homeward oriented. When the view of the landscape was prevented by screens that surrounded the arena, the control pigeons exited from the arena approximately in the home direction, while the anosmic pigeons' distribution was not different from random. Our data suggest that olfactory and visual cues play a critical, but interchangeable, role for orientation at familiar sites.

Keywords: pigeon; homing; visual landmarks; olfaction

1. INTRODUCTION

The debate about homing pigeon navigational mechanisms has mainly concentrated on the map system that allows the birds to determine their position with respect to the home loft. A large body of evidence collected during a long series of experiments shows that homing pigeons: (i) possess a mental representation of the surroundings based on the distribution of olfactory cues dispersed in the environment, which has been called an 'olfactory map' (Papi *et al.* 1971; Papi 1990, 1995; Wallraff 1996, 2000; Wallraff & Andreae 2000); (ii) build up the olfactory map when young, by associating the odours carried by the winds to the home loft with the direction from which the winds blow (Wallraff 1966; Gagliardo *et al.* 2001); and (iii) determine the direction of displacement by recognizing the prevalent odours at the release site (Ioalè *et al.* 1990), and then orient by using a compass system (Schmidt-Koenig 1961).

It has often been reported that the olfactory stimuli become redundant for homing from familiar locations, which can be identified by the anosmic birds on the basis of other kinds of stimuli experienced during previous releases (Benvenuti *et al.* 1973, 1992; Papi & Casini 1990; Wallraff *et al.* 1993). We could presume that pigeons might recognize a previously visited site on the basis of its characteristic features, in other words on the basis of visual cues. Nevertheless, some authors have denied the involvement of visual landmarks in orientation from familiar locations. This has been on the basis of the observation that after phase-shifting, pigeons tend to deviate their initial orientation even from very familiar sites (Füller *et al.* 1983; Wiltschko & Wiltschko 1998). Moreover, conditioning experiments showed that the pigeons preferentially use the sun compass rather than intramaze landmark beacons to locate the food reward in an outdoor arena (Chappell & Guilford 1995; Gagliardo *et al.* 1996). Evidence that pigeons actually do use visual landmarks when released from familiar locations was

collected by Braithwaite and other authors (Braithwaite & Guilford 1991; Braithwaite & Newman 1994; Burt *et al.* 1997). The authors showed that the birds that had been kept in opaque boxes for a few minutes before being released homed consistently more slowly than those kept in transparent boxes, which had a preview of the surroundings before taking off. Nevertheless, this technique does not allow us to evaluate the effect of the manipulation of the visual information on the orientation of the birds. On the other hand, since the standard method for studying pigeons' orientation consists of releasing a pigeon and then recording its bearing when vanishing from the observer's view, preventing the pigeons from exploiting the visual information of the surroundings would imply a direct manipulation of the visual sensory system by, for example, applying opaque lenses (Schmidt-Koenig & Schlichte 1972; Benvenuti & Fiaschi 1983). In our experiment we adopted an alternative method, pioneered by Chelazzi & Pardi (1972), which consists of recording the orientation of homing pigeons while exiting from a circular arena (Mazzotto *et al.* 1999). By using this method we were able to prevent the access to the release site visual information without interfering with the pigeons' visual system.

2. MATERIAL AND METHODS

Forty-seven adult and experienced homing pigeons were used in the experiments. The birds were housed in a loft in the Arnino field station (10 km southwest of Pisa) and were allowed to perform spontaneous daily flights. All the birds were released in flock seven times from each of the three sites used for the experimental tests (see table 1 for details on the release sites). An additional training release was performed from each site. During this release, in order to simulate the condition of the experimental test, each bird was kept for 1–2 min in a round cage placed on a pedestal before being released singly.

Moreover, the pigeons were trained to exit from a circular arena described in Mazzotto *et al.* (1999) and placed in the Arnino field station at a distance from the home loft varying from 20 to 50 m. The arena (1.8 m in diameter) was made of

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Table 1. *Orientation at the exit of the arena.*

(Release site: name of the release site, home direction and distance are indicated. Group, A, anosmic pigeons; group C, controls; N, birds released; n, birds for which the orientation in the arena was recorded; α, mean vector direction; r, mean vector length; $p(R)$, results of the Rayleigh test; $p(V)$, results of the V-test; *, **, ***: $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively; n.s., not significant; hc: $r\cos(\alpha-\beta)$, where β is the home direction.; t_a: median of the time spent in the arena.)

	release site	date	group	N	n	α	r	$p(R)$	$p(V)$	hc	t_a
VIS +	Arnaccio	06/07/00	A	23	21	291°	0.45	*	**	+ 0.42	7′00″
	270° 12.7 km		C	22	21	255°	0.37	n.s.	**	+ 0.36	0′50″
	Calambrone	07/07/00	A	23	21	010°	0.42	*	**	+ 0.41	0′30″
	356° 7.4 km		C	22	22	355°	0.23	n.s.	n.s.	+ 0.23	0′07″
	La Costanza	06/06/00	A	24	21	190°	0.67	***	***	+ 066	0′14″
	185° 18.1 km		C	23	23	198°	0.57	***	***	+ 0.56	0′07′
VIS −	Arnaccio	15/06/00	A	23	22	218°	0.37	*	n.s.	+ 0.22	0′07″
	270° 12.7 km		C	23	21	263°	0.36	n.s.	**	+ 0.36	0′12″
	Calambrone	20/06/00	A	22	22	108°	0.18	n.s.	n.s.	− 0.07	0′48″
	356° 7.4 km		C	23	23	007°	0.20	n.s.	n.s.	+ 0.19	0′53″
	La Costanza	22/06/00	A	21	21	279°	0.31	n.s.	n.s.	− 0.02	1′03″
	185° 18.1 km		C	22	22	146°	0.36	n.s.	*	+ 0.28	0′13″

non-magnetic material and placed on a 1.2 m high pedestal. The floor of the arena consisted of an opaque plastic sheet. The ceiling of the arena consisted of a net, which allowed both a full view of the sky and free circulation of the air. There were aluminium bars hanging down around the edge of the arena. The birds were able to escape from the arena by pushing through the bars, which were familiar to the pigeons since they were the same as those used at the entrance to their loft. At the centre of the arena there was a remotely operated release box made of a net, where the pigeons were kept for 2 min before the beginning of the test.

In order to let the pigeons familiarize themselves with the arena, three pre-training sessions were performed. In each session the pigeons were put in the arena in groups of three subjects at a time. The pigeons quickly learned to escape from the arena. Afterwards the pigeons were trained singly to exit from the arena for one more session. For the subsequent seven sessions of training the arena was surrounded by a screen, which prevented the pigeons from viewing the landscape. The screen was made up of eight 2 m × 3 m blue plastic sheets attached to each other by means of aluminium stakes. The distance between the screen and the edge of the arena was *ca.* 2.5 m.

The day before the first experimental release 24 pigeons (A-group) were made anosmic by washing their olfactory mucosae with a 4% $ZnSO_4.7H_2O$ solution, according to the procedure described in Guilford *et al.* (1998). The remaining 23 pigeons (C-group) were treated with Ringer solution.

All the experimental releases took place in sunny conditions, with no or light wind. Each bird was placed in the release box of the arena. After 2 min this box was opened by the experimenter pulling a rope while sitting under the arena out of the view of the bird. The escape bearing was recorded by using a compass referring to the midpoint between the bars lifted by the pigeon. After take-off the pigeon's flight was observed using 10 × 40 binoculars and the azimuth of the vanishing bearing was recorded. Both the time spent by each individual in the arena before taking off and its vanishing time were also recorded.

If a bird spent more than 20 min before exiting from the arena, we tried to catch it in order to release it later. If the bird escaped as the experimenter approached, the exit direction was not recorded.

For each of the three familiar sites two test releases were performed: in one release the view of the landscape was allowed (VIS +) and in one release the screens placed around the arena prevented view of the surroundings (VIS −).

For each release two bearing distributions were obtained: one referring to the pigeons' directional choices while exiting from the arena and the second referring to the birds' vanishing bearings. These distributions were tested for randomness by means of both the *V*- and the Rayleigh test (Batschelet 1981). The Watson U^2-test was used to compare the orientation of control and anosmic birds. For the directional choices in the arena, two individual mean vectors, one for the VIS + and one for the VIS − condition, were calculated by pooling the data obtained from each single pigeon in the three tests and setting the home direction to 360°. Therefore for most of the birds each vector was calculated from three bearings. The individual mean vectors of a few pigeons were calculated from two data. If only one bearing was recorded the datum was excluded from the second-order statistics.

The Hotelling test (Batschelet 1981) was applied on the individual mean vectors in order to test for randomness of the pigeons' orientation in the cage. The Hotelling test for paired samples of angles (Zar 1984) was used in order to compare, for each experimental group of birds, the orientation in the arena with and without the view of the landscape.

The times spent in the arena and the vanishing times of C- and A-pigeons were compared by means of the Mann–Whitney *U*-test.

3. RESULTS

The median times spent in the arena before taking off by C- and A-pigeons are reported in table 1. According to the Mann–Whitney *U*-test the A-pigeons spent a significantly longer time than the C-birds before exiting the arena in two out of three VIS + releases (La Costanza and Arnaccio, $p < 0.05$ in both tests). In the VIS − condition no difference between A- and C-birds was detected.

The directional choices of the pigeons when exiting the arena are reported in table 1 and figure 1, in both visual conditions.
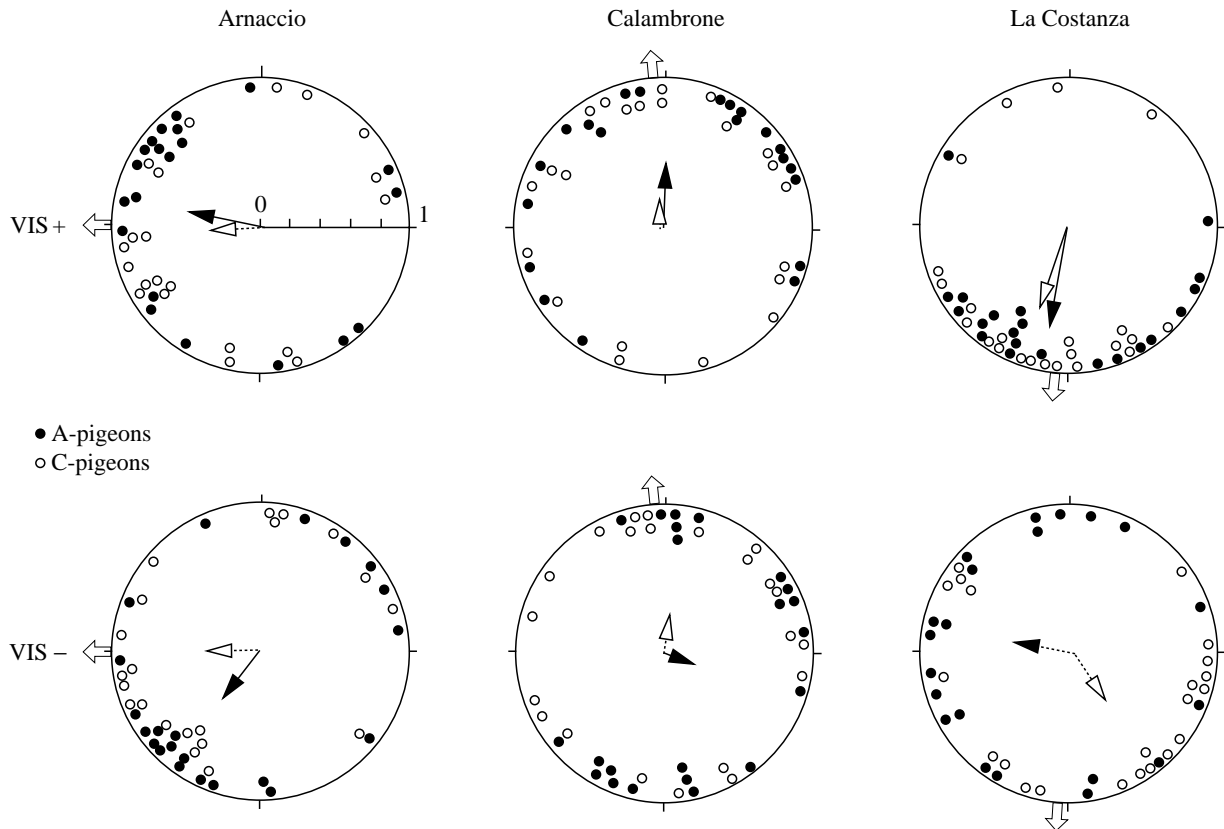
Figure 1. Orientation in arena at the three familiar release sites. The upper and the lower row diagrams refer to the releases in the VIS + and VIS − condition, respectively. Each symbol represents a single bird. The open and filled symbols refer to the smelling (C) and anosmic (A) pigeons, respectively. The outer arrows represent the home directions. The inner arrows represent the distribution mean vectors (dashed arrows for $p > 0.05$ according to the Rayleigh test). For details, see table 1.

Due to some scattering, which has also been reported in a previous paper describing pigeon orientation at the release site in the same arena (Mazzotto *et al.* 1999), the distributions of C-pigeons in the VIS + condition were significantly different from random according to the Rayleigh test only in one out of three releases (La Costanza, see table 1). However, for the same distributions, the *V*-test, which takes into account the home direction, gave significant results in two out of three releases (Arnaccio and La Costanza, see table 1).

The orientation in the arena of the A-birds in the VIS + releases was even better, although not significantly, than that of controls (Watson U^2-test, $p > 0.05$). In fact, the A-pigeon distributions in the arena were significantly oriented in the three releases, according to both the Rayleigh and the *V*-test.

In the three VIS − releases, both C- and A-pigeons in the arena were generally more scattered than in the VIS + tests. The only exception is represented by the significantly oriented distribution of the A-birds at Arnaccio (see table 1 for the Rayleigh test). However the anosmic birds were never significantly oriented according to the *V*-test ($p > 0.05$), while the control pigeons were homeward oriented in two out of three releases (Arnaccio and La Costanza, see table 1 for the *V*-test). The orientation of A- and C-pigeons within the arena did not differ significantly (Watson U^2-test, $p > 0.05$) in all VIS − releases.

Since the bearings' distributions collected by using this method are generally noisier than what we could expect by recording vanishing bearings (see also Mazzotto *et al.* 1999), we pooled the data by calculating the mean directional choice with respect to home for each bird. The distributions of the mean directional choice of each pigeon in the arena are reported in figure 2. The second-order distributions of C-pigeons were different from random in both VIS + and VIS − conditions and the resultant second-order mean vector direction was close to the home direction (Hotelling test, $p < 0.001$ and $p < 0.05$ in VIS + and VIS −, respectively; see also figure 2 for the second-order mean vector values).

In the VIS + condition, the second-order distribution of A-pigeons turned out to be different from random and the second-order mean vector direction was close to the home direction (see figure 2). On the contrary, in the VIS − condition the A-birds were not able to determine the home direction in the arena (Hotelling test, $p > 0.25$).

Moreover, the control pigeons' orientation in the arena was similar in both visual conditions (Hotelling test for paired data, $p > 0.05$) while, on the contrary, the A-birds' distribution when the view of the surroundings was allowed (VIS +), was significantly different from the distribution displayed by the same birds in the screened condition (VIS −) (Hotelling test for paired data, $p < 0.025$).
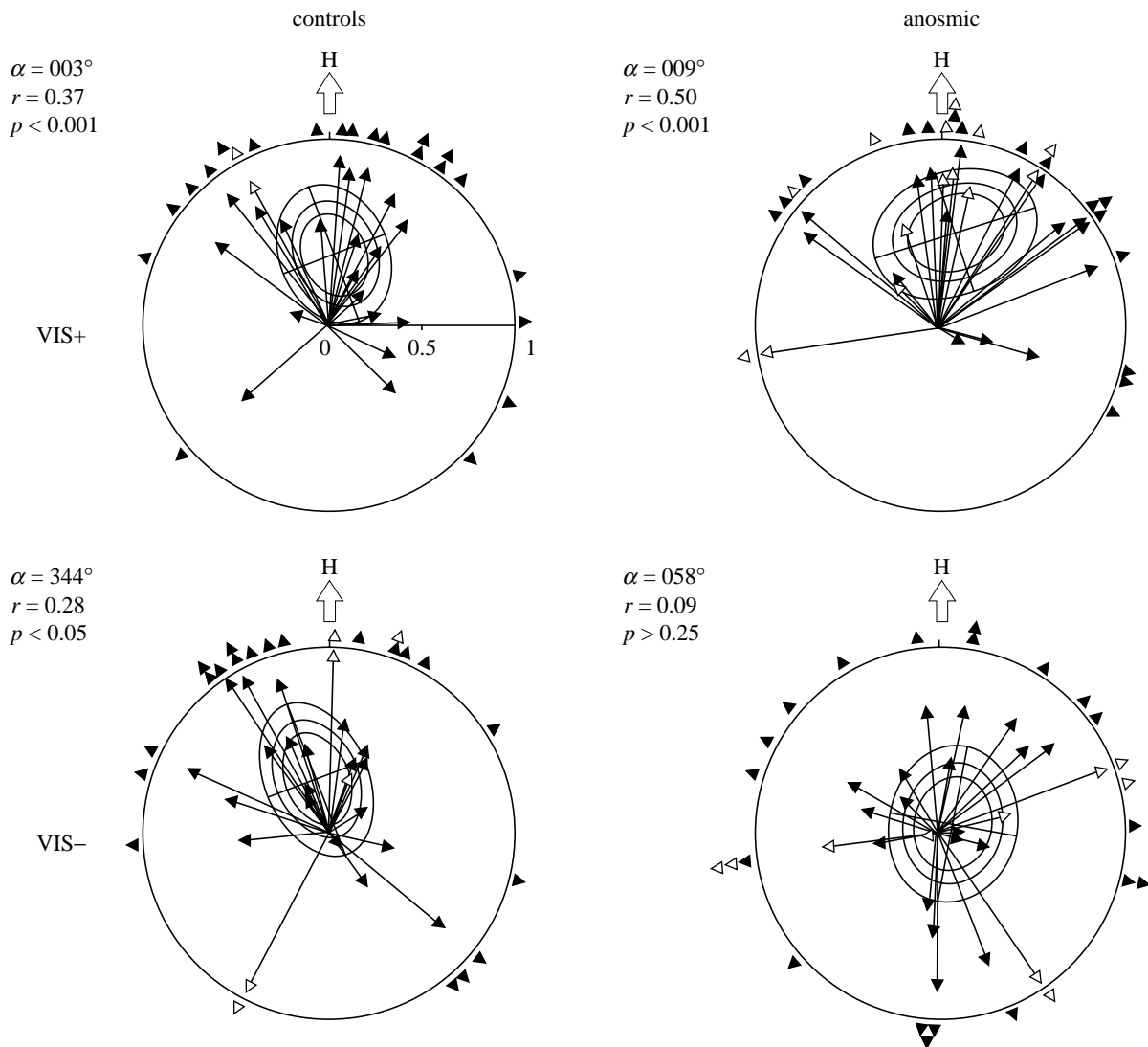
Figure 2. Second-order distributions for the orientation in the arena. Each vector represents the mean orientation with respect to the home direction (set in 360°) of a single bird. Filled symbols represent the vectors calculated from three data. Open symbols represent vectors calculated from two data. Confidence ellipses (95%, 99%, 99.9%) are reported; *a*, second-order mean vector direction; *r*, second-order mean vector length; *p* values according to the one sample Hotelling test. For other explanations, see § 3.
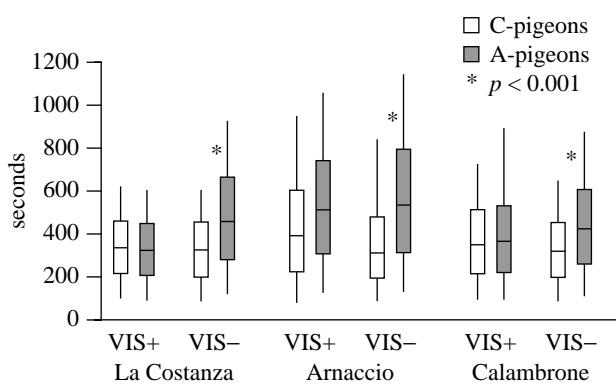

Figure 3. Vanishing times. In the diagram are indicated the range (vertical line), the median (horizontal line), the second and the third quartile (vertical rectangle). The Mann–Whitney *U*-test was used to compare the control (C) and the anosmic (A) pigeons in the VIS + and VIS − conditions. Other explanations in the text.

The difficulty of the anosmic birds in determining the home direction before taking off in the VIS − condition was also indicated by the longer time taken to disappear from the observer's view if compared with the C-birds. As reported in figure 3, the A-pigeons' vanishing times were significantly longer than those of the controls in all the VIS − releases (Mann–Whitney *U*-test, $p < 0.0001$). On the contrary, C- and A-pigeons took a similar amount of time to vanish when they were able to observe the environment before taking off (Mann–Whitney *U*-test, $p > 0.5$ at La Costanza and Calambrone; $p > 0.05$ at Arnaccio).

The orientation at vanishing recorded in the six experimental releases is reported in table 2. Both the anosmic (A) and control pigeons (C) were similarly homeward oriented in all the releases and the Watson U^2-test never revealed a significant difference among the two groups. This result is consistent with previous findings describing the orientation of anosmic pigeons from familiar locations

Table 2. *Orientation at vanishing.*

(Release site: name of the release site, home direction and distance are indicated. Group A, anosmic pigeons; group C, controls; N, birds released; n, birds for which vanishing bearings were recorded; α, mean vector direction; r, mean vector length; $p(R)$: results of the Rayleigh test; $p(V)$: results of the V-test; *, **, ***, $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively; hc: $r \cos(\alpha - \beta)$, where β is the home direction; t_v, median vanishing time.)

	release site	date	group	N	n	α	r	$p(R)$	$p(V)$	hc	t_v
VIS +	Arnaccio	06/07/00	A	23	18	260°	0.64	***	***	+ 0.63	3′29″
	270° 12.7 km		C	22	19	270°	0.93	***	***	+ 0.93	2′49″
	Calambrone	07/07/00	A	23	20	346°	0.95	***	***	+ 0.94	2′25″
	356° 7.4 km		C	22	21	353°	0.96	***	***	+ 0.96	2′17″
	La Costanza	06/06/00	A	24	21	201°	0.97	***	***	+ 0.93	1′57″
	185° 18.1 km		C	23	22	203°	0.96	***	***	+ 0.92	2′01″
VIS −	Arnaccio	15/06/00	A	23	22	253°	0.44	**	**	+ 0.42	3′43″
	270° 12.7 km		C	23	20	266°	0.70	***	***	+ 0.70	1′59″
	Calambrone	20/06/00	A	22	22	347°	0.95	***	***	+ 0.94	2′48″
	356° 7.4 km		C	23	23	357°	0.96	***	***	+ 0.96	2′03″
	La Costanza	22/06/00	A	21	20	201°	0.97	***	***	+ 0.93	3′04″
	185° 18.1 km		C	22	22	209°	0.95	***	***	+ 0.87	2′03″

(Papi 1986; Wallraff & Neumann 1989; Benvenuti *et al.* 1992).

4. DISCUSSION

By measuring the orientation of the pigeons in a circular arena at the release site (Mazzotto *et al.* 1999) it was possible to evaluate the relevance of both the visual characteristics of the familiar locations and the olfactory cues in determining the home direction.

The main issue pointed out by our data is that homing pigeons do use visual information to orient from previously visited sites. The orientation in the arena of both anosmic and smelling birds is definitely improved by the view of the landscape, but in the case of the anosmic birds the visual cues turned out to be the only factor useful in determining the direction of displacement.

The use of visual cues has been denied on the basis of the strong tendency of the clock-shifted pigeons to deviate despite their good knowledge of the topographical features of the release site (Füller *et al.* 1983; Luschi & Dall'Antonia 1993; Wiltschko & Wiltschko 1998). However, other authors have shown that clock-shifted pigeons can sometimes solve the conflict between the sun compass directional information and the topographical information by relying on the latter (Bingman & Ioalè 1989; Gagliardo *et al.* 1999; Bonadona *et al.* 2000; Holland *et al.* 2000). On the whole, the data reported in the literature (see Wallraff *et al.* (1999) for a discussion on the topic) indicate that homing pigeons possess two orientation strategies over familiar areas: (i) they use visual landmarks for recognizing the release sites and consequently for recalling the compass direction leading them home; in this case the directional information is exclusively given by the compass system (Füller *at al.* 1983); and (ii) they fly back home, or better pilot home, by relying on a topographical map based on landmarks—the directional information is given by the spatial relationship among the landmarks (Bonadona *et al.* 2000). The relationship between the two strategies and the factors determining the preference for one or the other by the pigeons certainly deserves further investigation. Actually

our data are consistent with both strategies, since the recognition of the familiar location on the basis of its visual features might be important in both cases. However, our experimental plan does not allow us to determine which strategy our pigeons used.

Our data are consistent with the olfactory navigational hypothesis (Papi 1990; Wallraff 1990, 1996). In fact olfactory cues, redundant when the anosmic pigeons were able to rely on visual information, became critical in the VIS− condition. Therefore olfactory and visual cues seemed to be the only cues used by the pigeons in the recognition of the familiar locations in our experiments, in contrast to what Benvenuti & Fiaschi (1983) observed.

The orientation of both anosmic and smelling birds at vanishing was extremely similar. However, we observed a striking difference in the two groups' vanishing times when the pigeons could not see the surroundings prior to taking off. In fact the anosmic birds took significantly longer times to vanish from the observer's view in the VIS− condition releases. This finding is in agreement with what Braithwaite & Guilford (1991) observed: they detected consistently longer times in homing from very-short-distance familiar locations when the pigeons did not have access to the landscape view prior to the release. The longer vanishing times displayed by the A-pigeons with respect to the C- birds in the VIS− tests are also consistent with the idea that the smelling birds can exploit olfactory information about which site they have been displaced to when already in the arena. By contrast, the anosmic pigeons seemed to start to understand where they were only once they had taken off, by observing the landscape while circling around the area before heading home.

In conclusion, our report offers direct evidence that homing pigeons do use both visual landmarks and olfactory information to orient towards home from familiar locations, and that visual cues become critical for determining the home direction when olfaction is impaired.

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