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Pigeon Navigation: Effects of Wind Deflection at Home Cage on Homing Behaviour*

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Summary. From fledging time up to the test releases, two groups of experimental pigeons were housed in two cubic cages supplied with deflectors which deviated the winds through to the inside approximately 70° clockwise (CW-birds) or counter-clockwise (CCW-birds). Test releases were made at 9.0, 23.5, and 105.3 km from the loft. With respect to that of control birds, the mean bearing of CW-birds was always deflected clockwise, and that of CCW-birds was always deflected counter-clockwise. Control birds performed better than CW-birds in homing from the first release site, and better than both experimental groups from the second release site.

These results agree with the olfactory hypothesis of pigeon navigation (Papi *et al.*, 1972).

Introduction

According to a recent hypothesis, homing pigeons released in an unfamiliar site establish the home direction using olfactory cues (Papi *et al.*, 1972). This ability is thought to be acquired during the first months of life by learning to recognize the characteristic odour of the loft area as well as the "foreign" odours carried by the winds. Of course, this presupposes that over different areas the constituent odours of the air change, and therefore give rise to different patterns of olfactory stimulation in the birds. This assumption granted, it follows that, when, for example, a north wind blows, the birds learn to recognize the characteristic odour of the areas located north of the loft. At the same time, since pigeons are able to determine compass directions (see Keeton, 1974, for references), they associate this odour with the north direction. If, then, the birds are released from a site north of the loft, they would recognize the odour at the release site as being one which comes from the north. The birds would then react by flying in the opposite direction, south, which would be determined by means of the sun compass or another compass orientation mechanism.

This hypothesis has received support from a series of recent experiments performed with the specific intent of testing it (see Baldaccini *et al.*, 1974, for references). Moreover, the hypothesis agrees with the results of previous experiments which showed that homing capacity is very poor in pigeons kept in aviaries with the side walls fenced by such materials as wood, glass or cloth (Kramer, 1959a, b; Wallraff, 1966, 1970). In order to obtain further evidence, we have performed the present experiment in which the winds blowing through the birds' cages were deflected. If the hypothesis be correct, the headings recorded in test releases should have deflected in conformity with the amount of wind deflection

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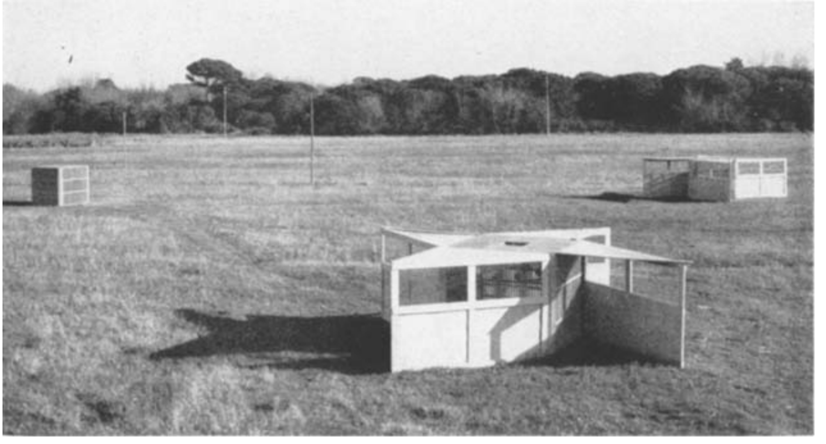

Fig. 1. View of the three cages at Arnino. The cage with counter-clockwise deflectors is in the foreground

at the home cage. Therefore, if the winds blowing through an aviary were deflected by 90° clockwise, the birds would associate the odour of, for example, northerly areas, with the east direction and would, when released north of the loft, head west instead south. By testing the pigeons at different distances from the loft, we also attempted to determine at what range the olfactory mechanism is used by homing pigeons.

Methods

I. The Cages

Three cubic cages, each side measuring 2.10 m, were built for this experiment, and installed on the grounds of our laboratory at Arnino, near Pisa. Two cages were constructed for the birds of the experimental groups, and one for the control group. Each cage was placed at one vertex of a triangular area, 32 m apart from the other two. The cages were oriented identically, with the side walls facing the cardinal points. The side walls were made of wire-netting with vertical strips of ply-wood arranged perpendicularly to the netting. These strips were 10 cm wide, 0.6 cm thick, and placed 5 cm apart. The roof was covered by wire-netting and glass. The birds could return to the cages from training flights and test releases through a trap-door situated in the middle of the roof. The perches were 62 cm below the roof and arranged as shown in Fig. 2.

The control birds' cage was a simple cube, but the two cages employed for the experimental groups were provided with large vertical wind deflectors (Fig. 1). The deflectors were attached to the vertical edges of the cage and extended for a length of 3.00 m. They were made of wooden boards, with tarred cardboard in the lower half and panes of glass in the upper half, which allowed the birds to see outside when resting upon their perches. Each deflector formed an angle of 45° with the cage wall. The space between the deflector and the cage wall was covered by a triangular roof of tarred cardboard, which appeared to be an extension of the cage roof. The deflectors of one cage deviated the wind clockwise through the cage, while those of the other cage counter-clockwise (Fig. 2).

Other devices for wind deflection might have functioned more precisely, but the system we used of flat surfaces and strips was preferable because of its simplicity and low cost. However, it did have some disadvantages. The mean value of wind deflection varied according to the direction from which the wind was blowing. Moreover, inside the cage, the

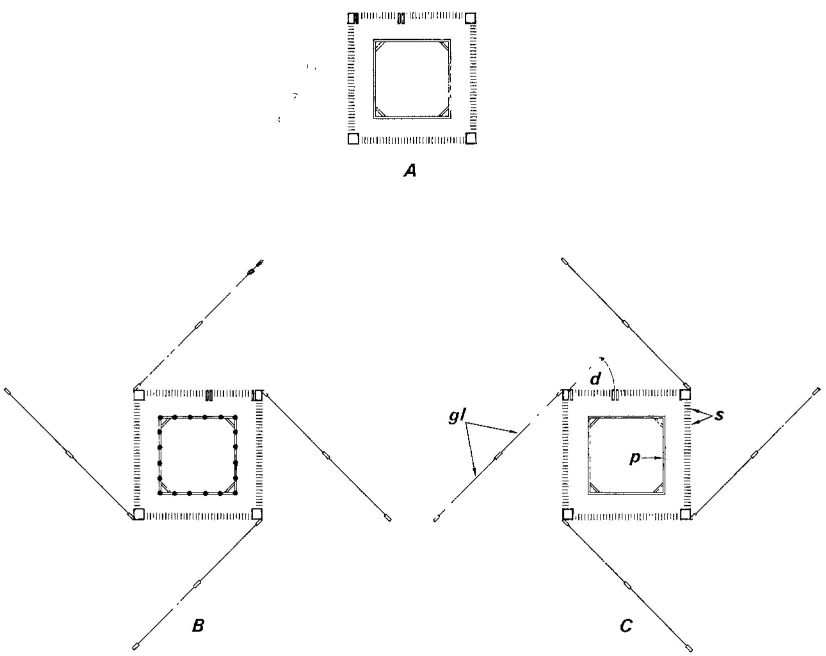

Fig. 2A—C. Horizontal section of the cages at the level of the perches (p). (A) cage of control birds; (B) cage with counter-clockwise deflectors; (C) cage with clockwise deflectors. On the perches of cage (B), the filled circles indicate the position of the vanes in the scale model. *d* door; *gl* panes of glass; *s* vertical strips. Other explanations in the text

degree of deflection was different in different points, and phenomena of turbulence occurred. In order to measure wind deflection, a 1:10 scale model of the cage with counter-clockwise deflecting screens was built and exposed to an air current of velocity 8–9 m/sec. The wind deflection was recorded by means of 20 small vanes placed upon the perches (see Fig. 2). Measurements were made with a side wall of the cage facing the wind, as well as after rotating clockwise the cage model by 15°, 30°, 45°, 60°, and 75°. In the spots where turbulence occurred, the intermediate value between the extreme positions of the vane was assumed as the wind direction in that spot. Wind deflection always occurred in the expected way, the mean values of deflection in the six positions of the model being 80°, 82°, 74°, 67°, 56°, 67°. Even if these values were only approximate, we could conclude that an average wind deflection of about 70° occurred in the cages of the experimental birds.

Wind deflection also occurred to some degree inside the control birds' cage, because the vertical strips tended to channel the wind perpendicularly to the cage wall. According to observations made on the scale model of the control birds' cage, deflections of approximately 30° and 12° would be expected from winds blowing from directions of 15° and 30° from the cardinal point, respectively. When a corner of the cage faced the wind, clockwise and counter-clockwise deflections were observed in some points, but these deviations compensated each other.

II. Treatment of the Birds

The homing pigeons used in the experiments were bought from the breeders in the Valle Padana at the time of fledging. Some arrived at our Arnino laboratory on April 18, some on April 24, 1974. All of them were kept in a large room until May 24, when they were divided by lots into three groups and transferred to the cages. Thirty-one pigeons were put in the cage with clockwise deflectors (CW-birds), 32 in the cage with counter-clockwise deflectors (CCW-birds), and 30 in the cage without deflectors (control birds). Before the test releases, flights outside the cage were permitted on six occasions. Three times the trap-doors of the cages were left open for 2 days. Later, three training releases from very short distances were carried out, 150 m E, 400 m NNW, and 550 m SW of the aviary. On all these occasions, the birds wore a mask applied to the upper beak which gently pressed the nostrils (for details, see Papi *et al.*, 1973a). Twenty-three birds did not return from either spontaneous flights or after the training releases. Another 9 birds, that had remained outside their cages with the mask for more than 7 consecutive days, were not used on the test releases. Consequently 19 CW-, 22 CCW-, and 20 control birds were available for the experiments.

III. Test Releases

The birds were carried to the release sites in baskets inside of a van. They could not see outside, but were well ventilated by two broad pipes which conveyed air from the outside to the baskets. All the experiments were begun early in the morning and were over, at the latest, one hour after sun culmination. The releases were made under clear sky or, at least, with the sun disk visible. Birds were tossed singly and observed with 10×40 binoculars until they vanished from sight. Releases of one to three birds of one group were alternated with those of the two other groups. Each experiment was carried out in two or three days, with a daily release of a nearly equal number of birds of each group.

Three test releases were made at increasing distances from the loft.

1st Experiment. August 12 and 13, 1974. The test site was Campaldo near Pisa, 9.0 km from the loft, home direction 208°. All the birds were released.

Weather conditions during releases: August 12, clear sky, wind was initially barely perceptible from E, then turned to SW (3–4 m/sec) and finally to WSW (5–6 m/sec). August 13, clear sky, initially no wind, later a gentle breeze from ESE, which turned to SW.

2nd Experiment. August 14 and 16, 1974. The test site was near Fornacette, 23.5 km from the loft, home direction 273°. All the birds which had returned in time from the first experiment were released, except for one, which we were not able to capture.

Weather conditions during releases: August 14, clear sky, initially a gentle breeze from E, later no wind. August 16, clear sky, wind initially from E (2–3 m/sec) soon dropped, then from WNW (2 m/sec) and afterwards from NW (3 m/sec), finally from W (4 m/sec).

3rd Experiment. September 2, 6, and 9, 1974. The test site was on a plain near Giuncarico, 105.3 km from the loft, home direction 326°. All the birds which had returned in time from the 2nd experiment were released, except for one, which we were not able to capture.

Weather conditions during releases: September 2, clear sky, initially no wind, later SSW wind growing stronger up to 6 m/sec. September 6, sky initially 7/8 covered, later clear, became again overcast until the sun was clouded over. Therefore, the releases had to be stopped. Wind initially from NE (2–3 m/sec), later calm, thereafter S wind (3 m/sec) which turned to SSW (up to 8 m/sec). September 9, clear sky, initially no wind, then ESE wind (2 m/sec), which turned to S (3–4 m/sec) and finally to SSW (5–6 m/sec).

IV. Statistical Methods

Bearings were tested for randomness by the Rayleigh test (Batschelet, 1965). The three sets of bearings in each experiment were compared by the Mardia multisample test (Mardia, 1972) and by the Mardia-Watson-Wheeler test (Batschelet, 1972). Homing performances and vanishing times were tested by the Mann-Whitney U test (Siegel, 1956).

Results

I. Initial Orientation

The bearing distributions of the three groups were different from random in every experiment (value of the test statistic z and probability are given below each diagram, see Figs. 3–5). The mean vectors of the control birds' bearings were deflected at most 34° from the home direction. In every experiment the mean

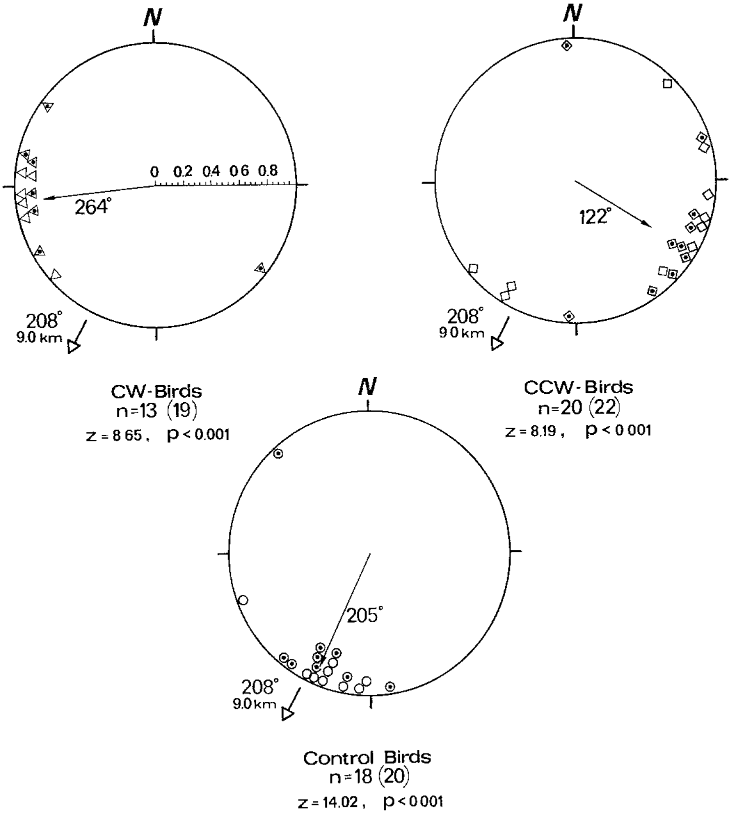

Fig. 3. Initial orientation of the three bird groups in the 1st test release. Each symbol on the periphery of the circles indicates the bearing of one bird. The outer arrow indicates home, the direction and distance of which are given; the inner arrow represents the mean vector, whose length can be read with the scale in the first diagram. Open and dotted symbols refer to birds released on August 12 and 13, respectively. The number of bearings (n) and of birds released (in parentheses) are given. Other explanations in the text

vectors of the CW- and CCW-birds were deflected with respect to that of control birds in the expected direction, i.e. clockwise in CW-birds, and counter-clockwise in CCW-birds. The values of this deflection in the three experiments were 59°, 45°, and 102° for the CW-birds, 83°, 36°, and 121° for the CCW-birds.

The three bearing samples of each experiment were first tested for homogeneity by Mardia's multisample test. The following values were obtained: $W = 41.999$, $p < 0.001$, in the 1st experiment; $W = 27.271$, $p < 0.001$, in the 2nd experiment, and $W = 38.467$, $p < 0.001$, in the 3rd experiment.

Since differences among the samples resulted in all the experiments, the Mardia-Watson-Wheeler two-sample test was also applied. We obtained:

1st Experiment. Control vs. CW-birds, $U = 20.751$, $p < 0.001$; control vs. CCW-birds, $U = 21.245$, $p < 0.001$; CW- vs. CCW-birds, $U = 18.111$, $p < 0.001$.

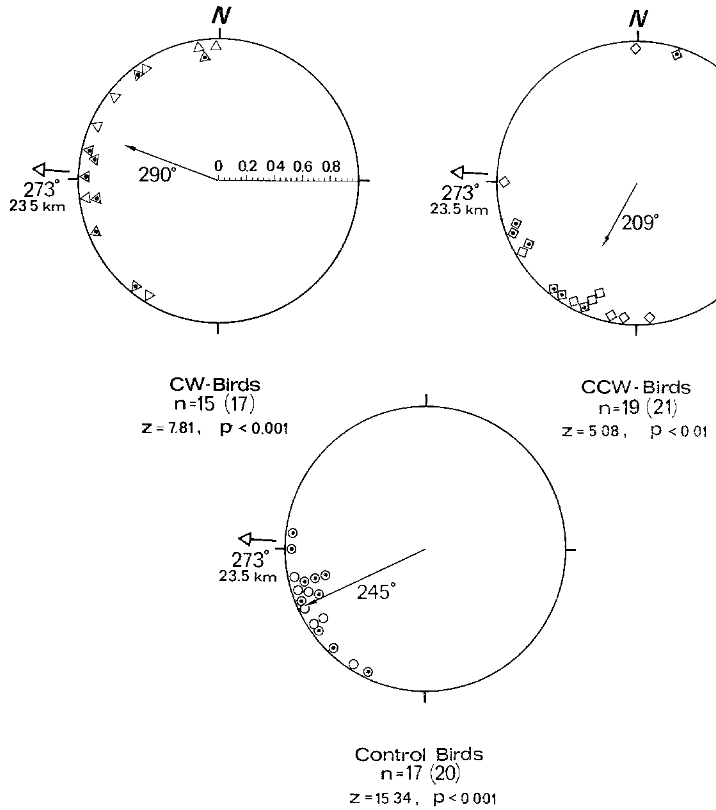

Fig. 4. Initial orientation in the 2nd test release. Open and dotted symbols refer to birds released on August 14 and 16, respectively. For other explanations see Fig. 3 and text

2nd Experiment. Control vs. CW-birds, U = 13.739, $p < 0.01$; control vs. CCW-birds, U = 9.606, $p < 0.01$; CW- vs. CCW-birds, U = 13.814, $p < 0.01$.

3rd Experiment. Control vs. CW-birds, U = 9.408, $p < 0.01$; control vs. CCW-birds, U = 18.559, $p < 0.001$; CW- vs. CCW-birds, U = 15.301, $p < 0.001$.

Thus the three groups of birds, compared two by two, showed a difference in their orientation in every experiment.

In all the experiments, the number of released birds was greater than the vanishing points we could record (the values are given in Figs. 3–5). This is due to the fact that some birds perched in the surroundings of the release points or disappeared early behind vegetation or other objects, or more rarely joined other birds previously released. Considering each experiment separately, no significant difference was seen in comparing the behaviour of the three groups of birds just after being released. However, considering all three groups together, the ratios between birds which disappeared regularly and birds which did not were 51:10, 51:7, and 33:23 in the 1st, 2nd, and 3rd experiments, respectively. A significant difference was found when comparing the third ratio with both the first ($\chi^2 = 7.604$, $p < 0.01$) and the second ratio ($\chi^2 = 10.908$, $p < 0.001$). This difference is not due to a greater number of visual obstacles present in the 3rd release site, but to the behaviour of the birds. Indeed, contrary to the 1st and 2nd experiments, all the lost bearings of the 3rd experiment involved birds which perched in the surroundings.

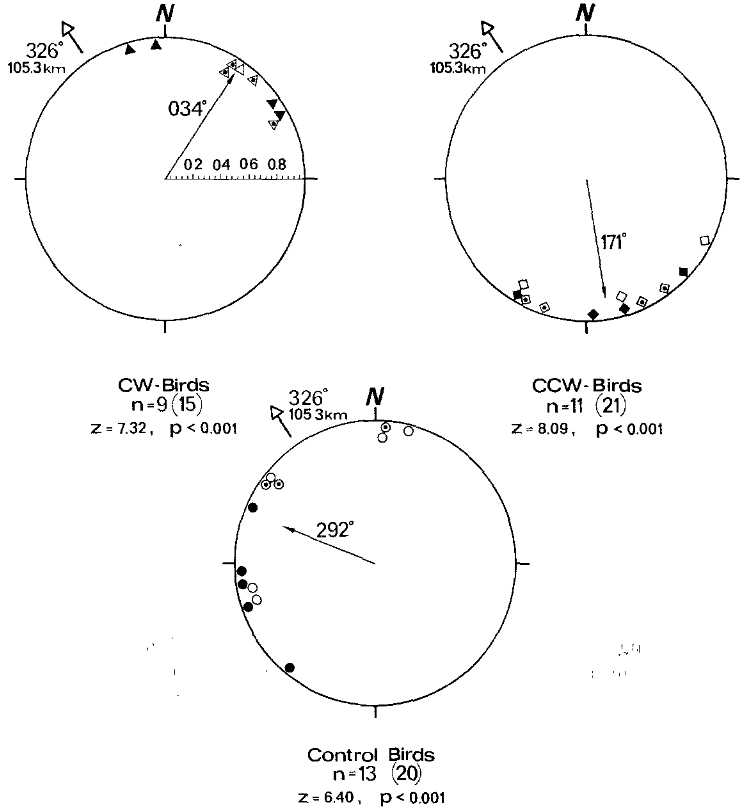

Fig. 5. Initial orientation in the 3rd test release. Open, dotted, and filled symbols refer to birds released on September 2, 6, and 9, respectively. For other explanations see Fig. 3 and text

II. Vanishing Times and Homing Performances

A comparison of the vanishing times did not reveal significant differences among the bird groups in any of the test releases.

In the 1st and 2nd experiments, the majority of both the experimental and control birds homed during the day of their release. Many pigeons reached their cages in a short time, and only one CW-bird never returned from the 2nd test release. In contrast, homing performances were poor in the 3rd experiment. Only two control and one CW-bird homed during the day of their release; 7 control, 6 CW-, and 11 CCW-birds were lost.

In Fig. 6, pigeons are positioned according to their homing times. The following significant differences were seen: 1) In the 1st experiment CW-birds had performances inferior to both control (U = 110, $p < 0.05$) and CCW-birds (U = 95, $p < 0.002$); 2) in the 2nd experiment control birds showed better performances than both CW- (U = 65, $p < 0.002$) and CCW-birds (U = 141.5, $p < 0.05$).

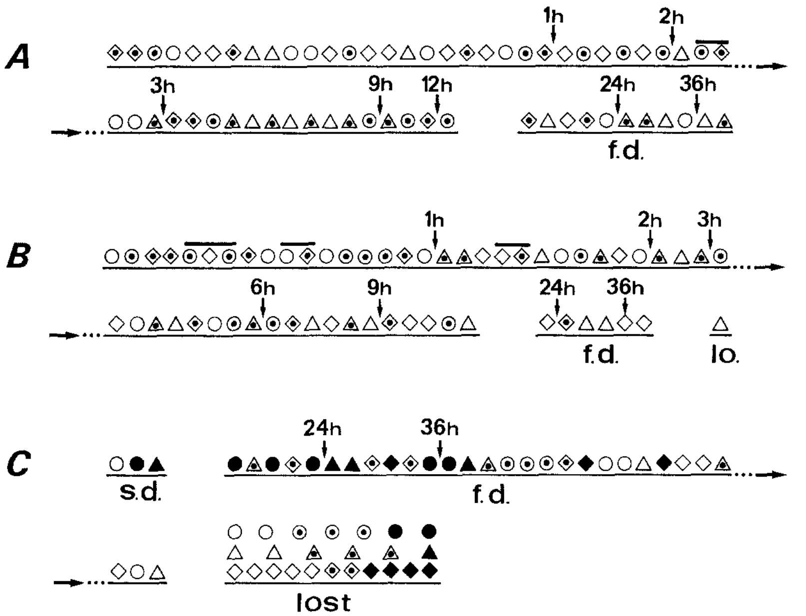

Fig. 6A—C. Homing performances in the three experiments. Each symbol refers to one bird and is positioned according to the time spent to return home. A, B, and C: homing performances from 1st, 2nd, and 3rd test release sites (explanations for the symbols as in Figs. 3, 4, and 5, respectively). Lines are placed over symbols corresponding to birds with the same homing time. *s.d.* homed in the same day of the release, *f.d.* in following days; *lo.* birds lost

Discussion

From the data concerning the initial orientation, it was found that the bearings of the two experimental groups deviated as expected in consequence of the wind deflectors applied to their cages. The fact that differences in homing performances, when observed, were due to the slower re-entries of experimental birds, confirms that the experimental birds had greater difficulties in finding their loft.

The degree of deviation shown by the experimental group birds with respect to the mean bearing of the control birds was roughly as expected in the 1st experiment, smaller than expected in the 2nd experiment, and greater than expected in the 3rd experiment. There is no convincing explanation for these differences. Nevertheless, it should be pointed out that, combining all the experiments, the mean value of the bearing deviations (74°) is nearly equal to that of the wind deflection observed inside the cage model (70°).

These results show that information acquired at home during the first months of life is utilized by pigeons in determining flight direction when they are released far from the loft. This acquisition of information is based, in part at least, on perception of stimuli which are propagated horizontally and can be reflected by sheets of wood and/or glass. Moreover these stimuli must be different in some parameter according to the direction from which they come, otherwise one could not explain how deflection of the stimuli could influence the initial orientation of the birds in the way which was observed.

These conclusions correlate well with the olfactory hypothesis of pigeon navigation. However, one might object that other kinds of stimuli were also deviated by the cages' deflectors (e.g. sounds). Actually, on the basis of the present results, one can not directly assume that the pigeons were informed by the winds about the odours prevailing in the areas surrounding the loft. This assumption, however, appears justifiable if one also considers the results of previous experiments, which can be summarized as follows. 1. Pigeons deprived of olfactory perception show poor homing performances (Papi *et al.*, 1971, 1972; Benvenuti *et al.*, 1973a; Baldaccini *et al.*, in press). 2. Homing behaviour is disturbed by odorous substances applied near to or on the nostrils (Benvenuti *et al.*, 1973b). 3. Pigeons which at home had been prevented from breathing through the nostrils in open air, are incapable of correct initial orientation (Papi *et al.*, 1973a; Baldaccini *et al.*, 1974). 4. Pigeons subjected in their aviary to an artificial odorous wind sent from a specific direction show the tendency to fly in the opposite direction when the same odorous substance is applied to the beak before releasing (Papi *et al.*, 1974).

The deflection of the vanishing bearings was consistent in all three test releases despite the different home distance (from 9 to over 100 km). In our opinion, this result is not to be interpreted as evidence that pigeons displaced by more than 100 km recognize over the release area odours which had been carried by the winds to the loft. More probably, the birds determined the direction of displacement during the first part of the outward journey, when the vehicle crossed areas where odours were more familiar to them. This interpretation agrees with recent findings (Papi *et al.*, 1973b, and unpublished data) which indicate that stimuli perceived during the outward journey influence the initial orientation.

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