

# THE FUNCTION OF OLFATORY INPUT IN PIGEON ORIENTATION: DOES IT PROVIDE NAVIGATIONAL INFORMATION OR PLAY ANOTHER ROLE?

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## Summary

In 1972, Papi and his colleagues reported that anosmic pigeons were severely impaired in orientation and homing performance. This observation was followed up in a series of experiments involving numerous elaborate experimental manipulations. On the basis of their results, the hypothesis of olfactory navigation was proposed. Attempts to replicate these findings at other lofts produced widely differing effects, which suggested a highly variable role of olfaction. However, meteorological data, as well as certain other aspects of the findings, throw doubt on the role of odours as navigational cues. (1) Odours of the required characteristics and distribution do not seem to exist. (2) Some effects of 'olfactory' manipulations do not seem to

depend on the availability of odours. (3) Olfactory treatments proved mostly effective, but often the effect was not as predicted. In view of these findings, explanations other than olfactory orientation cannot be excluded; accepting olfactory input as navigational information seems premature. Some of the findings are in agreement with the assumption that olfactory manipulations impair the birds' general processing and integration of information in some unknown way.

Key words: olfactory navigation, olfactory 'map', homing, navigational information, pigeons, *Columba livia*, odour.

## Introduction

In 1972, Papi and his colleagues first reported that olfactory deprivation severely impaired the orientation and homing performance of pigeons, *Columba livia*. These findings seemed to suggest that odours were of crucial importance in pigeon homing. The hypothesis of olfactory navigation marked the beginning of an entirely new field of research in homing. In a series of elegant experiments, involving numerous sophisticated experimental manipulations, Papi and his coworkers collected an impressive amount of evidence documenting the effectiveness of olfactory treatments in Italian pigeons (for summaries, see Papi, 1982, 1986, 1991). Replications of the experiments in other countries, however, yielded widely differing results. Wallraff (e.g. 1980, 1981, 1986) could confirm the Italian findings in southern Germany and became a firm protagonist of the olfactory hypothesis. Yet in upstate New York, USA, and at other lofts in Germany, olfactory manipulations only rarely caused a clear effect (e.g. Keeton, 1980; Schmidt-Koenig, 1987; W. Wiltschko *et al.* 1987*b,c*). These discrepancies led to the well-known controversy among scientists about the role of olfactory input and its general importance for orientation.

The variability in the effects of olfactory manipulations indicates that odours are not the sole cues on which navigation is based, as was initially assumed by Papi and his coworkers. Yet one might still take odour to be one of many navigational factors playing a highly variable role. However, physical limitations and meteorological data render a role of odours as

navigational cues questionable. Also, the findings on olfaction are rather inconsistent, so that accepting the olfactory hypothesis seems premature.

## The availability of suitable odours and physiological requirements

The olfactory hypothesis assumes that pigeons at their home loft associate wind-borne odours with the direction from which the wind blows; from this knowledge, they derive the home direction when they encounter these odours at a release site (e.g. Papi *et al.* 1972; Papi, 1976). Wallraff (1980, 1989*a,b*) later proposed a gradient 'map' of odours, assuming that birds can locate their position by comparing odour concentrations and/or odour combinations. This requires the detection and interpretation of minute differences. It is unclear how pigeons and other microsmatic species could perform this task (cf. Wenzel, 1991).

However, a more crucial question is whether predictable odour gradients exist at all. Meteorologists such as Becker and van Raden (1986) flatly deny that odour gradients, as required by the olfactory hypothesis, exist in nature. Waldvogel (1987) analyzed empirical data on aerial transportation of aerosols; he also pointed out that the normal distribution of airborne substances renders a general use of odours as navigational factors impossible (Waldvogel, 1989). Ganzhorn and Paffrath (1995), who studied the pattern of air pollutants as a model for

the distribution of airborne substances, came to the same conclusion. Any pattern is highly variable; it is continuously disturbed, modified and rearranged by meteorological factors such as wind, turbulence and precipitation, so that a predictable distribution of odours in the form required by the olfactory hypothesis does not exist. This is, no doubt, a most powerful argument against the olfactory navigation hypothesis.

### The data from experiments on olfactory navigation

In view of the meteorologists' statements, one may ask how the numerous effects of olfactory manipulations are to be interpreted. These data come from experiments where groups of pigeons are released away from their home loft. They are set free singly and observed with binoculars until they vanish. The vanishing bearing of each pigeon is taken with a compass; from the bearings of the group, the mean vector is determined by vector addition, its direction and length representing the most important variables of initial orientation. Helpers at the home loft record the returning birds; homing times (often converted into homing speeds) and return rate (percentage of birds returned) are the variables of homing performance.

In experiments on olfaction, treated pigeons and untreated controls are released alternately, and their homing data are compared. Olfactory manipulations were found to affect both initial orientation and homing performance, but the manifestations of these effects do not form a consistent picture.

### The effect of olfactory deprivation

Various methods were used to render pigeons permanently or temporarily anosmic, namely olfactory nerve section, zinc sulphate ( $ZnSO_4$ ) applied to the nasal mucosa, insertion of small plastic tubes into the nostrils, stuffing the pigeons' nostrils with cotton held in place by a tape mask, transportation in air-tight containers with filtered or bottled air, application of local anaesthetics or a combination of the latter. The results obtained are largely independent from the method used.

At unfamiliar sites, effects on initial orientation were observed at distances from less than 10 km to beyond 100 km. On the basis of pooled data, the effect was usually described as 'disorientation'. The data from individual releases, however, reveal two different patterns of response: (1) an increase in scatter and (2) oriented behaviour in directions which differ from those preferred by the controls, which, being different at the various sites, add up to seemingly 'random' distributions when pooled. An obvious pattern with respect to the conditions under which each type of response occurs did not emerge. Homing performance of anosmic pigeons is also impaired: they take considerably longer to return to their home loft and their return rate is markedly lower than that of controls.

Deficits in initial orientation and homing performance are in agreement with what one might expect when navigational information is lacking, but they might also be the results of unspecific trauma. Certain aspects of the findings caution

against a simple interpretation that would favour the olfactory hypothesis.

### Possibility of non-olfactory effects

The effectiveness of some treatments was shown not to be related to olfactory impairment. For example, local anaesthetics affected orientation in a similar way when the pigeons had access to natural odours during displacement and at the release site until immediately before release, at least when applied for the first time (R. Wiltschko *et al.* 1989). Moreover, some of the treatments might interfere with sun compass orientation: Dornfeldt (1979) reported that olfactory deprivation slowed down the homing speed only under sun, but not under overcast sky; Bingman and Ioalè (1989) and Wallraff *et al.* (1994) observed that anosmic pigeons did not respond to clock-shifting in the normal way. A series of clock-shift experiments suggested that transporting pigeons in air-tight containers ventilated with natural air also impairs their use of the sun compass (R. Muth and R. Wiltschko, unpublished data; Fig. 1). In view of these findings, it cannot be excluded that some of the effects attributed to the loss of olfactory information may have different causes.

### Behaviour at familiar sites

Olfactory deprivation is effective only at unfamiliar sites, not at familiar ones. This observation is usually explained by the assumption that pigeons at familiar sites rely on landmarks (see Papi, 1986); Wallraff and Neumann (1989) speak of 'pilotage'. However, several findings argue against this interpretation. (1) Anosmic birds could still orient at familiar

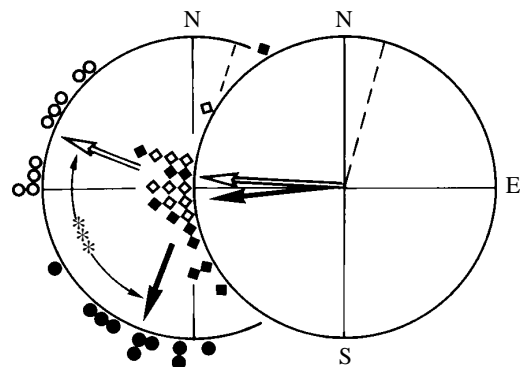


Fig. 1. Transportation in air-tight containers ventilated with natural air impairs the use of the sun compass: orientation of control pigeons transported in open wooden boxes as usual (left-hand circle, circular symbols) and of pigeons transported in air-tight containers (right-hand circle, diamond-shaped symbols) released together at the same site. The home direction is indicated by a dashed radius. Symbols at the periphery of the circles mark vanishing bearings of individual pigeons: open symbols are those of birds living in the natural photoperiod; filled symbols are those of pigeons whose internal clock had been shifted (6 h fast). The arrows represent the mean vectors of the various groups, drawn proportional to the radius of the circle (=1). The asterisks indicate a significant difference in direction ( $P < 0.001$ , Watson Williams test; R. Muth and R. Wiltschko, unpublished data).

sites even when deprived of vision by frosted lenses (Benvenuti and Fiaschi, 1983). (2) The ‘familiarity’ includes other sites in the vicinity where the landmarks are different (Wallraff and Neumann, 1989; R. Wiltschko and Wiltschko, 1989). (3) Untreated birds were shown to ignore landmarks even at very familiar sites when clock-shifted (Füller *et al.* 1983). Thus, existing evidence does not support a use of landmarks at familiar sites, and it is difficult to see why odours – if they are crucial navigational cues at unfamiliar sites – should suddenly cease to play an important role after one homing flight. Together, these findings do not support a role of odours as navigational cues.

*A paradoxical pattern of responses*

The pigeons’ response to olfactory impairment depends on the way in which they are housed and raised (W. Wiltschko *et al.* 1987a). Because of this, pigeons that normally did not respond to olfactory impairment and ones that responded strongly to such treatment could be released together from the same site. The behaviour of such birds results in an odd pattern: of the first group, untreated controls and anosmic pigeons oriented alike, which shows that their headings were independent of odours. However, their orientation was identical with that of the controls of the second group, which must be assumed to be based on olfaction since the anosmic birds of the second group preferred significantly different directions (R. Wiltschko and Wiltschko, 1989; Fig. 2). This phenomenon was observed at several sites where pigeons normally show considerable deviations from the home direction, so-called release site biases (see Keeton, 1973), and seems to imply that, for the second group, olfactory information always indicated the same direction as did non-olfactory information for the first group. This appears highly unlikely when the direction is different from home.

In summary, the various experiments in which pigeons were subjected to olfactory impairments produced effects which

were highly variable. Many of the results indicate an involvement of olfactory input in homing, but they do not prove that odours provide navigational information.

**Experiments designed to manipulate the ‘olfactory map’**

Since the effects of deprivation are only indirect evidence for the role of a factor, attempts were made to obtain more direct evidence by manipulations resulting in effects that could be predicted by the olfactory hypothesis. One possibility was to manipulate the olfactory ‘map’: pigeons are assumed to learn the distribution of odours by exposure at the home loft during the first months of their life, which provided an opportunity to alter the pigeons’ ‘map’ by suitable treatments at the loft.

A number of experimental approaches attempted to make use of such test designs; they included differential shielding at the home loft allowing access of wind only from defined directions, ‘deflector’ lofts deflecting the incoming air clockwise or counterclockwise, as well as forced associations of specific artificially introduced odours with certain wind directions (for summaries, see Papi, 1986, 1991). These manipulations mostly produced a significant change in initial orientation which, in the pooled data, seemed to correspond qualitatively with expectations. The behaviour varied widely, however, and the results of individual experiments were not always consistent with predictions under the olfactory navigation hypothesis (e.g. Ioalè, 1982; Ioalè and Benvenuti, 1983). A prominent example are the ‘deflector loft’ experiments. The incoming air was deflected by 60–80°, which should have resulted in a rotation of the ‘olfactory map’ by a corresponding angle. The bearings of the experimental birds deviated from those of controls in the expected direction, but the size of the deflection was markedly smaller than that predicted by the olfactory hypothesis (Fig. 3; data from Baldaccini *et al.* 1975, 1978; Papi, 1976). Homing was only slightly affected, even when the pigeons had to return from

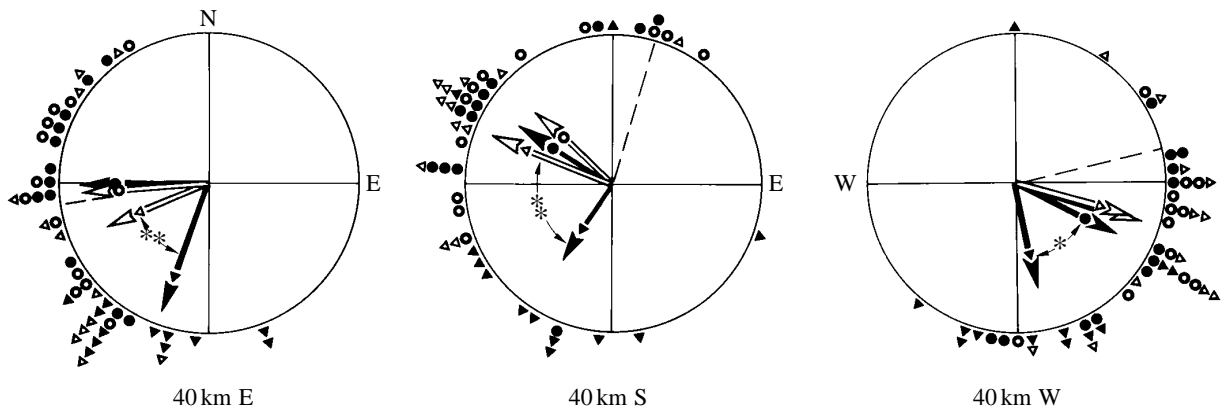


Fig. 2. Unexplained aspects of the effect of olfactory deprivation: orientation of anosmic birds (filled symbols) and controls able to smell (open symbols) from two groups of pigeons raised and kept in different ways: group 1 (circular symbols) did not use olfaction, as indicated by the lack of difference, whereas group 2 (triangular symbols) used olfaction, as indicated by the significant differences between anosmic birds and controls. Yet the birds of group 1 preferred the same directions as the controls of group 2. Symbols as in Fig. 1, significance levels: \* $P < 0.05$ ; \*\* $P < 0.01$  (from R. Wiltschko and Wiltschko, 1989).

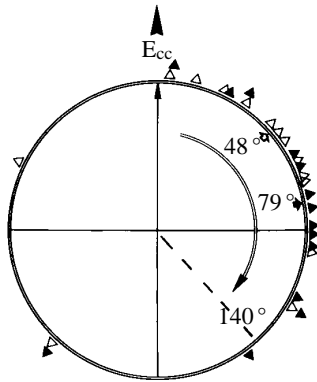


Fig. 3. Effect of housing pigeons in 'deflector lofts' in which the incoming air was deflected 60–80° clockwise or counterclockwise: orientation of the birds from the clockwise-deflecting loft is given with respect to the mean heading of the birds from the counterclockwise loft ( $E_{cc}$ , drawn upwards). The deflection predicted by the olfactory hypothesis, approximately 140°, is marked by a dashed radius. The symbols at the periphery of the circle indicate the angular difference between groups at individual releases, at familiar sites (open symbols) and at unfamiliar sites (filled symbols). The small arrows inside the circle at 48° (familiar sites) and 79° (unfamiliar sites) mark the medians of the releases (data from Baldaccini *et al.* 1975, 1978; Papi, 1976).

directions where information should be lacking in their olfactory 'map' or when a rotated 'map' should have given them false information.

The results of 'deflector loft' experiments, which were replicated by Kiepenheuer (1978) and Waldvogel *et al.* (1978), were initially quoted as proof for the use of olfactory information (e.g. Papi, 1982, 1986). Later studies, however, gave rise to serious doubt about whether the deflections were indeed caused by airborne odours. Deflections were also observed in anosmic pigeons and in pigeons that had been unable to determine the original direction of odours (Kiepenheuer, 1979, 1982); reflected light cues were found to cause similar deflections (Phillips and Waldvogel, 1982). These findings make one wonder whether the deflections observed in these and analogous experiments (e.g. Ioalè and Benvenuti, 1983; Foà *et al.* 1986; Ioalè *et al.* 1990) are truly based on olfaction; they might be induced by wind from one direction only, or by other non-odorous factors, or they may represent conditioned responses to preferred specific directions. In summary, although manipulations attempting to interfere with the normal development of the 'olfactory map' were mostly successful, the results do not provide clear evidence for a role of odours as factors forming the navigational 'map'.

#### Manipulations of olfactory input during displacement and during release

Several experiments attempted to provide pigeons with meaningful, but 'false', information simulating by odorous substances a route or a release site different from the one

actually used. Most of these experiments yielded inconclusive results (e.g. Baldaccini *et al.* 1982; Kiepenheuer, 1986; Schmidt-Koenig and Ganzhorn, 1988). One experiment by Benvenuti and Wallraff (1985) appeared to be successful. The rationale was to make groups of pigeons believe from the odours to which they were exposed that they had been released from site A, while they had actually been released at site B; the design was rather complex, involving six groups of pigeons and two release sites. Three groups of pigeons were each made anosmic and transported to either site, where two of them were given access to the natural air for a certain time period; after that, they were made anosmic again. The control groups now stayed at this site A where they had been allowed to smell until they were released: the experimental birds were transported to the other site B and released there, together with the controls that had had access to odours at site B. Each third group of pigeons was displaced together with the experimental birds first to A, then to B, but was not allowed to smell at either site. The results showed very large scatter; when pooled, none of the groups was homeward-oriented. However, Benvenuti and Wallraff (1985) observed that the mean bearings of the experimental birds showed a significant directional tendency when pooled with respect to the mean of the controls released at site A where the experimental birds had had access to natural air (Table 1, upper line).

Benvenuti and Wallraff (1985) quoted their findings as proof for olfactory navigation. However, the data do not exclude a different interpretation: when the mean bearings of the third, totally anosmic, group were used as a reference, the experimental birds also showed a common directional tendency (Table 1, lower line). The reverse procedure, using the means of the experimental pigeons as a reference, revealed a corresponding significant directional tendency in the anosmic birds. These calculations suggest that the observed behaviour is not due to olfactory cues. It appears to be caused by the component of the procedure which the birds had in common, namely, the route of the outward journey to site A. This interpretation is in agreement with the observation of Kiepenheuer (1985), who performed a similar experiment, but used different routes in transporting his pigeons; he found no agreement in directional tendency between the experimental birds and the controls released at the site where the experimental birds had been allowed to smell.

#### Open questions about the role of olfactory input

The findings presented so far make the physical and the physiological bases of olfactory navigation doubtful; in particular, the meteorological data argue strongly against a role of odours as navigational cues. Experiments designed with the olfactory hypothesis in mind yielded a number of interesting results; yet the findings are not as clear as one might wish. The emerging picture is not free of inconsistencies. The unexplained discrepancy in the manifestation of the effects of olfactory impairment and of attempted manipulations of the olfactory 'map' serve as an example: anosmic birds are

Table 1. Behaviour of pigeons allowed to smell natural air at site A, but released at site B

Reference	German releases			Italian releases			All releases		
	<i>N</i>	<i>r</i>	<i>F</i> (2,2)	<i>N</i>	<i>r</i>	<i>F</i> (2,4)	<i>N</i>	<i>r</i>	<i>F</i> (2,8)
Controls released at A	4	0.49	10.34	6	0.39	24.01**	10	0.40	42.59***
Anosmic pigeons	4	0.26	1.83	6	0.44	110.61***	10	0.34	8.28*

Data from Benvenuti and Wallraff (1985).

*r* indicates the distance of the centre of distribution of the respective vectors from the origin of coordinates.

*F*(2,*N*-2) gives the test statistic of the Hotelling test; significance indicates a common tendency in the reference direction. Significance levels: \**P*<0.05, \*\**P*<0.01, \*\*\**P*<0.001.

impaired only at unfamiliar sites, and their homing performance is markedly reduced; birds with a manipulated olfactory 'map', in contrast, also show deflections at familiar sites (see Fig. 3), while their homing performance is only slightly affected. These differences show that effects resulting from the various olfactory manipulations do not necessarily represent a single, homogeneous phenomenon; the effects of olfactory deprivation might be of quite a different nature from the effects of olfactory manipulations at the home loft.

Open questions further concern observed deviations from the control direction, which are mostly attributed to a 'preferred compass direction', a phenomenon that is likewise unexplained and the existence of which is not undisputed (see R. Wiltschko, 1993, for a discussion). Odd asymmetries and other details of the pigeons' behaviour also await explanations. Benvenuti and Wallraff's statement (1985, p. 744) 'As usual in this kind of experiment, individual releases rarely fit theoretical expectations in the ideal way, and often they show some peculiarities inviting speculative interpretations' applies to almost all experiments on olfactory navigation. The theoretical background of the olfactory hypothesis and the precise role that odours are assumed to play in the navigational process are likewise unclear (see Schmidt-Koenig, 1987, for details). Aside from these problems, it must be considered that some effects initially reported as olfactory effects may be of a different nature. At the moment, no experiment unequivocally proves the use of odours as navigational cues. Hence, it does not appear justified to accept that they provide navigational information.

What possible alternative explanations exist? Of course, I cannot offer a consistent interpretation of all 'olfactory' data. Olfactory impairments are known to have side-effects interfering with a number of non-olfactorily controlled responses, such as tonic immobility and vestibular and optokinetic nystagmus (e.g. Wenzel and Rausch, 1977; Dornfeldt and Bilo, 1990). I would like to point out some additional observations which indicate in what direction we might want to look. (1) Olfactory deprivation appears to impair the motivation to return home, which is indicated by the observation that great losses of permanently anosmic pigeons also occur at the loft and when such birds are trained together with intact controls (e.g. Papi *et al.* 1989; Schmid and Schlund, 1993). (2) Some olfactory manipulations seem to interfere with

the sun compass (Dornfeldt, 1979; Bingman and Ioalè, 1989; Wallraff *et al.* 1994; see Fig. 1) and with the recording of directional information during the outward journey (W. Wiltschko *et al.* 1987b). (3) Olfactory deprivation is effective only at unfamiliar sites, which means that pigeons have no previous experience and have to interpret an entirely new combination of navigational factors.

These observations seem to suggest that olfactorily manipulated birds are somehow impaired in the general processing of information, such as route-specific information, integrating time and sun azimuth for sun-compass orientation, or extrapolating 'map' factors at unfamiliar sites. The assumption that olfactory input is involved in the processing of non-olfactory information is further supported by the observation that treatments such as exposure to irregularly alternating magnetic fields affected orientation only when the pigeons had access to natural air during the treatment (Wallraff *et al.* 1986; Papi and Ioalè, 1988). Earlier experiments (cf. Wenzel and Rausch, 1977; Wenzel, 1974) had already indicated that anosmic birds are impaired in tasks not controlled by olfaction, such as responses to visual stimuli (Wenzel and Salzman, 1968). Hence, it may be worthwhile to follow up the idea of an involvement of olfactory input in general information processing.

## Conclusions

The open questions, especially about its physical basis, cause most researchers to remain sceptical about the olfactory navigation hypothesis. Even among its protagonists, a certain uneasiness is indicated. Defending their hypothesis, they repeatedly point out that there is no alternative to olfactory navigation (e.g. Papi, 1991; Wallraff, 1991, 1993). This may be true, but the lack of an alternative is certainly no valid reason for accepting a specific hypothesis. It would be like convicting a defendant simply because there is no other suspect.

As it is, we need research which does not take a role of odours as navigational cues for granted, but asks the crucial specific questions about what happens when olfaction is impaired and how the various olfactory manipulations really affect the organism.

## References

- BALDACCINI, N. E., BENVENUTI, S., FIASCHI, V., IOALÈ, P. AND PAPI, F. (1978). Investigation of pigeon homing by means of 'deflector cages'. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 78–91. Berlin, Heidelberg, New York: Springer.
- BALDACCINI, N. E., BENVENUTI, S., FIASCHI, V., IOALÈ, P. AND PAPI, F. (1982). Pigeon orientation: Experiments on the role of olfactory stimuli perceived during the outward journey. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 160–169. Berlin, Heidelberg, New York: Springer.
- BALDACCINI, N. E., BENVENUTI, S., FIASCHI, V. AND PAPI, F. (1975). Pigeon navigation: Effects of wind deflection at home cage on homing behaviour. *J. comp. Physiol.* **99**, 177–186.
- BECKER, J. AND VAN RADEN, H. (1986). Meteorologische Gesichtspunkte zur olfaktorischen Navigationshypothese. *J. Orn.* **127**, 1–8.
- BENVENUTI, S. AND FIASCHI, V. (1983). Pigeon homing: Combined effect of olfactory deprivation and visual impairment. *Comp. Biochem. Physiol.* **76A**, 719–725.
- BENVENUTI, S. AND WALLRAFF, H. G. (1985). Pigeon navigation: Site stimulation by means of atmospheric odours. *J. comp. Physiol.* **156**, 737–746.
- BINGMAN, V. P. AND IOALÈ, P. (1989). Initial orientation of anosmic homing pigeons based on information gathered at familiar release sites remains homeward directed following clock-shift. *Behaviour* **110**, 205–218.
- DORNFELDT, K. (1979). Beeinträchtigung der Navigation der Brieftaube (*Columba livia*) durch Xylocain-Behandlung der Nasenhöhle. *Verh. dt. zool. Ges.* **1979**, 218.
- DORNFELDT, K. AND BILO, D. (1990). Effects of intranasal application of the local anaesthetic Xylocain on vestibulo-, opto-collic and postural reflexes of the head and on tonic immobility in homing pigeons: implications for experiments on pigeon homing. *J. exp. Biol.* **149**, 95–111.
- FOÀ, A., BAGNOLI, P. AND GIONGO, F. (1986). Homing pigeons subjected to section of the anterior commissure can build up two olfactory maps in the deflector lofts. *J. comp. Physiol. A* **159**, 465–472.
- FÜLLER, E., KOWALSKI, U. AND WILTSCHKO, R. (1983). Orientation of homing pigeons: Compass orientation vs piloting by familiar landmarks. *J. comp. Physiol.* **153**, 55–58.
- GANZHORN, J. U. AND PAFFRATH, D. (1995). Patterns in air pollution as model for the physical basis for olfactory navigation in pigeon homing. *J. Orn.* **136**, 159–165.
- IOALÈ, P. (1982). Pigeon homing: Effects of differential shielding of home cages. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 170–178. Berlin, Heidelberg, New York: Springer.
- IOALÈ, P. AND BENVENUTI, S. (1983). Pigeon homing: Further experiments on shielded lofts. *Comp. Biochem. Physiol.* **76A**, 725–733.
- IOALÈ, P., NOZZOLINI, M. AND PAPI, F. (1990). Homing pigeons do extract directional information from olfactory stimuli. *Behav. Ecol. Sociobiol.* **26**, 301–305.
- KEETON, W. T. (1973). Release-site bias as a possible guide to the 'map' component in pigeon homing. *J. comp. Physiol.* **86**, 1–16.
- KEETON, W. T. (1980). Avian orientation and navigation: New developments in an old mystery. In *Acta XVII Congr. Intern. Ornithol.*, vol. I (ed. R. Nöhring), pp. 137–158. Berlin: Deutsche Ornithologen-Gesellschaft.
- KIEPENHEUER, J. (1978). Pigeon homing: A repetition of the deflector loft experiment. *Behav. Ecol. Sociobiol.* **3**, 393–395.
- KIEPENHEUER, J. (1979). Pigeon homing: Deprivation of olfactory information does not affect the deflector effect. *Behav. Ecol. Sociobiol.* **6**, 11–22.
- KIEPENHEUER, J. (1982). Pigeon orientation: A preliminary evaluation of factors involved or not involved in the deflector loft effect. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 203–210. Berlin, Heidelberg, New York: Springer.
- KIEPENHEUER, J. (1985). Can pigeons be fooled about the actual release site position by presenting them information from another site? *Behav. Ecol. Sociobiol.* **18**, 75–82.
- KIEPENHEUER, J. (1986). Are site-specific airborne stimuli relevant for pigeon navigation only when matched by other release-site information? *Naturwissenschaften* **73**, 42–43.
- PAPI, F. (1976). The olfactory navigation system of the homing pigeon. *Verh. dt. zool. Ges.* **69**, 184–205.
- PAPI, F. (1982). The homing mechanisms of pigeons. *Nature* **300**, 293–294.
- PAPI, F. (1986). Pigeon navigation: Solved problems and open questions. *Monit. zool. ital.* **20**, 471–517.
- PAPI, F. (1991). Olfactory navigation. In *Orientation in Birds* (ed. P. Berthold), pp. 52–85. Basel: Birkhäuser.
- PAPI, F., FIORE, L., FIASCHI, V. AND BENVENUTI, S. (1972). Olfaction and homing in pigeons. *Monit. zool. ital.* **6**, 85–95.
- PAPI, F., GAGLIARDO, A., FIASCHI, V. AND DALL'ANTONIA, P. (1989). Pigeon homing: Does early experience determine what cues are used to navigate? *Ethology* **82**, 208–215.
- PAPI, F. AND IOALÈ, P. (1988). Pigeon navigation: New experiments on interaction between olfactory and magnetic cues. *Comp. Biochem. Physiol.* **91A**, 87–89.
- PHILLIPS, J. B. AND WALDVOGEL, J. A. (1982). Reflected light cues generate the short-term deflector-loft effect. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 190–202. Berlin, Heidelberg, New York: Springer.
- SCHMID, J. AND SCHLUND, W. (1993). Anosmia in ZnSO<sub>4</sub>-treated pigeons: loss of olfactory information during ontogeny and the role of site familiarity in homing experiments. *J. exp. Biol.* **185**, 33–49.
- SCHMIDT-KOENIG, K. (1987). Bird navigation: Has olfactory orientation solved the problem? *Q. Rev. Biol.* **62**, 31–47.
- SCHMIDT-KOENIG, K. AND GANZHORN, J. U. (1988). On the role of airborne information for the initial orientation of homing pigeons: Test for the mosaic map hypothesis. In *Current Topics in Avian Biology* (ed. R. van den Elzen, K.-L. Schuchmann and K. Schmidt-Koenig), pp. 299–304. Bonn: Deutsche Ornithologen-Gesellschaft.
- WALDVOGEL, J. A. (1987). Olfactory navigation in homing pigeons: Are the current models atmospherically realistic? *Auk* **104**, 369–379.
- WALDVOGEL, J. A. (1989). Olfactory orientation by birds. In *Current Ornithology*, vol. 6 (ed. D. M. Power), pp. 269–321. New York: Plenum Press.
- WALDVOGEL, J. A., BENVENUTI, S., KEETON, W. T. AND PAPI, F. (1978). Homing pigeon orientation influenced by deflected winds at home loft. *J. comp. Physiol.* **128**, 297–301.
- WALLRAFF, H. G. (1980). Olfaction and homing in pigeons: Nerve-section experiments, critique, hypotheses. *J. comp. Physiol.* **139**, 209–224.
- WALLRAFF, H. G. (1981). The olfactory component of pigeons' navigation: Steps of analysis. *J. comp. Physiol.* **143**, 411–422.
- WALLRAFF, H. G. (1986). Relevance of olfaction and atmospheric

- odours to pigeon homing. In *Orientation in Space* (ed. G. Beugnon), pp. 71–80. Toulouse: Privat, I.E.C.
- WALLRAFF, H. G. (1989a). Simulated navigation based on unreliable sources of information (models on pigeon homing. Part 1). *J. theor. Biol.* **137**, 1–19.
- WALLRAFF, H. G. (1989b). Simulated navigation based on assumed gradients of atmospheric trace gases (models on pigeon homing. Part 2). *J. theor. Biol.* **138**, 511–528.
- WALLRAFF, H. G. (1991). Conceptual approaches to avian navigation systems. In *Orientation in Birds* (ed. P. Berthold), pp. 128–165. Basel: Birkhäuser.
- WALLRAFF, H. G. (1993). Correct and false olfactory orientation in homing pigeons as depending on geographical relationships between release site and home site. *Behav. Ecol. Sociobiol.* **32**, 147–155.
- WALLRAFF, H. G., KIEPENHEUER, J. AND STRENG, A. (1994). The role of visual familiarity with the landscape in pigeon homing. *Ethology* **97**, 1–25.
- WALLRAFF, H. G. AND NEUMANN, M. F. (1989). Contribution of olfactory navigation and non-olfactory pilotage to pigeon homing. *Behav. Ecol. Sociobiol.* **25**, 293–302.
- WALLRAFF, H. G., PAPI, F., IOALÈ, P. AND BENVENUTI, S. (1986). Magnetic fields affect pigeon navigation only while the birds can smell atmospheric odors. *Naturwissenschaften* **73**, 215–217.
- WENZEL, B. M. (1974). The olfactory system and behavior. In *Limbic and Autonomic Nervous Systems Research* (ed. L. V. DiCara), pp. 1–40. New York: Plenum Press.
- WENZEL, B. M. (1991). Olfactory abilities of birds. In *Acta XX Congr. Intern. Ornithol.*, vol. III (ed. B. D. Bell, R. O. Cossee, J. E. C. Flux, B. D. Heather, R. A. Hitchmough, C. J. R. Robertson and M. J. Williams), pp. 1820–1829. Christchurch, New Zealand: Ornithological Congress Trust Board.
- WENZEL, B. M. AND RAUSCH, L. J. (1977). Does the olfactory system modulate affective behavior in the pigeon? *Ann. N.Y. Acad. Sci.* **290**, 314–330.
- WENZEL, B. M. AND SALZMAN, A. (1968). Olfactory bulb ablation or nerve section and behavior of pigeons in nonolfactory learning. *Exp. Neurol.* **22**, 472–479.
- WILTSCHKO, R. (1993). Pigeon homing: release site biases and their interpretation. In *Orientation and Navigation – Birds, Humans and Other Animals*. Proc. Int. Conf. Royal Inst. of Navigation Oxford 1993, paper no. 15
- WILTSCHO, R. AND WILTSCHKO, W. (1989). Pigeon homing: olfactory orientation – a paradox. *Behav. Ecol. Sociobiol.* **24**, 163–173.
- WILTSCHKO, R., WILTSCHKO, W. AND KOWALSKI, U. (1989). Pigeon homing: An unexpected effect of treatment with a local anaesthetic on initial orientation. *Anim. Behav.* **37**, 1050–1052.
- WILTSCHKO, W., WILTSCHKO, R., GRÜTER, M. AND KOWALSKI, U. (1987a). Pigeon homing: Early experience determines what factors are used for navigation. *Naturwissenschaften* **74**, 196–198.
- WILTSCHKO, W., WILTSCHKO, R. AND JAHNEL, M. (1987b). The orientation behavior of anosmic pigeons in Frankfurt a. M., Germany. *Anim. Behav.* **35**, 1324–1333.
- WILTSCHKO, W., WILTSCHKO, R. AND WALCOTT, C. (1987c). Pigeon homing: Different effects of olfactory deprivation in different countries. *Behav. Ecol. Sociobiol.* **21**, 333–342.