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Olfactory navigation in birds

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Summary. Many bird species rely on an osmotactic mechanism to find food sources even at a considerable distance. Pigeons also rely on local odours for homeward orientation, and they integrate those perceived during passive transportation with those at the release site. It is possible to design experiments in which birds are given false olfactory information, and predictions about the effects of this can be made and tested. Pigeons build up their olfactory map by associating wind-borne odours with the directions from which they come; this was shown by experiments which aimed at preventing, limiting or altering this association. Some objections have been made to this conclusion; namely that even anosmic pigeons are sometimes homeward oriented, that they may be demotivated in flying or disturbed in their general behaviour, and that olfactory cues may be only one component of pigeon's navigational repertoire. The most recent experiments, however, confirm that pigeons derive directional information from atmospheric odours. The lack of any knowledge about the chemical nature and distribution of the odorants which allow pigeons to navigate hinders progress in this area of research.

Key words. Bird olfaction; orientation; navigation; homing pigeon.

Introduction

Until the 1950s, observations on bird behaviour in response to olfactory stimuli yielded conflicting results. Many zoologists considered the olfactory ability of birds to be very low and the question sometimes arose whether their olfactory apparatus had a different function from that of sensing odours. The opinion that birds have no olfactory ability was widely held in the 1940s, when an authoritative paper[120] reported the results of a series of physiological and behavioural tests performed on several species, which were found by the author to be insensitive to odours. More recently, however, a re-evaluation of the olfactory ability and the role of olfaction in a bird's life has been prompted by anatomical, physiological and behavioural evidence[10].

Anatomical studies have shown that the relative size of the olfactory bulbs, as measured by the ratio between the olfactory bulb diameter and that of the cerebral hemisphere, expressed as a percentage, varies between 3% and 37%[9]; this is an indication of differences in the importance of olfactory perception in different species. Electrophysiological recordings from the olfactory membrane, nerves, bulbs or associated single units showed clear responses to odorants according to intensity and quality of stimuli[62, 85, 93, 127]. Spontaneous visceral responses to odours, including respiration and heart rate changes, which can be strengthened by pairing the stimulus with an electric shock, have been successfully used to test olfactory sensitivity[84, 98, 121, 123].

A rather long series of both classical and operant conditioning experiments indicating that birds are poor at associating odours with other stimuli[22, 120] lent support to the idea that traditional conditioning methods were quite ineffective in demonstrating the sensitivity of birds to odours. A conditioned suppression method – although it was time-consuming – was eventually set up and successfully used[34, 86, 87, 91]. More recently, however, simple conditioning methods were also reported to yield positive results[28, 41, 46].

The olfactory sensitivity threshold was determined for a few species by using a small number of compounds, whose odour probably has little, if any, biological relevance for the birds tested[88, 89, 91, 98]. Many values lie between 10^{-5} and 10^{-7} M, and they are seldom as low as 10^{-9}. However, the threshold for certain substances of biological relevance might be much lower. In fact, even species with poorly developed olfactory bulbs may be specialized for sensing some compounds, whereas a large olfactory membrane tends to indicate a high capacity for discrimination between odours[2].

Use of odours in the life of birds

Little is known about the use that birds make of their sense of smell. Besides the olfactory orientation phenomena reported in later sections, a small number of other odour-dependent behaviour patterns have been reported or suspected. Odours arising from the secretion of the uropygial gland are thought to act as a pheromone in the rook and in the mallard[8, 45, 52] while the stomach oil of procellarids might be an olfactory mark[31, 84]. Young geese react to odours from certain plants by head-shaking[134], while starlings select some plants with insecticidal and anti-pathogenic properties on the basis of their smell, and incorporate them in the nest material[18, 19].

Orientation towards odour sources

A series of species, including the brown kiwi, corvids, honeyguides and procellarids is known to use the sense of smell to select or find food[10, 95]. The probable mechanisms involved in food finding are upwind orientation on perceiving an attractive smell or, in still air, orientation according to a gradient.

Some cases are worth mentioning, as they involve rather long, oriented flights. Honeyguides are attracted by the odour of lighted candles[90]; they probably find beehives by smell. When the greater honeyguide (*Indicator indicator*) shows the direction of a hive to man, the distance of the target can be deduced from its behaviour[44]. About a dozen procellarid species were found to be attracted by smells while flying over the sea. Sponges soaked with cod liver oil (or a volatile extract from it) were approached by birds flying upwind, whereas unscented sponges were disregarded[30, 36, 37, 47].

An interesting case of homing guided by olfactory cues has been investigated in leach's petrel[31]. The birds return to their burrows, which are hidden by a thick canopy, landing downwind and then walking upwind. In a Y-maze, birds significantly prefer an air current coming from their own nest material. Further evidence of olfactory orientation comes from experiments with anosmic birds which were unable to home.

Olfactory navigation without sensory contact with the goal

Homing ability from unfamiliar sites after passive displacement has been reported for many bird species[1, 63, 64] but the investigation of navigational mechanism(s) has been almost entirely carried out on the homing pigeon. This is one of the many pigeon breeds produced by artificial selection from the wild ancestor, *Columba livia*. In comparison with the ancestor and with other breeds, the homing pigeon shows a greater motivation to home[3]. Independently of body size, homing pigeons have larger brains than fantails and strassers[32], but the relative size of their olfactory bulbs with respect to the cerebral hemispheres ('olfactory ratio') does not significantly differ from that of strassers and fantails[65]. With an olfactory ratio of 18% the pigeon has olfactory bulbs which are of medium size in comparison with those of other birds.

In a homing experiment, pigeons are released one by one. By recording the direction in which each pigeon disappears from the visual field of the observer's binoculars, a vanishing diagram can be obtained, and this allows one to infer whether the initial orientation is randomly determined, or oriented towards home or some other point. Homing speed and homing success (the ratio of birds that home) are two further important parameters in homing behaviour. Intact birds that are transported by a van to a release site usually have an initial orientation towards home. In some regions, however, the initial orientation often fails to reveal a homeward tendency; under overcast skies the vanishing points usually show a much wider scatter.

Initial orientation often turns out to be the resultant between two tendencies – that of flying towards home and that of flying in a fixed compass direction. The latter is called 'preferred compass direction' (PCD), and it is peculiar to each loft[106]. It seems to be determined by the direction of the prevailing wind in the loft area (Ioalè, unpublished observations). Some authors do not accept the concept of a PCD and attribute deviations from the homeward direction to release site biases[128, 129].

Series of investigations that began early in the 1970s ascertained that the initial bearings of clock-shifted pigeons, when these were released in sunny conditions, were deflected with respect to controls[81, 82], as would be expected in animals that use a time-compensated sun compass. It was also observed that orientation in overcast conditions was not influenced by the clock shift but was disturbed by the application of magnets[48, 49]. As a result it was generally accepted that, in some unknown way, pigeons discover the home direction, and then adopt that direction using a solar or magnetic compass (Kramer's map-and-compass concept[59]).

Many hypotheses have been put forward as to how pigeons determine the home direction, but none of them have been verified experimentally. The involvement of olfactory cues in the homing process was eventually shown by Papi and co-workers[67–69, 71, 72] and repeatedly confirmed by Wallraff[103; 105, 107, 108]. The main findings and ideas of Papi's and Wallraff's teams are reported in subsections 1–4, while the objections to their conclusions are discussed in subsection 5, which includes the most recent results.

1. Olfactory navigation in the pigeon

Many release experiments have been performed to test the homing behaviour of pigeons made anosmic by a variety of methods. The safest way is that of sectioning both olfactory nerves, but an almost complete, though transitory, anosmia can be obtained in a simple way by spraying a local anaesthetic (Lidocain) through the nostrils. To minimize differences with respect to controls, one can sever one nerve in controls and in experimentals, and then plug the controlateral nostril in the experimentals, and the ipsilateral one in the controls. Finally, the insertion of thin plastic tubes into the nasal passages, which prevent air from reaching the nasal mucosae, produces anosmia without surgical or pharmacological intervention[69, 105, 110]. During transportation to the release site, one can prevent pigeons from perceiving odours in the natural environment by enclosing them in containers ventilated with pure or filtered air. Transportation during which both nostrils are plugged does not guarantee complete anosmia[110].

Homing ability from unfamiliar sites was heavily impaired by all these methods in terms both of initial orientation and homing success. In inexperienced pigeons with severed olfactory nerves, homing success decreases with increasing distance from the loft, and almost all birds are lost at release sites at a distance of more than 50 km (fig. 1). The distribution of the recovery sites shows that anosmic pigeons often fly over very long distances but are unable to approach home[109].

As shown by the deflecting effect of the clock shift[23, 27, 29], pigeons, if able to smell, use their olfactory map-and-compass mechanism even from familiar sites. However, the birds' behaviour indicates some additional reference to familiar site information[16]. In repeated releases from the same site, the deflection produced by clock-shift progressively decreases[23]. When made anosmic, pigeons still steer homeward, and they home from familiar sites[13, 33, 78], as familiar-site information alone is sufficient to guide birds. In this situation (familiar site plus anosmia), the sun compass mechanism is no longer used and clock shift has a merely marginal effect, resulting in an increased scattering of bearings[16].

Pigeons take into account the olfactory information picked up both at the release site and during the outward journey[69, 119]. If access to outside odours or to all smells is prevented during transportation, there is a heavy fall in homeward directedness in birds that have been released a few minutes or hours after they have started to smell natural odours again[6, 112]. However, the results of releases made the day after transportation indicate that a longer stay at the release site compensates for the lack of olfactory information en route, as if olfactory information at a specific site were not fully available at any one time[102, 115]. If initial orientation is compared in groups of pigeons: a) transported and released without any limitation on the perception of odours, b) transported without such limitations, but made anosmic by local anaesthesia a few minutes before release, c) transported anosmically and released after being allowed to smell at the release site, and d) prevented from perceiving odours during transportation and at the release site, there turns out to be a progressive deterioration in initial orientation (fig. 2).

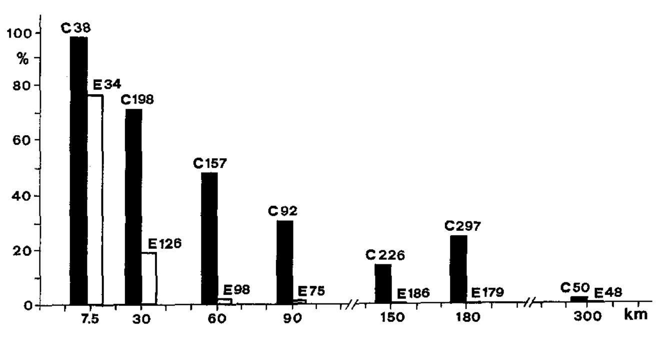

Figure 1. Percentage of pigeons which homed from different distances. Solid bars refer to control birds (C), open bars to anosmic birds (E); the number of birds released is given. All the birds belonged to the same loft and were homing-inexperienced. Source: data from Wallraff[109].

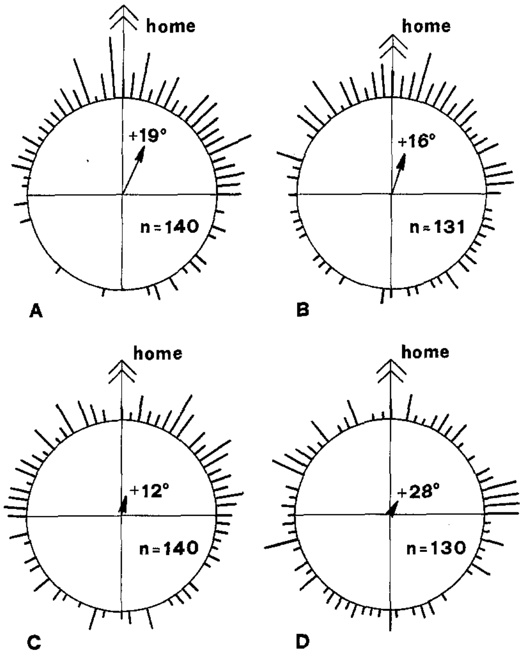

Figure 2. Vanishing diagrams of homing pigeons released: *A* without any limitation on the perception of atmospheric odours; *B* transported normally, but made anosmic a few minutes before release; *C* transported without access to atmospheric odours but released after being allowed to smell at the release site, and *D* prevented from smelling atmospheric odours during transportation and at the release site. The length of the bars at the periphery of the circle is proportional to the number of pigeons that vanished in the corresponding 5-degree sector. The inner arrow indicates the mean vector; its length decreases as the scattering of the bearing increases. It would be 1 if it were equal to the radius of the circle. Source: data from Wallraff et al.[112].

By combining anosmic transport and local anaesthesia, differences between controls and experimentals can be minimized, and it can be shown that in itself the anaesthesia does not disturb orientation. In these studies pigeons are transported in closed containers which are ventilated with filtered air for experimentals, and with non-filtered air for controls, and then both groups are released after the anaesthesia of the olfactory membranes. The controls are homeward oriented, unlike the experimentals, which are randomly oriented[112, 114].

2. *Detour and site simulation experiments*

Of course, pigeons do not rely on smells originating in the loft area in order to fly home, but on local odours, from which they derive information about their position with respect to their loft. This is shown by detour and site simulation experiments.

In a detour experiment, two groups of pigeons are carried to the same release site by two different routes, which are strongly divergent in the first leg. In most cases the two groups have a different initial orientation, each showing the tendency not to fly simply on the basis of the position of the release site, but according to a compromise between its position and that of the sites crossed during the outward journey[70, 76, 77].

Site simulation experiments were performed by allowing pigeons to smell atmospheric odours at only one site, at a distance of 15–55 km from the loft and located in the opposite direction from that of the release site. Birds were prevented from perceiving odours from outside and had their olfactory mucosae anaesthetized before release[15, 56]. The pigeons oriented according to the position of the site where they had had access to atmospheric odours and not according to the position of the true release site. In another series of experiments, pigeons did not orientate according to the position of the site where they had smelled atmospheric odours, but were disoriented[57]. Since the releases were carried out only 11–15 km from the loft, the olfactory information probably conflicted with information provided by familiar landmarks.

3. *The olfactory map and its acquisition*

The range of olfactory navigation is limited. At a very great distance from the loft, local odours no longer convey useful information, and pigeons are disoriented unless they can rely on odours during the first part of the outward journey in identifying the direction in which they are being displaced. For pigeons from Florence anosmically transported north of the Alps, the boundary appeared to lie between 500 and 700 km[43, 118], but pigeons from the Munich area were still able to steer in the home direction from a point 709 km north of the loft[104]. Thus, it has been shown that pigeons possess an olfactory map whose range is probably seasonally and geographically variable.

Since each pigeon possesses a map centred on its loft, the map itself must be regarded as the outcome of individual experience. However, previous homing experience is not necessary, and pigeons are able to navigate even if they have always been kept in an aviary[60, 61, 99, 100]. Under such constraints, from what kind of experience do pigeons derive their olfactory map?

We have suggested that young pigeons, in their loft, build up their map by associating wind-borne odours with the direction from which they come[72]. If so, pigeons released far from the loft can determine the home direction, provided that the prevailing odour at the release site has already been sensed at the loft as one of the odours brought by the wind. The home direction is opposite to the one from which that particular odour was usually perceived in the loft.

It may be noted that, at the moment when orientation occurs at the release site, there is no need for a wind to be blowing; this would, in fact, be a disturbance, because it would bear odours from other areas. It is interesting to note that a navigation mechanism based on an olfactory map has been hypothesized by Baker[4] without reference to any specific animal, and without knowing the mechanism described by us. Baker's model also supposes that the olfactory map is acquired on the basis of odours carried by winds to an animal's usual home, whereas a direction-fixing towards home from distant sites would only be possible when a wind is blowing.

Our idea is consistent with the results of a long series of previous experiments in which pigeons were kept all the time in aviaries shielded in different ways[60, 61, 99]. When the shields prevented the flow of air currents, pigeons were unable to home and it was eventually concluded that oriented dynamic processes in the atmosphere were involved in navigation[100]. After the discovery of the effect of anosmia on homing, new experiments were performed with pigeons kept in screened lofts, or exposed to winds with their nostrils plugged. The results showed that exposure to winds with open nostrils is a prerequisite for the acquisition of homing ability[73].

Further experiments aimed at testing how pigeons build up their map, by using special cages. When the loft is only open to winds from two quadrants (fig. 3 A), the pigeons are homeward oriented, provided that releases are from directions included in those quadrants[39, 101]. However, when the loft is screened from all directions but one (fig. 3 B), the birds fail to orientate homeward even when released from the direction open to the wind[40]. This result seems to show that birds need to compare wind-borne odours from at least two directions; otherwise, it must be considered a result that contradicts the hypothesis[83]. Many authors quote the experiments performed by keeping the birds in lofts equipped with deflectors which produce a clockwise or counterclockwise deviation of the winds, from whatever direction they come (fig. 3 C). The result is that birds released from any direction consistently deflect clockwise or counterclockwise, according to the arrangements of the deflectors[5, 7, 20, 53, 96].

Other results consistent with those reported above have been obtained by keeping pigeons in corridor lofts equipped with fans (fig. 3 D). When a wind blew from one of the two quadrants bisected by the corridor axis, the birds were subjected to an artificial wind produced by a fan and blowing from the opposite direction. In releases from the directions of the corridor axis, the birds orientated in a direction opposite to that of home. The homing performances were poorer than those of controls, and in some releases disastrous[38, 42].

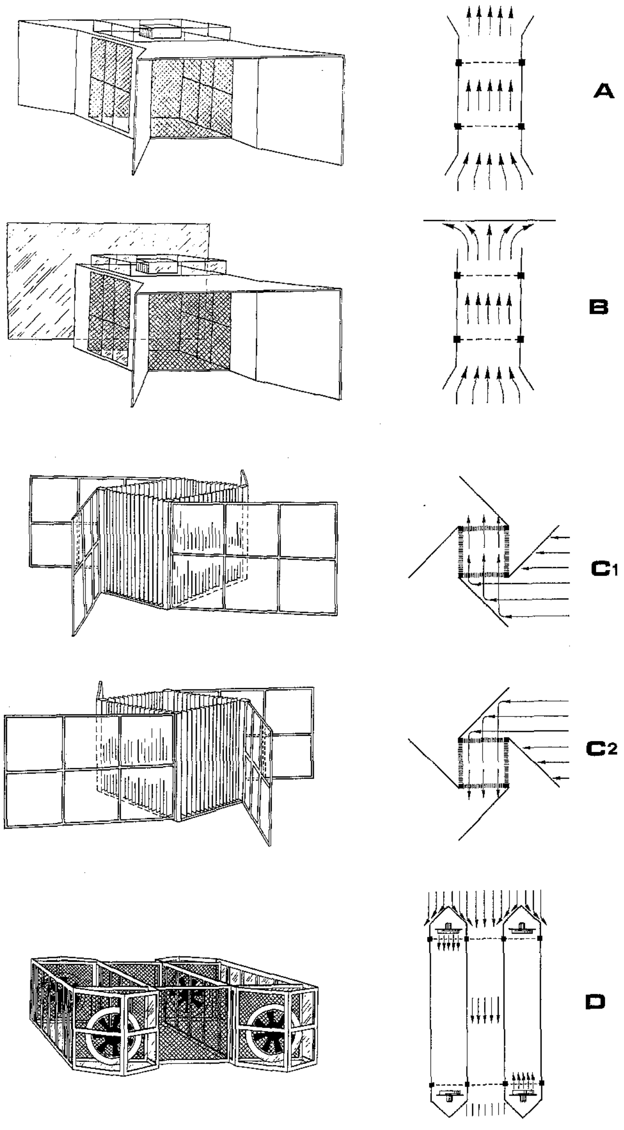

Figure 3. Sketches and horizontal sections of the cages used in the experiments aiming to test whether pigeons associate wind-borne odours with the direction from which they come. *A* Cage open to winds blowing from two quadrants, and *B* from one quadrant. *C* Deflector lofts deflecting the wind clockwise (C1) or counterclockwise (C2). *D* Corridors with fans. In the central corridor the birds are exposed to natural winds blowing along the corridor axis, in the left corridor, to an air current blowing in the same direction, in the right corridor to an air current from the opposite direction. From Papi[69].

Another experiment, which aimed at testing the hypothesis mentioned above about how pigeons build up an olfactory map, was carried out using artificial winds laden with odours. Two groups of pigeons were denied exposure to natural wind but were intermittently exposed to artificial odour-bearing air currents. One group of pigeons was able to smell odour A from the North and odour B from the South, whereas another group was treated in the reverse way. The test experiments took place at a site to the west of the loft. One or the other of the odorous substances was placed near the pigeon's nostrils. The pigeons then flew in the opposite direction (North or South) from that from which they were used to sensing that particular odour in the corridor loft. Thus each group of pigeons flew North or South according to whether they were made to smell odour A or B and the pigeons belonging to the two groups went in opposite directions when they received the same odour[75].

4. Hypotheses about the map

Previous theories on pigeon navigation were based on the fact that certain known physical parameters were capable of allowing the identification of a subject's geographical position. The height of the sun at local noon and the time at which the sun passes the meridian may supply a bird with information about latitude and longitude, while the total intensity of the magnetic field, and its inclination, could give further indications of latitude. The importance of such cues was tested experimentally by depriving birds of astronomic or magnetic cues, or by giving them false cues of this kind. The conclusion was reached that the birds do not possess either an astronomic map[50], or a magnetic one[105].

This has increased attention and interest in olfactory navigation, where, however, the theoretical situation is not fully understood. Considering that birds which are deprived of olfactory information, or which are given false information, do fly in the expected way, one possible inference was that odorants distributed in the atmosphere may be able to provide an indication of geographical position. Papi and his group have put forward the concept 'that there exist odorant substances, which, for every area give rise to a different pattern of olfactory stimulation, that is, to a characteristic prevailing odour'[72].

This is a vague formulation, yet no other statement is justified given the present state of knowledge. Nonetheless, it does give an indication of qualitative differences between smells perceivable in different areas. These differences may derive from regional differences in vegetation and in soil composition. This hypothesis, which has been nicknamed 'the mosaic hypothesis' by Wallraff[103], seems better able to explain olfactory navigation over short distances than the rival hypothesis proposed by Wallraff himself. He has suggested that there are olfactory gradients which are operative over large areas, and which are due to circumscribed sources which free long-living odorants. For further detailed discussions on these advantages and disadvantages of the mosaic and gradient models, the reader can refer to Wallraff[103,111].

It should, in any case, be pointed out that so far neither of these two models has been empirically supported by data on the distribution of gaseous substances in the atmosphere, and that the two hypotheses are working proposals in response to the need to offer a model for the physical substrate of the map. The doubts which remain in this connection do not undermine the validity of the findings that prove the existence of a long-distance navigation mechanism that, unlike all others in the animal domain, is based on an olfactory map. The orientation of pigeons is very approximate and their direction is often corrected as they get nearer their loft. Thus we do not need to hypothesize a theoretically perfect direction-fixing mechanism, or that the physical substrate on which navigation is based must give precise homing cues.

Little has been done so far to test whether other bird species use the same homing mechanism. Nesting swifts were made anosmic and then released 45–66 km from home. Most of them, unlike controls, were unable to reach home, even though the differences between experimental birds and controls had been minimized by severing only one nerve and plugging only one nostril[21]. In the case of starlings subjected to bilateral cutting of the nerves and then released at a distance of 130 km, the homing success of experimentals (25%) was half that of controls (52%)[116].

It is still not known how far olfactory navigation is involved in migratory flights.

5. *Critiques, discussions and most recent findings*

Various authors have criticized the conclusions reached by the teams of Papi and Wallraff. The authors of these criticisms claim: a) that they have obtained conflicting results, b) that the results of Papi and Wallraff can be interpreted differently, c) that it is hard to identify the physical substrate of the olfactory map.

It is generally agreed that permanent and temporary anosmia reduce homing success and/or homing speed[35, 51, 78, 130–133]. The main text of a recent review[83], and even its summary, make the statement that anosmic pigeons are able to home. This is incorrect if it refers to pigeons released from unfamiliar sites, and misleading if it refers to pigeons released over familiar areas. Some authors have argued that the initial orientation of anosmic pigeons is not influenced by anosmia which, at most, could lead to an increase in scattering. Some of these claims were unjustified because methodological errors had been made, or because no allowance had been made for the fact that pigeons tend to fly in a set direction, or because observers expected to find an effect produced by anosmia even when controls were unable to steer home[69]. The orientation of pigeons from Cornell, which had been found to be only slightly affected by anosmia[78, 133], was investigated further by S. Benvenuti and I. Brown[12] using a procedure which was correct, even if complete anosmia during passive transportation was not guaranteed. These experiments were carried out on two groups of pigeons; the first group were trained up to a distance of 25 km, but their freedom in spontaneous flights was restricted (Cornell training procedure), whereas the other group were not trained but they were always free to fly in the loft area (Italian procedure). As shown by initial orientation, controls in both groups displayed a weak but significant homeward tendency, whereas the orientation of the anosmic birds did not differ from random. The authors conclude that 'the results show that Cornell pigeons use olfactory cues for navigation' but do not exclude the existence of an auxiliary non-olfactory mechanism, since they observed a residual homeward tendency in experimentals, which was not, however, significant.

Another case of contradictory results has been reported by R. Wiltschko and W. Wiltschko[130]. They raised two groups of pigeons in a single building, keeping the first on the roof, so that this group was exposed to wind, and the other group in the courtyard; they also trained the two groups in different ways. The orientation of the pigeons that had been kept on the roof was drastically affected by anosmia, while the pigeons that had been kept in the courtyard were homeward oriented even when anosmic. In both groups, however, the experimentals had worse homing performances than controls. This experiment has been repeated twice in Italy[14] following the Wiltschkos' procedures, but the results were different, because both groups of anosmic pigeons failed to show a homeward orientation. In yet another case, the residual capacity of anosmic pigeons to orient homewards[103, 104] turned out to be illusory after further investigations[113].

No other results of any importance that conflict with those of Papi's and Wallraff's teams can be found in the literature. On the other hand different interpretations are often made of the same findings. The results of detour experiments have led to many disagreements[77]. These disagreements arise from the fact that a detour does not always produce the expected effect, or else from the finding that the discrepancy between the groups does not reach a significant level. Naturally, this depends on differences in the interference between odours perceived en route and those at the release site. Despite this, when a sufficient number of experiments have been carried out and correctly interpreted, they have always ended up by giving positive results, not only in Italy, but also in Switzerland, Germany, and the United States[77], so that even one of the most critical authors, K. Schmidt-Koenig, concludes that 'one may, with certain reservations, accept that there is some detour effect'[83]. He immediately adds that 'there is still no convincing evidence for an olfactory basis for this effect', but fails to inform the reader that there is a series of 13 experiments in which 308 experimental pigeons transported in an anosmic state, unlike the 281 controls transported in a normal state, showed no detour effect[77].

Further discussions have arisen out of the interpretation of results obtained with deflector lofts. These were first used in Italy but they have led to the same results in the United States[96] and in Germany[53]. In later, methodologically different attempts to ascertain the nature of the stimuli involved in the deflector loft effect, Kiepenheuer[54, 55] in Germany, and Waldvogel and Phillips[79, 97] in the States, obtained results which in part were in conflict with each other and with the olfactory interpretation.

Details of this controversy, which can be found elsewhere[69], are of little interest after the new findings of Foà et al.[24]. This team used pigeons with the interhemispheric anterior commissure severed in order to prevent a transfer of olfactory information from one hemisphere to the other. Every three days, they were moved from a clockwise deflector loft to a counterclockwise one, and then back again. When they were in the clockwise deflector loft, they had their right nostril plugged, and when in the counterclockwise deflector loft, they had the left nostril plugged. When taking off, the pigeons had only one nostril free. They deviated in a clockwise direction when the free nostril was the one they had had free in the clockwise deflector loft, and in a counterclockwise one in the opposite case. The birds behaved as if they had a different map in each hemisphere, one rotated clockwise, and the other counterclockwise. This result clearly demonstrates the involvement of the sense of smell in the deflector loft effect. The statement that this experiment 'proves only that the orientation mechanisms of pigeons are highly malleable and capable of making rather unusual adjustments'[95] is elegant in its choice of words, but all it is doing is to set up a smokescreen, which only serves to hide a simple reality.

The concept expressed by Keeton[50], that diminished sensory feedback from the nasal cavity reduces the motivation to fly, has been challenged on several occasions, on various grounds[69, 103]. The most important of these are that pigeons made permanently anosmic often make long flights, as shown by reports of lost birds, and that when anosmic birds are released from known places they are quite capable of flying home.

Other authors point out that severing the olfactory nerves of pigeons has effects on behaviour patterns which are not primarily related to olfaction such as learning, extinction-induced aggression, and tonic immobility[124–126] even when many other forms of behaviour appear to be quite normal[72]. This has raised the suspicion that cutting the olfactory nerves may lead to disturbances in homing behaviour that are independent of the removal of olfactory information[83, 95, 130]. This suspicion does not take into account the following facts which have already been mentioned, namely that, a) even when olfactory deprivation is achieved without cutting the nerves, it has the same effect, b) when only one of a pigeon's nerves is cut, its homing behaviour is influenced to a degree depending on which nostril is plugged, and c) pigeons with both nerves cut show almost normal behaviour when tossed from sites made familiar by previous releases (or located not far from them[117]).

More recently, the same effect as that induced by olfactory deprivation has been obtained by removing a portion of the dorsolateral telencephalon in pigeons (Papi and Casini, unpublished data). This area, which is recognized as being comparable to the mammalian pyriform cortex[66], is reached by projections from the olfactory bulb[80]. Operated birds behave like intact controls when released from familiar sites but are impaired in both initial orientation and homing from unfamiliar sites. Since the birds show electro-olfactographic and cardiac responses to odorous stimuli, it is reasonable to conclude that their imcompetence in homing is due to a breakdown in their processing of olfactory information. This is also supported by the fact that in rats the cortex pyriformis was found to be involved in olfactory discrimination tasks and in acquiring neural representations of olfactory cues[92]. In the case of pigeons, it could be argued that the disturbance in question is aspecific, but it would be very strange if one single type of aspecific disturbance could be induced in such a variety of different ways – for example cutting the nerves, removing a portion of the telencephalon involved in the processing of olfactory information, or inserting plastic tubes in the nasal passages – without the sense of smell being involved.

According to Waldvogel[95], wind-borne odours might be used in orientation without this necessarily implying the existence of an olfactory map. In coastal regions, there are often prevailing breezes which carry a specific odour, and these could supply compass information. Even so, it is not at all clear how an extra compass could help pigeons to solve navigational problems, and in any case, odours are necessary for the steering of pigeons which, like those of Bavaria, live far from the sea.

Two other proposals that have been made are that odours 'serve merely as a motivation factor that acts to focus the bird's attention on other navigational cues'[95] and that information from airborne factors needs to match other information[57, 83]. The intention of these hypotheses is to explain the results that had been obtained by allowing pigeons to smell in one place and then releasing them in another, without having to admit that odours supply directional information. There is, however, the experiment mentioned above involving winds laden with odours, which shows that, even for a single release site, orientation varies with the odorant which pigeons are sensing.

It is also worth noting a new experiment carried out with winds laden with odours which refutes the two hypotheses just mentioned. In this case the pigeons did not live sheltered from natural winds, but were continually exposed to them, by being kept in two cages made of wire netting. The pigeons in one cage were also exposed at intervals to an artificial NNW-wind which carried a strong odour of benzaldehyde, whereas the others were given no treatment. When the two groups where exposed to benzaldehyde during transportation and at the release site, the controls had a homeward orientation, while the experimentals flew SSE – that is, in the direction opposite to that from which they had been used to receiving the odour – and this happened independently of the home direction (fig. 4; Ioalè et al., unpublished data). On the other hand, if the birds were not exposed to benzaldehyde prior to release, the experimentals as well as the controls flew towards home. This experiment demonstrates that an odorant becomes significant for orientation only if it is perceived as being carried by a wind. It will then supply a directional clue, which is independent of the geographic position of the bird.

To explain the apparent differences in results obtained over different areas it has been argued that pigeons use a redundant series of cues of various kinds to navigate[50], and among these they choose those which yield the most reliable information for navigation over the region where they live[132]. Naturally, these authors believe that the most reliable information in Italy is olfactory in character. In an attempt to test whether pigeons are also capable of using non-olfactory cues for navigation, we made a group of pigeons permanently anosmic at fledging time – before they could perceive odours in the loft area. These pigeons were free to fly ad libitum and were trained by flock releases along with intact controls. When they were released singly from unfamiliar places, the experimentals turned out to be incapable of initial homeward orientation, and most of them (89%) were lost[74]. The early cutting of olfactory nerves should have favoured reliance on non-olfactory cues, but this did not happen. At this point the only explanation available to critics is that in Italy alone the sense of smell is the only aid to orientation.

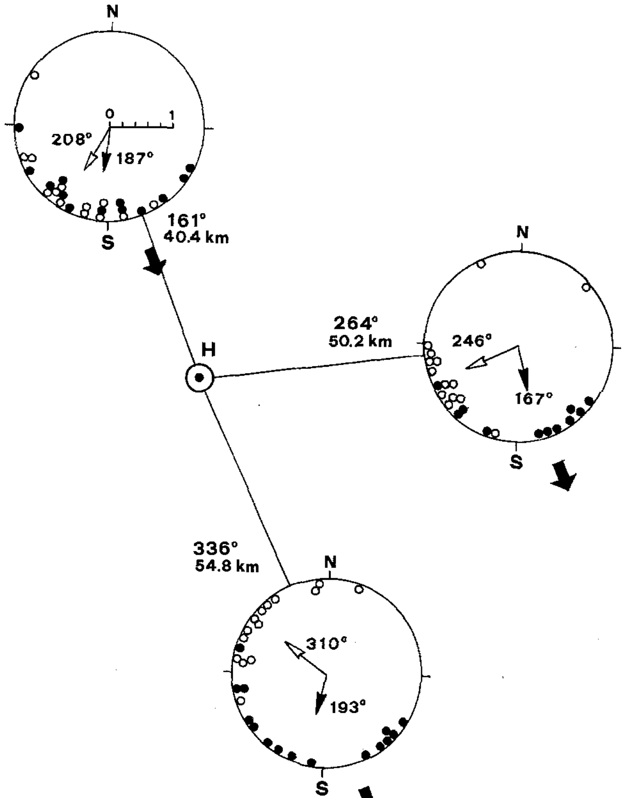

Figure 4. Initial orientation of pigeons exposed at the loft to an odorous wind from NNW (solid symbols) and controls (open symbols). The three vanishing diagrams refer to three test releases from different directions. Controls were homeward oriented, whereas experimentals oriented towards a direction opposite to that from which they had been used to receiving the odour (SSE, black arrow outside the circle). Each dot indicates the vanishing bearing of a bird. Ioalè et al., unpublished data.

It is, however, true that pigeons perform better in Italy than in Germany. This does not depend on genetic factors, as pigeons of the same stock behaved differently in the two countries and only marginal differences were found when the performances of the two stocks raised and tested in the same area were compared[25, 26, 58]. It turns out that the environmental conditions are conducive to navigation to different extents, according to seasonal and spatial variations of the climate. This is compatible with a mechanism of olfactory navigation, and on the other hand there is no evidence that cues of different nature are used over different regions.

The hypothesis of the genetic discrepancy between different strains of pigeons is not only undermined by the comparison between German and Italian pigeons but also by that between Italian pigeons and pigeons from Cornell. Pigeons of the Cornell strain, born and raised in Italy, have been compared with Italian pigeons. In the tests the controls in the two groups were orientated towards home, while birds from the two experimental subgroups which had been transported and released anosmically were equally disoriented[14].

Considering all the foregoing, it may be concluded that while there are several differences arising from different evaluations of the results, the only discrepancies of any importance between different sets of findings are those related to the initial orientation of anosmic pigeons. In a few cases there is a residual orientation, or even a good orientation, towards home comparable to that of controls[130]. These cases call for an explanation. In my opinion there may be an auxiliary mechanism which helps to fix the homeward direction, and which only comes into play in certain situations. This mechanism, however, does not reduce impairment in homing, so that it seems to be based on information gathered on the outward journey. The calculation of the direction of the target, which is made during the outward journey, cannot be corrected during the return journey, and if it is made inaccurately, it leads to failure.

Other discrepancies which have been reported are of minor importance or are only apparent. Some results could be explained without reference to the sense of smell, but this, in contrast with the principle of economy, would call for a contribution from many different factors, when only one factor could be sufficient.

The only important objection that can be made to the mechanism of olfactory navigation is that the physical substrate on which it is based is unknown. By means of experiments in which pigeons breathed filtered air, it was shown that the olfactory cues used by pigeons consist of substances that are dispersed in the atmosphere, very probably in molecular form, whereas no use seems to be made of substances present as liquid or solid aerosols[114]. So far, however, there is no proof that one or more gaseous substances present in the atmosphere possess the reliability and continuity needed for navigation, even if that navigation is rather imprecise.

According to two meterologists[11], long-living substances generally do not have any significant gradients, while those of short-living compounds are strong but temporally and spatially variable. It is not, however, clear whether substances with intermediate characteristics may exist. Waldvogel[94, 95] recently made a considerable effort to test the possibility of olfactory navigation in the northwestern United States on the basis of the data collected in a study of long-range atmospheric transport. In this study (CAPTEX '83) the tracer used (perfluoromonomethyl-cyclohexane) was released in aerosol form from two release points and then monitored at ground level. Unfortunately for our purposes, aerosols represent the least appropriate physical state, given that it is known that their elimination does not affect the navigational capacity of pigeons. Moreover, Waldvogel assumes that a) the pigeon's olfactory threshold, which has been determined for only a few substances, cannot be situated at a lower level for certain odorants of special significance, and b) that even in the United States, pigeons' navigational maps allow them, at a distance of hundreds of kilometers, to determine their position with respect to the loft without picking up olfactory information en route. Besides this, Waldvogel only had access to data at distance of over 300 km from the source of the tracer. With these premisses and under these conditions, it is hardly surprising that the author's conclusions were negative with reference to the region in question. Despite all these limitations, his study is the result of a serious effort made in the right direction.

Conclusions

It can be stated that there is much evidence in favour of olfactory navigation, and that it constitutes a coherent picture. The data relative to the acquisition of the map are in accordance with the homing behaviour under natural and experimental conditions, and only a few conflicting data call for further study. It is possible that a non-olfactory auxiliary mechanism based on information picked up en route functions in some cases; research in this direction might turn out to be very valuable. Many objections have been raised to the suggested mechanism of olfactory navigation, but this continues to be the focus of attention for a clear majority of researchers. Among the positive results of this line of research, the following generally recognized achievements deserve mention: a) there is a sensory input, and its elimination leads to impairment of homing, but only from unfamiliar places, b) information gathered en route is used in orientation, and c) initial orientation can be deflected in a foreseeable way according to the conditions in which pigeons have been kept (deflector experiments). Knowledge of the homing behaviour of the pigeon has already reached the point where pioneering experiments on the central mechanisms that underlie homing have become possible[17]. It is true that at present there is a lack of data on the physical bases of olfactory navigation, but this lack cannot be considered to be evidence against the essential role of the sense of smell in homing even from large distances. It should, in fact, act as a stimulus to further research in this direction.

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Spatiotemporal programs and genetics of orientation

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Summary. A number of migratory bird species have endogenous annual rhythms that regulate the entire annual cycle including the migratory portion. Moreover, captive migrants display inherited migratory activity; this could theoretically also be used by free-living migrants as a time-program for migration. Finally, this heritable migratory activity is oriented in a seasonally appropriate direction even in naive birds. These characteristics should enable inexperienced migrants isolated from contact with experienced conspecifics to utilize a heritable vector-navigation program to migrate from the breeding grounds to the winter quarters. That is, migrants should reach goal areas they have never experienced by migrating in programmed directions, for as long a period as the genetically fixed time-program for migratory activity induces them to do so. The time-course of migration as established by trapping stations, theoretical influences of environmental variables on migratory programs, and also compensatory behavior and migratory backup measures, are discussed. The present evidence supports the view that a large number of migrants are essentially brought to their wintering areas by vector-navigation systems.

Key words. Bird migration; orientation; navigation; circannual rhythms; genetic programs; inheritance.

Introduction

A worldwide effort (primarily during the past 80 years) of marking ('ringing') individual migratory birds and carrying out population censuses clearly demonstrated that most migrants do not move to winter quarters which vary at random, but are capable of precisely oriented movements between well-defined species- and population-specific breeding grounds and wintering areas[41, 56]. The most difficult task in such a system of movements is the first outward journey from a known area (the breeding grounds) to a totally unknown region (the prospective wintering area). In all later seasons both areas are known. In some highly social groups of birds (e.g., storks, cranes, geese) the problem can be solved by tradition; the offspring are led by experienced adults[50]. It is not possible, however, for there to be any social transmission of migratory information in birds such as brood-parasitic cuckoos, in which migrating fledglings never become acquainted with their parents or other adults before their first migratory journey. This is an extreme example, but the same holds true for the vast majority of migrants that either fly individually, or in varying flocks of inexperienced conspecifics[50]. Since these birds are also able precisely to reach specific winter quarters[41, 56] it is logical to propose that they are equipped with endogenous orientation programs. And because these lonely wanderers, even when commuting over thousands of kilometers, regularly perform their long-distance movements according to rather fixed schedules[34] they must have spatiotemporal programs. In the following sections our present knowledge of such programs is summarized.

Endogenous time-programs

The involvement of endogenous programs in the control of migration has been proposed for a long time. As far back as 1702 von Pernau[44] assumed that a 'hidden urge' in the individual bird was responsible for triggering the initiation of the migratory journey. Later on, it was proposed that endogenous time-programs might control the entire migratory journey (at least during the first migratory season from the breeding grounds to the winter quarters)[51]. About 20 years ago, such programs were actually demonstrated in European warblers[15, 26], and they have currently been established in about 20 bird species of about 10 families[31]. An example is given in figure 1.

In order to demonstrate the existence and performance of endogenous rhythms, organisms have to be kept under constant experimental conditions. Thus, periodicity should not occur within a period length in which the supposed endogenous rhythm would be most likely to