An amazing discovery: bird navigation based on olfaction

Hans G. Wallraff discusses the impact of Floriano Papi and colleagues' classic paper 'The influence of olfactory nerve section on the homing capacity of carrier pigeons', published in the *Monitore Zoologico Italiano* in 1971.

Around 1970 it was well known that homing pigeons and other birds are able to return to their home site when passively displaced to unfamiliar areas several hundreds of kilometres away. It was additionally known that birds can use the sun, together with an endogenous clock, to determine compass directions and that pigeons actually make use of their sun compass to navigate home. However, using a compass alone, a pigeon cannot find out in what direction it has to fly. A complete sun-navigation hypothesis, including the assessment of a bird's current position relative to its home, had been discussed in the 1950s and 1960s, but eventually it was disproved. Similarly, the magnetic field of the earth had just been established as a second basis for compass orientation, but as an indicator for position it could be almost excluded as well (later confirmed). While there were no recognisable environmental signals that birds might use to deduce positional ('map') information, some peculiarities of the pigeons' homing behaviour began hinting at the nature of such signals. However, researchers working in the field (including myself) failed to provide a satisfactory interpretation of these hints.

Eventually, the decisive observation was performed by Floriano Papi from the University of Pisa, Italy. Realising that previous searches for the sensory basis of homing had ignored the sense of smell, Papi and his colleagues published a short communication in a little-known journal where they reported on the behaviour of ten pigeons with sectioned olfactory nerves that were released individually 54 km west of their loft in Florence (Papi et al., 1971). These pigeons, in contrast to untreated control birds, did not depart homeward. Only three returned 1–2 days later, whereas 9 of the 10 control birds homed before nightfall. The authors commented on their results cautiously, leaving it open whether their nerve cuts might have non-specifically interfered with some general preconditions for home-flying or whether the results might indicate that olfaction was directly involved in the homing mechanism. Based on additional results and arguments, they soon decided in favour of the latter alternative and presented a first tentative hypothesis for a functional principle of olfaction-based navigation (Papi et al., 1972). They assumed that winds arriving at the home loft from different directions carry particular relevant odours that prevail in the areas from which they come. Using their compasses, pigeons would, over several months at home, associate the varying odours with the concurrent wind directions, would recognise them again when released somewhere abroad, and would then fly in the direction toward which the wind at home had blown while they had smelled the respective prevailing odours.

In spite of the apparent soundness of these experiments, the scientific community did not celebrate the inference that pigeon homing (and perhaps goal-oriented avian navigation in general) appears to be based on olfactory signals as a groundbreaking discovery. Instead, the inference encountered disbelief. I myself considered it impossible that airborne odours perceived some hundreds of kilometres away from home might in any way be helpful in determining the direction toward home. Though I considered it possible that pigeons could distinguish, by smell, between air arriving at the loft from a forest in the north, a lake in the east, a town in the west etc., I could not visualise how such experiences might help in a remote unfamiliar area with many forests and towns in the intervening distance between a pigeon's current location and its home. I considered it necessary to search for the 'real causes' of Papi's results. However, neither I nor anybody else succeeded in giving a non-navigational explanation.

While others maintained their scepticism, the researchers in Pisa extended their experimental approach. Beyond simple nerve-cutting, they conducted a variety of experiments that were in line with their hypothesis and confirmed the necessity and specificity of olfactory input for home-finding from unfamiliar sites within a radius of about 30–100 km of the home loft. Five years after the initial report, Papi presented a respectable range of additional results (Papi, 1976). Most enlightening was the predicted involvement of winds at the home site. If pigeons really associated alterations in their olfactory input with simultaneous changes of wind direction, experimental deflection of the incoming winds to the left or right in a home aviary over several months should cause a corresponding deflection of the initial flight course of pigeons at distant sites. In fact, experimental results agreed with that prediction (Baldaccini et al., 1975). Contemporaneously, these new experiments implied a possible explanation of earlier findings by Gustav Kramer and later by me. We had found that pigeons kept in an aviary surrounded by vertical walls made of wood or glass were, in contrast to birds from unscreened aviaries, unable to orient homeward from sites 150 km away. In retrospect, these results should have guided my attention to airborne scents carried by winds sooner. I had considered their possible involvement, but I had dismissed the idea that birds might respond to volumes of air transported over such long distances. Papi hypothesised that when pigeons are displaced so far, they refer to odours perceived during the initial part of the outward journey. Later it turned out that he was right as far as Italy is concerned, but not with respect to wider and flatter countries, where olfaction-based

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navigation operates over distances of 300 km and more, even if the birds had been prevented from smelling natural air during the outward journey.

Although I could not understand how navigation based on olfaction and experience of winds at the home site might work, I was unable to reject the conclusion that it does work. Henceforth, I felt challenged either to refute the conclusion or to confirm it. I focussed my experimental research on this problem, both in parallel and in cooperation with the Papi group. Further investigations revealed that homeward orientation of pigeons can be disrupted not only by deactivation of the receiver, but also by elimination of the message to be received: breathing clean air that has passed through a charcoal filter prevents homeward orientation. Moreover, if pigeons having smelled natural air at a distant site for a few hours, are thereafter transported in filtered air to another site in the opposite direction from home and released there under nasal anaesthesia, they fly along a compass direction that points homeward from the first site, i.e. now away from home. After several years of continued research, it was possible to enumerate 17 different kinds of experiment that yielded a coherent collection of findings supporting olfaction-based navigation (Wallraff, 2005b). The principal results were also confirmed in a number of wild-living bird species, even for distances as great as 800 km (for details and further references see Papi, 1986, 1989, 1991; Wallraff, 2004, 2005a,b; Gagliardo, 2013; Gagliardo et al., 2013).

Traditionally, attempts to explain long-distance homing are linked with the idea of bi-coordinate navigation that uses some physical gradients as coordinates (such as geomagnetic intensity decreasing gradually from the poles to the equator). However, at first sight, it appears impossible that the concentration of any trace gas, which is highly dispersed and dilute in the continually varying atmosphere, might form a sufficiently stable and wide-ranging gradient (e.g. Becker and van Raden, 1986; Waldvogel, 1989). Yet at a second glance, when proportional relations between two or more particular gases are considered instead of single chemical compounds, it turned out that, in Germany, sufficiently stable ratio gradients ranging over at least 400 km do exist, which theoretically could be exploited for navigation. If ratios between compounds are used, at least three or more substances should be involved to form a multi-coordinate system centred at the pigeons' loft. Closer analyses of air samples from a large area suggest that varying winds slightly move this whole system across the loft and thereby provide information about the compass alignments of the various ratio gradients. We need not propose that a bird is aware of the individual compounds separately; their varying proportional mixture may result in perceived qualities of olfactory input that vary depending on wind direction at home and on the position of remote sites around. These mixture qualities can be set in relation to each other. Model calculations revealed that pigeon homing can be satisfactorily simulated by comparing appropriately selected trace gases sampled within a radius of 200 km around a virtual home site with samples collected at that site under varying wind conditions over a longer period of time (Wallraff and Andreae, 2000; Wallraff, 2004, 2005a,b, 2013). Thus, Papi's *prima facie* hypothesis that winds carry navigationally exploitable olfactory signals to the home site appears applicable even for long-distance homing.

So far, I have presented my own perspective of our current understanding of the role of olfaction in pigeon navigation and the developments that have led to this position. However, the field has been dogged by controversy (cf. Able, 1996). After a decade of early uncertainty, the small community of researchers actively working in the field split into proponents and opponents of olfactory navigation. The latter had an immediate advantage when conveying their opinions to the general public, as any argument that renders long-distance olfactory navigation questionable makes intuitive common sense. Yet I do not fully understand the 'resistance by scientists to scientific discovery' (Barber, 1961) that persists in this particular case. While initial doubts are natural, the continued accumulation of diverse, yet complementary and statistically well-proven results should eventually have convinced the sceptics. Opponents challenged the conclusion that olfaction-based navigation works by arguing against hypotheses trying to explain how it operates (e.g. Schmidt-Koenig, 1987). Others suspected olfactory effects on a non-olfactory navigation system that is based on other, yet unknown sensory inputs (e.g. Wiltschko, 1996; Jorge et al., 2010; Phillips and Jorge, 2014; but see also Wallraff, 2014a). Recent attempts to identify such sensory inputs have revealed no more than presumed influences of either infrasonic (Hagstrum, 2013) or gravitational (Blaser et al., 2014) anomalies on homing routes of pigeons, while factual evidence is lacking (cf. Wallraff, 2014b). Nonetheless, such contributions perpetuated the impression that the physical basis of navigation is a controversial matter. Circular reasoning then made it possible to ignore the bulk of publications on pigeon homing since 1971 on the grounds that the physical basis of the avian 'map' is still controversial (reviews by Wiltschko and Wiltschko, 2003, 2009). However, a broadly debated issue, which comprises a substantial amount of empirical findings, deserves critical inspection and assessment (for detailed discussions from my point of view, see references and other publications referenced therein).

If we desist from distractions in the literature and focus, instead, on the empirical results accumulated over the past four decades, we gain a rather clear picture of where we are. On the one hand, these results strongly suggest that goal-oriented avian navigation is crucially based on chemical substances whose fairly regular spatial distributions in the atmosphere evidentially imply exploitable positional information. On the other hand, the functional details of the system remain unsolved. A final solution of this problem should meet the three following requirements. (1) It is most urgent to investigate the atmospheric boundary layer covering diverse types of landscape in different regions of the earth with respect to differently oriented wide-ranging gradual changes of proportions between some of the many airborne trace gases. The effects of winds in this context need a closer inspection as well. The final objective is an understanding of the origin of such long-range regularities. These tasks are challenges for atmospheric chemistry.
(2) Chemical compounds whose specific mixtures would be suitable as indicators of position should be identified and their actual use by birds tested: a challenge for both atmospheric chemists and biologists.
(3) The birds' sensory and neural capacity to process atmospheric data in an appropriate way should be investigated: a challenge for biologists.

The threefold challenge for future research implies problems that may be more difficult to solve than the work that has already been performed. Nonetheless, the decisive first steps have been taken and we have a perspective of what should be done in the future. Floriano Papi and his ten anosmic pigeons opened an unforeseen and most amazing alley toward a solution for the long-standing mystery of how birds find their way home from far distant areas where they had never been before. Following this alley is currently the sole recognisable chance to reach a final solution.

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