

Pigeon homing from unfamiliar areas

An alternative to olfactory navigation is not in sight

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The conclusion that pigeons and other birds can find their way home from unfamiliar areas by means of olfactory signals is well based on a variety of experiments and supporting investigations of the chemical atmosphere. Here I argue that alternative concepts proposing other sources of geospatial information are disproved by experimental findings or, at least, are not experimentally supported and hardly realistic.

The first scientific searches for mechanisms enabling goal-oriented avian navigation focused on the three systems used by human navigators for centuries, i.e., on the magnetic field of the earth, on celestial bodies, and on dead reckoning (in animals: path integration during the trip away from home). These candidate systems have been examined thoroughly by homing experiments with passively displaced pigeons; none of them turned out to imply a 'map' function providing information on the birds' current position relative to their home site.¹ An unexpected sense, however, olfaction, which in theory had never been considered potentially useful for long-distance navigation, proved to be crucial. With sectioned olfactory nerves, pigeons failed to orient homeward.² Since that discovery in 1971, a large range of empirical evidence has been accumulated¹⁻⁸ which would not have left any doubt that homing pigeons find their way home over hundreds of kilometers by deducing positional information from atmospheric trace gases perceived by the sense of smell, if such a conclusion would not have provoked intuitive disbelief. Despite this understandable scepticism, the study supplemented by this *Addendum* article⁷ confirms that a

navigation system using natural airborne volatiles is a realistic model.

In the following, I substantiate my conclusion that no competing alternative or additional mechanism is recognizable that might explain how pigeons navigate home from unfamiliar areas. To prevent any misunderstandings, it should be noted that the question is not whether a particular sensory input is involved in the homing process as a whole, but only whether it provides information on the current position of the birds relative to their home site, i.e., so-called 'map' information. There is general agreement that birds have 'compasses', even two, a sun compass and a magnetic compass,^{1,5,9,10} and that these compasses are necessary components of various considered homing systems. Furthermore, it should be emphasized that I exclusively discuss home-finding from reliably *unfamiliar* areas where any knowledge of learned local features (e.g., visual landmarks) cannot be helpful.

The Potential Sensory Basis of an Avian 'Map' as Conceived by Humans

In most theories, navigation toward a defined home site based on external geospatial signals (i.e., any mechanism except egocentric path integration¹¹) requires some kind of coordinates, in physical terms gradients of some quantifiable variables, whose compass alignments must be known in order to enable extrapolation from the home position to any more or less distant position in any arbitrary direction. It is well known that pigeons can obtain this knowledge (if actually necessary)

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while living at their home site in an aviary (Figs. 3.7,¹ 3.8¹) and hence while they cannot determine the compass alignments of increase and decrease of possibly relevant variables during exploration flights around their loft. This general problem is not solved by any preconceived navigation hypothesis that proposes the use of a compass-aligned coordinate system (unless it proposes inherited knowledge which would fit only if coordinates were worldwide equally oriented).

Sensing geomagnetism

In a global scale, the magnetic field of the earth has, in principle, a north-south gradient of total intensity as well as of inclination. Even on a global map, however, the isolines of the two variables do not at all run in parallel and west-east everywhere, but in some regions they deviate from each other by up to 90° so that, in theory, they could be used there as two coordinates (Fig. 1¹²). In most areas, however, they can hardly be used that way. On smaller regional and local scales, the geomagnetic topography is often so irregular and unpredictable that extrapolations from one position to another without local exploration are impossible.

Various responses of pigeons to various kinds of artificial magnetic fields or to natural anomalies have been reported. As far as they did not clearly concern compass orientation, they were mostly suspected to affect a 'map sense'. However, no kind of artificial magnetic treatment or sectioning of presumably relevant nerves have prevented pigeons from returning to their loft at speeds similar to those of untreated control birds.^{1,13-16} Some observed effects on initial orientation alone, i.e., without an effect on homing performance, merely indicate that magnetic stimuli exert some transient disturbance of the birds' behavior, but they do not prove that the pigeons derive relevant 'map cues' from magnetic stimuli (cf. Figures 6.4,¹ 6.5¹). Similarly, proven or claimed irregular or in a particular way oriented responses of pigeons flying over a local topography with variably oriented gradients of magnetic intensity¹⁷⁻¹⁹ do not imply evidence that magnetic signals are used to guide the way home.

Observing celestial bodies

From the 1950s to the early 1970s, the sun (and the stellar sky for migratory birds) was the focus of experimentation and debate not only as a basis of compass orientation, but also as a potential basis of goal-oriented 'map' navigation by pigeons.^{20,21} I refrain from discussing results and arguments for and against sun navigation as for about four decades the topic has no longer been promoted by anybody.^{1,22,23}

Sensing force of gravity

Recently, Blaser et al.²⁴ suggested a "gravity vector theory" which proposes that pigeons determine the direction of the gravity vector, i.e., the vertical, at their home site and in some way memorize its absolute alignment in space, thus keeping it available at any other location as well. When displaced to a distant site, they deduce from the angle between the vertical measured there and the memorized home vertical the direction (azimuth) and possibly the distance toward home (1° difference = 111 km distance). The logic of this procedure is simple (see Figure 1²⁵); in principle, it would be easily applicable by an extraterrestrial player, provided that he is sensitive enough to measure the tilt angle of ca. 0.5° between the verticals determined at two sites 50 km apart from each other together with its azimuthal orientation. It remains unclear, however, how the underlying physical and neural machinery might operate in the real earthbound world in which, as far as I know, only the centripetal gravity vector at its current position is accessible to an organism. If the pigeons, nevertheless, would refer to the azimuth of the tilt angle, they would not need an extra compass and should not be affected by a shift of their time-dependent sun compass (even if they would use the current arbitrary sun position to stay on course). In reality, however, the initial bearings of pigeons are deflected away from the tilt azimuth by a clock-shift, in unfamiliar areas by an angle well corresponding to the angle between expected and real sun azimuth; thus, not even some conflict is indicated (Fig. 5.2,¹ C vs. A).

To test for possible influences of gravity anomalies, Blaser et al. released pigeons from two lofts, one situated in a strong anomaly, the other 8 km apart in a gravitationally almost quiet area, at a site about 50 km distant in the same direction from

both lofts. Initial orientation and paths of the two groups were clearly different and are interpreted as being related to the topographical isolines of gravity. However, responses to other features, e.g., visual or olfactory, and/or effects of preceding training releases from different directions to the two lofts are also possible. A single descriptive case study cannot reveal causal connections.

Hearing infrasound

During the 1970s and somewhat later, infrasonic waves propagating from oceanic coasts, mountain ridges etc. along the earth's surface over hundreds and thousands of kilometers were considered to assess their possible suitability as a regional triangulation network.^{26,27} Pigeons can perceive infrasound at frequencies as low as 0.05 Hz, provided that their inner ear with the cochlea is intact.²⁷ With their cochleae removed, however, pigeons homed from unfamiliar areas over a distance of 150–160 km at the same speeds as control birds and their initial bearings were clearly oriented toward home.²⁸

Irrespective of these findings, Hagstrum has revitalized the idea of "infrasonic 'map' cues" in a number of more recent publications.^{29,30} They include, however, neither a clearly described concept of a theoretical navigation system based on infrasound nor any indication exceeding the level of assumption that particular orientation patterns of pigeons might have been elicited by hearing infrasonic input. No statistical evidence of anything is presented (see Supplemental Material).

Sensing undefined stimuli

Many related reviews and other publications remain open about the types of physical parameters used by pigeons to determine their current position relative to their home site, merely mentioning a number of debated possibilities and arguments without reaching evaluative decisions. Some studies explicitly question or exclude that any 'map cues' used by pigeons are perceived by olfaction, although without suggesting an alternative sensory input³¹⁻³³ (see ref. 8). Other studies operate with fictitious "geophysical gradients" as if they were realities.^{9,10} However, waiting for the emergence of yet undiscovered geophysical factors and sensory inputs, while denying the proved

crucial role of olfactory cues, implies no perspective for a solution to the problem of goal-oriented navigation.

Using a multifactorial 'map' system

Indecisiveness about crucial navigational mechanisms has sometimes led to the assumption that pigeon navigation relies on a multitude of environmental signals (e.g., magnetic, olfactory, infrasonic, and/or unknown) to obtain information on the direction toward home. None of these signals is thought to be generally essential because birds may opportunistically employ different types of cue depending on varying circumstances.^{9,10,34} However, as long as the components of such a redundant system are not clearly determined and checked for their functional involvement, it explains everything and nothing.

Not all of the factors involved in the homing flight of a pigeon are components of a navigational process, and therefore not all of them must be counted as 'map factors'. Some factors merely distract the bird from a course it would have chosen on a purely navigational basis. Most obvious are distractions caused by the visual topography, e.g., attraction by a village or avoiding flying over a forest (cf. Figure 3.21¹), but magnetic noise during flight over a magnetic anomaly also appears to temporarily distract pigeons from flying homeward more directly (what they do when magnetoreception is prevented,¹⁹ thus indicating that it is not part of the home-finding system).

A redundant multifactorial, at least bifactorial home-guiding system is actually used within areas that have been familiarized during preceding homing flights, so that henceforth the pigeons can refer to learned visual landmarks in addition to olfactory cues^{1,5} (cf. Figures 8.1,¹ 8.5¹). However, such vision-guided homing^{35,36} using a 'familiar area map' must not be confused with 'true' navigation, which, in its pure form, can only be investigated at locations sufficiently far away from any visually distinctive familiar features. Pigeons having *reliably* no olfactory access to natural air before and after take-off, if released *reliably* without visual access to familiar landmarks, are, according to current knowledge, unable to direct their courses homeward.^{1,3-8}

Thus, under these conditions no nonolfactory 'map cues' can help.

The Real Sensory Basis of an Avian 'Map' as Evolved by Birds

Birds were obviously more successful than humans in detecting environmental parameters that are useful for home-finding over fairly short distances (20–50 km) as well as over distances that extend (at least in some regions) to 200, 300, and > 500 km. A large volume of empirical evidence has been presented and discussed elsewhere,^{1,3-7} which induces the conclusion that the chemical atmosphere is the decisive medium and that olfaction is the decisive sense that enable goal-oriented navigation over unfamiliar territories.

(Also this conclusion has not been left without contradiction. Suggesting that olfactory signals do not contain navigational information, but merely activate an unknown 'non-olfactory map system', Jorge et al.^{32,33} deny even this remaining sensory basis of pigeon homing and thus drop back to a zero point of any understanding of goal-oriented avian navigation. However, their inconsistent 'activation hypothesis' does not withstand critical inspection and is incompatible with a number of experimental findings.⁸ In their reply to my critique, Phillips and Jorge³⁷ do not challenge my arguments.)

Olfactory navigation, as I presently see it,^{1,5,7} implies a solution of a problem that other hypotheses based on gradients can hardly resolve (see above): birds do not need to move across environmental gradients during exploration flights to determine their alignments, because the atmospheric ratio gradients are moved by winds across the birds at home, even if they are confined in an aviary (cf. Figure 1⁶).

In the context of navigation, I am reluctant to speak about atmospheric *odors*, because we immediately associate the word *odor* with our subjective perceptions and connected emotions. The processing of airborne chemosignals by navigating birds, however, which must not allow adaptation to continuous olfactory inputs, is certainly not fully analogous to our everyday experience of the sense of smell. Therefore, we should be cautious in drawing rash conclusions about what appears possible or

impossible in a field that we erroneously may consider trivial and well known to ourselves.

Concluding Remarks

It appears unlikely that a global system of any kind (geomagnetism, celestial bodies, gravity) can be used by animals for goal-oriented navigation over hundreds of kilometers as well as down to 50 and 20 km. On the other hand, a regional system such as olfactory navigation must have and obviously has some upper range limits which appear to be quite variable depending on relevant geographical conditions (cf. Figures 7.15–17¹). The title of this article restricts the problem to pigeon homing, although olfactory navigation is certainly applied by most or all other avian navigators as well.^{1,5,38} I do not exclude that some of them, covering in their migrations several thousand kilometers, make use of additional less precise nonolfactory, most probably magnetic global indicators of position or at least of latitude.³⁹ Such coarse indicators operating in larger scales, however, are inappropriate for guidance to a small familiar home area around a geographically well-defined location.

All the aforementioned alternatives to olfactory navigation are theoretically unconvincing and experimentally disproved or, at least, not supported in any way. There is no indication that pigeons, when passively displaced to definitely unfamiliar areas, can gain any *nonolfactory* information about their position relative to their home loft. The *olfactory* information, however, which is obviously available to the pigeons, is not yet deciphered in its material components, i.e., the chemical compounds actually used by birds are not yet identified and the formation of the observed regularities in the gradual changes of their proportional composition in the atmosphere over hundreds of kilometers^{1,5-7} is not yet coherently elucidated. Instead of perpetuating doubts about the *existence* of olfactory navigation without having a competing alternative in mind, we should concentrate future efforts of research on trying to decode the *functionality* of olfactory navigation and to understand its atmospheric basis.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

Supplementary Material

Supplementary material may be found here: <https://www.landesbioscience.com/journals/cib/article/28565/>

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