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THE DEBATE OVER OLFACTORY NAVIGATION BY HOMING PIGEONS

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In the years since 1971, when Papi and his colleagues first proposed that odors played an important role in the homing navigation of pigeons, the hypothesis has remained controversial. Although the idea seemed intuitively unreasonable to nearly everyone working in the field at that time, empirical support from a wide variety of experiments emanating from Papi's laboratory in Pisa has stimulated a quarter of a century of experiments, theorizing, advocacy and dissent. The issue is reviewed here in contributions by Hans Wallraff, one of the chief proponents of olfactory navigation, and Roswitha Wiltschko, who remains skeptical about the involvement of odors in pigeon homing. At the Editors' request, I provide here a personal perspective on the debate from one who has had no involvement in the issue and, indeed, has never released a homing pigeon.

The literature on olfaction in pigeon homing is now quite large. Recent summaries of the empirical data and theoretical arguments, both for and against, can be found in Papi (1991, 1995), Wallraff (1990), Schmidt-Koenig (1987), Schmidt-Koenig and Ganzhorn (1991) and Waldvogel (1989). Many of the relevant original papers are cited in the chapters by Wallraff and Wiltschko. It is not my purpose here to provide a thorough review of the relevant literature. Rather, I will focus on the general issues involved in the debate and attempt to weigh up the evidence.

Experimental data

An astounding array of different types of experiments has been performed to test the olfactory hypothesis. They fall into two broad categories: (1) those that attempt to remove the presumably relevant stimulus (odors), and (2) those that attempt to manipulate predictably the putative olfactory map.

Releases of anosmic pigeons

A seemingly straightforward prediction of the olfactory navigation hypothesis is that anosmic pigeons should not be able to home. A variety of invasive techniques have been employed to produce long- and short-term anosmia (olfactory nerve section, plugging the nostrils with cotton, inserting tubes into the nasal passages, application of local anesthetics to the nasal epithelia). In most of the homing experiments, no direct attempt was made to verify anosmia among the subjects, and some of the methods (e.g. nasal plugs) probably do not produce an acceptable degree of olfactory loss. Long-term anosmia can be produced by properly performed olfactory nerve section and by application of zinc sulfate; local anesthetics such as xylocaine can be effective for 1–2 h, but results can be variable if great care is not taken in their application.

In cases where one can feel confident that pigeons were anosmic, the data consistently show striking effects both on initial orientation (vanishing bearings are usually random) and homing performance when pigeons are released at unfamiliar (but not at familiar) sites.

Numerous concerns have been raised about the procedures employed to induce anosmia and about the interpretation of the results. The predicted effects of the experimental treatment are random vanishing bearings and poor homing performance, rather general deficits that might occur for many reasons (control pigeons fly off in random directions with disconcerting frequency). Many have raised the possibility that well-known behavioral side-effects of anosmia in other species (motivational, learning and attentional deficits) might indirectly affect the pigeons' motivation or ability to process (non-olfactory) navigational information. This is a legitimate concern, and there is little relevant empirical evidence with which to evaluate its validity. However, the existing evidence does not support at least a general motivational deficit. It is well-documented that nerve-sectioned and other anosmic pigeons both orient and home adequately from familiar release sites. Thus, if their motivation to home is impaired, it is only impaired at unfamiliar sites. It is not obvious why that should be the case. Wallraff (1988) showed that anosmic (nerve-sectioned) pigeons flew distances comparable to those flown by controls (but in random directions), suggesting that they were similarly motivated to home but did not know the correct direction.

A less invasive means of eliminating access to potentially relevant odors involves transporting the pigeons in sealed containers supplied only with filtered air. The pigeons are able to smell all odors within the container (which can become substantial during a lengthy transport). Local anesthesia is applied before release. This procedure also has marked effects on initial orientation and on homing success, apparently identical to those of long-term anosmia. Because anesthetics are used to produce anosmia prior to release, these experiments are open to some of the same criticisms noted above.

Overall, the data from experiments in which pigeons were denied olfactory exposure to air *en route* to and at the release site form a consistent picture that clearly supports the olfactory hypothesis. Concerns remain about the side-effects of the

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procedures used to produce anosmia and of anosmia itself, and although there is no direct evidence that such effects have caused the results, they have been impossible to eliminate experimentally. Because of these problems and because these tests do not directly manipulate odors *per se*, the results from anosmic pigeons alone do not constitute a conclusive test of olfactory navigation. However, they do not stand alone.

Attempts to manipulate the odor map

A large variety of experiments have attempted directly to manipulate the odor environment so as to produce a predictable effect on the orientation of the pigeons. This approach has the potential to provide strong tests of the hypothesis because one can manipulate the putative orientation cue, and the predicted effects are usually a change in direction rather than the more problematical disorientation. Experiments have focused on three aspects of homing navigation: (1) attempts have been made to alter the odor environment at the loft so that pigeons will develop a predictably altered ‘map’; (2) pigeons are known to use information acquired during transport to the release site (route-based or outward journey information) in the homing process and attempts have been made to mislead them by providing false odor information; (3) outward journey information is not necessary for pigeons to home well from distant, unfamiliar sites and experiments have been designed to determine whether pigeons can be fooled about the release site on the basis of odors.

The olfactory navigation hypothesis posits that pigeons learn an odor ‘map’ by associating odors perceived at the home loft with the directions from which they are carried by winds, or by sampling odor gradients during exploratory flights. Attempts to manipulate the development of that map have involved changing the directions of wind (deflector lofts, wind-reversal experiments), shielding the birds from winds coming from certain directions, and exposing the pigeons to artificial odorants coming from certain directions. Much controversy has surrounded the cause of the consistent changes in initial flight bearings produced by deflector lofts, and it is probably best simply to disregard those experiments at present. The wind-reversal experiments (Ioalè *et al.* 1978; Ioalè, 1980) have produced compelling results. By employing fans at the ends of corridor-shaped lofts, it was possible to expose pigeons to natural air and odors which came from a direction opposite to the actual wind direction. The simple prediction is that the experimental pigeons should learn a reversed odor map and, when released from a direction along the axis of the corridor, should fly in the opposite direction to the controls. This is a very specific prediction and the results were striking: wind-reversed experimentals had vanishing bearings on average directly away from home, whereas controls flew towards home when released from the same site. One could argue that the flight directions of these birds simply reflect some sort of directional response to winds experienced in the loft, but that criticism seems to be answered by a more recent study (Ioalè *et al.* 1990). In this experiment, the pigeons were housed in open cages. Experimental pigeons were exposed to a fan-produced air current carrying the scent of benzaldehyde. When released with exposure only to the natural air during transport and at the release site, both experimentals and controls were homeward-oriented. If they were simply responding to fan wind, experimentals should have flown in quite different directions. When both groups were exposed to the odor of benzaldehyde during transport and at the release site, controls were homeward-oriented whereas experimentals vanished in directions approximately opposite to that from which they had perceived benzaldehyde at the loft.

These experiments make specific predictions about the initial orientation of the pigeons and are not subject to criticisms concerning the detrimental effects of the procedures. They directly manipulate odor and, taken together, it is difficult to explain the results by anything other than the most contrived alternative hypothesis. (There are some complicating details of these experiments to which I shall return later.) Similar points can be made concerning the site simulation experiments in which pigeons exposed to air from one release site are in fact released (without smelling any air) from a site in the opposite direction from home. Benvenuti and Wallraff (1985) obtained impressive results in which controls flew homewards and experimentals flew in more or less opposite directions, towards the ‘false’ home direction. With substantially smaller sample sizes and poorer orientation, Kiepenheuer (1985) obtained similar results. No artificial odors or winds are involved in these experiments, and I do not see how the results can be explained without involving airborne cues. I am not bothered by the common directional tendency between experimentals and controls noted by Wiltschko (her Table 1). Such directional biases not related to the home direction are observed frequently in pigeon releases. Whether they are due to a loft-specific preferred compass direction, produced by factors unique to the release site, or are due to something else, they do not negate the basic interpretation of the site simulation experiments.

A consistent and somewhat peculiar feature of the olfaction experiments is that anosmic pigeons released from familiar sites are essentially unaffected (i.e. they head homewards), whereas the various manipulations discussed here tend to produce the same effects as at unfamiliar release sites. The impotence of anosmia suggests that the pigeons are using some other feature(s) of the site that have become effective through prior experience. Wallraff believes that these are visual landmarks, but there seems to be little persuasive evidence that this is the case. The lack of an influence of anosmia and the occurrence of effects of manipulations of odors and air do not seem particularly contradictory to me. In the one case, the putative map information has been eliminated and thus the animal cannot respond to it. In the other, the information is present, but in an altered state.

The physical substrate

From the outset, the implausibility of the existence of the necessary physical substrate has made olfactory navigation seem far-fetched. It is not obvious how gradients of odors useful over ranges of hundreds of kilometers could be maintained in the dynamic atmosphere. This remains a major unresolved problem and has been cited as sufficient grounds to reject the olfactory hypothesis out of hand. But science does not work this way. Hypotheses can only be rejected through the results of empirical tests, not on the basis of theoretical considerations. Models are useful in raising questions and focusing research, but all are based on a variety of untested assumptions. Without knowing what substances in the atmosphere constitute the basis for an olfactory map, what can we conclude about their distribution in space and time?

We may have tended to assume that the pigeon's navigational map is a good deal more sophisticated than that which exists or is necessary. To explain the level of performance revealed by pigeons, a 'map' need not be particularly precise (Wallraff, 1989). It might contain no distance component, but simply indicate the direction towards home. Trying to discover the physical basis of olfactory navigation is a question of central importance that needs to receive much more attention. However, I do not find the unlikelihood of a mechanism a powerful argument against its existence. I am reminded that we were assured, on the basis of apparently sound theoretical arguments, that hummingbirds could not fly across the Gulf of Mexico and that terrestrial animals could not detect the Earth's magnetic field. One of the general themes in our developing understanding of animal orientation systems has been that studies of behavior have revealed responses whose sensory basis was discovered only later when the question was forced by empirical behavioral data. Ethology has always fared best when we have followed the leads provided by the spontaneous behavior of our animal subjects, and that is how I think we should best proceed in this case.

Olfactory sensitivity

Coupled with our lack of knowledge about relevant aspects of the atmosphere is the primitive state of our understanding of the olfactory abilities of birds. Most of the work that has been done has involved potent artificial odorants. Without knowing what substances pigeons are using, it is difficult to ask a refined question, but it is surprising that no one has attempted to use conditioning techniques to ask whether pigeons can discriminate relevant samples of natural air. When olfactory homing was proposed as the mechanism by which salmon return to natal streams, some of the earliest experiments tested whether the fish could discriminate water from different streams. If pigeons could be induced to reveal a robust discrimination ability under controlled laboratory conditions, much could be learned rapidly about the possible physical and physiological bases of an olfactory map.

The question of replication

One of the major barriers to widespread acceptance of the olfactory hypothesis has been the failure of some of the results from Papi's group to be replicable in other places. Even when considerable effort was made to employ identical procedures, rather different results were obtained at lofts in the United States, Germany and Italy (Wiltschko *et al.* 1987*b*). The differences seem not to be due to genetic stock, but may have to do with the different rearing procedures employed at the various pigeon lofts or with aspects of the local environment around the loft. There has been a strong emphasis on releases with anosmic pigeons in the replications (as noted above, not the strongest evidence) and there are no published replication attempts of many of the most compelling experiments. In addition, the conclusions of too many of these studies have relied on sample sizes much smaller than those presented by the proponents, on control pigeons either not oriented at all or not homeward-oriented, and on data with other qualitative problems.

Replication of the experiments by Papi, Wallraff and their colleagues remains a worthy goal, but to be credible the results must be based on quantitatively and qualitatively comparable data. The results must be able to pass a number of tests. (1) Are the control pigeons homeward-oriented? If not, it is dangerous to draw any conclusions about homing navigation. Pigeons may be well-oriented in directions other than homewards. It is not clear in many cases why this is so. Wallraff is convinced that it is often based on a loft-specific directional bias (preferred compass direction); others are inclined to attribute the biases to factors at the release site. Whatever the case, it is not clear how or if the biases are directly related to homing, though they can have a devastating impact on homing experiments. (2) In attempts to produce anosmia, can we be certain that the birds were completely prevented from smelling natural air during the critical times and at the critical places? Occlusion of nostrils is apparently inadequate and local anesthetics work only for short duration (1–2 h). (3) When release at unfamiliar sites is a component of the design, can we be certain that the pigeons are really inexperienced in the region of the release? Only when these baseline criteria are met can we put much confidence in the results of experiments designed to test the olfactory hypothesis.

Conclusion

Where does all this bring us? In empirical science, our judgment at any time is based on the weight of evidence. I find the accumulated evidence convincing that olfaction plays a major, sometimes primary, and sometimes perhaps even exclusive, role in what we call the 'map' component of homing. Papi and Wallraff believe that atmospheric odors provide the necessary and sufficient basis for the map (e.g. Wallraff's thesis 6). While I agree that there is no alternative hypothesis supported by substantial data, Wiltschko makes the point that the absence of an alternative is not a valid basis for accepting the olfactory hypothesis. Papi and Wallraff may turn out to be right, but I am not yet convinced that odors comprise the *sole* map for *all* pigeons.

My reservations about the exclusiveness of olfactory navigation are based on several empirical results. The extent to which pigeons rely on olfactory navigation seems to be a function of how and where they are raised and housed. When Wiltschko *et al.* (1987*a*) raised pigeons according to Papi's procedures, they seemed to use olfaction. Pigeons reared in a loft sheltered from winds were largely unaffected by anosmia and were homeward-oriented, suggesting that they possessed some other navigational capability. In the experiments of Ioalè *et al.* (1978, 1990; Ioalè, 1980) discussed above, there was conspicuously more variance in the vanishing bearings of experimentals *versus* controls. This suggested to the authors and suggests to me that there may well be other conflicting information to which the birds have access, resulting in some ambiguity in selecting the departure direction. Homeward orientation from familiar sites by presumably anosmic pigeons wearing frosted lenses might be interpreted in the same way (Benvenuti and Fiaschi, 1983). The comparative study of Wiltschko *et al.* (1987*b*) and the intriguing results regarding the importance of the loft environment described in Walcott's chapter continue to point to a navigational map based on multiple cues. The relative weighting of these cues depends on the environmental conditions around the loft and the types and amounts of experience the pigeons have in the loft vicinity. This is admittedly vague and there is no very compelling hypothesis for what the other cues might be, but that doesn't mean there are none.

The overall situation with regard to olfactory navigation by pigeons is reminiscent of that with magnetic orientation some years ago. The weight of a large amount of evidence supported magnetic orientation, but there were some conspicuous inconsistencies and failures of replication. If we required unanimity of results in studies of bird navigation, we would be confident of almost nothing. Today, virtually everyone in the field accepts magnetic orientation as a matter of course. In the case of olfactory navigation, I think the burden of proof clearly rests with those who still believe that odors play no role in homing.

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