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EDITORIAL

Olfactory navigation versus olfactory activation: a controversy revisited

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Abstract

In the early 1970s, Floriano Papi and colleagues proposed the olfactory-navigation hypothesis, which explains the homing ability of pigeons by the existence of an odor-based map acquired through learning. This notion, although supported by some observations, has also generated considerable controversy since its inception. As an alternative, Paulo Jorge and colleagues formulated in 2009 the olfactory-activation hypothesis, which states that atmospheric odorants do not provide navigational information but, instead, activate a non-olfactory path integration system. However, this hypothesis is challenged by an investigation authored by Anna Gagliardo and colleagues and published in the current issue of the *Journal of Comparative Physiology A*. In this editorial, the significance of the findings of this study is assessed in the broader context of the role of olfaction in avian navigation and homing, and experiments are suggested that might help to finally resolve the olfactory-navigation versus olfactory-activation controversy.

Keywords Pigeon · Homing · Atmospheric odorants · Olfactory-navigation hypothesis · Olfactory-activation hypothesis

Introduction

As one of the editors of the *Journal of Comparative Physiology A*, I always take great pleasure in receiving and handling manuscripts on animal navigation, migration, and homing. This was also the case when Anna Gagliardo, Enrica Pollonara, and Martin Wikelski submitted the paper that is published in the journal's current issue (Gagliardo et al. 2018). In this study, the authors present findings that the authors interpret as inconsistent with the so-called olfactory-activation hypothesis. This hypothesis states that olfactory stimuli play a role in navigation of pigeons during homing, yet their function is restricted to the activation of navigational systems based on non-olfactory cues (Jorge et al. 2009, 2010).

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The olfactory-activation hypothesis has challenged earlier claims by other authors, most notably Floriano Papi and co-authors (Papi et al. 1971, 1972), that pigeons learn at their home lofts to associate atmospheric odorants with the direction of winds, which serve as vehicles of these odorants. According to this hypothesis, which has become known as the olfactory-navigation hypothesis or olfactory-map hypothesis, pigeons use this information to construct an odor-based map. In combination with a compass system, this positional information enables them to return to their loft after displacement.

Although some experimental data are in agreement with the olfactory-navigation hypothesis (for reviews see Wallraff 2004, 2005), skepticism has persisted since the publication of Papi and colleagues' paper in 1971. This skepticism was fueled more recently by the experiments conducted by Paulo E. Jorge and colleagues, in which they demonstrated that the orientation of pigeons exposed to artificial odorants that did not contain any navigational information was undistinguishable from the behavior of pigeons exposed to natural odorants, as long as the birds had access to these odorants during displacement (Jorge et al. 2009, 2010). On the other hand, the pigeons were disoriented when they were deprived of odors during displacement. These observations prompted the authors to propose that odors do not provide navigational information but, instead, activate a non-olfactory path integration system. Exactly this hypothesis is challenged by the current paper of Gagliardo and colleagues. Based on GPS tracking experiments, their study has failed to find support for the idea of a mere activational role of olfactory stimuli, but seems to be in agreement with the olfactory-navigation hypothesis (Gagliardo et al. 2018).

Readers who have followed the development of avian navigation research may be puzzled at this point. Over nearly five decades, they have witnessed cycles of both support and disapproval of the olfactory-navigation hypothesis, leaving perhaps some of them wonder in which direction the pendulum might swing next. A weakness that prevents us from reaching a final verdict is that no experimental result published so far has proven the olfactory-navigation hypothesis (or an alternative to it) unambiguously. However, as history teaches us, controversies have preceded many scientific theories before they became widely accepted (Sherwood 2011). Controversies did not stop Bill Keeton from inviting Floriano Papi to collaborate with him to test the olfactory-navigation hypothesis. Nevertheless, when the American and Italian teams could not agree on the interpretation of the results they had obtained through their joint experiments, they spelled out the differences in two separate sections in the Discussion of their paper published in the *Journal of Comparative Physiology A* (Papi et al. 1978)—something that might well be unique in science, but, at the same time, underscore the openness and collaborative spirit of Keeton (Zupanc 2015).

In the tradition of this openness, I have asked Charles Walcott, Wolfgang Wiltschko, and Roswitha Wiltschko—each of them a pioneer in avian navigation—to share with the readers of the *Journal of Comparative Physiology A* their assessment of why experiments have so far failed to provide unambiguous clues about the role of olfaction in avian navigation, and how future experiments should be designed to accomplish a better understanding of this phenomenon. Their statements are presented in the following two sections, the first written by Charles Walcott, the second by Wolfgang and Roswitha Wiltschko.

Charles Walcott: pigeons are opportunists

The olfactory-navigation hypothesis, that pigeons could use olfactory information to return to their home loft, has always appeared improbable. Odors seem so ephemeral, so changeable, and insubstantial. Yet Floriano Papi and his colleagues (Papi et al. 1972; Wallraff 2014) have made a very strong case that homing pigeons use them to find their way home. One of the problems has been the difficulty of repeating the Italian experiments. Here in Ithaca, anosmic pigeons both orient and home from unfamiliar sites. Further, one crucial experiment with the deflector loft showed that pigeons were responding to sun reflections not deflected winds (Waldvogel et al. 1988). This difference of opinion led Paulo E. Jorge and colleagues (Jorge et al. 2009, 2010) to try an experiment in which pigeons were exposed to nonsense odorants at a false release site. When released at a location in the opposite direction from home, both the control pigeons, which had been exposed to natural odorants at the false release site, and those exposed to nonsense odorants, oriented as if they had been released at the false release site. In the paper published in the current issue of the *Journal of Comparative Physiology A*, Anna Gagliardo and colleagues have tried to repeat this experiment using Italian pigeons and have shown that exposure to artificial odorants on the way to the release point has little or no effect on either initial orientation or homing (Gagliardo et al. 2018).

So why might these differences arise? Two possible effects come to mind: first, the pigeons were very different in the age, training, and experience, and second, differences in the environment seem to alter the cues that pigeons pay attention to.

For the first of these, the Italian group raises pigeons in an open loft where they are free to come and go. They used young, inexperienced pigeons who had never been trained or released away from their loft. Jorge et al (2010) used old, experienced pigeons who had been given training flights up to 5 km in the cardinal directions around the loft. The Wiltschkos (Wiltschko and Wiltschko 1985; Schiffner and Wiltschko 2013) have shown that young pigeons on their first flights may well rely on different cues; they are, for example, very susceptible to variations in the magnetic field on the way to the release point.

The second point has to do with geographic locations. My colleagues and I spent several summers finding that our homing pigeons raised at Fox Ridge Farm, in Lincoln, Massachusetts, were disoriented at magnetic anomalies, places where the earth's magnetic field was disturbed (Walcott 1978). When, after Bill Keeton's death, I moved to Ithaca, I was unable to repeat these experiments with Ithaca pigeons. Going back to Massachusetts, our old lofts at Fox Ridge Farm were not available so we set up a portable loft about 1.5 km away at Codman Farm and stocked it with Ithaca and Boston pigeons. Neither group of pigeons raised at Codman Farm were disoriented at magnetic anomalies. So, I pleaded with my former landlord, and we set up a portable loft at the old site at Fox Ridge Farm and stocked it with pigeon siblings, one group raised at Codman and the other at Fox Ridge. Both groups of birds were trained together and oriented well at normal sites. But at magnetic anomalies, the Fox Ridge Farm birds were disoriented, while their siblings from Codman Farm were well oriented towards home (Walcott 1992).

Another example of the same kind of effect was the experiment carried out by the Wiltschkos (Wiltschko and Wiltschko 1989) in Frankfurt. Anosmic pigeons from their loft surrounded by buildings were well oriented towards home, whereas anosmic pigeons raised on the roof of the zoology building were disoriented. Additional experiments with anosmic pigeons in Italy, Germany, and the United States showed a profound disorientation in Italy, but little effect in either Germany or the U.S.A. (Wiltschko et al. 1987a).

What is striking about these experiments is that pigeons growing up in different environments may be attending to different cues. Fox Ridge Farm sits on a steep magnetic gradient; Codman Farm has almost no magnetic gradient at all. The Wiltschkos' birds, when brought up with free access to the wind, were disoriented after made anosmic, but pigeons from their old, sheltered loft were oriented (Wiltschko and Wiltschko 1989).

My conclusion from these experiments is that pigeons are opportunists, using information gained from the environment around the loft and on training releases to find their way home. And that different pigeons, at different stages of their development and at different locations may well be using different cues. The evidence is quite overwhelming that olfaction plays some role in this process, but exactly how it is used and under what circumstances is still mysterious.

What experiments can be done to resolve this issue? One obvious suggestion is to try to repeat the crucial Italian experiments with trained, experienced pigeons. It would also be interesting to see whether young untrained pigeons in Portugal behave more like the Italian ones when given false odorants. These two experiments might indicate whether the difference is due to loft location or to training. Finally, there is the curious finding that anosmic pigeons can fly in the home direction from familiar locations even when equipped with frosted lenses (Benvenuti and Fiaschi 1983). This observation begs for further investigation: what have the pigeons learned that makes a place 'familiar'?

Wolfgang and Roswitha Wiltschko: early learning appears to be critical

In the early 1970s, an Italian group led by Floriano Papi forwarded the hypothesis of olfactory navigation, claiming that atmospheric odorants are the most important, if not the sole navigational factors (Papi et al. 1971, 1972; for a summary see; Papi 1986). The proposed role of odors was met with considerable skepticism, the more, since not all findings seemed totally compatible with claims of the olfactory protagonists (for a discussion of this issue see Wiltschko 1996). In 2009, Jorge and colleagues offered an alternative by suggesting the olfactory-activation hypothesis: odorants do not carry navigational information, but activate the processing of navigational information. Their claim was supported by experimental data obtained in Portugal (Jorge et al. 2009, 2010, 2014). In the present issue of the *Journal of Comparative Physiology A*, Anna Gagliardo and colleagues report that they repeated one of the critical experiments and were not able to replicate these findings (Gagliardo et al. 2011, 2018).

Vivid controversies about the inability to replicate data obtained at other lofts seem to be a characteristic of the olfactory hypothesis right from the beginning. At his loft in Ithaca, Upstate New York, U.S.A., Bill Keeton could not reproduce the original Italian findings: his pigeons oriented despite of olfactory deprivation (Keeton and Brown 1976; Keeton et al. 1977; Hermayer and Keeton 1979); and we (Wiltschko et al. 1987b) could not replicate them either at our loft in Frankfurt, Germany. Italian and American researchers collaborated and performed joint experiments at Keeton's loft, but even this did not solve the problem because the two groups could not agree on the interpretation of their results, which led to the unique case of a paper with two separate discussions: Papi and Benvenuti took the slower homing speed and lower homing success as an indication of olfactory navigation; Keeton and Brown argued that the absence of a consistent effect on initial orientation spoke against olfactory navigation (Papi et al. 1978). In a later study, we could show that the response of pigeons to olfactory deprivation depended on the way the pigeons were raised and trained: pigeons from our loft in the garden, being routinely trained 40 km in the cardinal compass directions, failed to respond to olfactory deprivation as before, whereas birds from a loft on the roof, only a few meters away, with little training, were markedly affected (Wiltschko and Wiltschko 1989 for a more extended discussion).

We find the olfactory-activation hypothesis attractive because assuming that an activation is necessary only once when the bird is new at a site, it can explain a number of observations that the olfactory-navigation hypothesis left unanswered, like: the lack of an effect of olfactory deprivation at familiar sites, the expansion of that 'familiarity' beyond the site itself, and the difference between the findings at the different lofts, which can be attributed to the extent of early training (see Wiltschko and Wiltschko 2017 for a more extended discussion).

In the present study by Gagliardo and colleagues, there is, no doubt, a difference between the pigeons treated with natural air, and those treated with air containing artificial odorants. However, the difference appears gradual rather than principal, as many of the initial bearings still lie in the home direction, and the number of late and lost birds were more similar than one would expect if natural odorants carried essential navigational information (Gagliardo et al. 2018).

It is clear that the authors could not replicate the findings by Jorge and colleagues (Jorge et al. 2009, 2010, 2014), but they also cannot explain why the other findings were positive. Failures to replicate other researchers' results are problematic, and they are often caused by differences in methods, sometimes aspects the importance of which has not yet been realized. One of us made this experience in the 1960s, when the avian magnetic compass was first described (Merkel and Wiltschko 1965; Wiltschko 1968). This discovery was in stark contrast to the conclusion of eleven independent investigators or groups (listed by Wallraff 1972) who had tried to find evidence for the existence of navigational systems other than the ones based on celestial cues. This discrepancy of the findings was caused by methodological differences, like the cages used and the design of the experimental procedures. To what extent differences in methods may play a role in the present controversy concerning the olfactory-activation hypothesis is difficult to assess.

To solve this controversy, we need critical tests that can decide between a possible role of odorants as navigational cues and a role as activating agents, comparing the effects of natural and artificial odorants. It would be best if the two opponent groups would collaborate and run such experiments jointly in Italy as well as in Portugal. It seems very important to use pigeons with equal training experience (see Wiltschko and Wiltschko 1989), and identical methods and procedures agreed upon by both groups. Additionally, the birds should be released at more than one site in each country to exclude the influence of special conditions at a specific site. One would hope that this does not lead to a similar scenario as was encountered in the collaboration of Papi and Keeton, but finally resolve the issue.

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