

COMMENTARY

Considerations on the role of olfactory input in avian navigation

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ABSTRACT

A large amount of data documents an important role of olfactory input in pigeon navigation, but the nature of this role is not entirely clear. The olfactory navigation hypothesis assumes that odors are carrying essential navigational information, yet some recent experiments support an activating role of odors. This led to an ongoing controversy. An important, often-neglected aspect of the findings on olfaction is that olfactory deprivation affects avian navigation only at unfamiliar sites. The orientation of anosmic birds at familiar sites remains an enigma; earlier assumptions that they would rely on familiar landmarks have been disproven by the home-oriented behavior of anosmic pigeons additionally deprived of object vision, which clearly indicated the use by the birds of non-visual, non-olfactory cues. However, if odors activate the establishing and enlarging of the navigational 'map' and promote the integration of local values of navigational factors into this map, it seems possible that such a process needs to occur only once at a given site, when the birds are visiting this site for the first time. If that were the case, the birds could interpret the local factors correctly at any later visit and orient by them. This hypothesis could explain the oriented behavior of birds at familiar sites, and it could also help to reconcile some of the seemingly controversial findings reported in the literature, where the effect of olfactory deprivation was reported to differ considerably between the various pigeon lofts, possibly because of different training procedures.

KEY WORDS: Pigeon navigation, Olfactory input, Activation effect, Navigational map, Familiar sites, Cue integration

Introduction

The role of odors in pigeon navigation is still controversial, and findings with migratory birds add to the confusion rather than providing answers. Briefly reviewing the key findings on 'olfactory navigation' – the positive as well as the negative ones – we propose a modification of the olfactory activation hypothesis that can possibly reconcile the seemingly controversial findings in the literature.

The olfactory navigation hypothesis

In the early 1970s, Papi and colleagues (1971, 1972) first reported that homing pigeons deprived of smell were disoriented, and most of them did not return to their loft. This discovery started a new approach in pigeon navigation research and, during the following decades, led to an enormous number of various kinds of experiments to analyze the role of odors. The studies involved releasing birds made anosmic (see Glossary) in different ways, transporting them in filtered air, letting them smell at one site and releasing them at another, as well as attempts to provide them with a false odor map (see Glossary) by

raising them in lofts with altered wind conditions, etc. The early experiments have been well reviewed (e.g. Papi, 1986); the entire literature on the various olfactory experiments has been briefly summarized by Wallraff (2004) and Gagliardo (2013). The results document a crucial role for olfactory input and were interpreted as suggesting navigation by different odors and odor compositions based on a navigational 'map' that was established at the loft as wind from a different direction reached the birds (see Papi, 1986). The protagonists of the olfactory navigation hypothesis tended to consider odors as the only orientation cues used by birds to navigate.

Experiments with wild birds produced very similar results. Depriving displaced swifts (*Apus apus*), starlings (*Sturnus vulgaris*) or Cory's shearwaters (*Calonectris diomedea*) of the sense of smell led to disorientation and a marked decrease in the number of birds returning (e.g. Fiaschi et al., 1974; Wallraff and Hund, 1982; Gagliardo et al., 2013; Pollonara et al., 2015). Adult migratory birds displaced during migration normally compensate for the displacements, heading directly towards their goal area (e.g. Perdeck, 1958; Thorup et al., 2007); when deprived of olfaction, however, the migrants appeared unable to do so. Catbird (*Dumetella carolinensis*) and most lesser black-backed gulls (*Larus fuscus fuscus*) fell back on their innate migratory direction (Holland et al., 2009; Wikelski et al., 2015). Thus, for these wild birds too, determining the direction to a distant goal seemed to require olfactory input. Nevertheless, the findings on olfactory navigation, seen in their entirety, do not always form a consistent picture and are in some details not in agreement with predictions (for a critical review of the pigeon data, see Wiltshcko, 1996).

The olfactory controversy

The hypothesis of olfactory navigation, especially its universal claim that odors are the only orientation cues, met with considerable skepticism. One reason was that, at some other pigeon lofts, the findings did not support a crucial role for odors, as there was hardly any effect of olfactory deprivation on initial orientation (e.g. Keeton and Brown, 1976; Keeton et al., 1977; Schmidt-Koenig and Phillips, 1978; Wiltshcko et al., 1987a). A comparative study using the identical method of depriving pigeons of smell revealed the same difference in the responses of pigeons in Italy, Germany and Upstate New York as had been observed before (Wiltshcko et al., 1987b): a considerable effect in Italy, and negligible effects in Germany and North America. Another reason for doubt was that meteorological data and studies of air flow spoke against the existence of stable odor distributions as required for the assumed olfactory navigation (e.g. Becker and van Raden, 1986; Waldvogel, 1987; Ganzhorn and Paffrath, 1995) – indeed, reliable maps of odors did not seem to exist.

The effects of olfactory manipulations, where they occurred, were undisputed; what was controversial was their interpretation (see Wiltshcko, 1996). The supporters of olfactory navigation were convinced that odors carried crucial navigational information, in spite of what the meteorologists said. The possibility that odors may play yet another role was hardly ever considered.

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Glossary**Anosmic**

Unable to smell, deprived of odors.

Homing

Returning to one's home, e.g. to the pigeon loft, to the nest.

Internal clock

The animal's feeling for the time of day.

Navigational map

A mental representation of the spatial distribution of navigational factors.

Odor map

A navigational map based on different odors.

In 2009, Jorge and colleagues reported experiments with pigeons that were exposed during displacement to artificial odors from various plants such as lavender, eucalyptus, jasmine and others added to synthetic bottled air. These odors had the same effect as the natural odors that the control birds had experienced (Jorge et al., 2009). Another study supported these results: pigeons displaced in filtered air were allowed to smell at a 'false' release site, one group having experienced the local natural odors and another group the artificial odors. When subsequently released anosmically at a second site, the two groups oriented alike, namely as if they had to return from the 'false' site, whereas birds not allowed to smell at any site were disoriented (Jorge et al., 2010). These findings suggested that the specific chemical substances in the air were unimportant as long as the birds could smell anything and clearly argued against navigational information by odors; instead odors appeared to have an activation effect, activating a (non-olfactory) map system. This 'olfactory activation hypothesis' forwarded by Jorge and colleagues (2009, 2010) caused a vivid controversy about the role of odors (see Gagliardo et al., 2011; Phillips and Jorge, 2014; Wallraff, 2014) that currently has not been resolved.

Open question: orientation at familiar sites

One aspect of the olfactory navigation hypothesis has been largely neglected by its supporters: in spite of the disrupting effect at unfamiliar sites, olfactory deprivation proved largely ineffective at familiar sites. This was established in 1973 by Benvenuti and colleagues and was confirmed in later studies (e.g. Hartwick et al., 1977; Luschi and Dall'Antonia, 1993; see also Papi et al., 1978). As an explanation for this phenomenon, these authors proposed that birds would rely on visual landmarks and assumed piloting (i.e. following sequences of familiar landmarks; see Griffin, 1952) as a strategy for returning from sites that were familiar to the birds from previous flights. Findings from one study seemed to be in accordance with this assumption (Bingman and Ioalè, 1989). However, pigeons with a shifted internal clock (see Glossary) also showed the typical deflection when homing (see Glossary) from extremely familiar sites from which they had returned more than 50 times before (Füller et al., 1983). In another study, anosmic pigeons, too, were deflected in the typical way when released clock-shifted, documenting that these birds at familiar sites still determine their home direction as a compass course (Luschi and Dall'Antonia, 1993). These authors suggested that the birds would recognize the site by landmarks and remember the home bearing from previous return flights.

The assumption that navigation is based on visual landmarks was critically tested only once by Benvenuti and Fiaschi (1983) in a study that is largely ignored by the advocates of olfactory navigation: anosmic pigeons were released with frosted lenses that additionally deprived them of object vision. At familiar sites, these birds departed

in directions that were not different from those of controls. These findings clearly speak against a role of visual landmarks in their orientation, instead indicating that the birds determined their home direction by non-visual, non-olfactory cues, the nature of which remained unclear. And it raises the question why the birds do not use these unknown cues when the sites are not yet familiar.

Interestingly, the 'familiarity' that allows pigeons deprived of smell to orient is not restricted to the previously visited site itself, but seems to extend to the vicinity. Wallraff and Neumann (1989) observed that anosmic birds were oriented at 'unfamiliar sites' within the training area, a finding they could not interpret with the olfactory hypothesis alone. They attribute it to a topographical map of landmarks, in spite of the findings of Benvenuti and Fiaschi (1983). Displaced wild starlings could also navigate without olfactory input in an area around their home: there was no effect of olfactory deprivation up to about 60 km, whereas the return rate of anosmic starlings dropped dramatically at greater distances (Wallraff et al., 1995).

A recent study with migratory lesser black-backed gulls documents a phenomenon that could be of a related nature (Wikelski et al., 2015): when displaced south–southwest, anosmic gulls seemed unable to navigate, as predicted by the olfactory hypothesis, and left in their migratory direction. Birds displaced eastward, however, flew in similar directions to untreated controls despite the loss of smell. The eastern release point, in contrast to the western one, possibly lay within the general migration corridor of the respective gull population, and the authors speculate that the birds might have been there before – thus it was possible that the release site was not totally unfamiliar to them. But even in this case, it is rather unlikely that the gulls were familiar with the visual landmarks in such a large area, and it leads back to the question of what cues the anosmic birds use to navigate in an area that they might have visited before.

Activating the integration of local factors into the navigational map

So far, the olfactory navigation hypothesis has not been able to provide a satisfactory answer to questions about the nature of orientation at familiar sites. Can the olfactory activation hypothesis do this?

An activating effect of odors is supported by recent neurobiological studies which indicated an activation of neurons in the hippocampal formation and of the navigation circuitry by lateralized activation of neurons in the piriform cortex (Jorge et al., 2014, 2016). However, some older findings could also be interpreted in view of an activating role of odors, as they revealed effects of olfactory deprivation on tasks not involving odors, such as tonic immobility and optokinetic nystagmus (rhythmic movements) (Wenzel and Rausch, 1977; Dornfeld and Bilo, 1990) as well as responses to visual stimuli (Wenzel and Salzman, 1968). Even the strongly disruptive effect of irregularly changing magnetic fields on pigeon orientation was suppressed in birds that had been deprived of odors by being kept in purified air during its application (Wallraff et al., 1986).

The question is now: what precisely is activated by olfactory input? As the compass orientation remains intact (Luschi and Dall'Antonia, 1993), any activation appears to involve the mechanisms by which birds determine the home course. In a study with very young, inexperienced pigeons displaced for the first time, olfactory deprivation produced no effect (Wiltshko and Wiltshko, 1987). These birds had not yet developed a map and must be assumed to be still in a phase where they relied on reversing the net compass course

of the outward journey to obtain the home course (see Wiltschko and Wiltschko, 1985, for details) – this mechanism does not seem to be disrupted by olfactory deprivation. Hence, one should look for an activation effect involving the navigational map, the mental representation of the spatial distribution of the navigational factors. Pigeons establish this map by experience and then preferentially use it for navigation (see Wiltschko and Wiltschko, 1985, for discussion). The observation that olfactory deprivation is not effective at familiar sites suggests that olfactory input is perhaps not required for the navigational step of determining the home direction itself, but that odors are required to activate the neuronal pathways that integrate the local values of the navigational factors into the map, in particular if unfamiliar values or combinations of navigational cues are involved. This assumption would explain the lack of effect of olfactory deprivation at familiar sites, because here, the birds would have already integrated the local combination of navigational factors into their map during their first visit – having done so, they were able to use them for navigation and derive their home direction from them.

This hypothesis can also explain the phenomenon that ‘familiarity’ is not restricted to the ‘familiar’ site itself, but includes a certain area around sites that birds have previously visited. Environmental gradients, such as magnetic intensity, gravity, infrasound and possibly others not yet known, are considered as navigational factors included in the map (for review, see Beason and Wiltschko, 2015); in contrast to the view of landmarks, these gradients do not change so rapidly and will still be sufficiently similar and interpretable in a certain area around the site of a previous visit. Hence, the assumption that olfactory input is only required once for integrating a new combination of navigational factors into the map is in agreement with a few observations that pigeons deprived of smell were oriented at ‘unfamiliar sites’ in the vicinity of familiar sites (Wallraff and Neumann, 1989) and with the orientation of displaced wild starlings in the vicinity of their home (Wallraff et al., 1995). And finally, the above-mentioned assumption can also provide a plausible explanation for the recently reported ability of anosmic gulls released eastward to compensate for the displacement (Wikelski et al., 2015): if the birds had visited this part of their distribution range before, as Wikelski and colleagues (2015) assume, they could already have integrated the local cues into their map and thus were able to interpret them for navigation, even if they may not have visited the specific release site itself.

Contradictory findings at different pigeon lofts

The above hypothesis might also help to resolve some of the apparent discrepancies between findings reported in the literature. In Italy, olfactory deprivation and olfactory manipulations always had a marked effect (for review, see e.g. Papi, 1986; Gagliardo, 2013), but this was not always the case in other regions. Keeton’s attempts to replicate the Italian experiment at his loft in Upstate New York produced largely negative results (e.g. Keeton and Brown, 1976; Keeton et al., 1977). In a series of joint experiments performed by Papi and Keeton together at Keeton’s loft, the results were largely negative or inconclusive. There was no agreement on their interpretation – the Italian authors emphasized the lower homing speed and lower return rate as indications for olfactory navigation; the American authors pointed out that the initial orientation showed little effect and attributed the decrease in homing success to a lower motivation or stressful effects of the treatment, pointing out that the few experimental birds followed by aeroplane were observed to land (Papi et al., 1978). Experiments in Germany yielded different results depending on where they were performed. At Schmidt-Koenig’s

loft in Tübingen and our loft in Frankfurt, olfactory manipulations also failed to show a consistent effect (e.g. Schmidt-Koenig and Phillips, 1978; Wiltschko et al., 1987a), whereas pigeons from Wallraff’s lofts in Würzburg and near Munich responded to olfactory manipulation in a very similar manner to those in Italy (e.g. Wallraff, 1980, 1981; Wallraff et al., 1984; see Wallraff, 2004, for a review). These differences alone cannot be attributed to different ways of depriving pigeons of smell, although some of the various methods applied could have caused stress and discomfort and might thus have contributed to poorer orientation and homing of anosmic birds (for discussion, see Keeton et al., 1977; Papi et al., 1978). The already mentioned comparative study using identical methods in Italy, Upstate New York and Frankfurt clearly indicated that the pigeons responded differently to the same treatment (Wiltschko et al., 1987a).

In the course of this study, striking differences in the management at the different lofts had become evident; that is, in the procedures of rearing and training the test birds before the experiments began. In Frankfurt, we normally raised our pigeons in the same way as Keeton treated his birds in Upstate New York, with a standard training program that began when they were in their third month post-hatching consisting of numerous releases at slowly increasing distances up to 40 km in the four cardinal compass directions, plus diagonal flights. In Italy, the birds were housed in a more wind-exposed loft and, although they had access to the open for free flights, were not regularly forced to fly; they had only a few flock releases when they were older. Wallraff (e.g. 1980, 1981) mostly used inexperienced pigeons and normally did not subject his birds to any systematic training program involving flights in different directions over longer distances.

To test for an effect of loft management, sibling pigeons were raised in two different ways, one group in the normal Frankfurt way, the other in the ‘Italian style’. The first group of birds, when made anosmic, oriented like the untreated controls, while the birds raised in the Italian style were markedly affected by olfactory deprivation (Wiltschko and Wiltschko, 1989). This clearly showed that the response to olfactory deprivation depends on the way the pigeons were raised and their previous experience. Wind exposure may also be involved (Wiltschko et al., 1989); it is striking, however, that olfactory deprivation had usually little effect at lofts where the birds were intensively trained before the experiments – that is, where they had been provided with profound knowledge of the regional navigational factors.

Training flights familiarize pigeons with the spatial distribution of the navigational factors around their home loft. Birds are released only at specific points, but these sites form a network and probably allow the birds to extrapolate the course of the navigational factors between them. If olfactory input is required to activate the mechanisms for integrating the respective factors and forming the navigational map (see Glossary), the formation of this map is guaranteed, because birds have normal access to odors during all training releases. At the end of the training phase, the pigeons are generally familiar with the navigational factors in their home region, and this ‘familiarity’ allows them to also interpret the local cues at sites where they have not been released before – a possible parallel to the lesser black-backed gulls displaced to the eastern part of their distribution range (Wikelski et al., 2015).

Concluding remarks

The role of olfactory input in avian navigation – navigational information or activation effect – is still a matter of heated debate. The recent neurobiological studies (Jorge et al., 2014, 2016) support

an activation effect of odors in parts of the brain associated with orientation and navigation: also, the activation hypothesis can better explain many of the olfactory findings. In particular, the assumption that birds need olfactory activation only at truly unfamiliar sites and that it is no longer required once a regional map is established and the distribution of the navigational factors is generally known can account for the inefficiency of olfactory manipulations at familiar sites and provides a possible explanation for the seemingly contradictory findings at the various lofts.

When Papi and colleagues (1971, 1972) observed that olfactory input is involved in avian navigation, this was a very important discovery. But, unfortunately, the role of odors appears to have been misinterpreted, and the ensuing discussion was one-sided in the sense that alternatives to providing navigational information were largely ignored. It might prove helpful to reconsider the entire olfactory findings in view of a possibly activating role for odors in establishing the map and integration of new local cue combinations, as, ultimately, we want to solve the existing controversies and achieve a better understanding of the navigational processes of pigeons and other birds.

Competing interests

The authors declare no competing or financial interests.

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