

COMMENTARY

Requiem for a heavyweight – can anything more be learned from homing pigeons about the sensory and spatial-representational basis of avian navigation?

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ABSTRACT

The homing pigeon (*Columba livia*) has long served as a study species to exhaustively investigate the sensory and spatial (map)-representational mechanisms that guide avian navigation. However, several factors have contributed to recent questioning of whether homing pigeons are as valuable as they once were as a general model for the study of the sensory and map-like, spatial-representational mechanisms of avian navigation. These reservations include: the success of this research program in unveiling navigational mechanisms; the burgeoning of new tracking technologies making navigational experiments on long-distance migratory and other wild birds much more accessible; the almost complete loss of the historically dominant, large-scale pigeon loft/research facilities; and prohibitive university per diem costs as well as animal care and use restrictions. Nevertheless, I propose here that there remain good prospects for homing pigeon research that could still profoundly influence how one understands aspects of avian navigation beyond sensory mechanisms and spatial-representational strategies. Indeed, research into neural mechanisms and brain organization, social/personality influences and genetics of navigation all offer opportunities to take advantage of the rich spatial behavior repertoire and experimental convenience of homing pigeons. Importantly, research in these areas would not necessarily require the large number of birds typically used in the past to study the sensory guidance of navigation. For those of us who have had the opportunity to work with this remarkable animal, one research door may be closing, but a window into exciting future opportunities lies ajar.

KEY WORDS: Navigational map, Familiar area map, Migratory navigation, Olfaction, Geomagnetism, Bird

Introduction

Beginning in the 1950s, laboratories in the United Kingdom (Matthews, 1951) and Germany (Kramer, 1957) established the domesticated homing pigeon as the premier model for investigating the sensory basis and map-like properties of avian navigation. This continued up to the end of the 20th century while homing pigeon research flourished under the leadership of such notable scientists as William Keeton, Floriano Papi, Klaus Schmidt-Koenig, Charles Walcott, Hans Wallraff, and Roswitha and Wolfgang Wiltschko, whose research teams and large-scale pigeon-loft operations produced an enormous volume of data and influential papers (see Wallraff, 2005; Gagliardo, 2013; Wiltschko and Wiltschko, 2017a).

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However, only the Pisa lofts, now headed by Anna Gagliardo, continue in operation, and the pace of this rich history has substantially diminished because of a number of factors in addition to the vanishing of the large loft facilities. These factors include: (1) a growing consensus on the sensory and representational mechanisms underpinning pigeon navigation; (2) a technological expansion that enables a more complete analysis of the sensory and spatial (map)-representational mechanisms of navigation in long-distance migratory and other wild birds; and (3) prohibitive per diem costs imposed by universities as well as animal welfare regulations. Therefore, the question I raise here is whether the combination of a largely successful research program and other extrinsic factors has rendered the homing pigeon obsolete with respect to advancing our understanding of the sensory toolbox and spatial-representational mechanisms used by birds as a group to navigate. However, recognizing this does not mean the cupboard is bare, as there are still numerous other research challenges well suited for the use of homing pigeons as experimental subjects.

Are the sensory mechanisms of homing pigeon navigation known?

I would like to premise this section by admitting that a full understanding of any behavioral phenomenon is illusory, and is simply awaiting the next surprise. Having said that, a strong case can be made that, broadly speaking, the sensory mechanisms that guide homing pigeons after release from an unfamiliar location to the home loft are well understood, and that understanding is a testament to the researchers mentioned above, their students and collaborators. The intent here is not to thoroughly summarize the vast body of literature that enables the claim of understanding, but to offer a brief overview colored by my own interpretation of the accumulated knowledge regarding pigeons and homing. Detailed summaries and interpretations can be found in Wiltschko and Wiltschko (2003, 2017a), Wallraff (2005, 2014) and Gagliardo (2013).

It is in many ways remarkable that Kramer's (1957) 'map and compass' model of homing pigeon navigation and Wallraff's (1974) 'gradient' model of how Kramer's map would be structured are as relevant today as when they were first introduced (Fig. 1). The map and compass model captures homing pigeon navigation as a two-step process in which pigeons, when released from a distant, unfamiliar location, first determine their position relative to the home loft with use of their 'navigational map', and then transform that relational-spatial information into a homeward-oriented compass bearing. The gradient model captures the representation of the map in the form of two intersecting stimulus gradients, which need not necessarily be perceived through the same sensory modality, that vary predictably in space. The crucial point is that an approximate understanding of the rate of stimulus change in a gradient through space, which can be implemented as a neural

Glossary

Conditioning paradigm

A historically important, psychological experimental procedure by which the occurrence of a once neutral stimulus predicts the occurrence of another behaviorally meaningful stimulus presented at the same time or shortly thereafter. With repeated presentation of the paired stimuli, the previously neutral stimulus begins to elicit a behavioral response.

Functional lateralization

The observation that paired brain structures that reside in both brain hemispheres or in both sides of a nervous system, for example, the hippocampus on the left and right side of the cerebrum, have different physiological, emotional, behavioral or cognitive functions.

Hippocampal formation

Also identified as the dorsomedial pallidum in non-mammalian vertebrates, this brain structure is fundamental for the control of map-like, spatial navigation and memory for events contextualized by space and time.

Homing speed

Generally, the average speed of an animal during its return from a start location to a goal location. For a homing pigeon, this would be the average speed during the flight from the release site until reaching the home loft.

Multi-modal map

A map used by an animal to guide navigation that is composed of more than one sensory element. For example, some have proposed that the navigational map of homing pigeons is supported by both olfactory and geomagnetic inputs.

Olfactory cortex

The region of the forebrain/telencephalon that receives direct inputs from the olfactory bulbs and participates in the neural processing of olfactory information.

Olfactory navigational map

The well-supported observation that the navigational map of homing pigeons, and other birds as well, used to return home is based on sufficiently stable variation in the spatial–environmental distribution of atmospheric odors.

Telencephalic organization

Refers to how the various subdivisions of the telencephalon are structured with respect to, among other things, neuronal cell types, connectivity among subdivisions (connectome) and neurochemistry.

Vanishing bearing

Before the time of GPS flight path recordings, the direction a homing pigeon would disappear from binocular view with respect to a release location.

Wingbeat signature

Typically characterized by the wingbeat frequency and flap–pause ratio of a flying animal.

algorithm, would allow a pigeon to extrapolate its position relative to its home loft at distances beyond what they have experienced (unfamiliar locations) from as far away as the quality of the gradient change is spatially stable.

For decades, the challenge that dominated research into homing pigeon navigation was the sensory basis of the map and compass. It is now universally agreed that homing pigeons have two compass mechanisms: one reliant on the sun, the sun compass, and the other reliant on the Earth's magnetic field, the geomagnetic compass. Less agreed upon is the sensory basis(es) of the map and whether, like the compass cues, different maps can be constructed from different sensory inputs. Indeed, much of the controversy and public antagonism among researchers has been motivated by strongly held positions on the navigational map's sensory basis. However, what most researchers would now agree on is that atmospheric odors play a fundamental role in enabling homing pigeons to determine their location relative to home from unfamiliar locations (Wallraff, 2005,

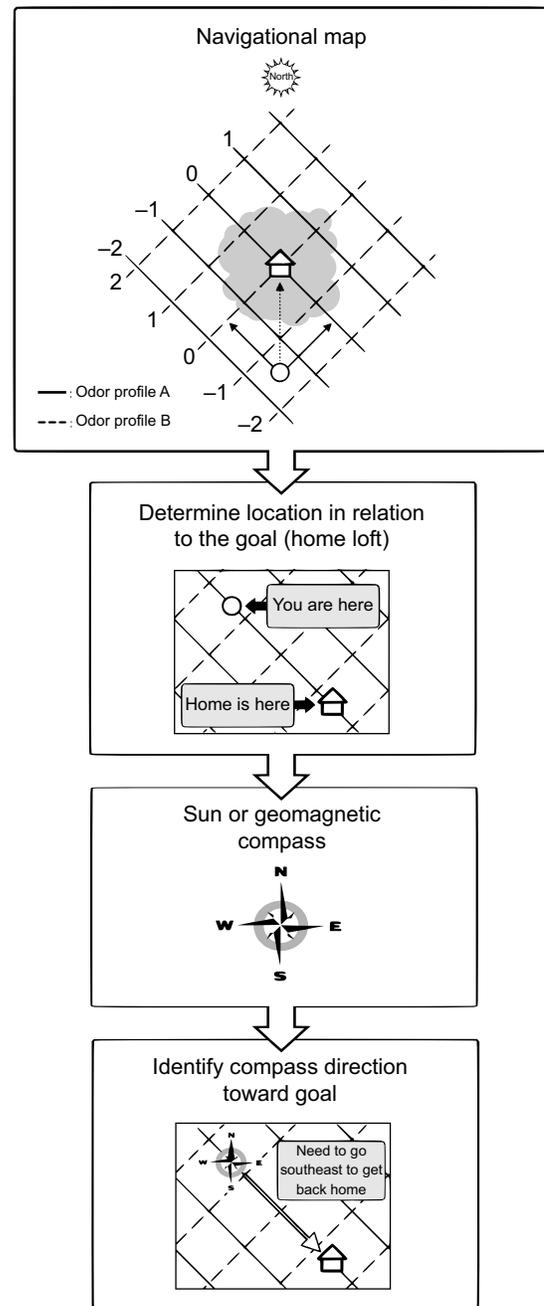


Fig. 1. Illustration of the complementarity of Kramer's (1957) 'map and compass' and Walraff's (1974) 'gradient' model of homing pigeon navigation. The map and compass model (bottom three panels) captures homing pigeon navigation as a two-step process in which a pigeon, when released from a distant, unfamiliar location, first determines its position relative to the home loft with use of its 'navigational map', and then transforms that relational-spatial information into a homeward-oriented compass bearing. The gradient model (top panel) captures the hypothetical representation of the map in the form of two intersecting stimulus gradients, in this example, two different odor profiles with intensities predictably varying along a northeast–southwest (odor profile A) and a northwest–southeast (odor profile B) axis. For advocates of a geomagnetic navigational map, the axes could be composed of variation in geomagnetic intensity or inclination. The crucial point is that an approximate understanding of the rate of stimulus change in a gradient, which can be learned through the experience of flying in the gray cloud of familiar space and implemented as a neural algorithm, would allow a pigeon to extrapolate its position relative to its home loft at distances beyond what they have experienced (unfamiliar locations outside of the gray cloud).

2014; Gagliardo, 2013; but see Wiltschko and Wiltschko, 2017b for a rebuttal of this position) – that is, the navigational map is olfactory in nature.

Less visible as a research topic is the recognized importance of familiar landmark and landscape features that pigeons exploit when they navigate closer to their home loft or over any previously experienced, familiar space. This ‘second map’ is of interest because it can be reliant on the avian hippocampus for its implementation (Herold et al., 2015; Bingman and MacDougall-Shackleton, 2017), and, when reliant on the hippocampus (see Gagliardo et al., 1999), its properties resemble those associated with the so-called cognitive map, as developed by O’Keefe and Nadel (1978).

Taken together, the brief outline above offers a credible and sufficient framework toward understanding the sensory guidance that pigeons use to navigate, a framework that is carefully and compellingly expounded by Wallraff (2005) and enables one to answer ‘yes’ to the question raised at the beginning of this section. When a pigeon is released from an unfamiliar location, it first relies on its olfactory navigational map (see Glossary) to approximate the direction of displacement with respect to the home loft. Wallraff (2005) also nicely describes the hypothetical properties of such an olfactory navigational map that addresses the intuitive obstacle of the disruptive effects of changing atmospheric conditions on the spatial reliability of chemical cues in the air. That information is then used to compute a homeward-oriented bearing directed by the sun or magnetic compass. As the pigeon gets closer to home and transitions from unfamiliar to familiar space, it begins to rely more on its hippocampal-dependent landmark/landscape map.

What is left to understand?

As hinted at above, many researchers in the field would be (perhaps justifiably) appalled by the simplistic sensory/representational guidance scheme of homing pigeon navigation outlined in the previous section. Certainly the mechanisms of homing pigeon navigation are much more nuanced than what I have summarized. As examples, questions remain about: the relationship between the sun and the magnetic compass; how might sun or magnetic-compass orientation interact with landmark-/landscape-derived spatial information; and does the navigational map necessarily need to rely on a gradient stimulus structure or can homing pigeons learn what is referred to as a ‘mosaic map’, in which positional information is extracted from spatially stable ‘patches’ of discrete sensory inputs? Given the adequacy of the navigational framework described above, which again is a simplified account of the much more carefully crafted thesis of Wallraff (2005), one can ask: have the big questions about the sensory guidance and spatial-representational structure of homing pigeon navigation been answered?

In my view, there are two conversations and one side note that are relevant with respect to this question. The first is the elusive and seemingly enduring question of whether something in addition to olfaction can support the homing pigeon navigational map. Here, one must acknowledge that there is tantalizing evidence that the Earth’s magnetic field, in addition to supporting the magnetic compass, can also support a geomagnetic map (Dennis et al., 2007; Wiltschko et al., 2010; Schiffner et al., 2011; Wiltschko and Wiltschko, 2017a). The evidence has prompted the idea of a navigational map that is multi-modal in nature (see Glossary; e.g. Wiltschko and Wiltschko, 2017a), which certainly has an intuitive appeal, and there is no reason why the multi-modality should be limited to olfaction and geomagnetism (see Hagstrum, 2000). Indeed, looking broadly at homing pigeon navigation, the system is

necessarily multi-modal with, minimally, an olfactory navigational map operational from distant, unfamiliar sites and a principally visual familiar landmark/landscape map closer to home. Nonetheless, one is still left with the question that if olfaction sufficiently explains the navigational map of homing pigeons (Wallraff, 2005; Gagliardo, 2013), why introduce the idea of multi-modality in the absence of any compelling support other than its trendy appeal? It is axiomatic that one must be objective about the possibility of a map based on something in addition to olfaction, and, as noted above, there is evidence that experimental treatments designed to disrupt the extraction of positional information from the Earth’s magnetic field (but some could also impact the geomagnetic compass) do influence the behavior of pigeons during homing. However, Anna Gagliardo routinely offers the sobering reminder that although magnetic treatments in homing pigeons have resulted in changes in behavior, those changes have never influenced the likelihood of pigeons returning home any slower than control-treated pigeons; in other words, there is little navigational impact of those treatments. Indeed, many magnetic treatments have no effect at all on homing behavior from unfamiliar locations (e.g. Holland et al., 2013), and one of the most used techniques designed to disrupt geomagnetic sensitivity in experiments investigating a magnetic map (e.g. Wiltschko et al., 2010), presumptive peripheral anesthesia of trigeminal nerve-coupled receptors, likely has no effect at all on geomagnetic sensitivity (Engels et al., 2018). Notable here is the contrast between the subtle effects of magnetic treatments on behavior compared with the complete failure of birds deprived of smell to navigate home successfully (Wallraff, 2005; Gagliardo, 2013). In my view, the most compelling evidence against anything other than an olfactory map in homing pigeons is the elegant study of Gagliardo et al. (2009). That study demonstrated that although cutting of the olfactory nerve in homing pigeons results, as expected, in a disruption of navigational ability, cuts of the trigeminal nerve – the presumptive source of peripheral geomagnetic-map inputs to the brain – have no impact on navigation. Finally, advocates of a geomagnetic map have not adequately addressed the challenge of how, over the distances they navigate (see Bingman and Cheng, 2005), homing pigeons would compensate for the temporal and spatial noise in the Earth’s magnetic field.

From some perspectives, the GPS technology that developed in the 1990s allowed for an almost transformative opportunity to reveal much more about the navigation of homing pigeons by providing complete reconstructions of the routes pigeons take to return home. Such route reconstructions supply data that informationally go well beyond the earlier experimental recording of simple vanishing bearings (see Glossary) taken with binoculars and homing speeds (see Glossary). However, and perhaps surprisingly, the GPS tracking seems to have revealed much more about how pigeons move and navigate over familiar space (Lipp et al., 2004; Gagliardo et al., 2007; Guilford and Biro, 2014) than how sensory mechanisms control the navigational map used from unfamiliar locations. For example, using GPS tracking, Gagliardo et al. (2016) investigated olfactory map navigation, and Schiffner et al. (2011) studied geomagnetic map navigation, but the former study would not be considered instrumental in supporting an olfactory map and the latter offers no convincing evidence for a geomagnetic map. Given the research that is being conducted in migratory birds (see below), it is challenging to see how studying pigeon homing with sophisticated GPS tracking devices will unveil anything new about the sensory or map/representational mechanisms that support avian navigation in general. That said, there are other aspects of pigeon navigational behavior – for example, the study of the

underlying neural mechanisms – that can be much more profoundly investigated with the use of GPS tracking (see below).

Finally, it must be noted that an often-discussed challenge to the olfactory navigation hypothesis has been developed by Jorge and colleagues (2009, 2010), who argue that olfactory stimulation is necessary to ‘activate’ the navigational map but positional information would be sourced to some other sensory input, e.g. geomagnetism. In other words, olfactory-deprived pigeons fail to home from unfamiliar locations not because atmospheric odors provide positional information, but simply because the navigational system was never ‘turned on’. However, as appealing as the ‘activational hypothesis’ may be for opponents of an olfactory navigational map, it is strongly contradicted by the available evidence (Gagliardo et al., 2001, 2011; Wallraff, 2014). Indeed, in a recent paper looking at thalamic activation under different homing treatments, Jorge et al. (2017), while still claiming an activational contribution from olfaction, also identify a direct role of olfaction in determining map-based position. Given, in my opinion, the overall untenable premise of the ‘activational hypothesis’, I continue to be amazed that it is arguably now the most debated issue regarding the sensory basis of the homing pigeon navigational map (see Walcott et al., 2018; Gagliardo et al., 2018).

The growth in understanding sensory guidance of navigation in migratory and other wild birds

The study of homing pigeons has been, in part, motivated by the assumption that, as an accessible experimental model, it could reveal much about how birds, and migratory birds in particular, generally navigate. However, the often staggering distances traveled by migratory birds, routinely thousands of kilometers, and their remarkable success in relocating back to their regular breeding sites both indicate that the navigational mechanisms employed, and their underlying sensory bases, are considerably more variable and collectively more complex than what is found in homing pigeons and their navigational system, which is operational over a few hundred kilometers (Bingman and Cheng, 2005). And indeed, with advances in tracking technologies and the data that will soon be available from the visionary ICARUS (International Cooperation for Animal Research Using Space) Initiative, headed by Martin Wikelski, investigating navigational mechanisms in wild birds is no longer limited by a lack of accessibility (see Guilford et al., 2011), and the ‘convenience’ of homing pigeons as an experimental model is not as appealing as it once was.

Tracking studies have already revealed tantalizing hints at the complex mechanisms that guide migratory navigation (e.g. Thorup et al., 2007), and some have even investigated supporting sensory mechanisms (Holland et al., 2009; Wikelski et al., 2015), which, perhaps surprisingly, hint at an important role of olfaction. Such field-based studies have been complemented by recent success investigating the sensory basis of migratory navigation using captive migrants tested in orientation cages. Whereas there is little compelling evidence for a geomagnetic map in homing pigeons navigating over relatively short distances (see above), for longer-distance migrants the evidence does point to at least partial positional information being derived from the Earth’s magnetic field (Deutschlander et al., 2012; Kishkinev et al., 2015). However, given that these experiments were carried out in orientation cages, one has to wonder whether the results from captive birds would generalize to free-flying birds in the wild. For example, in nesting shearwaters navigating over distances of up to 800 km, there is little support for a geomagnetic map (see Pollonara et al., 2015; Wikelski et al., 2015). Nonetheless, the apparent contrast between homing

pigeons and long-distance migratory birds, at least those tested in orientation cages, is consistent with hypothesized constraints on the plausibility of a geomagnetic map at shorter navigational distances because of the inevitable spatial and temporal errors in positional information derived from it (see Bingman and Cheng, 2005).

The advances in tracking technology are not limited to birds during migration, but can also be applied to the study of navigational and guiding sensory mechanisms used while moving between nest sites and remote feeding/displacement locations. For example, Pollonara et al. (2015) have demonstrated a role for olfaction in Scopoli’s shearwaters (*Calonectris diomedea*), a Mediterranean seabird, navigating to nest sites, and Orchan et al. (2016) have investigated the development of navigational abilities in stone curlews (*Burhinus oediacnemus*), both facilitated by GPS tracking technology.

The claim that the navigational mechanisms used by experienced migratory birds, perhaps returning to a breeding site several thousand kilometers distant, are necessarily richer or more complex than those used by homing pigeons appears unassailable. I do realize, however, that ‘complex’ is an easy word to use without really defining it. In support of the reasoning that the navigational mechanisms of migrants are more complex, beyond the obvious factor of distance, is that migrants are more likely to experience weather conditions that will displace them from any familiar, previous route and they often need to detour around geographical barriers. In other words, and admittedly an oversimplification, once a homing pigeon takes up a homeward bearing, it is unlikely to need to change that bearing in any substantial way until arriving close to home. By contrast, a migrant being blown off course by a weather system or choosing to detour around, for example, the Gulf of Mexico, and all this happening perhaps several thousand kilometers away from the goal location, would require a continual updating and re-orientation from any one preferred migratory bearing. It should also be noted that different species and populations of migratory birds navigate under a variety of conditions, laying the foundation for comparative investigations into the factors determining which array of possible sensory and representational mechanisms are favored under different environmental conditions. Given that homing pigeon research can only partially capture the complexity and diversity associated with distance and the mechanisms guiding the continual directional adjustments migratory birds need to make, the recent experimental accessibility of studying navigational mechanisms in migrating and other wild birds conspires to diminish the value of homing pigeons as a prototype or model species.

A glass half full

Although homing pigeons may no longer be as useful as a general model for the sensory mechanisms that guide avian navigation, there are nonetheless other aspects of avian spatial behavior where homing pigeons can be of enormous experimental value. The homing pigeon brain continues to be the avian brain in which overall telencephalic organization (see Glossary) is best understood (Shanahan et al., 2013), and therefore homing pigeons are still best suited for studies investigating the underlying neural mechanisms that guide navigation and doing so in a field setting. For example, homing pigeons have been crucial in understanding the importance of the avian hippocampal formation (see Glossary; Herold et al., 2015; Bingman and MacDougall-Shackleton, 2017) and olfactory cortex (see Glossary; Patzke et al., 2010) for navigation. The avian brain is characterized by a strong degree of structural and functional lateralization (see Glossary; Manns and Ströckens, 2014), and many

avian navigational mechanisms are similarly lateralized and best understood in homing pigeons (Bingman and Gagliardo, 2006; Gagliardo et al., 2011; Jonckers et al., 2015), including the lateralization of visual guidance during homing (Martinho et al., 2015; Pollonara et al., 2017). And even though we know of the sensory mechanisms that guide avian navigation, the underlying neural control of those mechanisms is still poorly understood [but see the important findings of Zapka et al. (2009) revealing the importance of the anterior forebrain ‘Cluster N’ in supporting the geomagnetic compass of migratory birds]. Using homing pigeons, Cordula Mora and colleagues (Mora and Bingman, 2013; Mora et al., 2014) have developed an operant conditioning paradigm (see Glossary) that can be used to examine the perceptual range of magnetic field detection and may lead to an understanding of the properties and limits of geomagnetic intensity and inclination sensitivity. However, and perhaps of more importance, the same paradigm could be used to identify the network of brain regions that support the geomagnetic compass, and, should homing pigeons ever be shown to possess a geomagnetic map (but see above), the brain regions that implement a geomagnetic map too.

GPS tracking has also been recently used to identify differences in wingbeat characteristics, which were reliably associated with differences in acceleration, body amplitude and airspeed when pigeons fly a familiar route (Taylor et al., 2017). From a mechanistic perspective, wingbeat signatures (see Glossary) could also be used as a proxy for identifying when homing pigeons switch between navigational and sensory mechanisms being employed and, by inference, the neural mechanisms engaged. A similar approach has been developed by Schiffner et al. (2011), who used behavioral indicators, but not wingbeat characteristics, to mathematically model inferences of shifts in navigational mechanism(s) active during a homing flight. Although admittedly less informative, recording changes in wingbeat patterns would also be much easier to use than recording directly from the brain (Vyssotski et al., 2009) to identify when pigeons may be making changes in the navigational mechanism(s) currently controlling behavior, but only as long as any changes in wingbeat characteristics owing to non-navigational factors, e.g. shifts in wind profile, can be excluded. The important point is that such detailed behavioral-modeling approaches for understanding dynamic changes in navigational strategy or mechanism are currently only feasible in homing pigeons (but see above) because of their size, which enables the carrying of both GPS recorders and accelerometers, and their faithfulness in returning home, which allows for the recovery of data that cannot be transmitted remotely.

The tracking of homing pigeons has also proved illuminating with respect to insights into how idiosyncratic spatial behavioral profiles of individuals, ‘spatial personalities’ and social interactions impact navigation (Nagy et al., 2010; Freeman et al., 2011; Portugal et al., 2017). This line of research is of considerable relevance to the growing literature on animal personality (e.g. Sih et al., 2012). ‘Social navigation’ studied in homing pigeons would likely offer important insights into the navigational consequences of group migrations, and application of this pioneering work in homing pigeons has already been used to study group migration in white storks (*Ciconia ciconia*; Flack et al., 2018). Homing pigeons and related forms of domesticated rock doves are well suited for uncovering correlations between genetic variation and spatial behavior characteristics (Domyan and Shapiro, 2017; Gazda et al., 2018), which will be facilitated by the complete genome sequencing of individual homing pigeons and members of other breeds of pigeon. Gazing to the future, the application of CRISPR-based

genome editing and the creation of transgenic pigeons could offer a vast, new frontier for understanding the genetics of navigation and associated neural support mechanisms, as well as perhaps the engineering of a super-navigator. Although genetic experiments would likely require large numbers of birds and resources (perhaps justifying the re-establishment of new, large-scale loft facilities), homing pigeons, because of their experimental accessibility, are likely much better suited than any other candidate migratory bird model for investigating the genetics of navigation.

Concluding remarks

It may seem unusual that someone on the margins of research into the sensory mechanisms of homing pigeon navigation should suggest that the big questions appear to be answered and the usefulness of homing pigeons for generally understanding the mechanisms of long-distance navigation in birds as a group may be ending. Indeed, those still actively working with homing pigeons would likely challenge this view. However, the sobering prognosis offered here is rendered more real by the almost complete loss of the historically dominant, industrial-scale pigeon-loft facilities and, perhaps more importantly, the burgeoning of new tracking technologies making navigational experiments on long-distance migratory and other birds much more accessible.

At the same time, the impact of homing pigeon research may still profoundly influence how researchers can understand aspects of avian navigation beyond sensory mechanisms and spatial-representational strategies – for example, the gradient properties of the navigational map or the landscape/landmark properties of a familiar-area map. Research into neural mechanisms and brain organization, social/personality influences and genetics of navigation all offer opportunities to exploit the rich spatial behavior repertoire and experimental convenience of homing pigeons. Importantly, research in these areas would not necessarily require the large number of birds historically used to study the sensory guidance of navigation, although for some imaginable genetic investigations, large numbers of animals would likely be needed. For those of us who have been blessed with the opportunity to work with this remarkable animal, one research door may be closing, but other exciting opportunities beckon.

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Competing interests

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