The role and ontogeny of maps in long-distance animal navigation



Joe Morford

St Anne's College

University of Oxford

A thesis submitted for the degree of

Doctor of Philosophy

Michaelmas 2023

Abstract

Impressive feats of long-distance animal navigation raise questions relating to the proximate causes of such behaviours: what mechanisms facilitate long-distance animal navigation? What is the ontogeny of such behaviours? I focus on how animals determine their position in relation to their goals to determine goalward directions in the first step (the *map* step) of a two-step navigational process termed map and compass navigation.

I begin by introducing a framework that deconstructs animal maps into three interlinked components: (1) map cues, (2) map structure, their organisation of spatial information, and (3) map navigation strategy, the way that animals approach goals and combine multiple map cues. I discuss the ontogeny of animal maps, clarifying the roles of inherited rules, imprinting and latent learning, and suggest that mechanisms for determining vectors of self-motion, known as path integration, could facilitate map learning by allowing animals to integrate changes in map cues with self-motion.

I use two general approaches to examine animal maps. First, I employ artificial neural networks as simple computational models of animal learning. This allows me to investigate the possible ontogenies of navigational behaviours and make predictions about how animals might learn to navigate. Using this approach, I investigate how animals might learn to combine intersecting environmental gradients to navigate with a grid map. I find that neural networks adopt a mechanism of combining environmental gradient cues through first determining displacements in each gradient field independently, leading to predictable orientation errors in some environments. This work clarifies how such mechanisms might arise and change through learning, allowing me to make more nuanced predictions of how navigational mechanisms might develop through learning. Using a similar approach, I investigate how collective decision-making processes

impact upon individual learning when animals navigate in groups. I find that leaders learn more quickly than followers, and that individuals in democratic groups, in which compromises are taken between individual preferences, learn by compensating for partner error unlike individuals in despotic groups and solo learners.

My second general approach involves experiments on two model species of long-distance navigation. I attempt to investigate whether Manx shearwaters utilise olfactants as navigational map cues, while minimising impact on the birds, by manipulating their access to olfactory cues before release after long-distance displacement. However, I find no clear evidence that they utilise olfactory cues in their navigation, leaving the sensory basis of their navigational map an open question. I investigate navigational ontogeny in homing pigeons, examining whether passive exposure to a novel release site is sufficient for navigational learning. I find no evidence that passive exposure to the release site impacts upon initial navigational performance and hence no evidence that this is sufficient for learning.

Overall, this work clarifies outstanding questions on the proximate causes of animal navigation, generates predictions on navigational learning, and produces incremental steps forward in our understanding of navigational mechanism and ontogeny in two model systems. Ultimately, advancing these theoretical and empirical approaches together will enable us to better identify and understand the proximate causes of long-distance animal navigation.

Acknowledgements

This work was made possible by the funding of a studentship on the Oxford Interdisciplinary Bioscience DTP, supported by the Biotechnology and Biological Sciences Research Council (UKRI-BBSRC). Additionally, I received funding from Merton College, Oxford and St Anne's College, Oxford. I am thankful to these institutions for facilitating and supporting my research. I would also like to express my thanks to the Wildlife Trust of South and West Wales, the Skomer and Skokholm Island Advisory Committee, Natural Resources Wales, the Copeland Bird Observatory, and the Northern Ireland Environment Agency for facilitating and supporting my fieldwork on Skomer Island and Lighthouse Island, Copeland, over the last few years.

I would like to express thanks to my examiners, Alex Kacelnik and Steve Portugal, for taking the time to read this thesis and for an extremely stimulating and enjoyable, if intense, viva. It was a very positive experience and felt like a good note on which to end this degree.

My biggest thanks must go to my supervisor, Tim Guilford, who has inspired and guided my scientific ideas since 2016. I am very grateful to Tim for always humouring my latest idea on signalling or navigation and giving hours of his time to wide-ranging and enjoyable discussion. I look back on our trip to Copeland in 2020 with particular fondness, especially my introductions to the delights of both neat vodka and jelly ear mushrooms during that time together. I hope we are able to continue sharing ideas and collaborating in the future. Likewise, huge thanks should go to my co-supervisor, Ollie Padget, who gave me my first opportunity to be involved in research over two brilliant summers working on nightjars on Canford Heath. This was an extremely formative, enjoyable, and rewarding experience. I am grateful to Ollie too for many of the key ideas and insights around which I have based my research over the last four years, and for supporting me during this time.

Next, I would like to thank all of my collaborators, who have supported me in a range of ways. First, I would like to thank Anna Gagliardo for hosting me in Arnino and for all of her support in working on the homing pigeons there. I learned a great deal from Anna but also had a lot of fun. I won't soon forget getting stuck in a ditch on day one! I would also like to thank Enrica Pollonara for collaborating with that work and Lorenzo Vanni for his assistance. Both Enrica and Lorenzo were very welcoming, kind, and generous and I really enjoyed my time with them in Arnino. Second, I would like to thank Julien Collet for collaborating and sharing ideas on collective behaviour, and Dora Biro for contributing to that project. Third, I would like to thank Jay Willis for hosting me for an internship and assisting me in a wide range of technical matters. Jay has always been very generous in lending me his time, materials, and ideas, and so often provided a different, interesting perspective. Finally, I would like to thank a range of people who have collaborated with me and assisted me on a range of projects over the last four years, some of which are still awaiting completion, including Inês Nolasco, Dan Stowell, Alan Grafen, Jonathan Green, Ming Liu, Adelaide Sibeaux, Lucy Larkman, Dave Wilson, and Allex Turner.

The experimental work on Manx shearwaters was a complex undertaking, and a very large number of people contributed to making this possible. Most of all, I would like to thank Sarah Bond, who showed genuinely extraordinary generosity in enabling and collaborating on all aspects of this project and without whom this project would have been impossible. I am extremely grateful to Bond for everything, from the repeated visits to my parents' house, to allowing the complete takeover of the van, to the endless time and mental energy given to planning and executing this project. Thank you. I also owe huge thanks to those carried out much of the fieldwork for this experiment on Skomer, especially Trina Siddiqi-Davies, Lewis Fisher-Reeves, Joe Wynn and Max Buckley. I would like to thank the whole team on Skomer for their support, both in this work and personally, especially the Skomer Warden, Leighton Newman, and the rest of the Skomer team, including Ceris Aston, Beth Thompson, Kelda McChesney, Eve Sharples and

Simon Davies. Huge thanks also go to Dale Sailing and its staff who made the work possible by transporting the birds and researchers, and Gary and Chrissie at Lockley Lodge for their support. Finally, I would like to thank all those who assisted with releasing the birds, including Emma Lockley, Paddy Lewin, Milo Reynolds, Penny Hilder Jarvis and Clem Collins Rice.

Most of the work achieved and the fun had over the past years is thanks to my wonderful friends within OxNav. I would like to thank everyone involved in the group for all of their contributions to my work and life during this time. I would like to thank Joe Wynn for an endless stream of mad ideas and for exciting me and supporting me from the moment of my first arrival in the group, Paddy Lewin for being a constant sounding board for bad ideas and for not taking my cynicism to heart, Trina Siddiqi-Davies for mutual support in the final miserable weeks and introducing me to the great sitcoms of Phoebe Waller-Bridge, Paris Jaggers for baffling me with ideas from neuroscience that remind me I have no idea what 'cognitive map' really means and for friendship over many years, and Lewis Fisher-Reeves for encouragement and solidarity through abs-and-arse workouts (along with Trina) and for all of your support, especially on Skomer. I would like to thank all the others who have contributed to making OxNav a good place to be over the last years, including Jonathan Rutter, Lucinda Zawadzki, Tash Gillies, Martyna Syposz, Jessy Phillips, Annette Fayet and Chris Perrins.

I would like to thank Thomas Miller and Biliana Todorova for contributing illustrations to this thesis. Thomas surprised me with the stylishly drawn Manx shearwater on a birthday, and Bil has repeatedly delighted me with whimsical illustrations to accompany papers presented at our journal club; I include two pertinent illustrations here. Thank you both for brightening up my thesis.

I owe thanks to Common Ground, and all of the very friendly people who work there, which became my only haven of productivity towards the end (gladly shared with Trina). Additionally, I

would like to thank Paul Sinton-Hewitt, A. Wainwright, and Hugh Munro for giving me purpose when others faded at various times over these past four years.

Finally, I would like to thank and appreciate those people who have supported me personally over these years. My housemates deserve thanks for putting up with me, especially my unsolicited lectures on animal navigation (Clem may have suffered this the worst); you are great friends and have injected a lot of fun into my life over many years (when Thomas isn't being a miserable so-and-so and Seb is in the house for once). I am grateful for the many friends made and times spent in Merton College Choir over six hectic years and countless trips to The Half Moon. Thank you to Victor Ajuwon for being a great mentor, inspiration, and friend over many years, based on a mutual love for talking about animal behaviour over beer. Many other dear friends have supported me personally over these years, among them Dan Brooks, Alice HJ, and Milo Reynolds. Most importantly, I would like to thank my family for all of their love and support over many years, especially Granny and Grandma, and my brother, Louis, who has always been sufficiently sharp and quick-witted both to correct my writing, in the absence of any background info, and more importantly to make me smile. Thank you to Mum and Dad for all of your love and immeasurable support over the years. Thank you for helping me build ridiculous contraptions in the garage, for ferrying me here and there, for letting me steal (and break!) the car, for walks up the hill together, and for everything else you do to help me succeed and be happy.

Declaration

The work described in this thesis was carried out at the University of Oxford between October 2019 and October 2023 under the supervision of Professor Tim Guilford and Dr Oliver Padget. All work was performed primarily by the author, with the contributions of co-authors acknowledged at the front of each chapter. No part of this thesis has previously been submitted for any other degree.

X

Contents

Thesis Introduction 1
General Introduction 2
Figure 1.1. The navigation of Manx shearwaters. 3
Map and compass navigation: the mechanism and ontogeny of animal maps 9
Figure 1.2. Map and compass navigation. 12
Figure 1.3. Map terminology and structure. 18
Figure 1.4. Cue distribution and map structure. 20
Figure 1.5. Map learning and path integration. 31
Almost there: learning to navigate approximately with a grid map 35
Figure 2.1. Navigating by vector addition, as in Benhamou, 2003, in orthogonal and non-orthogonal grids. 40
Table 1.1. The gradient fields of the simulated environments. 46
Figure 2.2. The simulated environments. 47
Figure 2.3. Model predictions in simpler environments. 50
Figure 2.4. Model predictions in a non-linear, non-orthogonal environment. 51
Figure 2.4. Model predictions in a non-linear, orthogonal environment. 52
Figure 2.5. Neural network learning curves. 56
Figure 2.6. Model fit in B1 environment. 57
Figure 2.7. Model fit in B2 environments. 58
Figure 2.8. Neural network error and the approximate model predictions in B2 environments. 60
Figure 2.9. Model fit in B3 environments. 62
Figure 2.10. Model fit in B4 environments. 64
Do olfactory cues underlie the map of a wild navigational model, the Manx shearwater, *Puffinus puffinus*? 71
Figure 3.1. Fresh air exposure treatment. 79
Figure 3.2. GPS tracks after release at Ogmore-by-Sea in 2021 and 2022. 82
Figure 3.3. Virtual vanishing time at 5km. 84
Figure 3.4. Mean Vector Lengths of Successive Orientations in first 2km. 85
Homing pigeon, *Columba livia*, navigational ontogeny: no evidence that exposure to a novel release site is sufficient for learning 93
Table 4.1. Experimental design and sample sizes. 100
Figure 4.1. Directional distributions of initial orientations. 105
Figure 4.5. Initial efficiencies. 109
Neural networks reveal emergent properties of collective learning in democratic but not despotic groups 115
Figure 5.1. Model outline. 122
Figure 5.2. Overall performance of solo and paired learners. 127
Figure 5.3. Democratic decision making: performance and contribution of each individual member. 129
Figure 5.4. Despotic decision making: performance and contribution of each individual member. 131
General Discussion 139
References 149

Chapter 1

Thesis Introduction

General Introduction

Joe Morford, Patrick Lewin, Tim Guilford

Author contributions

Joe Morford: Conceptualisation, Writing – Original Draft, Writing – Review and Editing, Visualisation. **Patrick Lewin**: Visualisation. **Tim Guilford**: Writing – Review and Editing.

How animals are guided on long-distance journeys, sometimes across seemingly featureless desert or ocean landscapes has long fascinated students of animal behaviour. How does a Manx shearwater (*Puffinus puffinus*; Fig. 1.1), only hatched a matter of weeks earlier on a small island off Belfast, find its way over thousands of kilometres and across the equator to its wintering site off the coast of Argentina? After a number of years at sea, this bird will find its way back to the same rock in the ocean, less than 25 acres in area, to breed likely metres away from its natal burrow (Brooke, 2013; Harris, 1966; Perrins et al., 1973; Wynn et al., 2022a). Breeding involves yet another navigational challenge for this bird: it must now forage, in coordination with its breeding partner, over hundreds of kilometres with sufficient efficiency to keep an egg warm and a chick well fed (Brooke, 2013). The Manx shearwater is by no means a remarkable outlier in terms of its navigation abilities, but one of a great number of examples of impressive long-distance navigators found across a variety of animal taxa from moths to salmon to turtles (e.g. (Egevang et al., 2010; Hansen et al., 1993; Lohmann et al., 1999; Warrant et al., 2016)).

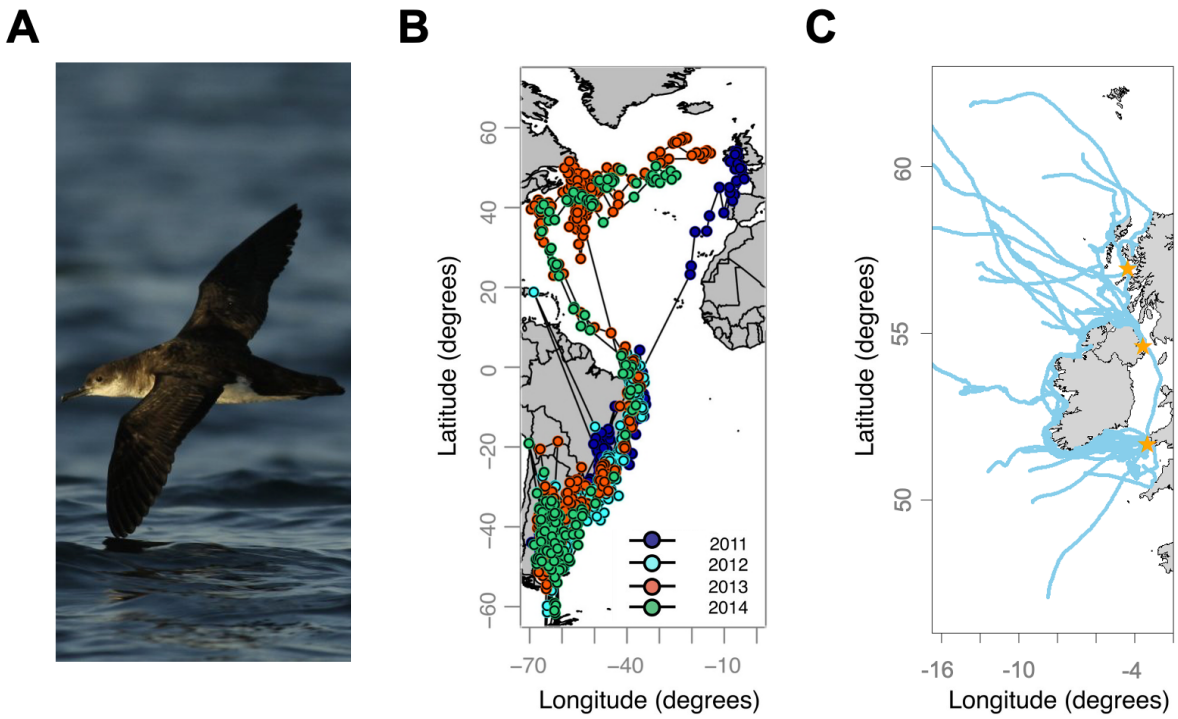


Figure 1.1. The navigation of Manx shearwaters. *(A) A Manx shearwater flying over the sea; photo taken by Joe Wynn. (B) Adapted from Wynn et al, 2022: geolocator positions for a Manx shearwater on its first outbound and return migration. (C) Selected GPS tracks of Manx shearwater homing trajectories to island colonies (orange stars) during the breeding season.*

Such examples of impressive long-distance movements in animals raise questions as to the *proximate* causes of long-distance navigation in animals (Mayr, 1961). These include questions relating to two of the four major problems for the field of ethology introduced by Tinbergen (Tinbergen, 1963). The first set of questions relate to *mechanism*: how is a Manx shearwater guided on its first migration? What mechanisms allow it to perform natal philopatry? How does it achieve such efficiency in its central place foraging? The second set of questions relate to the *ontogeny* of navigational behaviours: how does the *behaviour machinery* (Tinbergen, 1963) of long-distance navigation change during development? What ontogenetic mechanisms facilitate the development of impressive long-distance navigation abilities?

Various classes of mechanisms have been proposed and shown to play a role in guiding long-distance animal movements. These include mechanisms that facilitate movement that is directed but not towards a particular goal. Such mechanisms are sometimes not considered to represent *navigation*, but instead *orientation* (Able, 2001), and involve orienting with respect to topographic or other environmental features, such as coastlines or wind direction (Able, 2001), or using compasses, such as the azimuth angle of the sun, (Guilford and Taylor, 2014; Kramer, 1950; Kramer, 1953; Schmidt-Koenig, 1958; Schmidt-Koenig, 1990), the centre of rotation of the stars (Emlen, 1967a, b), or the inclination angle (Merkel and Wiltschko, 1965; Wiltschko and Wiltschko, 1972) or polarity (Marhold et al., 1997) of the geomagnetic field. Other mechanisms appear directed towards a particular region but do not involve mechanisms facilitating any course correction. Examples include the mechanism by which some birds execute first migration by following a certain compass orientation for a set duration of time, termed *vector navigation* (Berthold, 1996; Perdeck, 1958; Schmidt-Koenig, 1970). These contrast mechanisms that facilitate movement towards a defined goal. Animals may beacon towards their goal when in direct sensory contact with goal-emanating cues (Collett, 1987). Additionally, route-based mechanisms (Baker, 1984) such as following learned sequences of landmarks (Guilford and Biro, 2014) can guide animals towards goals. Information gathered on outward journeys from a 'home' goal can allow animals to navigate to goals through route reversal (Schmidt-Koenig, 1975) or mechanisms of determining vectors of self-motion, termed path integration (Mittelstaedt and Mittelstaedt, 1980). Finally, animals have been proposed to use a two-step navigational mechanism, termed map and compass navigation to approach goals (Kramer, 1953). The map step comprises the animal determining its position in relation to a goal or goals. In a range of taxa, this has been shown to involve visual (Gagliardo et al., 1999; Gagliardo et al., 2001b; Harten et al., 2020; Luschi and Dall'Antonia, 1993; Toledo et al., 2020; Tsoar et al., 2011), olfactory (Bonadonna and Gagliardo, 2021; Gagliardo, 2013; Papi et al., 1971, 1972; Wallraff, 1970; Wallraff, 2004) or magnetic cues (Boles and Lohmann, 2003; Chernetsov et al., 2008; Lohmann and Lohmann, 1994; Lohmann et al., 2001; Lohmann and Lohmann, 1996; Putman et al., 2014c).

Second, the compass step comprises the animal determining the relationship between its egocentric heading and the direction of a goal to orient in a goalward direction, using the compass cues introduced above.

The various mechanisms of long-distance animal navigation develop in animals in a range of ways. Some components of long-distance navigational behaviours involve following innate behavioural programmes, such as the vector navigation of some passerine birds on first migration, during which they orient in a set compass direction for a certain number of days. The ontogeny of long-distance navigation can also involve imprinting upon cues at the natal site (Brothers and Lohmann, 2015; Brothers and Lohmann, 2018; Wynn et al., 2022c; Wynn et al., 2020), and other relatively constrained learning programmes in early development, such as learning to orient using the centre of rotation of the night's sky (Emlen, 1967a, b) or latently associating olfactory map cues with wind direction (Gagliardo et al., 2001a; Odetti et al., 2003). Learning may also facilitate navigational ontogeny throughout development in a less constrained way, for instance in homing pigeons learning routes back to their home loft. Social learning can facilitate the development of long-distance navigational behaviours, such as migratory routes in certain avian taxa (Abrahms et al., 2021; Byholm et al., 2022; Mueller et al., 2013). Additionally, learning within groups can influence the development of navigational behaviours in various other ways, with dynamics of collective decision making impacting navigational learning (Burt de Perera and Guilford, 1999) through various mechanisms (Collet et al., 2023) such as influencing individual attention to salient navigational cues (Kano et al., 2021).

In this thesis, I focus on animal maps, which are introduced in detail in the second part of the thesis introduction: "Map and Compass Navigation: The Mechanism and Ontogeny of Animal Maps". In this section, I set out to clarify the links between findings on animal maps across different taxa and spatial scales and to highlight outstanding questions relating to the

mechanisms and ontogenies of animal maps. Subsequently, I use two general approaches to examine the mechanisms and ontogeny of animal maps, one theoretical and one experimental.

First, I use artificial neural networks as simple computational models of animal learning by training them to perform tasks based on animal navigation. Artificial neural networks have been shown to be capable of replicating various empirical features of animal learning (Ghirlanda and Enquist, 2007; Gluck, 1991; McClelland and Rumelhart, 1985; Peng and Chittka, 2017; Wisniewski et al., 2012). However, it is difficult to assess how analogous the training of artificial neural networks in this way is to navigational learning in animals, and so caution must be applied to any findings to ensure that they reflect modelled biology as opposed to the specifics of network implementation (Dawson, 2008; Franks and Ruxton, 2010). This method allows me to investigate the possible ontogenies of navigational behaviours in animals and make predictions for how animals might learn to navigate. Using this approach, I examine grid map navigation in Chapter 2, "Almost there: learning to navigate approximately with a grid map", and navigational learning in groups in Chapter 5, "Neural networks reveal emergent properties of collective learning in democratic but not despotic groups".

Second, I present results from displacement experiments in two model species of animal navigation, Manx shearwaters (*Puffinus puffinus*) and homing pigeons (*Columba livia*). These two model species have contrasting life-histories and ecologies but have both become avian models for navigation over long distances. Homing pigeons have been studied more extensively and are arguably easier to use as an experimental model, especially to study the ontogeny of navigation, as shearwaters spend years at sea after fledging, difficult to observe and study. Nonetheless, Manx shearwaters represent an interesting and important model species with which to examine navigation in a wild system, over longer distances, and across relatively featureless marine environments. These procellariform seabirds breed on islands in the north Atlantic, raising a single offspring each year in nesting burrows within densely populated colonies. The breeding season

involves regular travel over tens or hundreds of kilometres, both during incubation, during which the male and female of a breeding pair alternate multi-day stints of incubation and offshore foraging, and chick-rearing, involving at-sea foraging during the day and provisioning trips at night (Brooke, 2013). Outside of the breeding season, Manx shearwaters migrate across the equator to the south Atlantic, wintering off the east coast of South America, thousands of kilometres from their breeding colonies (Guilford et al., 2009). After their first migration, immature shearwaters often do not return to their breeding colonies until three or more years after fledging, but upon returning, exhibit high levels of philopatry (especially males) to their natal site (Brooke, 2013; Harris, 1966; Perrins et al., 1973; Wynn et al., 2022a). In general, the ecology of these birds involves navigational challenges at a range of spatial scales, from finding their breeding burrow in the dark of the night in dense colonies, to returning over thousands of kilometres to their natal subcolony to breed after years away. The remarkable long-distance navigational abilities of these birds have been recognised and experimentally investigated since the middle of the last century (Lack and Lockley, 1938; Lockley, 1942; Matthews, 1953b). More recently, they have become an emerging model species for the study of the mechanisms facilitating long-distance animal navigation in wild systems (Padget et al., 2018; Padget et al., 2019; Wynn et al., 2020). Here, in Chapter 3, "Do olfactory cues underlie the map of a wild navigational model, the Manx shearwater, *Puffinus puffinus*?", I extend this work, examining the navigational map of Manx shearwaters; I investigate whether olfactory cues might underlie their navigational map, using an innovative approach to minimise impact on the birds by manipulating their access to olfactory cues before release, but otherwise with their olfactory system intact.

In stark contrast to Manx shearwaters, homing pigeons are a domesticated variety of the rock dove that have traditionally been used to carry messages and raced for sport, but have additionally been studied as a navigational model for several decades (Wallraff, 2005a; Wiltschko and Wiltschko, 2017b). These birds are bred, and trained, to return to their home loft when released following displacement, and it is this behaviour which has formed the basis for the

convenient study of navigation in this model species. Initially, the vanishing bearings (the direction from the release site in which they disappeared from view) and the homing durations of pigeons could be used to determine the effect of various experimental manipulations upon their navigational mechanism and ontogeny (Wallraff, 2005a). More recently, this method has been revolutionised by technological advances, most importantly facilitating the GPS tracking of the homing trajectories of birds, but additionally enabling collection of a range of data during homing navigation, from head direction (Kano et al., 2018) to electrical brain activity (Vyssotski et al., 2009). Further, the propensity of homing pigeons to flock has facilitated the study of collective behaviour using similar methodologies, enabling study in a range of areas, from navigational decision-making in groups (Biro et al., 2006), to predator avoidance (Sankey et al., 2021), to cultural inheritance of homing routes (Sasaki and Biro, 2017). Here, I use homing pigeons as a navigational model to investigate the ontogentic mechanisms that facilitate the development of their navigational map; this is reported in Chapter 4, "Homing pigeon, *Columba livia*, navigational ontogeny: no evidence that exposure to a novel release site is sufficient for navigational learning".

Map and compass navigation: the mechanism and ontogeny of animal maps

Joe Morford, Joe Wynn, Patrick Lewin, Paris Jaggers, Lewis Fisher-Reeves, Adelaide Sibeaux, Oliver Padget, Tim Guilford

Author contributions

Joe Morford: Conceptualisation, Investigation, Writing – Original Draft, Writing – Review and Editing, Visualisation. **Joe Wynn**: Writing – Review and Editing. **Patrick Lewin**: Writing –Writing – Review and Editing. **Adelaide Sibeaux**: Writing – Review and Editing. **Oliver Padget**: Supervision. **Tim Guilford**: Writing – Review and Editing, Supervision.

Abstract

Map and compass navigation, a two-step navigational process in which animals use a map to determine the direction of goals and a compass to orient in goalward directions, appears to account for a wide variety of navigational behaviours across animals. These range from visual landmark navigation in highly familiar environments, to returning long distances from novel far-off sites (true navigation) and compensating for displacements from migratory trajectories (migratory true navigation). However, while extensive investigation of the sensory basis of maps in various taxa has implicated roles for visual, olfactory, and magnetic cues, many of the details of their mechanism and ontogeny are less well understood. Here, we introduce a framework that deconstructs the mechanisms with which animals use maps into three key interlinked components: (1) *cues*, the nature of the environmental properties that animals use to determine

goalward directions; (2) *structure*, the organisation of information used to determine the goalward direction, distinguishing discrete and continuous map structures; (3) *strategy*, how animals use maps to approach their goals and combine multiple map cues. We then consider the ontogeny of these three components of animal maps, and clarify the roles of inherited rules, imprinting and latent learning, drawing upon selected examples. We suggest that some examples of map and compass navigation, including those which require extrapolation of gradients or involve flexible navigation between multiple goals, are likely to require extensive learning. However, the mechanisms by which animals resolve the spatial arrangement of cues to learn maps, especially over large scales, are little understood. We discuss the role of mechanisms for determining vectors of self-motion, known as path integration, in the learning of maps over relatively small spatial scales in mammals and consider whether path integration could play a similar role in map learning in other taxa and over larger spatial scales, by allowing animals to integrate changes in map cues with vectors of self-motion. This would imply that path integration is more taxonomically widespread and plays a greater role in navigational learning than currently appreciated. This review helps to clarify links between disparate findings and raises questions about navigational mechanisms and ontogeny that, in conjunction with the increasing availability of large tracking datasets of animal movements, should help to better our understanding of map and compass navigation across taxa and spatial scales.

Introduction

In the 1950s, Kramer introduced the idea that homing navigation involves a two-step mechanism, termed 'map and compass' navigation (Kramer, 1953). First, the map step involves determining an animal's position in relation to 'home', other goals, or other known parts of the environment. Most simply, this could comprise determining the direction of a goal, but might involve determining both the direction and distance to a goal or goals. Second, the compass step involves determining how to orient in the direction of the goal by determining the relationship between the direction of the goal and the animal's egocentric heading. This conceptual framework for examining animal navigation is still central to research today (Gagliardo, 2013; Holland, 2014; Lohmann et al., 2022; Wiltschko and Wiltschko, 2003). Evidence supporting a two-step navigational process has accumulated through experiments that have independently manipulated the perception of map cues and compass cues of animals (Baldaccini et al., 1975; Benvenuti and Wallraff, 1985; Chernetsov et al., 2017; Dall'Antonia et al., 1999; Ioalè et al., 1978; Kishkinev et al., 2021; Papi et al., 1974; Schmidt-Koenig, 1990; Wiltschko and Wiltschko, 1995), demonstrating that navigation, in these instances, involves a two-part mechanism: a map and compass (Fig. 1.2).

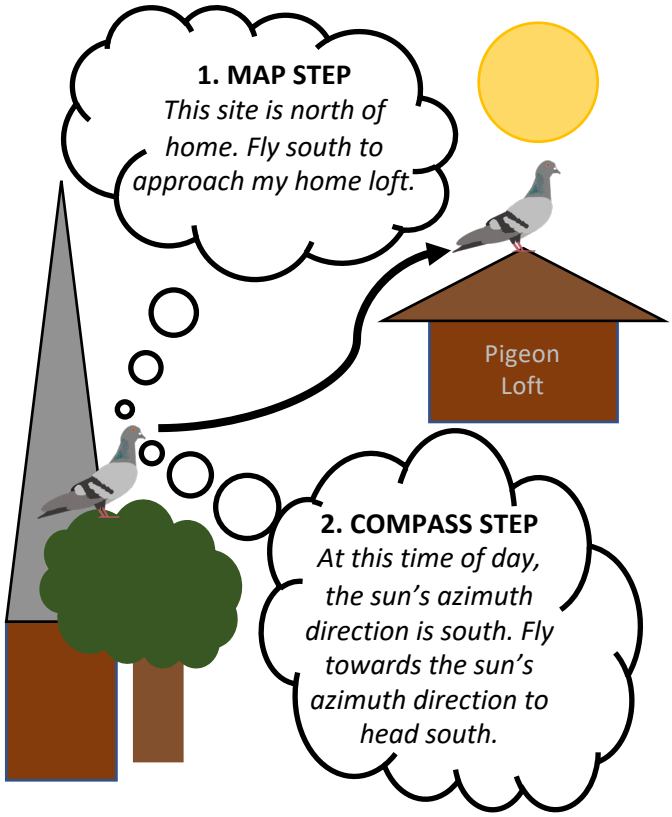


Figure 1.2. Map and compass navigation. *A homing pigeon is shown using a two-step process to navigate to its home loft. The map step allows the pigeon to determine the compass direction of the goal, and the compass step allows it to move in that direction by relating the goalward compass direction to its heading.*

Here, we focus on the mechanism and ontogeny of the map step of map and compass navigation. Tinbergen identified mechanism ('causation') and 'ontogeny' as two of the four major problems to be addressed by the research field of ethology, along with 'survival value' (adaptive value), and 'evolution' (Tinbergen, 1963). Lots of research on navigational maps in animals has focussed upon the sensory basis of maps, while many of the details of their mechanism and ontogeny are less well understood (Wynn and Liedvogel, 2023). We introduce a framework on the mechanisms with which animals use maps in map and compass navigation with the aims of, first, clarifying the links between ideas and findings on animal maps across taxa and spatial scales, and second, generating questions on the less well studied and understood aspects of animal maps. This framework deconstructs animal maps into three interlinked components: (1) map cues, the

environmental properties that are the basis of an animal's map; (2) map structure, the organisation of information used to determine the goalward direction; (3) map navigation strategy, the way in which animals use maps to determine a goalward direction, including how goals are approached and how multiple map cues are combined.

We then consider the ontogeny of animal maps, in particular in relation to the three components set out in our framework. Tinbergen gave particular emphasis to ontogeny and defined it as the "change of behaviour machinery during development". He argued that addressing simple questions about how behaviour changes during development and what underlies these changes is the key to understanding this major problem for the field of ethology (Tinbergen, 1963). We address how map and compass navigation changes through development and discuss the roles of inherited rules and predispositions, imprinting and latent learning. Finally, we discuss mechanisms of map learning and consider the role of mechanisms for determining vectors of self-motion, termed path integration, in map learning across taxa and spatial scales.

Map mechanisms framework

a) Cues

Map cues comprise any environmental properties that an animal can perceive and use to determine goalward directions. In order to be useful for determining goalward direction, any such environmental properties must be sufficiently temporally stable and vary sufficiently perceptibly and predictably in space. Extensive research on animal maps has focussed upon the sensory basis of animal maps and, in particular, on map cues perceived through three sensory modalities: magnetic, visual, and olfactory cues. Within each of these modalities, a range of cues are potentially available with various underlying spatial distributions. Several cues derived from the geomagnetic field have been implicated in providing animals with maps; these are magnetic inclination (Lohmann and Lohmann, 1994), magnetic intensity (Lohmann and Lohmann, 1996) and magnetic declination (Chernetsov et al., 2017; Kishkinev et al., 2021). Second, a large variety of visual cue types could provide animals with map information from landmark features (Collett et al., 1986) and their geometric relationships (Benhamou and Poucet, 1998; Cheng, 1986, 2005; Greene and Cook, 1997) to landscape features such as arrays of distant landmarks (Harten et al., 2020; Toledo et al., 2020), and prominent overflown features (Biro et al., 2007; Kano et al., 2018; Lau et al., 2006; Vyssotski et al., 2009). Third, there are a range of olfactants that animals might use to navigate with an olfactory map. However, while there is a large body of literature demonstrating the role of olfactory cues as a navigational map in homing pigeons, *Columba livia* (for reviews, see (Gagliardo, 2013; Wallraff, 2004)), and other birds (Benvenuti et al., 1993; Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015), the identities and distributions of these olfactants have proved difficult to unravel. The only exceptions are experiments in which animals have learned to navigate using introduced artificial odours in homing pigeons (Papi et al., 1974) and laboratory mice, *Mus musculus* (Fischler-Ruiz et al.,

2021). Some research has investigated the large-scale spatial distributions of putative olfactory map cues, indicating that, in certain regions, the ratios of olfactants or the concentrations of individual olfactants appear to be sufficiently temporally stable and spatially variable to be utilised as a map cue by animals (Wallraff, 2000; Wallraff, 2013; Wallraff and Andreae, 2000; Zannoni et al., 2020). Linking experiments on olfactory navigation in animals to olfactant distributions remains the final step in unravelling the map cues that are the basis of navigation with an olfactory map. Finally, aside from the three aforementioned groups of map cues, various other sources of map cues have been suggested, including the sun arc (Matthews, 1953a; Matthews, 1951), the Coriolis force (Yeagley, 1947, 1951), infrasound (Hagstrum, 2000; Patrick et al., 2021) and gravity vectors (Blaser et al., 2014; Dornfeldt, 1991). However, there is currently relatively limited or no evidence demonstrating that these cues act as the basis of navigational maps in animals.

b) Structure

Map structure is the organisation of information used to determine the directions of goals. We distinguish between maps with discrete and continuous structures, as shown in Fig. 1.3. Maps with discrete structures, in which different places or regions are recognised and function distinctly in providing animals with directions to goals, have been invoked using a large number of different terms, sometimes with reference to maps based on cues in a particular sensory modality. These include mosaic maps (Papi et al., 1972; Wallraff, 1974), topographic maps (Wallraff, 1988), familiar area maps (Baker, 1978), cognitive maps (O'Keefe and Nadel, 1978; Tolman, 1948), sketch maps (Jacobs and Schenk, 2003), magnetic signposts (Collett and Collett, 2011), and site-specific compass orientation (Gagliardo et al., 1999; Gagliardo et al., 2001b; Luschi and Dall'Antonia, 1993). While these all comprise maps with discrete structures, they can nonetheless differ in the density and integration of their organisation of spatial information. At one end of the spectrum, discrete maps can be structured such that they provide animals with

only the directions to single goals from each distinctly recognised place. This could facilitate moving along the next step of a migratory trajectory (e.g. in juvenile loggerhead turtles, *Caretta caretta*, utilising magnetic signposts (Collett and Collett, 2011; Lohmann et al., 2001), or return to a single goal, for example the home loft of homing pigeons or the breeding island of pelagic seabirds engaged in central place foraging. At the other end of the spectrum, a map with discrete structure might be fully integrated, encoding all of the spatial relationships between each of the recognised places in the map. This would potentially facilitate novel shortcutting between different places and is the most common conception of mammalian cognitive maps (O'Keefe and Nadel, 1978). Generally, maps with discrete structures can differ in the density and integration of their organisation of directional information, but all involve distinct recognition and orientation in response to different places or regions in space.

By contrast, maps with continuous structures allow animals to exploit predictable spatial patterns in environmental cues to obtain continuous map information. This allows them to determine their direction to goals flexibly through space, rather than recognising discrete regions. There is the potential for magnetic and olfactory cues, amongst other cues, where they are distributed along spatial gradients in the environment, to be utilised by animals as maps with continuous structure, termed grid maps, gradient maps or bearing maps (Gould, 1982; Jacobs and Schenk, 2003; Papi, 1990; Putman et al., 2011; Wallraff, 1974; Wallraff, 2004; Yeagley and Whitmore, 1947). Predictable variation in the spatial arrangement of familiar visual landmarks could also provide animals with continuous spatial information. For instance, taking back-bearings from two or more visual landmarks of known position can reveal a navigator's location at their point of intersection and hence facilitate determination of goalward directions at novel locations. This is termed resection by intersection (Johnson, 1970; Mooers, 1972), and similar mechanisms include utilising triangular geometry between a novel site and two known sites (triangulation/self-triangulation (Baker, 1984; Johnson, 1970)) and utilising the distances to known sites to determine position (trilateration/multilateration). The involvement of these mechanisms in map

and compass navigation has been suggested to explain the partial effect of experimental manipulations on time-compensated sun compass use in birds (Padget et al., 2018). Egyptian fruit bats, *Rousettus aegyptiacus*, appear to use the spatial arrangement of familiar visual landmarks to navigate from novel sites; this has been described as self-triangulation and as cognitive map navigation (Harten et al., 2020; Toledo et al., 2020; Tsoar et al., 2011). However, the term cognitive map has been mainly used elsewhere to describe maps with a fully integrated discrete structure rather than maps with continuous structure facilitating goalward navigation from novel sites through triangulation or other similar mechanisms. Exploiting predictable variation in the spatial distributions of cues could potentially facilitate 'true navigation', the ability to navigate to a goal after displacement to novel far-off sites without direct sensory contact with the goal, and 'migratory true navigation', the ability to correct or compensate for displacements from a migratory trajectory (see (Holland, 2014) for review). How the predictable variation in the spatial distribution of cues is organised in an animal's map will impact upon the accuracy and efficiency of the animal's navigation. Environmental gradients are often noisy and do not necessarily vary in simple linear and orthogonal patterns (Bostrom et al., 2012; Wallraff and Andreae, 2000; Wynn et al., 2022b; Zannoni et al., 2020; Åkesson and Alerstam, 1998). It is therefore possible that animals might approximate spatial gradients, potentially as varying linearly and/or orthogonally in space, as illustrated in Fig. 1.4. This might generate predictable patterns in orientation error in animal movements which could allow us to assess the way in which animal maps are structured, as has been set out in modelling work by Turner and colleagues (Turner et al., 2016).

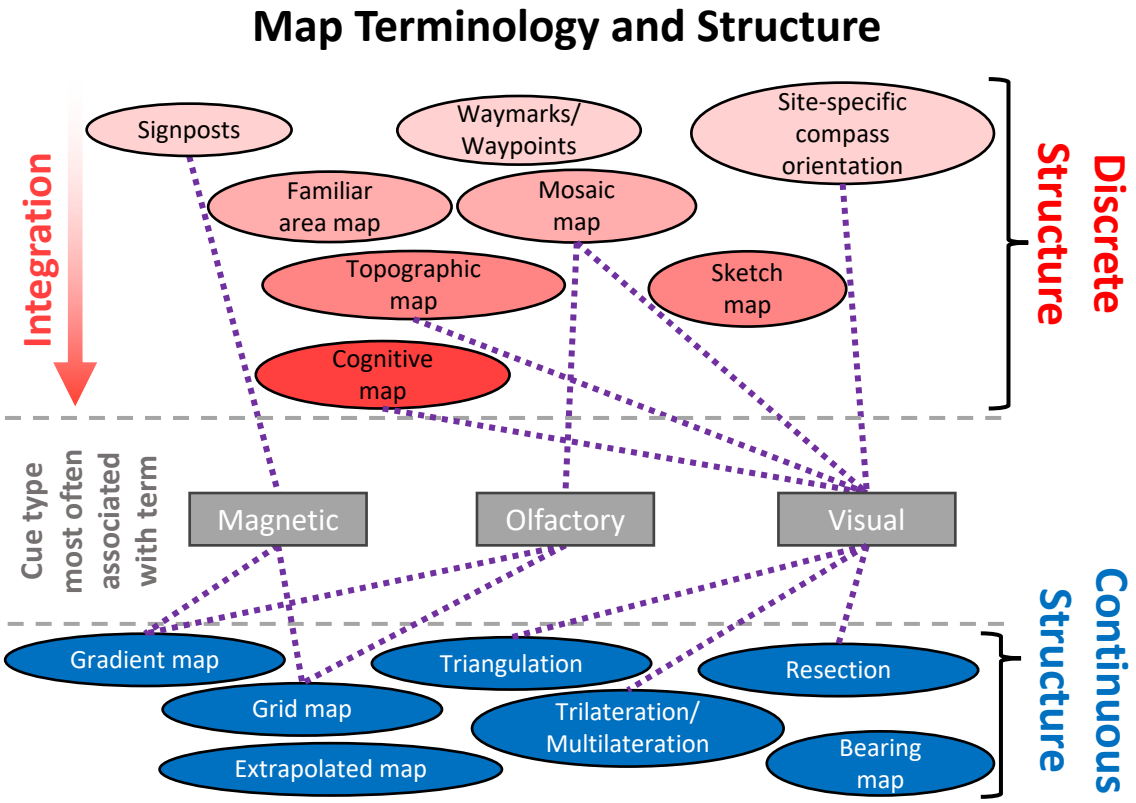


Figure 1.3. Map terminology and structure. We have grouped the different terms for animal maps into those that describe maps with discrete structure (red, top section) and with continuous structure (blue, bottom section). Terms used to describe maps with a discrete structure are placed according to their integration of directional information in the described maps: e.g. the term 'cognitive map' typically describes fully integrated maps encoding all of the spatial relationships between recognised places, whereas the term 'signpost' describes a map encoding single goalward directions from each site. Various terms have predominantly been used in reference to map cues in a particular sensory modality; in these cases, we have connected terms with dotted lines to the cue type or types with which they are most often associated in the literature.

The structure of information used by animals to determine a goalward direction is somewhat limited by the underlying spatial distribution of map cues. For instance, if it smells of olive oil north of the goal and turpentine south of the goal, without any further variation in the distribution of these olfactants, the organisation of information that the animal could use in its navigational map

is limited to comprising a simple discrete structure by this underlying olfactant distribution. However, the structure of an animal's map is not determined by the underlying spatial distribution of map cues but also depends on the way in which the animal perceives and orients in response to the cue. Even if a cue is distributed along gradients in space, an animal might perceive and/or orient in response to discrete ranges of the cue's value. This animal could be said to have a map with a discrete structure; this is illustrated in Fig. 1.4. In some regions magnetic inclination varies with latitude (Bostrom et al., 2012; Wynn et al., 2022b; Åkesson and Alerstam, 1998), and, for instance, forms a relatively predictable and stable gradient over the migratory trajectory of loggerhead sea turtles circumnavigating the North Atlantic gyre (Lohmann et al., 2001). Nonetheless, if these hatchling turtles only recognise and respond to the magnetic coordinates of specific, distinct regions of the migratory trajectory, the structure of their map does not constitute a continuous gradient or grid, but a discrete structure, of a limited set of regions or coordinates (Collett and Collett, 2011; Lohmann et al., 2001; Putman et al., 2014c). Similarly, if an animal perceives distinct patches of olfactants in different regions, and uses these to orient towards goals, we can consider the structure of this olfactory map to have a discrete rather than continuous structure, even if the olfactants are distributed along gradients in space (Gagliardo, 2013). It therefore remains currently unclear whether the olfactory maps of homing pigeons and some seabirds are organised with a discrete or continuous structure, despite air sampling studies examining the spatial distributions of olfactants through space (Wallraff, 2000; Wallraff, 2013; Wallraff and Andreae, 2000; Zannoni et al., 2020). Correlative analysis of the homing tracks of Manx shearwaters have showed that they orient on the goalward beeline direction despite intervening obstacles, and that departure time from distant sites is predicted by the goalward beeline distance; these results appear consistent with a map with continuous structure encoding the direction and distance to their breeding colony (Padget et al., 2019). Further experimental and correlative studies that utilise high-resolution animal tracking data and aim to determine how animals organise spatial information are required to better understand the structure of animal maps.

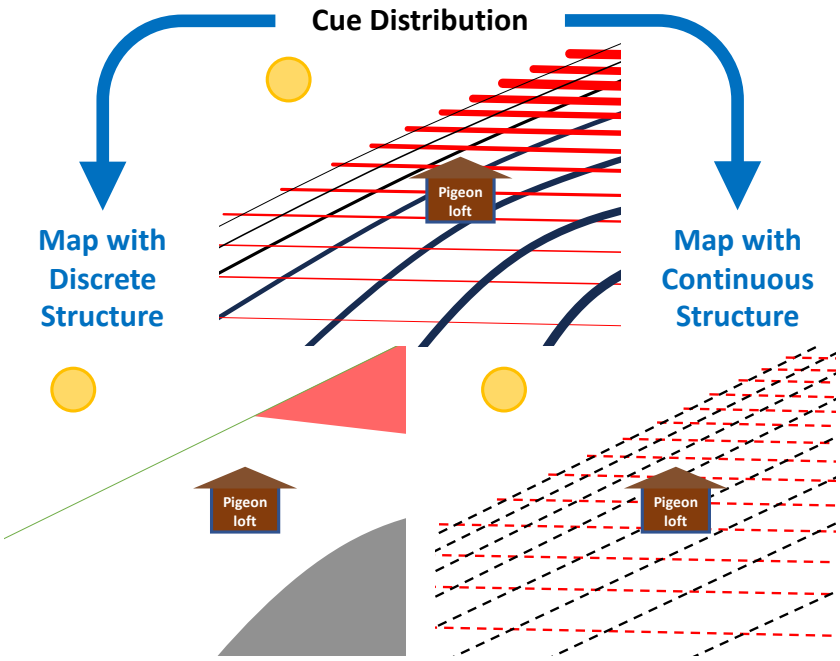


Figure 1.4. Cue distribution and map structure. *An environment with two cues distributed along gradients in the environment (red and black solid lines) is shown in the top panel. The bottom panels show two ways in which a map of this environment could be structured. On the left, a representation of a map with a discrete structure is shown, comprising two regions, one with high values of the red cue and one with high values of the black cue, that can be recognised and function distinctly in providing animals with a goalward direction to the home loft. On the right, a representation of a map with a continuous structure is shown, with a linear approximation of the two gradient fields facilitating approximate goalward orientation towards the pigeon loft continuously through the environment.*

c) Map navigation strategy

There are various navigation strategies that animals could employ to navigate goalward with a navigational map. These encompass strategies relating to both how animals approach their goals and how animals combine multiple map cues to determine goalward directions. For instance,

animals with discrete map structures might approach their goal by navigating along a sequence of waypoints/waymarks, orienting at each waypoint towards the next (Lohmann et al., 2022). This is consistent with the orientation responses of hatchling loggerhead turtles in response to recognised regions on their migratory trajectory (Lohmann et al., 2001). Additionally, this could be one of the mechanisms involved in homing pigeon navigation along familiar, stereotyped, and sometimes relatively inefficient routes (Biro et al., 2004; Meade et al., 2005), in which map and compass navigation between waypoints on a route may be combined with other route-following mechanisms to provide navigational guidance (Biro et al., 2007). Alternatively, animals could orient directly towards their goal using their navigational map; in some circumstances, this might represent a more efficient navigation strategy. In other cases, for instance if intervening obstacles are present, this might represent a less efficient navigational strategy; nonetheless, this strategy appears to be employed by Manx shearwaters in their homing flights from far-off sites despite the presence of intervening obstacles (Padget et al., 2019).

Animals might also exploit a range of strategies for combining multiple map cues to orient in goalward directions. Various examples of map and compass navigation have been shown to involve multiple map cues: visual and olfactory map cues in homing pigeon and Scopoli's shearwater (*Calonectris diomedea*) navigation (Gagliardo et al., 2001b; Padget et al., 2017; Pollonara et al., 2015); magnetic inclination and intensity in migratory navigation of hatchling turtles (Lohmann and Lohmann, 1994; Lohmann and Lohmann, 1996; Putman et al., 2011); multiple components of the magnetic field in reed warbler (*Acrocephalus scirpaceus*) migratory navigation (Kishkinev et al., 2021). When multiple different map cues are utilised by animals simultaneously, we can ask how animals combine these cues to determine goalward directions. Does one source of map information take precedence over others? Are multiple cues used together to disambiguate location? How do animals behave if different map cues conflict? Experiments putting featural landmark and geometric information into conflict in rats have revealed that they will learn both sources of map information but that geometric information

takes precedence over featural information when the two are put into conflict (Batty et al., 2009; Benhamou and Poucet, 1998; Wall et al., 2004). Over larger spatial scales, in one study, reed warblers appeared to ignore changes in magnetic map cues if the cues were presented in unrealistic combinations (Kishkinev et al., 2021). These studies reveal how the combination of map cues can be important in determining the orientation responses of animals.

Various strategies for navigating using cues distributed along spatial gradients have been proposed. For instance, it has been suggested that animals might travel along map isolines or coastlines to find a goal located at a known value of a single gradient cue (Lohmann et al., 2022; Lohmann and Lohmann, 2006). Similarly, on return migration, Eurasian reed warblers appear to orient in a particular compass direction until they intercept a known value of magnetic inclination (Wynn et al., 2022c). Additionally, to navigate with multiple gradients, a simple putative strategy of approaching the goal in each gradient alternately has been suggested (Lohmann et al., 2022; Lohmann et al., 2007). However, combining positional information from multiple gradients could facilitate more efficient goalward navigation. In the case of grid maps of two orthogonally varying gradients, it seems intuitive that the vectors of displacement in each gradient field could be summed to provide the homeward vector. However, in cases where animals may use grid maps comprising non-orthogonal and/or non-linearly varying gradients, combining the gradients to determine the homeward vector is likely to be more complex. Various models of how animals might combine multiple gradients, in particular when they vary non-orthogonally and non-linearly, have been suggested in theoretical models of grid map navigation (Benhamou, 2003; Turner et al., 2016). Different models vary in the apparent simplicity of how they combine gradients, as well as in the assumed structure of underlying gradients. Contemporary developments in animal tracking technology (Beardsworth et al., 2022; Couzin and Heins, 2022) may allow us to quantify spatial patterns in navigational performance and test the predictions of these theoretical models. Further cue conflict and combination experiments could also provide better understanding of how different sources of map information are combined.

The ontogeny of maps

Next, we consider the ontogeny of map cues, structures and navigation strategies employed by animals. Finally, we discuss the mechanisms by which animals learn maps for map and compass navigation and explore the role of mechanisms for determining vectors of self-motion, termed path integration, in map learning across taxa and spatial scales.

a) The ontogeny of map cues

What are the roles of inherited rules and learning in determining what map cues animals utilise? How do the cues they utilise depend upon their developmental environment? How do the cues they utilise change through development?

The cues that animals use as a map could rely upon inherited rules and even be developmentally fixed. For example, hatchling loggerhead turtles and juvenile salmon appear to inherit rules for orientation in response to certain magnetic cues: magnetic inclination and magnetic intensity (Lohmann and Lohmann, 1994; Lohmann et al., 2001; Lohmann and Lohmann, 1996; Minkoff et al., 2020; Putman, 2015; Putman et al., 2011; Putman et al., 2014a; Putman et al., 2013; Putman et al., 2014c; Putman et al., 2015; Putman et al., 2020; Scanlan et al., 2018). Some systems largely controlled through inherited rules might also involve some learning: imprinting upon the magnetic cues at the natal site, for instance, involves an inherited predisposition accompanied with rapid, relatively fixed learning. Examples include the imprinting of loggerhead sea turtles, Manx shearwaters, and Eurasian reed warblers upon magnetic cues at their natal site (Brothers and Lohmann, 2015; Brothers and Lohmann, 2018; Lohmann and Lohmann, 2019; Wynn et al., 2022c; Wynn et al., 2020). In cases of imprinting, learning is likely to be extremely

constrained, with animals predisposed to use particular cues and learning therefore restricted to variation in the values of those cues.

Other more complex learning programmes might also be relatively highly constrained in which cues can be learned and when learning can occur, or less constrained, facilitating learning map cues flexibly depending upon the developmental environment. Homing pigeons have been shown to have a sensitive learning period for developing an olfactory map using wind blowing through their home loft in the three to four months after fledging (Gagliardo et al., 2001a). During this period, they associate changes in olfactants with the wind direction (Gagliardo, 2013; Gagliardo et al., 2001a; Odetti et al., 2003). This mechanism appears to involve the latent learning of olfactory cues while confined to their home loft, such that olfactory map cues are learned before they are utilised for navigation. It is therefore likely that inherited predispositions and constraints determine the cues that are latently learned during this sensitive learning period. The nature of these inherited predispositions is not yet clear: hypothetically, pigeons could learn any olfactant or ratio of olfactants that changes with wind direction; conversely, they might be primed to learn specific olfactants. However, homing pigeons can also learn to use map cues outside of this sensitive learning period. Older homing pigeons can learn olfactory and visual map cues when free-flying, rather than confined to the loft, outside of this sensitive learning period (Odetti et al., 2003). Learning map cues perceived through multiple sensory modalities and outside of this sensitive learning period may be less constrained by inherited predispositions. Moreover, if animals are flexible in what map cues they learn depending on which are most pertinent in their environment, this might explain the range of different cues implicated in homing pigeon navigation in different experiments and at different locations (Guilford and Burt de Perera, 2017; Wiltschko et al., 1987).

Visual landscapes represent an example in which the specific map cues used during navigation seem less likely to be developmentally fixed, with the spatial and temporal change in visual

landscapes potentially preventing successive generations of homing pigeons from using the same visual map cues. Discrete map structures of visual cues ('site-specific compass orientations') must therefore be learned by pigeons as they obtain experience of their environment. However, these cues might still be constrained in various ways, for instance in regard to the size, distance, or geometric features of the visual cues used.

b) The ontogeny of map structure

How animals organise map information may also change through development and involve inherited constraints and predispositions as well as learning. In some cases, an organisation of map information appears to rely on inherited rules, such as the discrete map structure of sea turtles and salmon: a small number of regions on their migratory trajectory in which these animals orient in specific compass directions in response to magnetic cues (Lohmann and Lohmann, 1994; Lohmann et al., 2001; Lohmann and Lohmann, 1996; Minkoff et al., 2020; Putman, 2015; Putman et al., 2011; Putman et al., 2014c; Putman et al., 2015; Putman et al., 2020; Scanlan et al., 2018). The structure of the magnetic map utilised by turtles and salmon may remain developmentally fixed, or could develop through learning, but this is less well understood. The use of magnetic cues in the homing navigation of green turtles (*Chelonia mydas*) displaced up to 100km from their nesting islands (Luschi et al., 2007) appears indicative of a more complex map structure than a small number of inherited signposts. This suggests that a simple, discrete inherited map structure may have been extended and developed through learning. The number of discrete regions that the turtles recognise and orient in response to might have increased through development. Further, it is possible that these animals have developed the ability to exploit the gradient structure of the magnetic field and utilise a continuous magnetic map through learning.

One suggestion regarding the ontogeny of magnetic map structures is that an inherited grid map of magnetic gradients could be calibrated by the magnetic coordinates of the natal site (Putman, 2015). This would represent a developmentally fixed learning event, analogous to imprinting, in combination with relatively complex inherited rules, and is consistent with some experimental work on salmon (Putman et al., 2014b). The advantage of a system of calibration would be that it could alleviate one of the problems of inheriting a complex magnetic map: secular variation, the way in which the magnetic field varies through time (Wynn et al., 2022b). Another possible interplay of inheritance and learning in the ontogeny of map structure could involve the parameterisation of a relatively constrained map structure. For instance, it has been suggested that animals might use maps of one latitudinal and one longitudinal cue, forming an orthogonal grid map (Gould, 2008; Lohmann et al., 2007; Putman et al., 2011). This could represent a constrained structure which animals parameterise through learning map cues that vary with latitude and longitude. Alternatively, some animal map structures might be relatively unconstrained by inherited predispositions and instead be flexible and dependent on the structure of the available cues within the developmental environment of animals. Learning map structures likely involves determining how cues vary locally, and this might then facilitate extrapolation to areas beyond an animal's range of experience (Kishkinev et al., 2021; Turner et al., 2016), potentially through generalisation of associations learned through local, familiar area navigation (Guilford and Burt de Perera, 2017). Hence, learning likely plays an important role in the ontogeny of relatively more complex map structures in certain systems, but inherited predispositions to learn maps with certain structures and to approximate and extrapolate cue distributions in certain ways might also be crucial.

c) *The ontogeny of map navigation strategy*

The ways in which animals develop map navigation strategies remain relatively unexplored. Some strategies such as loggerhead turtles migrating by following a series of waypoints may rely upon

inherited rules, at least on first migration (Lohmann et al., 2001). However, the roles of inherited rules in following map isolines or coastlines, and the ways in which these strategies change through development as animals learn, are unknown. Similarly, rules for combining map cues, such as responding to different map cues independently, prioritising some map cues over others, or only responding to realistic combinations of map cues, might change as animals develop and learn or comprise inherited, fixed rules. Homing pigeons trained to find hidden food in a rectangular environment relied upon featural landmark and geometric spatial information to differing extents depending upon their training environment (Kelly et al., 1998). This demonstrates how rules for combining spatial information can be influenced through learning and depend upon the developmental environment of animals. However, the ontogenies of rules for combining discretely structured map cues for map and compass navigation over larger spatial scales in animals are little known.

Similarly, mechanisms of combining continuously structured map cues to determine the direction of goals could be fixed, inherited systems, or might emerge through learning. While various theoretical models of gradient combination in grid map navigation, associated with specific predictions on the spatial distribution of orientation errors, have been postulated (Benhamou, 2003; Turner et al., 2016), their ontogeny has been little considered. These questions may appear difficult to investigate; however, contemporary developments in animal tracking technology provide the potential to test the predictions of navigational models, and quantify navigational performance, not only in relation to its spatial distribution, but also its changes through development. This has the potential to better our understanding of the ontogeny of navigation strategies in animal maps, as well as the ontogeny of map cues and structure.

d) *Map learning and the role of path integration*

As set out above, learning likely plays an important role in the ontogeny of animal maps in many examples of map and compass navigation. During map learning, animals need to resolve the spatial arrangement of map cues. However, beyond the simplest instances involving imprinting on the map cues at the natal site, there are few systems in which map learning mechanisms are well understood. When learning cognitive maps in new environments over relatively small spatial scales, mammals may associate map cues with vectors obtained during exploration through tracking their own travel. By integrating distance and direction information, they are able to compute a 'home' vector that takes them back to a familiar reference point or 'home base' by the straightest possible path (Etienne and Jeffery, 2004; Fischler-Ruiz et al., 2021; McNaughton et al., 1996; McNaughton et al., 2006; Savelli and Knierim, 2019; Wang, 2016; Whittington et al., 2022). This vector allows animals to determine the distance and direction between sites of interest. Mechanisms of tracking vectors of self-motion are termed 'path integration' or 'dead reckoning' (Mittelstaedt and Mittelstaedt, 1980), and involve utilising compass or idiothetic (angular self-motion) directional cues in combination with speed or distance estimation through mechanisms such as stride integration and optic flow integration (Cheung et al., 2007, 2008; Vickerstaff and Cheung, 2010; Wittlinger et al., 2007). Therefore, path integration has the potential to provide an animal accurate distance and direction information between discrete maps cues or sites during the map learning process, at least for small scale navigation. Similarly, it has been suggested that bees and ants might associate snapshot views with path integrated vectors to learn a map, although clear evidence that this occurs is lacking (Collett and Collett, 2000; Müller and Wehner, 2010; Wehner, 2008).

However, it is unclear whether similar learning mechanisms involving path integration could scale up to facilitate map learning in animals performing map and compass navigation over larger spatial scales. First, while path integration has been found in a wide range of taxa, including a range of insects (Chittka et al., 1995; Müller and Wehner, 1988; Neuser et al., 2008), spiders (Moller and Görner, 1994), crabs (Layne et al., 2003; Zeil, 1998), birds (von Saint Paul, 1982), rodents

(Etienne et al., 1988; Mittelstaedt and Mittelstaedt, 1980), and dogs (Séguinot et al., 1998), it has been little studied in taxa that exhibit map and compass navigation over long distances. Further, the only study finding evidence of path integration in birds was conducted in geese that were walking, rather than flying, to their goal (von Saint Paul, 1982). Second, learning a map through mechanisms involving self-motion cues would require path integration that is not overly susceptible to noise over the spatial scales at which map cues vary; it is unclear whether this is possible for instances of map and compass navigation over large spatial scales.

One map learning mechanism that does not appear to involve path integration is the mechanism of learning an olfactory map in homing pigeons, in which pigeons associate the direction of the wind with detected olfactants in their home loft (Gagliardo, 2013; Gagliardo et al., 2001a; Odetti et al., 2003). This allows homing pigeons to somewhat resolve the spatial arrangement of map cues without themselves moving. However, even if learning from wind-driven olfactants allows individuals to resolve the spatial arrangement of olfactory cues relative to their home loft (e.g. it smells of turpentine in the south), it remains unclear how this process could facilitate certain map navigational abilities such as determining the distance to navigational goals (e.g. (Padget et al., 2019)), or navigating to multiple targets (e.g. (Blaser et al., 2013)). Further, in many other examples of map and compass navigation, a mechanism of learning maps while confined to a single site seems unlikely or even impossible. Animals must move to experience how certain map cues, for instance magnetic cues and visual cues over large spatial scales, vary in space. Indeed, this may also be the case for odour cues in many environments, in which animals are not exposed to the wind sufficiently to learn a map, or in which the winds do not provide sufficient information about how odours vary in space. It is therefore probable that, in some cases, the ontogeny of maps may involve learning during movement, by tracking how cues vary through space. This likely necessitates the integration of changes in map cues with vectors of self-motion, despite the limited evidence currently available to support the idea that path integration takes place in the relevant taxa and across sufficient spatial scales.

With path integration, learning discrete map structures, including site-specific compass orientations and mosaic olfactory maps, could then involve an association between map cues at a site and a self-motion vector between sites. Further, learning continuous map structures could involve the integration of changes in map cues, such as magnetic or olfactory gradient values, with path integrated vectors (Fig. 1.5). Integrating self-motion vectors with changes in map cues would potentially enable learning how different cues vary through space and facilitate development in the structuring of map information and map navigation strategy through learning. This mechanism of learning may play a role in the ontogeny of animal maps, and it is unclear how maps could be learned without some way of tracking self-motion, with the exception of learning odours carried on the wind.

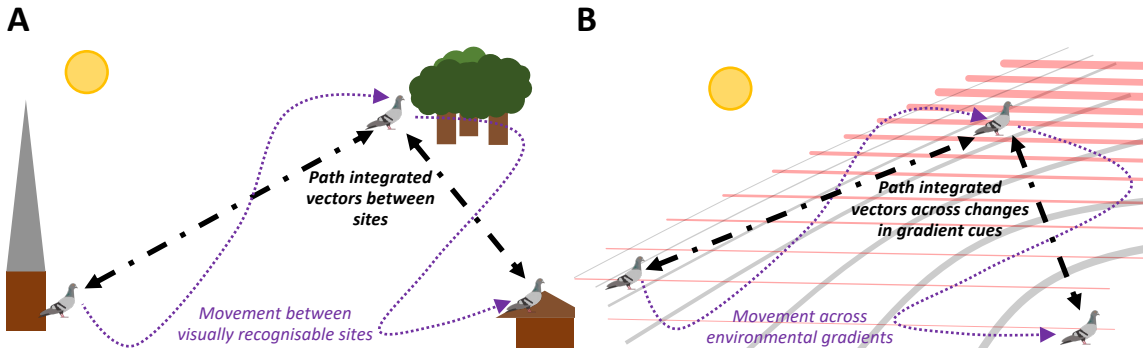


Figure 1.5. Map learning and path integration. *Map learning may involve the integration of changes in map cues with vectors of self-motion as animals explore their environment. Panel A shows how learning a map with discrete structure could involve an association between the visual map cues at a site and a path integrated vector between sites. Similarly, Panel B shows how learning continuous map structures could involve the integration of changes in map cues, such as magnetic or olfactory gradients, with path integrated vectors, to enable learning of how map cues vary through space.*

General conclusions

There are many outstanding and exciting questions relating to the mechanisms and ontogeny of the map step of map and compass navigation in animals. We have set out a framework that deconstructs animal maps into three interlinked components: map cues, map structure and map navigation strategy. The sensory basis of animal maps has been extensively researched, and hence the cues that underlie animal maps are the best understood of these three components. We set out a classification of map structures that distinguishes discrete and continuous map structures and helps to clarify the links between findings on the organisation of spatial information in different taxa and across various spatial scales. Our understanding of the map navigation strategies employed by animals, beyond theoretical ideas and models, is currently relatively limited. These strategies include the way in which animals approach their goals and their mechanisms of combining multiple map cues. There is a role for inherited rules and imprinting in the ontogeny of maps in some animals, but the roles of learning predispositions and the mechanisms of more complex learning programmes still require investigation. Path integration plays an important role in the learning of cognitive maps in mammals, but it is unclear how learning of maps occurs in other taxa and across larger spatial scales. We suggest that path integration might play an unappreciated role in map learning in some animals using map and compass navigation by allowing animals to integrate self-motion vectors with changes in map cues as they move and learn even across large spatial scales. This would imply that path integration is more widespread, taxonomically and in context, that currently appreciated. We suggest that experiments could examine whether path integration occurs in relevant taxa and over the spatial scales required for learning a large-scale navigational map. Finally, we hope that contemporary advances in the availability of large tracking datasets of animal movements will allow us to test the assumptions and predictions of navigational models, to shed light upon the navigational mechanisms that animals employ, in particular the way in which animals structure spatial information and employ navigation strategies during movement, and how these change through

development. This has the potential to better our understanding of the mechanisms of animal maps, and their ontogeny, in different systems.

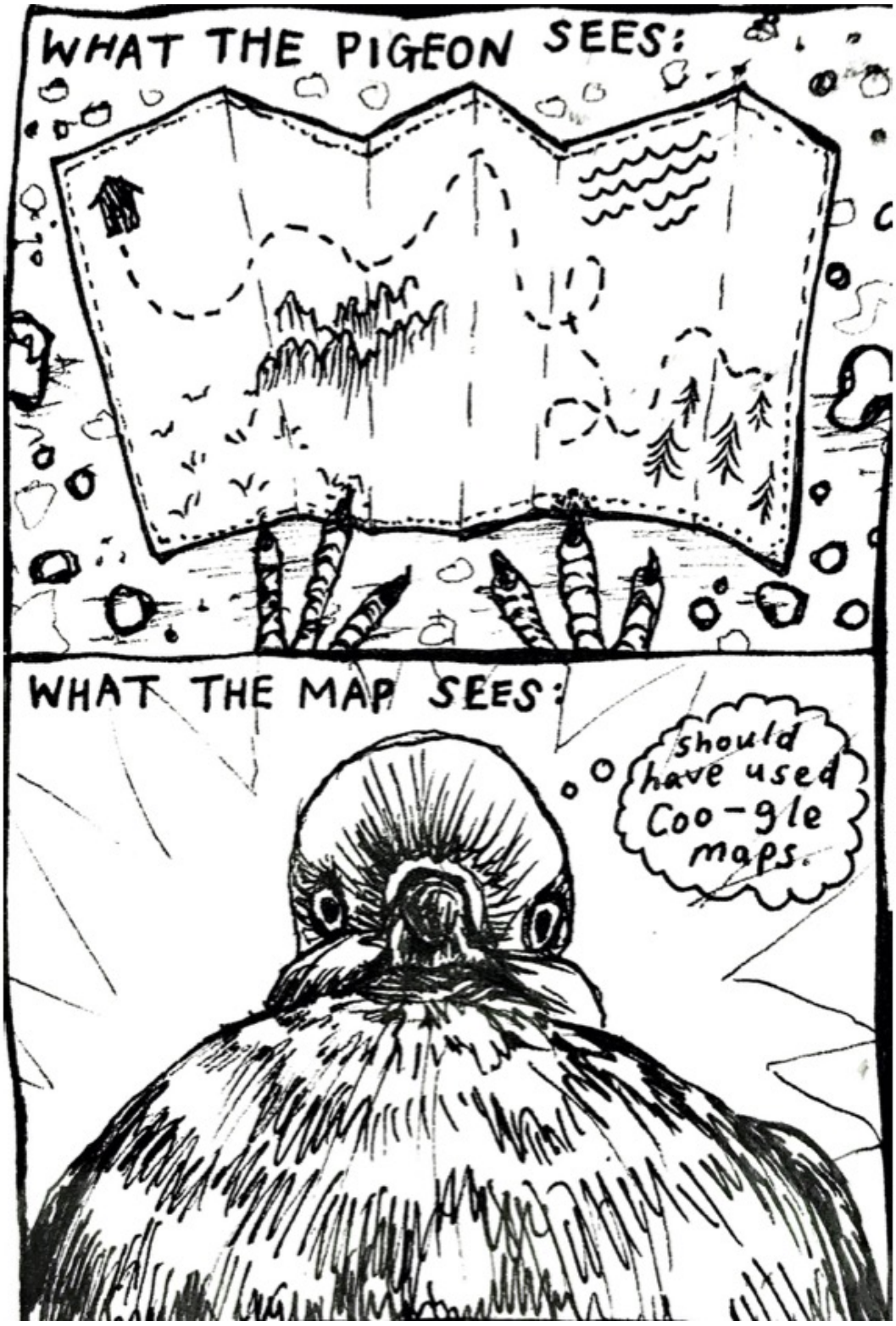
Chapter 2

Almost there: learning to navigate approximately with a grid map

Joe Morford, Patrick Lewin, Paris Jaggers, Joe Wynn, Tim Guilford, Oliver Padget

Author contributions

Joe Morford: Conceptualisation, Methodology, Software, Formal analysis, Investigation, Writing – Original Draft, Writing – Review and Editing, Visualisation. **Patrick Lewin**: Conceptualisation, Methodology, Writing – Review and Editing. **Paris Jaggers**: Conceptualisation, Writing – Review and Editing. **Joe Wynn**: Conceptualisation, Writing – Review and Editing. **Tim Guilford**: Conceptualisation, Supervision. **Oliver Padget**: Conceptualisation, Methodology, Writing – Review and Editing, Supervision.



Biliana Todorova

Abstract

Grid map navigation, based on two or more intersecting environmental gradients, has been invoked as a mechanism to account for impressive navigational abilities across a range of taxa. Further, both magnetic and olfactory cues are utilised as maps by various animals and are distributed along gradients in the environment, providing the potential to be utilised as grid maps by animals. However, the precise mechanisms by which animals navigate using cues distributed along gradients are difficult to unravel: first, how do animals extrapolate the spatial distribution of gradients, and second, how do they combine spatial information from multiple gradients? Various models of how animals might extrapolate and combine spatial gradients have been set out, but the ontogeny of these mechanisms has been little considered. To investigate how these mechanisms might arise and change through learning, we used artificial neural networks as simple computational models of animal learning. We trained neural networks to navigate using bicoordinate grid maps in a range of simulated environments and assessed whether they conformed to various previously proposed navigational models. We consistently found, across a range of simulated environments, that neural networks initially adopted a strategy of determining vectors of displacement in each gradient field independently before summing these to approximate goalward directions. This is termed the approximate model and produces predictable orientation errors in non-orthogonal grid environments. This lends support to the suggestion that this model represents a relatively simple mechanism that animals might adopt to navigate approximately in complex environments. However, by the end of training, neural networks no longer conformed to the predictions of the approximate model, hence the neural networks adopted this mechanism of combining gradient fields for a limited period only. Thus, if animals learn mechanisms to combine gradient fields in order to navigate, the predictions of these models might only be met in certain stages of development. Conversely, the neural networks seemed to extrapolate gradients in different ways depending on the environment. These results allow us to make more nuanced predictions of how animals might develop mechanisms of grid

map navigation through learning. We suggest that these predictions should be tested in the coming years as large tracking datasets of animal movements accumulate.

Introduction

The idea that animals navigate with a grid map of intersecting environmental gradients has been repeatedly suggested to account for impressive navigation abilities across a range of taxa (Baker, 1984; Gould, 1982; Papi, 1990; Putman et al., 2011; Wallraff, 1974; Wallraff, 2004; Yeagley and Whitmore, 1947). In particular, grid maps have been invoked to explain observations of true navigation, the ability to navigate to a goal from novel, unexperienced and far-off sites, without access to familiar landmarks, goal-emanating cues, or information about the displacement route (Griffin, 1952; Holland, 2014; Keeton, 1974). Grid map navigation is a type of map and compass navigation, through which animals navigate with a two-step process: using a map to determine the direction (and potentially the distance) of a goal, and using a compass to determine the relationship between the goalward direction and their egocentric heading and so orient towards the goal (Kramer, 1953). Navigating with a grid map involves exploiting the continuous and predictable distribution of gradients in space, facilitating goalward navigation flexibly through space. Various components of the magnetic field are distributed along spatial gradients and appear to be utilised by animals as map cues (Benhamou et al., 2011; Chernetsov et al., 2008; Chernetsov et al., 2017; Kishkinev et al., 2020; Kishkinev et al., 2013; Kishkinev et al., 2010; Kishkinev et al., 2015; Kishkinev et al., 2021; Lohmann and Lohmann, 1994; Lohmann et al., 2001; Lohmann and Lohmann, 1996; Lohmann et al., 2004; Luschi et al., 2007; Minkoff et al., 2020; Pakhomov et al., 2018; Putman, 2015; Putman et al., 2011; Putman et al., 2014a; Putman et al., 2013; Putman et al., 2014c; Putman et al., 2015; Putman et al., 2020; Scanlan et al., 2018). Similarly, some animals have been shown to utilise an olfactory map in their long-distance navigation, including homing pigeons (for reviews, see (Gagliardo, 2013; Wallraff, 2004)), and seabirds (Benvenuti et al., 1993; Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015), potentially facilitated by stable spatial gradients of olfactory cues over large spatial scales (Wallraff, 2000; Wallraff, 2013; Wallraff and Andreae, 2000; Zannoni et al., 2020).

Grid map navigation appears to require both information regarding how gradients are distributed in space, allowing animals to structure their map, and a strategy for the combination of multiple gradients to determine the direction of a goal. The complexity of both of these steps is likely to depend on how the gradients are distributed in space. For instance, navigating with non-linearly and non-orthogonally varying gradients may require complex mechanisms to achieve accurate performance. Further, gradients that vary at close to parallel with each other have typically been assumed to be unsuitable for use in grid map navigation, owing to the magnifying effect on positional inaccuracy of any error in such environments (Bostrom et al., 2012; Wynn et al., 2022b; Åkesson and Alerstam, 1998). Conversely, if two gradients which vary linearly and orthogonally are used to navigate, determining the distribution of these cues and how to combine them may be simpler. Accurate navigation could be achieved through computing a vector of displacement from the goal in each gradient field separately and performing vector addition to determine a goalward vector (Fig. 2.1A). In non-orthogonal gradient fields, the same mechanism would produce predictable biases in orientation, as shown in Fig. 2.1B. Nonetheless, Benhamou suggested that this might be a mechanism by which animals might approximately navigate in non-orthogonal grid environments (Benhamou, 2003), and this has been termed the approximate model of combining gradient fields (Turner et al., 2016)

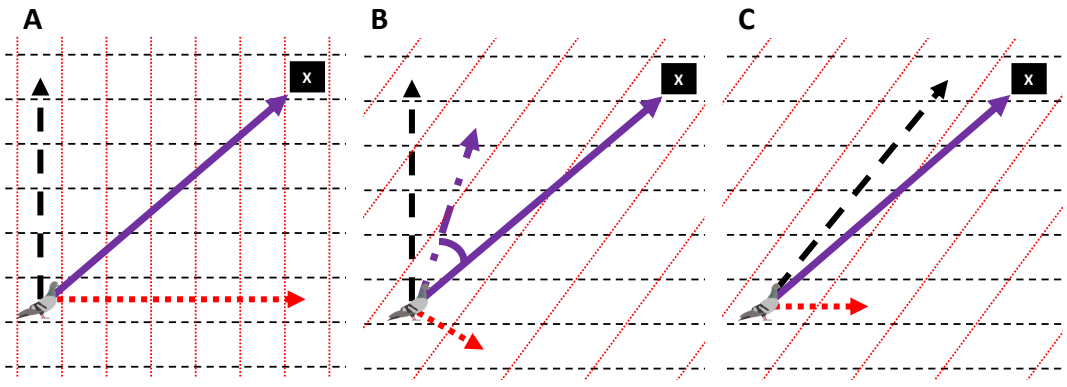


Figure 2.1. Navigating by vector addition, as in Benhamou, 2003, in orthogonal and non-orthogonal grids. *An animal is shown navigating towards a goal using two gradients (in black dashed and red dotted lines). In panels A and B, the animal is shown computing its displacement*

in each gradient field independently (the black dashed and red dotted arrows) and then using vector addition to determine an overall vector of displacement from its goal. (A) In an orthogonal grid, this produces an exact vector towards the goal (purple solid arrow); (B) in a non-orthogonal grid, this produces an approximate vector (purple dot-dash arrow) towards the goal, with a predictable error in orientation (shown marked between purple dot-dash arrow and purple solid arrow). (C) The exact goalward vector (purple solid arrow) can be computed in non-orthogonal grid environments by taking both gradient fields into account conjointly when determining the vector of displacement in each gradient field, before performing vector addition.

This navigational model was suggested by Benhamou to be simpler for animals to execute than taking the gradient fields into account conjointly to produce an exact goalward vector in non-orthogonal grids (shown in Fig. 2.1C). This has been expanded upon by Turner and colleagues, in a study in which they examine navigation in more complex gradient fields (e.g. curvilinear or exponentially-varying fields), and suggest a range of navigational models that animals might utilise (Turner et al., 2016). These models, first, involve different strategies of combining multiple gradients. Second, when the gradients vary in complex patterns, they involve different ways of extrapolating the gradients to generate a map structure from their distributions. In these models, they assume that two gradients are linearly extrapolated by animals, even if the fields in fact vary curvilinearly or exponentially. They model two ways in which animals might extrapolate the gradient fields: extrapolating using the direction and magnitude of the fields at either the single target/goal location, or at the 'release' locations (any locations at which they orient goalward). To these, we add a third model of how animals might extrapolate the field here: using the average vector along which the fields vary across the distribution of experienced locations. Additionally, they model three mechanisms by which animals could combine two gradient fields to produce goalward orientations: the approximate model (the mechanism modelled by Benhamou and introduced above), which involves determining the displacement in each gradient field independently before performing vector addition; the directional model, which uses only the

direction with which the gradient fields vary, ignoring their magnitudes, and weighing the direction of displacement in each gradient field equally before averaging them to orient; and the correct model, which takes the fields into account conjointly when determining the vector of displacement in each gradient field, before performing vector addition to find the correct vector home with linear gradient fields. In simple grid environments, with gradient fields varying linearly and orthogonally, only the directional model produces orientation errors, with the other two models computing exact goalward vectors. With gradients varying linearly but non-orthogonally, both the directional and approximate model produce distinctive patterns of orientation error, with the correct model taking the two fields into account conjointly to determine the exactly accurate goalward vector. In more complex environments with curvilinear and exponentially-varying gradients, each of these models, in combination with a mechanism for linearly extrapolating the gradient fields, produces predictable patterns of orientation errors in space.

One factor that has received little consideration is the ontogeny of grid map navigation mechanisms. Tinbergen emphasised ontogeny as one of the major problems or questions for the field of ethology, defining it as the change in behaviour machinery during development (Tinbergen, 1963). The mechanisms involving map structuring through extrapolating gradient fields and the strategies for combining multiple gradients to determine goalward vectors can be considered as some of the behaviour machinery involved in grid map navigation. One possibility is that animals might be predisposed to utilise particular map structures and strategies for combining multiple gradients, and so these mechanisms might be relatively invariant through development. In this case, if animals utilise some of the mechanisms of extrapolating and combining gradients that have been proposed (Benhamou, 2003; Turner et al., 2016), we might expect to find patterns of orientation errors in animal tracking that match up with the predictions of these models. Conversely, these mechanisms might arise and change during development through learning, and hence our expectations might be more nuanced: whether we would expect

to find the signature error patterns of these proposed models, and at what point in development, is not immediately clear.

We sought to examine how mechanisms of grid map navigation might arise and change through learning by training artificial neural networks to compute goalward directions in simulated environments. We used artificial neural networks called multi-layer perceptrons which can act well as simple computational models of animal learning and have been shown to be capable of replicating various empirical features of animal learning (Ghirlanda and Enquist, 2007; Gluck, 1991; McClelland and Rumelhart, 1985; Peng and Chittka, 2017; Wisniewski et al., 2012). Neural networks were trained to use gradient information to output directions towards a single goal in the centre of the environment at a large number of locations within a simulated environment. At various stages of training, we tested whether the errors of the networks conformed to predicted error patterns under different models of grid map navigation. It is difficult to assess how analogous the training of artificial neural networks in this way is to navigational learning in animals, and caution must be applied to any findings to ensure that they reflect modelled biology as opposed to the specifics of network implementation (Dawson, 2008; Franks and Ruxton, 2010). We therefore used two different implementations in order to ensure that the results did not rely on the precise way in which the networks outputted the direction to the goal or were optimised through training. This method allowed us to examine the ways in which, at least in theory, grid map navigation mechanisms could change through development. This facilitates more nuanced predictions about how signature error patterns of navigational models might manifest through development and in adult animals. This might prove useful in the coming years as contemporary developments in animal tracking technology facilitate the proliferation of large datasets in which these predictions can plausibly be tested.

The artificial neural networks

We utilised two implementations to train multi-layer perceptrons to compute goalward directions using simulated gradients. In both implementations, neural networks had 2 input neurons, each representing the value of one of the two gradient cues in the simulated environment, and 6 Dense hidden layers (1st: 10 neurons; 2nd: 100; 3rd: 200; 4th: 500; 5th: 200; 6th: 100) with Rectified Linear Unit (ReLU) activation functions (Chollet, 2015; Gulli & Pal, 2017). In the first implementation, we treated the task as a regression problem; the neural networks had a single output neuron constrained between 0 and 1 with a sigmoid activation function. This output represented the predicted direction of the goal, with units of degrees/360. To control for any biases generated by the implemented baseline direction of the output (an output of 0 degrees/360), a baseline direction was randomly assigned to each neural network, such that an output of 0 degrees/360 corresponded to a random direction. The loss function, which is optimised during training, was the squared directional error of each neural network prediction. Standard gradient descent was used to optimise the networks during training (learning rate = 0.001; Nesterov momentum = 0.9). In the second implementation, we treated the task as a categoric problem; the neural networks had 20 output neurons, with sigmoid activation functions, each representing an equally sized sector of the circle, with the neural networks estimating which of the sectors encompassed the goal direction. Like in the first implementation, to avoid biases generated by the implementation of the directions represented by the set of 20 sectors, and to improve the coverage of the results, the directions represented by the set of sectors was randomly assigned to each neural network. A binary crossentropy loss function in combination with the Adam optimiser was used in this implementation. In both cases, network training took place over a single epoch and with a batch size of one; hence networks were effectively trained with information relating to a single spatial location at a time and each location only once, in an effort to constrain learning in a biologically realistic way. This neural networks were implemented in Python 3.10.7 (Van Rossum and Drake Jr, 1995), with the libraries: keras

(Chollet, 2015), sys, numpy (Harris et al., 2020), scipy (Virtanen et al., 2020), matplotlib (Hunter, 2007) and tensorflow (Abadi et al., 2016).

The simulated environments

The artificial neural networks were trained and tested to output goalward directions in a range of simulated environments. In all environments, the target of the neural networks was set at (0, 0) in the Cartesian coordinate system. Possible training locations were generated through all combinations of sets of distances and directions from the target, with the set of distances spaced 0.025 units apart between 0.025 and 4 units from the target, and the set of directions spaced 4 degrees apart, from the y axis all the way round the circle. This procedure generated a greater density of training locations closer to the target. Testing locations were regularly spaced every 0.1 units along both the Cartesian x and y axes from -5 to 5 in both axes. The training and test locations are shown in the top left panel of Fig. 2.2.

Every simulated environment comprised two gradient fields. Seven different environments were simulated, conforming to the first four general cases modelled by Turner and colleagues (their 5th case is excluded, which examines gradient fields containing anomalies). In all cases, one field (A) varied linearly. The second gradient field varied either: (B1) linearly and orthogonally to field A; (B2i and B2ii) linearly and non-orthogonally to field A; (B3i and B3ii) non-linearly and non-orthogonally to field A at the target; (B4i and B4ii) non-linearly and orthogonally to field A. The equations of gradient A and gradient B in each of the simulated environments are given in Table 1.1, where the x and y represent the axes of a Cartesian coordinate system, and each k represents a constant value determined such that all of the gradients varied over the same range within the simulated environment. The seven simulated environments are shown in Fig. 2.2. The simulated environments will be referred to in relation to their B gradient henceforward (e.g. environment B2i).

Table 1.1. The gradient fields of the simulated environments. *The equations defining the gradient fields of the 7 simulated environments are shown. Gradient A is the same in every*

simulated environment, whereas there are 7 versions of gradient B, conforming to 4 general cases. x and y represent the axes of a Cartesian coordinate system and each k represents a constant value, chosen to standardise the range of the gradient field in the simulated environment.

Gradient A:		
All Cases	$A = (x - k_{1_A})/k_{2_A}$	
Gradient B:		
Case 1	$B1 = (y - k_{1_B1})/k_{2_B1}$	
	i	ii
Case 2	$B2i = (x - y - k_{1_B2i})/k_{2_B2i}$	$B2ii = (x - 2y - k_{1_B2ii})/k_{2_B2ii}$
Case 3	$B3i = (x - (y-1)^2 - k_{1_B3i})/k_{2_B3i}$	$B3i = (x - 0.2(y + 2)^2 - k_{1_B3ii})/k_{2_B3ii}$
Case 4	$B4i = (e^x - k_{1_B4i})/k_{2_B4i}$	$B4ii = ((6 - x)^3 - k_{1_B4ii})/k_{2_B4ii}$

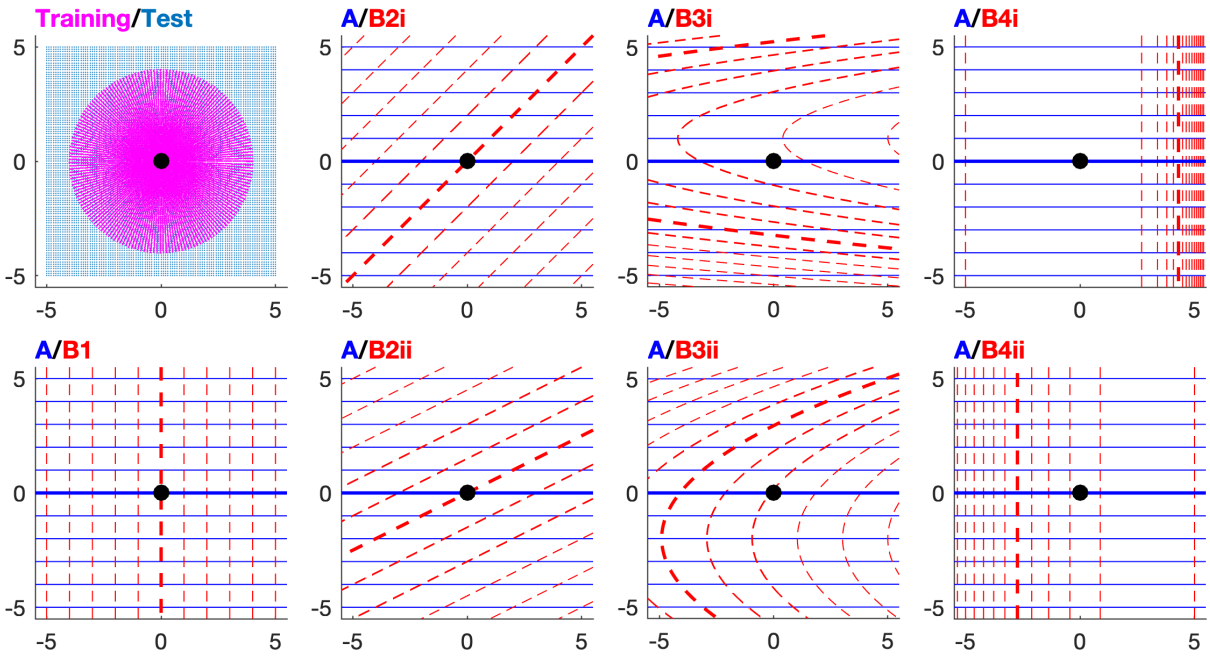


Figure 2.2. The simulated environments. *The top left panel shows the locations used to train (in magenta) and test (in blue) the neural networks within the simulated environments. The other seven panels show the seven simulated environments in which neural networks were trained and tested, each comprising two gradients. Gradient A is the same in every environment and is shown with solid blue contour lines; gradient B is different in each environment and is shown with dashed*

red contours. The contour lines are spaced one unit apart in gradient value; where the gradient value is equal to zero, a thicker contour line is used. In every environment, the goal location is the same, at the origin of the Cartesian coordinate system, and represented by a black point in each panel.

Generating predictions with navigational models

We use and extend the navigational models set out by Benhamou and by Turner and colleagues in previous modelling studies (Benhamou, 2003; Turner et al., 2016). See Turner et al, 2016 for mathematical descriptions of these models. The neural networks were tested in how closely their testing outputs conformed to each of the navigational models. The models include three ways in which two linear gradient fields are combined to generate goalward directions:

1) **The Approximate Model (APPROX)**. This comprises computing a vector of displacement from the goal in each gradient field independently and then determining an overall vector of displacement through vector addition (see Fig. 2.1).
2) **The Directional Model (DIRECTIONAL).** This model ignores the magnitudes with which the gradient fields vary, using only the directions along which they vary. The model comprises computing the direction of displacement from the goal location in each gradient field, and then weighing the two directions equally, irrespective of the magnitude of the displacement in each of the gradient fields.
3) **The Correct Model (CORRECT).** This model computes the correct direction home using two linear gradient fields. It comprises taking the fields into account conjointly to compute a vector of displacement in each gradient field and then determining an overall vector of displacement through vector addition.

In simpler environments, with linear gradient fields, the correct model produces accurate orientation predictions, whereas the approximate model produces orientation errors in non-orthogonal environments and the directional model produces orientation errors in all environments. The orientation errors produced by the approximate model and the directional model in simulated environments with gradient A and either gradient B1, B2i or B2ii are shown in Fig. 2.3.

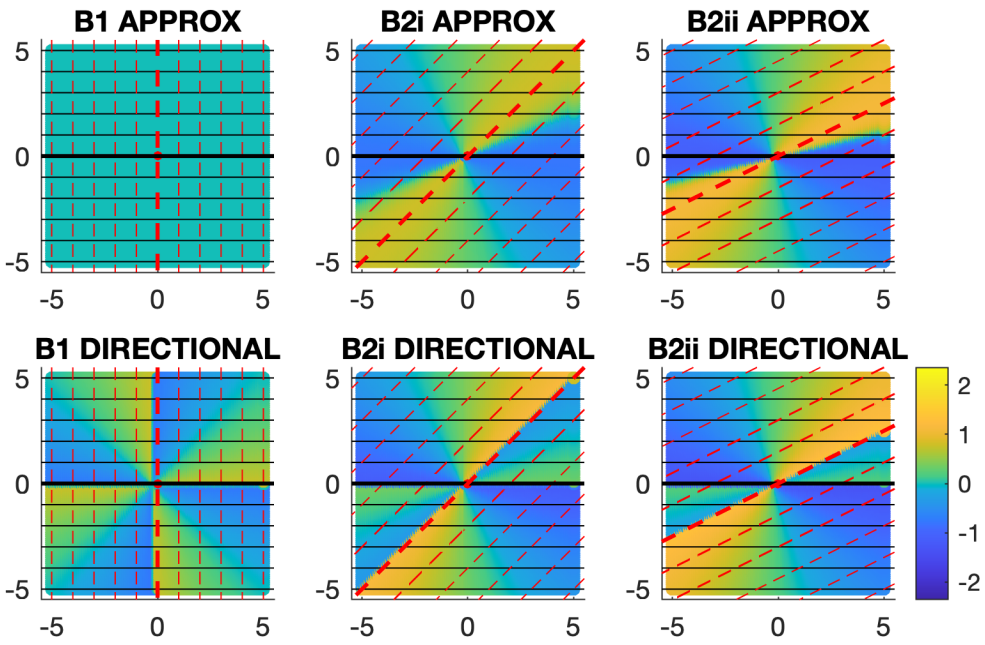


Figure 2.3. Model predictions in simpler environments. *The orientation errors for the testing locations predicted by the approximate and directional models in orthogonal (B1) and non-orthogonal (B2i and B2ii) linear environments are shown by the heatmaps. The angular error scale in radians is shown bottom-right, with anticlockwise error positive (brighter colours) and clockwise error negative (darker colours). The gradients are represented as in Fig. 2.2.*

In more complex environments with non-linear gradient fields, these models are extended to include linear extrapolations of the non-linear gradient fields. Three mechanisms of linear extrapolation are modelled, extending the models of Turner and colleagues:

1) **Target-based extrapolation (T).** The gradients are linearly extrapolated from the target/goal location with the direction and magnitude of the fields at the target site.
2) **Release-based extrapolation (R).** The gradients are linearly extrapolated from each release (training or test) location, with the direction and magnitude of the fields at each of those sites.
3) **Training-based extrapolation (Tr).** The gradients are linearly extrapolated using the average vector along which the fields vary across the distribution of training locations.

These three models of combining gradient fields in combination with three models of linearly extrapolating gradient fields produce 9 navigational models with different orientation error

predictions in complex environments, with non-linear non-orthogonal gradients such as in the simulated environment with gradients A and B3i, as shown in Fig. 2.4.

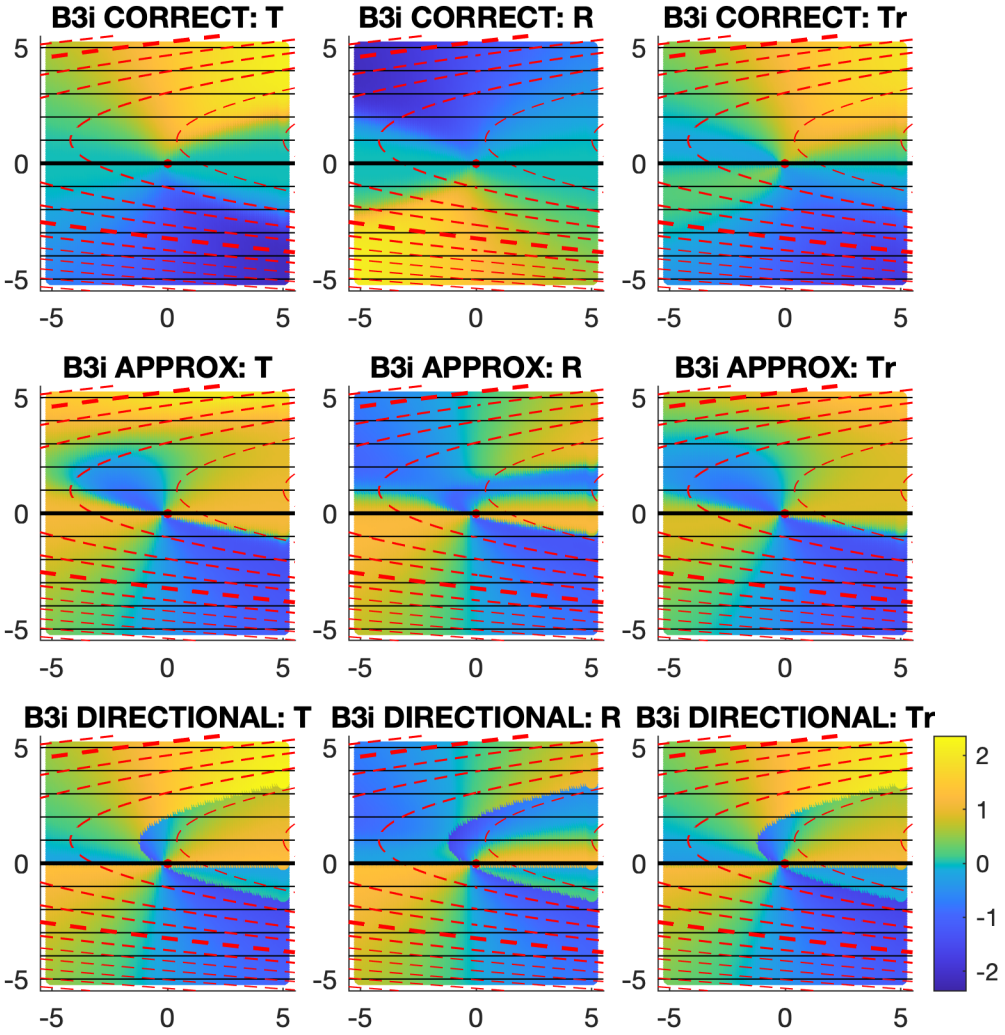


Figure 2.4. Model predictions in a non-linear, non-orthogonal environment. *The predicted orientation errors at the testing locations of the nine different navigational models in the simulated environment with gradients A and B3i are shown. The angular error scale in radians is shown bottom-right, with anticlockwise error positive (brighter colours) and clockwise error negative (darker colours). The gradients are represented as in Fig. 2.2.*

In certain environments, some of the models become equivalent, meaning that not all of the models can necessarily be distinguished. For instance, in environments with gradients varying non-linearly but orthogonally, the correct and approximate models make identical predictions of

orientation error, and the different models of extrapolation make identical predictions when combined with the directional model of combining gradients. This is the case in the simulated environment with gradients A and B4i, as shown in Fig. 2.5.

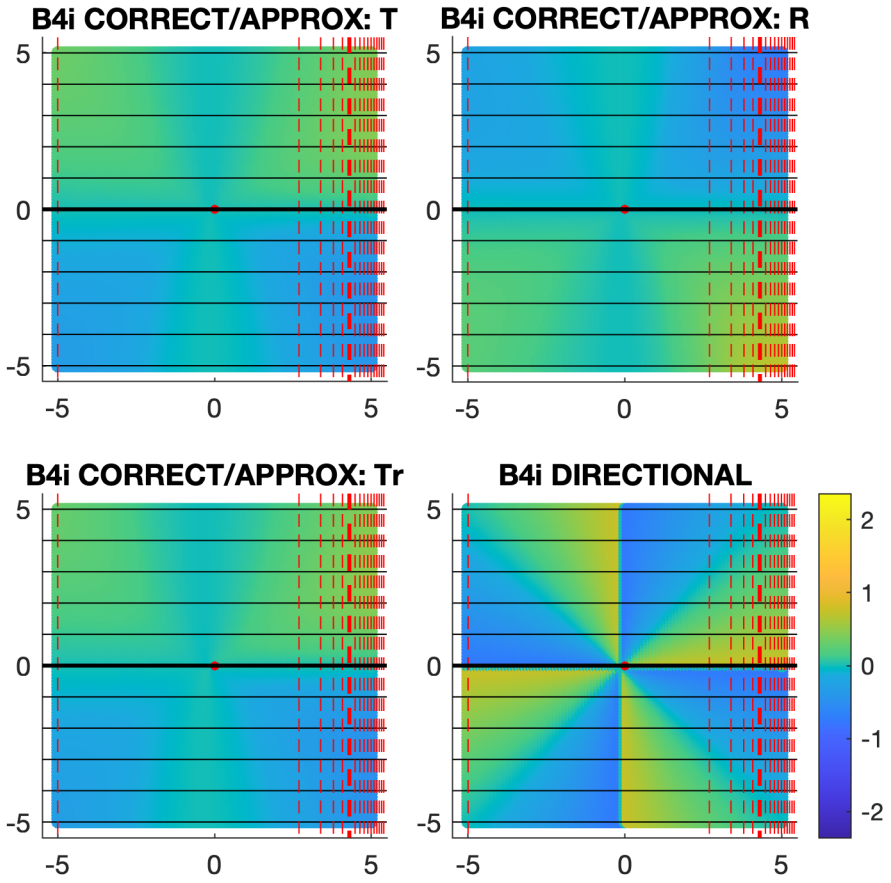


Figure 2.4. Model predictions in a non-linear, orthogonal environment. *The predicted orientation errors at the testing locations of different navigational models in the simulated environment with gradients A and B4i are shown. The angular error scale in radians is shown bottom-right, with anticlockwise error positive (brighter colours) and clockwise error negative (darker colours). The gradients are represented as in Fig. 2.2. The correct and approximate models make identical predictions in this environment, and there is no predictive distinction between directional models with different linear extrapolations of the gradients.*

Testing neural network performance against model predictions

Artificial neural networks were tested at various stages of training: after 0, 100, 250, 500, 1000, 2000, 4000, 8000 and 14000 training datapoints. The neural networks were tested at the testing locations shown in the blue points in Fig. 2.2A. Neural network performance was tested against perfectly accurate performance and against every navigational model with unique, non-zero predictions of orientation error. The absolute error of the neural network output was calculated at every testing location for each artificial neural network, and the mean was taken across the testing locations, to produce a mean error for each neural network. The absolute difference between model predictions and the neural network output was calculated at every testing location for each artificial neural network, and the mean was taken across the testing locations, to produce a mean absolute difference for each neural network to a given navigational model's predictions. This was computed for each of the navigational models. The fit of the different navigational models to the performance of the population of neural networks was then assessed using linear mixed effect models, of the general formula:

Mean Absolute Difference ~ Navigational Model + (1 | Neural Network ID)

Navigational Model was a categoric explanatory variable. Neural Network ID was modelled with a random intercept. At each stage of training, the best-fitting model (with the lowest mean difference to the neural network outputs) is reported, along with significance at 5% significance level of a *t*-test (using Satterthwaite's method (Kuznetsova et al., 2017; Satterthwaite, 1946)) to compare the fit between the best fitting model and the next best fitting model, and the significance at 5% significance level of a *t*-test to compare the fit between the best fitting model and perfectly accurate performance (included in the statistical analysis as an additional

navigational model), which was used as a baseline to assess model performance. Statistical analysis and graphical output was produced using Matlab (The-MathWorks-Inc., 2021)and R (R-Core-Team, 2018; RStudio-Team, 2020), using the R packages: circular (Agostinelli and Lund, 2022), plyr (Wickham, 2011), ggplot2 (Wickham, 2016), lme4 (Bates et al., 2015), vctrs (Wickham et al., 2023) and lmerTest (Kuznetsova et al., 2017).

Results

Under each of the two neural network implementations, we trained 200 artificial neural networks in environments B3i and B3ii, for which there were a greater number of navigational model predictions, and 100 artificial neural networks in each of the other five simulated environments. In each of the simulated environments, the learning curves of the neural networks under the continuous implementation are shown in the left panel of Fig. 2.5 and those under the categoric implementation are shown in the right panel. As expected, under both implementations and in each simulated environment, neural networks began with an average absolute error of approximately half pi radians with no training, before improving through training. As can be seen in the figure, neural networks achieved better performance most quickly in the simplest simulated environment with linear and orthogonal gradient fields (B1), and more slowly in the most complex environments, particularly B3i and B4i.

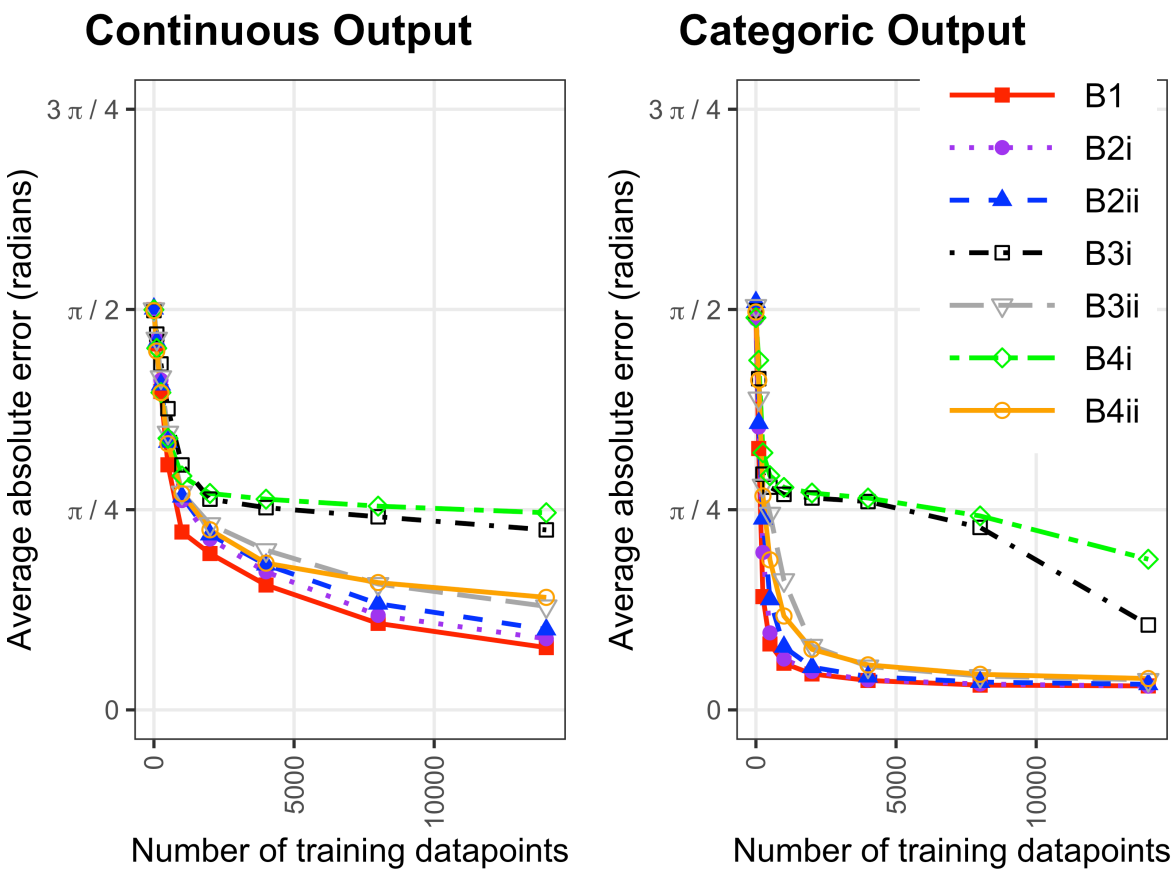


Figure 2.5. Neural network learning curves. *These learning curves show the absolute error averaged across testing datapoints and across the neural networks at various stages of training. Each curve represents the performance of neural networks trained in different simulated environments comprising different gradients. Performance of neural networks implemented with a continuous output are shown in the left panel, and those implemented with a categoric output on the right.*

Only one navigational model, the directional model, predicts orientation errors in the B1 environment comprising linear, orthogonal gradients. The fit of the directional model to the outputs of the neural networks was assessed relative to the baseline of perfectly accurate performance, and these results are presented in Fig. 2.6. At all stages of training, the neural networks conformed better to perfectly accurate performance than the directional model's predictions.

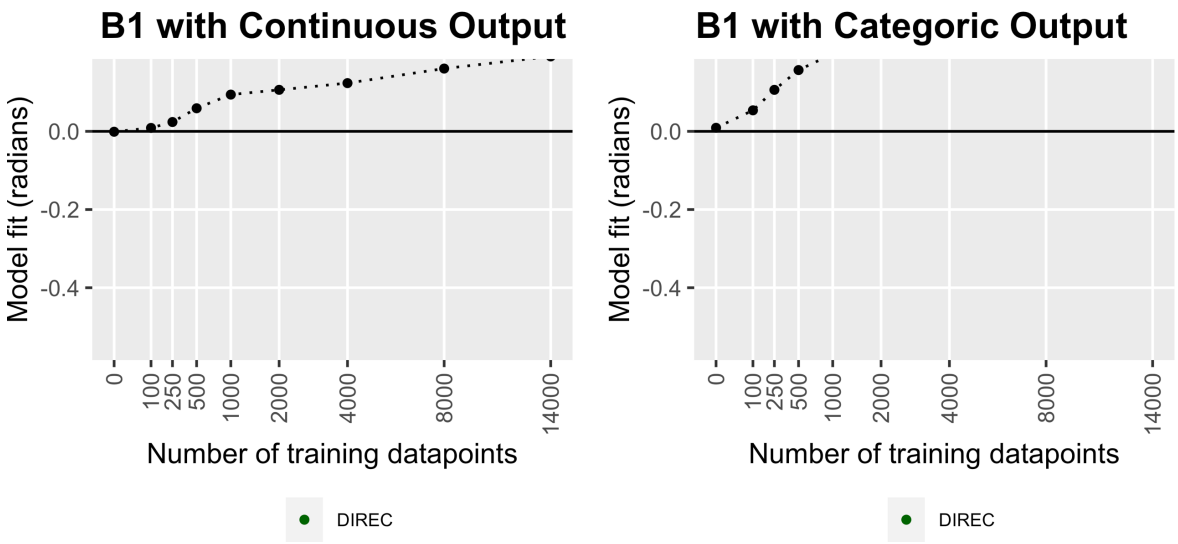


Figure 2.6. Model fit in B1 environment. *The fit of the directional model relative to the baseline of perfectly accurate performance (no error) is shown. The y axis represents the average absolute difference between the neural network outputs and the directional model predictions minus the average absolute error of the neural network outputs. A negative number indicates a better fit of the neural network outputs to the predictions of the navigational model than to the baseline of perfectly accurate performance. The x axis is square root transformed. Results from neural networks under the first implementation (continuous) are shown on the left, and those from neural networks under the second implementation (categoric) on the right.*

Likewise, 100 neural networks under each implementation were trained in two environments with linearly but non-orthogonally varying gradients, environments B2i and B2ii. In these environments, both the directional and approximate models predict orientation errors. In both environments and under both implementations, after some training, the approximate model fitted the neural network outputs best, and significantly better than the perfectly accurate solution, as shown in Fig. 2.7. In each of these cases, the approximate model also fitted significantly better than the directional model at some stage of training, except for the B2ii environment under the categoric output neural network implementation (no significant difference between the approximate and directional model at any stage of training). However, in

all these cases, at the end of training, the perfectly accurate solution fitted the artificial neural network outputs significantly better than the approximate model.

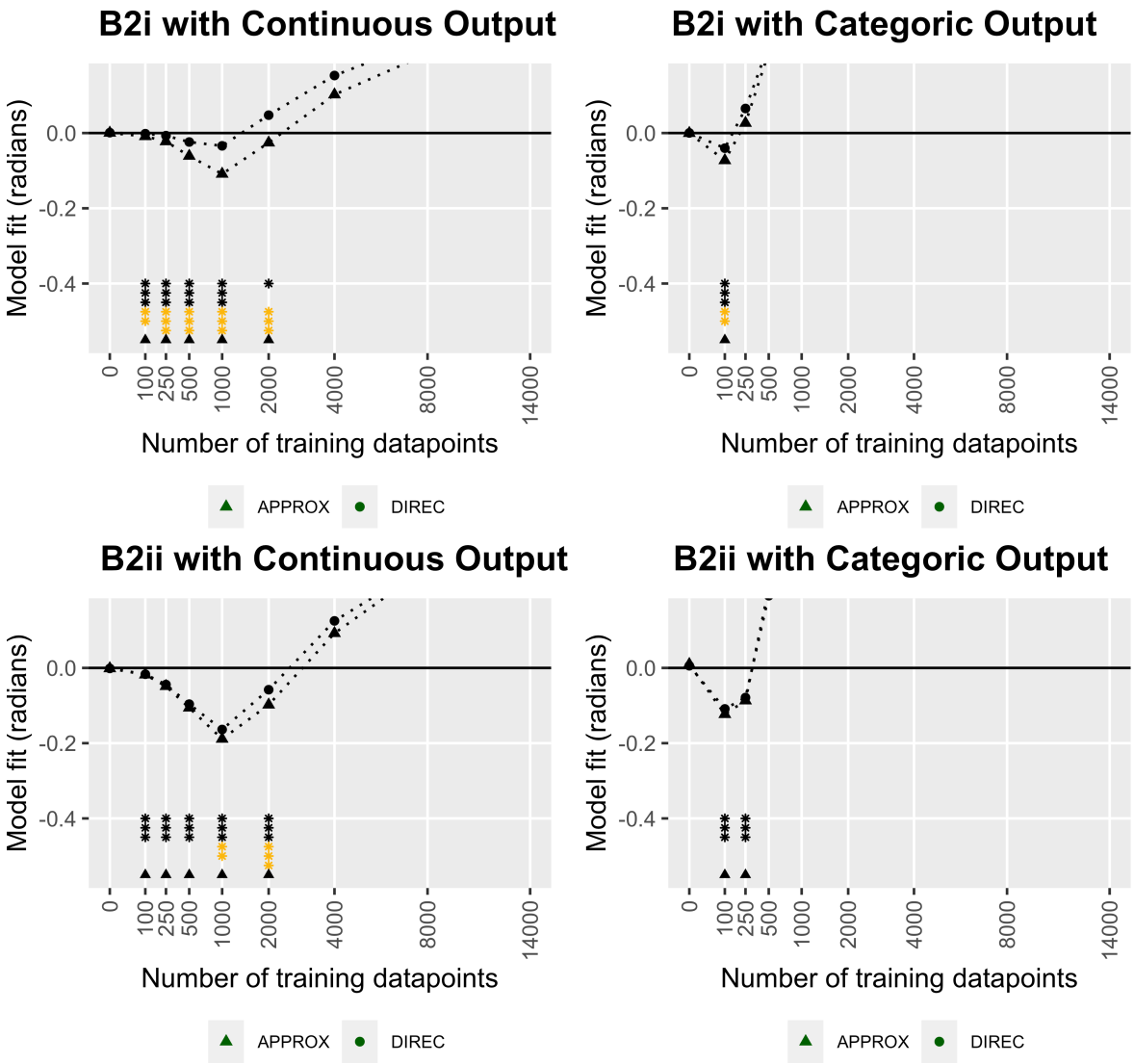


Figure 2.7. Model fit in B2 environments. *The fit of the approximate and directional models relative to the baseline of perfectly accurate performance (no error) is shown. The y axis represents the average absolute difference between the neural network outputs and the model predictions minus the average absolute error of the neural network outputs. A negative number indicates a better fit of the neural network outputs to the predictions of the model than to the baseline of perfectly accurate performance. Combination model (APPROX=approximate; DIREC=directional) keys are shown under the figures. The x axis is square root transformed.*

Results from neural networks under the continuous implementation are shown on the left, and those under the categoric implementation on the right. Black stars show where the neural network predictions are significantly closer to that model's predictions than to the perfectly accurate solution. In these cases, the identity of the best fitting model is shown by a symbol on the x-axis. Gold stars show where the best fitting model is a significantly better fit than the next best fitting model.

The predicted orientation errors of the approximate model at testing locations in B2i and B2ii across the range of possible directions from the target, and the error of the neural networks across these directions are shown in Fig. 2.8, at the stage of training at which the approximate model was the best fitting model by the largest margin. In each environment and under each implementation, the performance of two random neural networks is shown as well as the average performance across the population of neural networks. Visual inspection reveals a very close fit of the model predictions to the average neural network error despite relatively poorer fit of the predictions of the model to the performance of random neural networks.

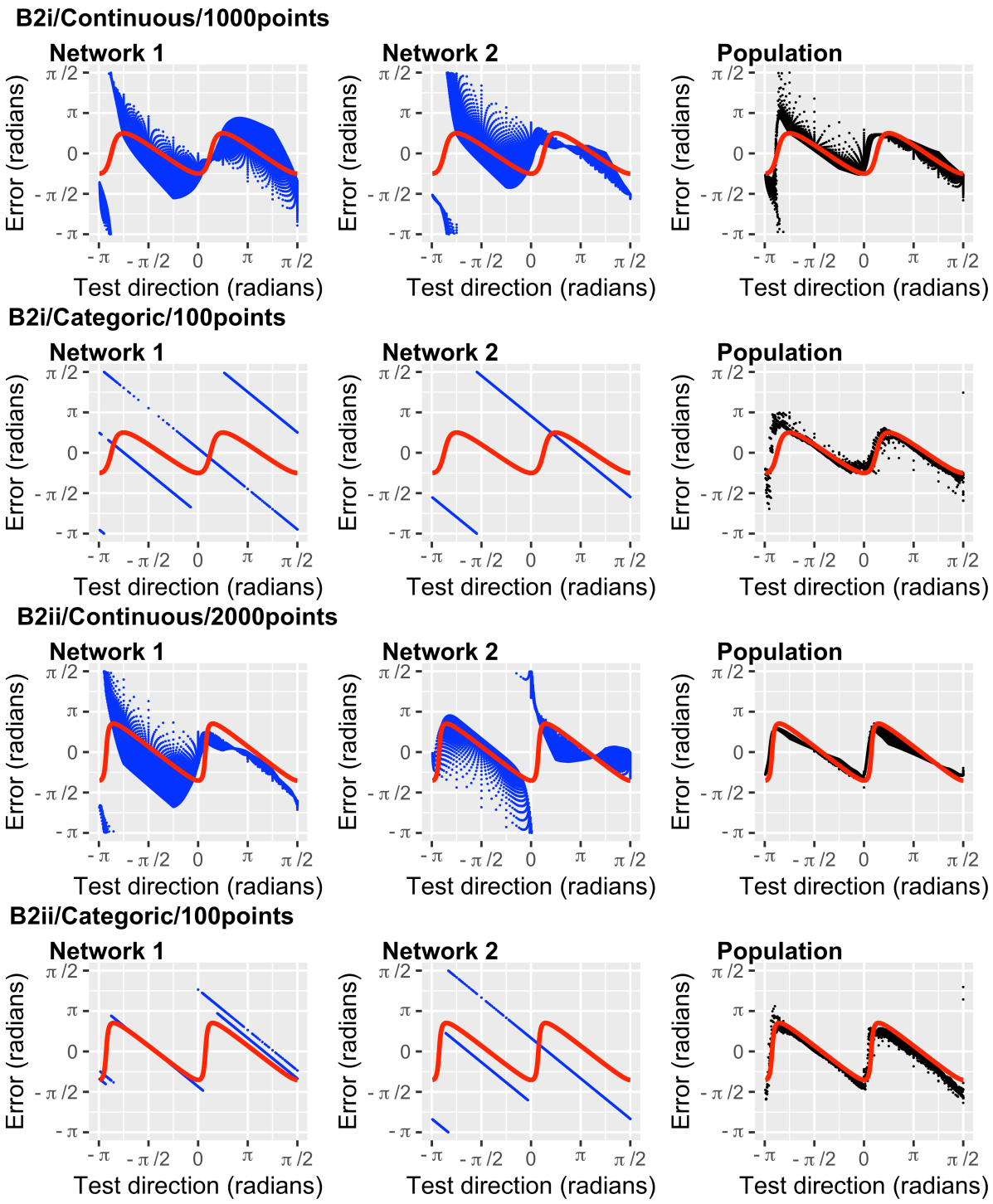


Figure 2.8. Neural network error and the approximate model predictions in B2 environments. *From each neural network implementation, in each of environments B2i and B2ii, the performance of two randomly selected neural networks and the population of neural networks is shown at the stage of training at which the approximate model is the best fitting model by the largest margin. Each blue point represents the performance of the neural network at a single testing location, with its direction from the target on the x-axis. Each black point represents the*

average performance of the neural networks at a single testing location. The predicted error under the approximate model at different directions from the target is shown by the red lines.

Under more complex simulated environments, there are a greater range of navigational models that predict orientation errors. These involve both a model for combining the two gradients (directional, approximate, and correct models) and a model for extrapolating the gradients (target-based, release-based and training-based extrapolations). In the environments with gradients varying non-linearly and non-orthogonally at the target site, B3i and B3ii, 200 neural networks were trained under each of the two neural network implementations. In environment B3i, under both implementations, the approximate model with release-based extrapolation was the best-fitting model after some training, fitting the neural network outputs significantly better than perfectly accurate performance. Under the continuous output implementation, this model significantly outperformed all other models in later training, whereas under the categoric implementation, this model significantly outperformed all other models except for the directional model with release-based extrapolation. At the end of training, under the continuous implementation, the approximate model with release-based extrapolation was still the best-fitting model, whereas under the categoric implementation, the neural network outputs were significantly closer to the perfectly accurate solution than any of the model predictions. Similarly in environment B3ii, under both implementations, the approximate model with release-based extrapolation was the best-fitting model at some stage of training, fitting the neural network outputs significantly better than perfectly accurate performance and all other models. Uniquely, under the categoric implementation, after 100 training datapoints, the correct model with release-based extrapolation was the best fitting model but did not fit significantly better than the approximate model with release-based extrapolation. At the end of training, the neural network outputs were significantly closer to the perfectly accurate solution than any of the model predictions. These results are shown in Fig. 2.9.

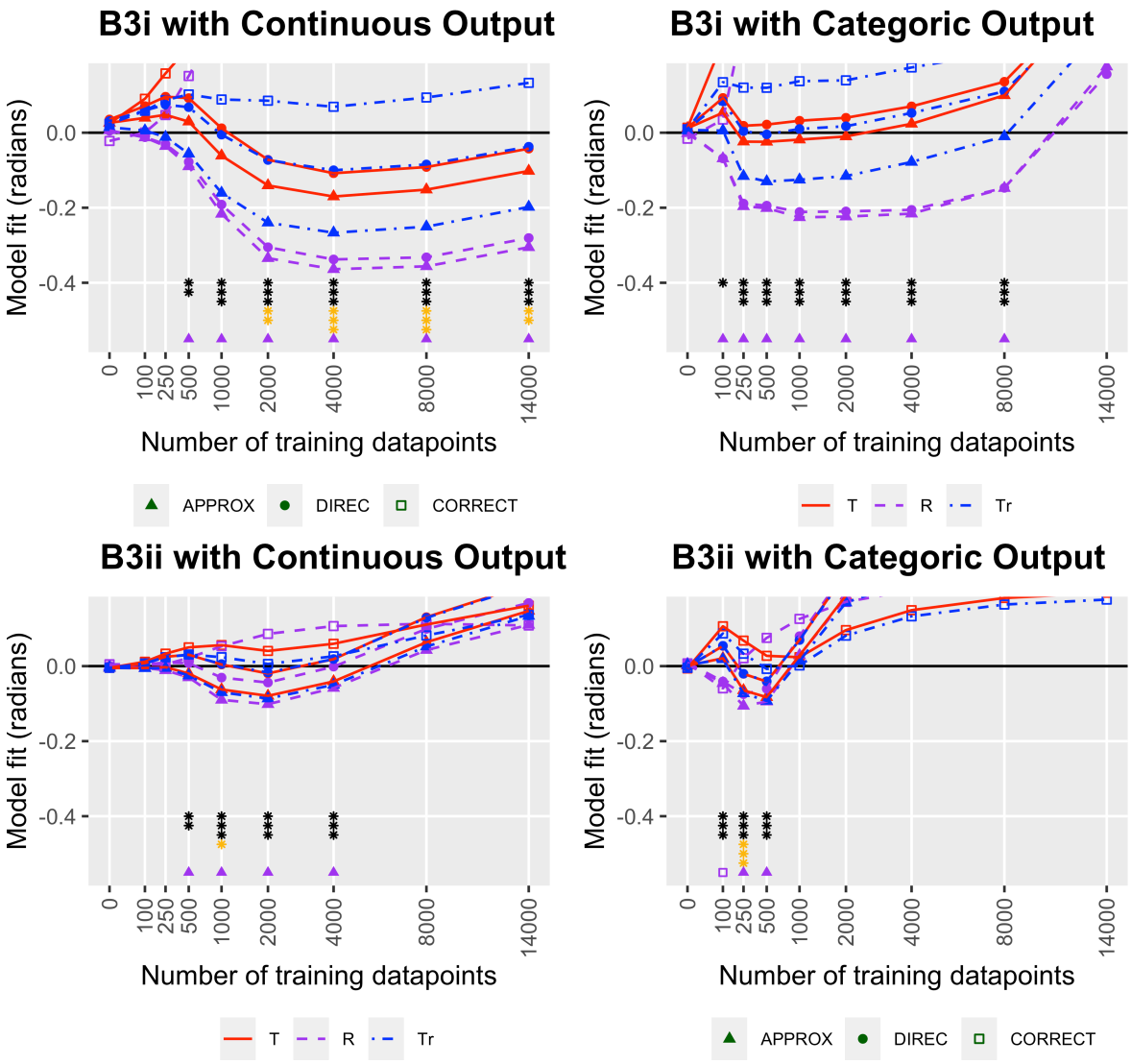


Figure 2.9. Model fit in B3 environments. *The fit of the navigational models relative to the baseline of perfectly accurate performance (no error) is shown. The y axis represents the average absolute difference between the neural network outputs and the model predictions minus the average absolute error of the neural network outputs. A negative number indicates a better fit of the neural network outputs to the predictions of the model than to the baseline of perfectly accurate performance. Combination model and extrapolation model (T=target-based; R=release-based; Tr=training-based) keys are shown under the figures. The x axis is square root transformed. Results from neural networks under the continuous implementation are shown on the left, and those under the categoric implementation on the right. Black stars show where the neural network predictions are significantly closer to that model's predictions than to the*

perfectly accurate solution. In these cases, the identity of the best fitting model is shown by a symbol on the x-axis. Gold stars show where the best fitting model is a significantly better fit than the next best fitting model.

Finally, we trained 100 neural networks under each implementation in environments with non-linearly and orthogonally varying gradients, B4i and B4ii. In these environments, the approximate and correct models produce the same predictions for directional error and so become the approximate/correct model. Here, in every case, the approximate/correct model with training-based extrapolation was the best-fitting model at some stage of training and significantly outperformed the perfectly accurate solution; this can be seen in Fig. 2.9. In three out of the four cases, this model significantly outperformed all others after some training. The exception was the B4ii environment under the categoric output implementation, in which this model outperformed all others except for the approximate/correct model with target-based extrapolation. At the end of training, in the B4ii environment, the neural network outputs under both implementations were significantly closer to the perfectly accurate solution than to any of the navigational models, whereas in the B4i environment, the approximate/correct model with training-based extrapolation was still a better fit to the neural network outputs at the end of training.

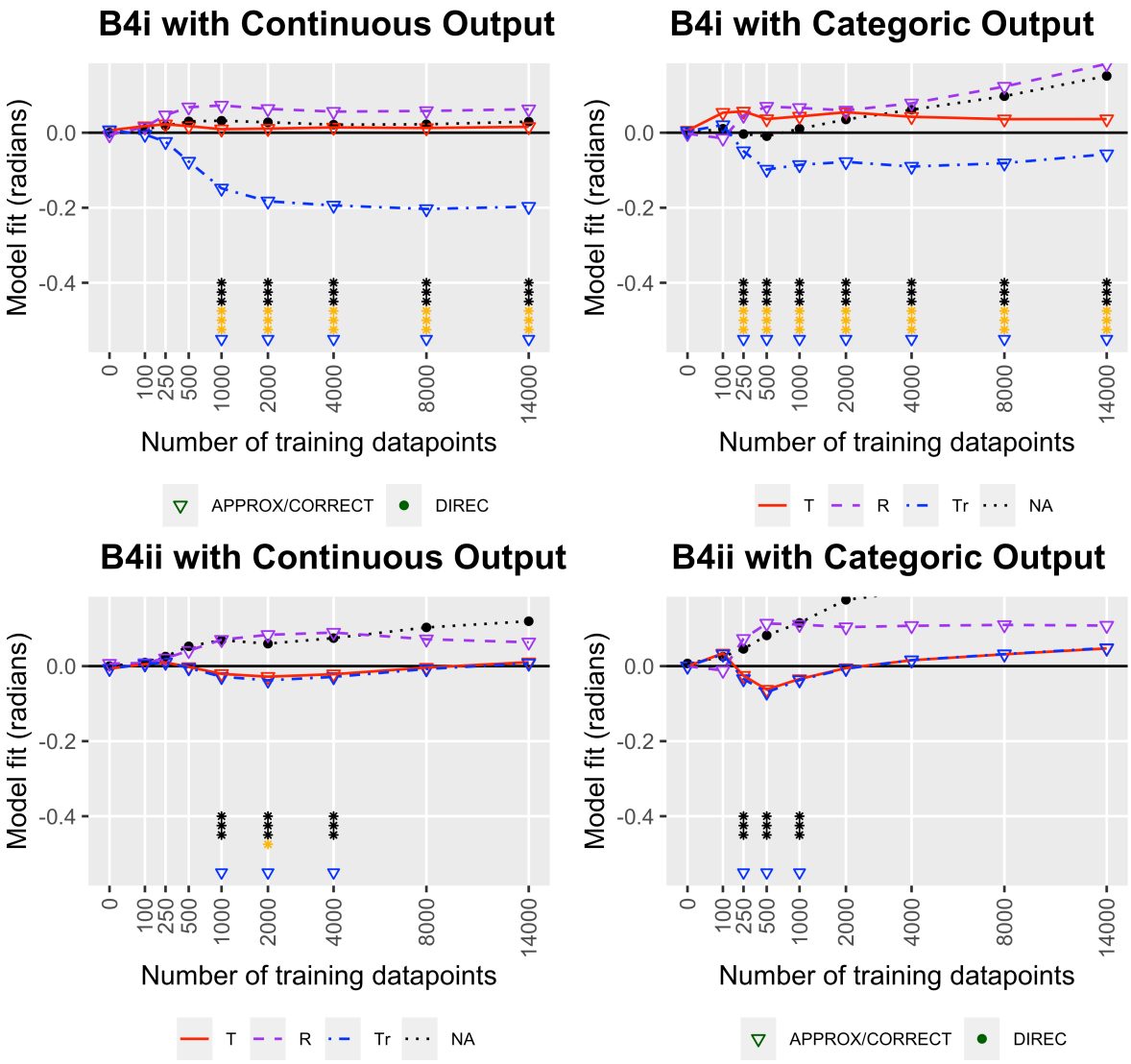


Figure 2.10. Model fit in B4 environments. *The fit of the navigational models relative to the baseline of perfectly accurate performance (no error) is shown. The y axis represents the average absolute difference between the neural network outputs and the model predictions minus the average absolute error of the neural network outputs. A negative number indicates a better fit of the neural network outputs to the predictions of the model than to the baseline of perfectly accurate performance. Combination model and extrapolation model (T=target-based; R=release-based; Tr=training-based) keys are shown under the figures. The x axis is square root transformed. Results from neural networks under the continuous implementation are shown on the left, and those under the categoric implementation on the right. Black stars show where the neural network predictions are significantly closer to that model's predictions than to the*

perfectly accurate solution. In these cases, the identity of the best fitting model is shown by a symbol on the x-axis. Gold stars show where the best fitting model is a significantly better fit than the next best fitting model.

Discussion

Overall, our results indicate that the artificial neural networks adopt the approximate model suggested for animal navigation by Benhamou, in a range of environments, after some training (Benhamou, 2003). This model involves computing a vector of displacement from the goal in each gradient field independently and determining an overall vector of displacement through vector summation. It produces predictable orientation errors in non-orthogonal gradient fields as shown in Fig. 2.1. Across non-orthogonal and linear environments (B2i and B2ii), non-linear and non-orthogonal environments (B3i and B3ii), and non-linear and orthogonal environments (B4i and B4ii; in which it cannot be distinguished from the correct model), the approximate model (combined with a model of extrapolation in non-linear environments) fitted the predictions of the artificial neural networks best of all the navigational models and significantly better than the perfectly accurate navigational solution at some stage of training. In some cases, as detailed above, the approximate model also significantly outperformed all other navigational models. Additionally, Fig. 2.8 allows visual inspection of the close fit between the error predictions of the approximate model across the range of directions from the target and the signed errors at each training datapoint averaged across the population of neural networks at intermediate stages of training in B2i and B2ii. This is despite the much poorer visually-inspected fit of the predictions of the model to the outputs of random neural networks within the population. This demonstrates how the signature of this navigational mechanism can emerge clearly at the level of the population despite being more difficult to detect in the outputs of individual neural networks.

However, in most cases, by the end of training (after 14000 training datapoints), the perfectly accurate navigational solution fitted the artificial neural network predictions better than the approximate model and all other navigational models. The only exceptions were the neural networks with a continuous output implementation trained in environments B3i and B4i, and the neural networks with a categoric output implementation trained in environment B4i. These two

environments were particularly complex (Fig. 2.2) and the neural networks learned to navigate in them more slowly (Fig. 2.5) than in the other environments. We expect that, given sufficient training, these results may have conformed to the patterns observed in the other scenarios, with the perfectly accurate navigational solution eventually fitting the artificial neural networks better than any of the navigational models. In sum, these results appear to indicate that after initial training the neural networks adopt the approximate model to perform grid map navigation, but that after more training, the neural networks improve upon this solution and converge on the perfectly accurate solution. This may lend support to the idea that the approximate model is simpler to execute than the perfectly accurate solution (Benhamou, 2003), and hence is adopted by the artificial neural networks first, but that the neural networks improve upon the approximate model solution later in training.

In more complex environments with non-linear gradient fields, there are a range of possible mechanisms that could be employed to navigate. The models that we tested here assumed a linear extrapolation of the gradient fields following Turner and colleagues (Turner et al., 2016), in combination with a mechanism of combining the two gradients. We tested three models of linearly extrapolating the gradient fields: extrapolating about the target, about each 'release site' (the training and test locations), and extrapolating with the average vector along which the gradients vary across training sites. However, various mechanisms that do not involve a linear extrapolation of the field are possible, and hence the mechanisms modelled here are a small set of the potentially available mechanisms by which navigation could take place in these complex environments. Nonetheless, the consistent finding that the approximate model, in combination with a mechanism of linearly extrapolating the gradient fields, fitted the neural network outputs best at some stage of training provides reasonably strong evidence that this model captures the mechanisms adopted by the neural networks across a wide range of environments. In environments with non-linear and non-orthogonally varying fields (B3i and B3ii), we found evidence for the neural networks adopting release-based extrapolation, whereas, with non-linear

and orthogonally varying fields (B4i and B4ii), we found evidence for the networks adopting training-based extrapolation. The reasons for this difference are unclear but could stem from the fact that in the former environments, both the direction and magnitude of the fields vary in space, whereas in the latter environments, the directions in which the fields vary remain constant through space.

These results held across both implementations of neural networks, in which neural networks either outputted direction via a single continuous output neuron or categorised direction into one of twenty segments with categoric output neurons. This shows that these results were not entirely contingent on the specifics of the neural network implementations, and hence may have captured something more general about how learning of these modelled navigational tasks might occur.

These findings have potential implications regarding the predictions of these navigational models for animal navigation. First, they lend support to the suggestion that the approximate model is simpler to execute than a perfect navigational solution in non-orthogonal environments, and might therefore be adopted by animals (Benhamou, 2003; Turner et al., 2016). Second, while it is possible that animals have fixed mechanisms for extrapolating and combining gradient fields such that the predictions of these models might be met consistently through development, these results demonstrate that if animals learn mechanisms to combine gradient fields in order to navigate, the predictions of these models might only be met in certain stages of development. These mechanisms might then be adopted at some stage of learning and not necessarily maintained through development, but instead improved upon through learning. This is an important qualifier to the predictions of these navigational models and could be crucial for the testing of these model predictions. However, the role of evolution, as well as learning, in tuning the mechanisms by which animals extrapolate and combine gradient cues has not been examined in our models and could predispose animals to navigate and learn to navigate in specific ways.

Finally, these results show how navigational mechanisms adopted by animals could be difficult to detect at the individual level but could emerge clearly at the population level. We anticipate that the proliferation of large tracking datasets of animal movements might allow the predictions of these navigational models to be tested in the coming years. We suggest that full lifetime tracks of animal movements could be particularly valuable for testing for the adoption of these navigational models by animals and facilitate a better understanding of the precise mechanisms and ontogeny of long-distance navigational abilities in animals.

Chapter 3

Do olfactory cues underlie the map of a wild navigational model, the Manx shearwater, *Puffinus puffinus*?

Joe Morford, Sarah Bond, Katrina Siddiqi-Davies, Lewis Fisher-Reeves, Joe Wynn, Andy Morford, Patrick Lewin, Oliver Padget, Tim Guilford

Author contributions

Joe Morford: Conceptualisation, Methodology, Software, Formal analysis, Investigation, Writing – Original Draft, Writing – Review and Editing, Visualisation. **Sarah Bond**: Methodology, Investigation, Writing – Review and Editing, Visualisation, Project Administration. **Katrina Siddiqi-Davies**: Investigation. **Lewis Fisher-Reeves**: Investigation. **Joe Wynn**: Methodology, Investigation. **Andy Morford**: Methodology, Investigation. **Patrick Lewin**: Investigation. **Oliver Padget**: Conceptualisation, Methodology, Supervision. **Tim Guilford**: Conceptualisation, Investigation, Writing – Review and Editing, Supervision, Project Administration.



Thomas Miller

Abstract

Manx shearwaters, *Puffinus puffinus*, are an emerging wild model of long-distance animal navigation. They have been shown to perform map and compass navigation with a time-compensated sun compass in their homing navigation during the breeding season, and magnetic cues have been implicated in their return to the natal colony after first migration. However, it is unknown whether they use olfactory cues in their navigational map, like homing pigeons and *Calonectris* shearwaters, or whether other cues are involved in their map and compass navigation. We set out to investigate whether olfactory cues underlie the navigational map of Manx shearwaters, utilising a less invasive methodology than destroying the olfactory mucosa of the birds, as has previously been carried out in other taxa. Therefore, we displaced Manx shearwaters long distances in filtered air, and manipulated the duration of their access to olfactory cues in fresh air before release, hypothesising that birds with longer access to olfactory cues might initially home more quickly and efficiently. Provisional results, in the first year of the study, indicated a potential relationship between the duration of access to olfactory cues and initial navigational performance. However, a larger sample size in the second year of the study failed to replicate those provisional results. Hence, we found no consistent evidence for olfactory cues underlying the navigational map of these birds and so the identity of the cues involved remains an open question. We believe that revealing the identity of the map cues of Manx shearwaters would represent a step change in our understanding of the navigational mechanisms of this model species, and hence experimental approaches should continue to address this question.

Introduction

Procellariform seabirds exhibit impressive abilities to navigate efficiently over long distances and through relatively featureless environments. In recent years, olfactory cues have been implicated in how these birds navigate, through experimentally inducing anosmia by the application of zinc sulfate to cause necrosis in the cells of their olfactory mucosa (Cancalon, 1982). This experimental manipulation disrupts their navigation, and hence olfactory cues have been attributed as underlying their navigational map (Bonadonna and Gagliardo, 2021). We set out to utilise a less invasive experimental approach to investigate whether olfactory cues might underlie the navigational map of an emerging model species of long-distance pelagic navigation, Manx shearwaters, *Puffinus puffinus*, by manipulating their access to olfactory cues before release after a long-distance displacement.

Kramer introduced the idea that birds might navigate with a map, to determine the direction of goals, and a compass, to determine goal direction in relation to heading and so orient goalward (Kramer, 1953). In homing pigeons, the use of olfactory cues as a navigational map, in combination with a time-compensated sun compass (Schmidt-Koenig, 1990), has been studied extensively (Gagliardo, 2013; Wallraff, 2004), and shown to facilitate their homing navigation from both familiar sites (Gagliardo et al., 2001b; Luschi and Dall'Antonia, 1993) and far-off sites, beyond the range of their previous experience (Gagliardo et al., 2021; Wallraff, 2014b), despite some controversy regarding the precise role of the olfactory cues (Gagliardo et al., 2011; Gagliardo et al., 2018; Jorge et al., 2009; Jorge et al., 2010; Phillips and Jorge, 2014; Walcott et al., 2018; Wallraff, 2014a, b; Wiltschko and Wiltschko, 2017a).

However, there is relatively limited research into the use of olfactory maps in wild birds. Procellariform seabirds, also known as 'tube-nosed' (Tubinares) birds, are a group in which olfactory information is known to play an important role in a range of ecological contexts

(Bonadonna, 2009), from acting as a foraging cue (Dell'Ariccia et al., 2014; Nevitt and Bonadonna, 2005; Nevitt et al., 1995), to facilitating nesting burrow recognition (Bonadonna and Bretagnolle, 2002; Bonadonna et al., 2001; Bonadonna et al., 2004; De León et al., 2003; Dell'Ariccia and Bonadonna, 2013; Zidat et al., 2023). *Calonectris* shearwaters, within the procellariforms, are the wild birds in which the use of olfactory cues as a navigational map is best evidenced and studied. Two species of *Calonectris* shearwater, Cory's shearwaters (*Calonectris borealis*) and Scopoli's shearwaters (*Calonectris diomedea*), have been shown to use olfactory cues in experiments that disrupted their access to olfactory information through application of zinc sulfate to their olfactory mucosa (Benvenuti et al., 1993; Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015). In these experiments, shearwaters with disrupted olfactory information exhibited impaired homing performance to their island colonies compared to controls. Additionally, one of these experiments examined both homing and foraging behaviour, finding an effect only on homing behaviour, potentially indicating a specific effect on the navigation of these birds, rather than a non-specific effect of the application of zinc sulfate such as on the motivation of the birds to home (Padget et al., 2017). Additional evidence for the use of an olfactory map in these two species, as well as the Cape Verde shearwater (*Calonectris edwardsii*), has been obtained through analysis of their free-ranging movement patterns (Abolaffio et al., 2018; Reynolds et al., 2015), showing that these patterns are consistent with theoretical expectations of an olfactory map navigational mechanism. However, outside of the *Calonectris* shearwater clade, it is unknown whether procellariforms utilise olfactory cues as a navigational map.

Manx shearwaters (*Puffinus puffins*), as an emerging model of long-distance animal navigation, are an interesting species in which to investigate map and compass navigation. The remarkable long-distance navigational abilities of these birds have been recognised and experimentally studied since the middle of the last century (Lack and Lockley, 1938; Lockley, 1942; Matthews, 1953b). Manx shearwaters are from the *Puffinus* shearwater clade, which split from *Calonectris*

(and *Ardenna*) shearwaters more than 15 million years ago (Estandía et al., 2021; Ferrer Obiol et al., 2022). These shearwaters have been shown to use a time-compensated sun compass in their homing navigation, like homing pigeons (Padget et al., 2018), which is likely indicative of map and compass navigation. This is further evidenced by a correlational analysis of their free-ranging homing that suggested Manx shearwaters navigate according to the beeline distance and direction of their colonies from far-off homing sites (Padget et al., 2019). These results present the possibility that Manx shearwaters navigate with highly similar mechanisms to homing pigeons; however, it is unknown whether they use an olfactory map, like homing pigeons and *Calonectris* shearwaters, and/or different sources of map information. A recent correlational study implicated a role for magnetic cues in the natal philopatry of Manx shearwaters; however, the extent of the role of magnetic cues in their navigation is currently unclear (Wynn et al., 2020). This opens the possibility that Manx shearwaters use a magnetic map to guide their homing, despite the fact that experiments on other procellariform taxa have found no evidence for the use of a magnetic map (Bonadonna et al., 2005; Mouritsen et al., 2003; Padget et al., 2017; Pollonara et al., 2015). Visual cues are another possible source of map information for Manx shearwaters; these play an important role in familiar area navigation of homing pigeons (Biro et al., 2004; Gagliardo et al., 1999; Gagliardo et al., 2001b; Guilford and Biro, 2014; Luschi and Dall'Antonia, 1993; Mann et al., 2014; Meade et al., 2006) and some procellariforms, especially in the absence of olfactory cues (Padget et al., 2017; Pollonara et al., 2015). Hence, olfactory, magnetic and visual cues could underlie the navigational map of Manx shearwaters, potentially singly or in combination. Overall, previous work on the map and compass navigation of these shearwaters, their use of a time-compensated sun compass, and their likely use of magnetic cues during migratory navigation, make the Manx shearwater an interesting model species in which to investigate the basis of a navigational map.

We set out to investigate whether olfactory cues play a role in the homing navigation of Manx shearwaters, utilising a methodology that was less invasive than application of zinc sulfate to the

olfactory mucosa of the birds, and which would specifically affect the navigation of these birds. We transported shearwaters from their breeding colony to a distant release site in filtered air. We allowed the birds access to the fresh air of the release site for a variable duration before releasing them and tracking their return journeys to the breeding colony with miniature onboard GPS devices. We hypothesised that shearwaters with longer exposure to the olfactory cues in the fresh air at the release site might initially home more quickly and efficiently. This design was based upon an experiment carried out by Wallraff and colleagues on homing pigeons, in which pigeons spending several hours with access to the fresh air at a release site prior to release were oriented significantly differently from controls that were kept in filtered air (Wallraff et al., 1984). Several other experiments have demonstrated that homing pigeons attend to olfactory cues prior to release, and utilise these cues in their subsequent navigation (Benvenuti and Wallraff, 1985; Dall'Antonia et al., 1999; Gagliardo et al., 2001b; Gagliardo et al., 2016; Kiepenheuer, 1985; Papi et al., 1984; Wallraff et al., 1984). We initially carried out this experiment in 2021, which indicated a potential relationship between duration with access to olfactory cues before release and the initial navigational performance of the birds. Subsequently, we repeated the experiment in 2022 with a larger sample size but failed to replicate the provisional results found in 2021. The results from both 2021 and 2022 are presented and discussed below.

Methods

This experiment was piloted in 2021 and then repeated in 2022 with a larger sample size. Adult Manx shearwaters, *Puffinus puffinus,* incubating eggs in breeding burrows at a colony on Skomer island (51°44'14.9"N, 5°17'00.9"W), were transported to a release site at Ogmore-by-Sea (51°27'15.8"N, 3°37'31.7"W), approximately 120km away. Before displacement, birds were fitted with igotU GT-120 miniature GPS loggers using TESA marine tape (total deployment mass between 15g and 16g; for more details see (Guilford et al., 2008)), which were programmed to take GPS fixes every 10 seconds. 27 shearwaters were released across 2 separate days in 2021 and 37 shearwaters were released across 3 separate days in 2022, with 21 and 28 usable GPS tracks of their homing trajectories obtained in the two years, respectively.

Birds were transported the initial 2-3km from their colony on Skomer Island by boat to Martin's Haven on mainland Wales in cardboard boxes. Subsequently, birds were transported by van from Martin's Haven to Ogmore-by-Sea, in airtight containers ventilated with air which had been passed through an activated charcoal filter. After arrival at Ogmore-by-Sea, the birds' containers were ventilated with fresh air, switched from filtered air, at this site for differing lengths of time, between 0 and 120 minutes. This applied treatment time was random with respect to release order. Subsequently, birds were transported on foot to the water's edge (<1km), where they were released singly at times when no gulls were in sight, to minimise the risk of predation. Birds were not released until the previous bird had disappeared out of sight. Birds were released between 1300 and 1900 BST. The final step of transportation to the water's edge and release took an average of 16 minutes. During these final steps of transport and release, the birds were exposed to the fresh air at the release site, and this is combined with the applied treatment time to constitute the total treatment time (the total duration of time exposed to fresh air at the release site). This is shown for each bird in Fig. 3.1, broken down into time ventilated with fresh air, and time for final steps of transport and release. Unfortunately, a confound emerged between

total treatment time and release time in the second release day (15th June) of 2021; this was not the case for any other release.

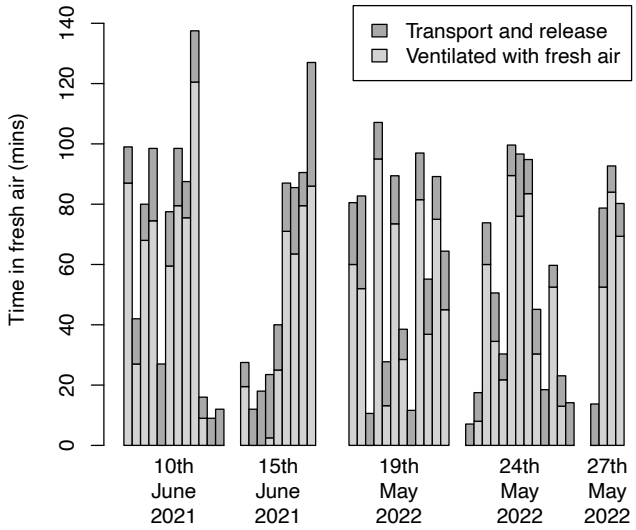


Figure 3.1. Fresh air exposure treatment. *The total amount of time exposed to the fresh air at the release site for each bird is shown, with each bar representing one bird from which a GPS track usable in the analysis was obtained. The bars are presented along the x-axis in order of release.*

The shearwaters were recaptured, and their GPS devices retrieved, upon their return to their breeding burrows on the first or second night following release. They were then returned back into their burrow and allowed to resume incubation.

As the shearwaters would have had access to olfactory cues after release, we expected any effect to manifest in the initial homing sections of the GPS tracks. We therefore isolated the sections of the tracks before the shearwaters left a 2km, 5km and 10km radius of the release site for the final time (in most cases, also the first time) to undertake three separate analyses. Additionally, analyses were undertaken separately on the 2021 pilot experiment data and the

2022 experiment data, as the pilot experiment was analysed at the end of 2021 before undertaking the experiment in 2022 with a larger sample size.

For each initial track section, we calculated three metrics: (1) the virtual vanishing time, the duration of time taken for the bird to leave the given radius of the release site for the final time; (2) the individual mean vector length of successive orientations from each GPS fix to the next within the initial track section; and (3) the efficiency index, calculated as the total length of the track section divided by the beeline distance moved.

These metrics were analysed with respect to the total treatment time using with linear models, with the general formula:

Metric ~ Treatment time (continuous predictor)

+ Release day (discrete factor)

+ Release time (continuous predictor; coded as minutes since noon)

Fit to the assumptions of linear modelling was checked by inspecting Q-Q plots and residual versus fitted value scatterplots. P-values were taken from the ANOVA table, calculated using Type II Sums of Squares (Fox and Weisberg, 2011). Release day and release time were included to account for any variance explained by different release conditions across the different times and days. Statistical analysis and graphical output was produced using R (R-Core-Team, 2018; RStudio-Team, 2020), using the R packages: circular (Agostinelli and Lund, 2022), ggplot2 (Wickham, 2016), stringr (Wickham, 2022), geosphere (Hijmans, 2022), car (Fox and Weisberg, 2011), rnaturalearth (Massicotte and South, 2023) and cowplot (Wilke, 2020).

Ethical note

This work was conducted after ethical approval by Natural Resources Wales (Licence: S089652/1 (2021) and S091097/1 (2022); granted under the Wildlife and Countryside Act

1981, amended by the Environmental Protection Act 1990), the Islands Conservation Advisory Committee for Skomer and Skokholm Islands, and the University of Oxford Department of Zoology's Local Animal Welfare and Ethical Review Body. Bird handling and GPS deployments were undertaken under licences granted by the British Trust for Ornithology.

In 2022, immediate effects on breeding success were compared between nests from which a bird had been displaced and controls, from the same part of the colony. Burrows were checked a minimum of 6 days after displacement procedures to check for whether the egg was still being incubated or whether the nest had failed. Of 38 nests from which a bird had been displaced, 5 nests failed in the days immediately subsequent to release, whereas 10 of the 36 control nests failed during the same period. Therefore, immediate failure was no higher in nests involved in the experiment compared to controls. Planned monitoring of these burrows later in the breeding season to obtain estimates of breeding success were cancelled owing to the Avian Influenza outbreak. Unfortunately, one bird released in 2022, despite being initially released successfully and flying rapidly from the release site, was attacked by a peregrine falcon (*Falco peregrinus*) when it was close to disappearing from sight. The peregrine caught the shearwater and flew with it back to its nest. This was very unexpected, as we had sought experienced advice before the experiment on the likelihood of a peregrine attack at sea, and the consensus was that this was extremely unlikely. Indeed, none of our experienced team, nor those from whom we sought advice, had ever observed a single instance of a peregrine falcon catching a shearwater. After this occurred, it was decided that it would not be safe or wise to release any more shearwaters from that site, and hence the experiment was stopped and the remaining shearwaters were released after dark at Martin's Haven, close to their breeding colony.

Results

The 50 homing GPS tracks that were used in the analysis are shown in Fig. 3.2, with 21 from 2021 and 28 from 2022. The tracks from 2021 and 2022 were analysed separately, with respect to the length of time each bird had access to the fresh air, containing the olfactory cues, at the release site before release (the treatment time). The analysis was focussed upon the initial sections of the tracks, within 2km, 5km and 10k from the release site. We hypothesised that, if Manx shearwater use olfactory cues as a navigational map, birds with longer access to the olfactory cues in the fresh air of the release site prior to release would leave the vicinity of the release site more quickly, would initially exhibit stronger orientation and would initially navigate more efficiently. This would be detected by a negative relationship between treatment time and virtual vanishing time, and positive relationships between treatment time and both individual mean vector length and efficiency index.

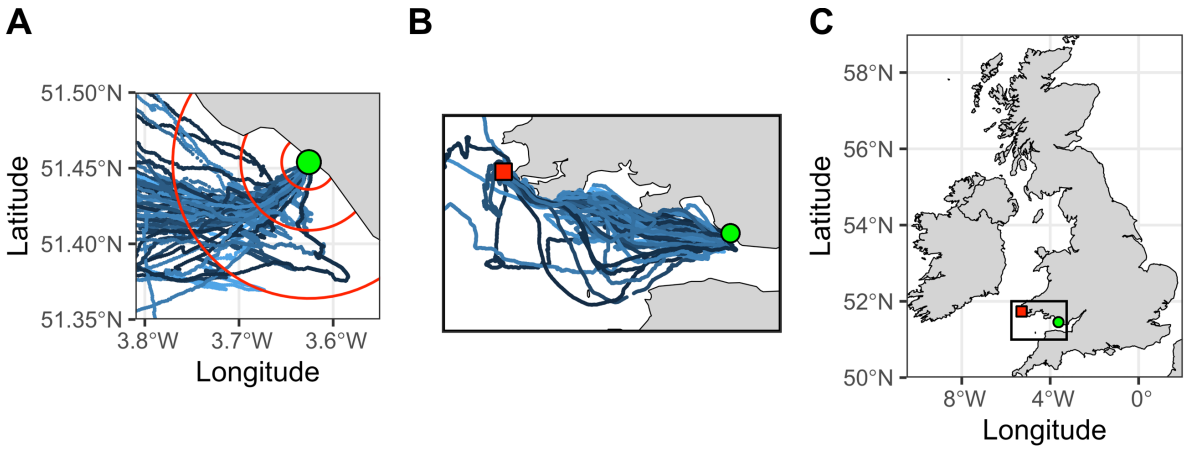


Figure 3.2. GPS tracks after release at Ogmore-by-Sea in 2021 and 2022. *The initial track portions after release and the full homing tracks are shown in panels A and B. A green circle indicates the release site at Ogmore-by-Sea, approximately 120km from the home colony of the birds, shown with a red square. The treatment of the birds is shown by the darkness of the points on the tracks: birds with longer treatment times have paler GPS points. The three distances (2km,*

5km and 10km) from the release site in which analysis was undertaken are represented in Panel A by the red arcs. The location of the map in Panel B within the British Isles is shown in Panel C.

Pilot analysis: 2021 tracks

We found a significant negative relationship between the virtual vanishing time of the birds at 5km and the and the treatment time (N = 21; effect size = -0.18; confidence interval = (-0.33, -0.040); P = 0.015). Hence, birds with longer access to the olfactory cues in the fresh air before release were quicker to leave 5km of the release site. This is shown in the top panel of Fig. 3.3. However, we found no significant relationship between the virtual vanishing times and the treatment time of the birds at 2km (N = 21; effect size = -0.0070; confidence intervals = (-0.027, 0.013); P = 0.46) or 10km (N = 21; effect size = 0.066; confidence interval = (-0.27, 0.40); P = 0.68). The release time was also found to be a significant predictor of virtual vanishing time at 5km from the release site (P = 0.043), but not at 2km (P = 0.43) or 10km (P = 0.65). On the other hand, the release day was a significant predictor of virtual vanishing time at 10km from the release site (P = 0.011), but not at 2km (P = 0.099) or 5km (P = 0.89).

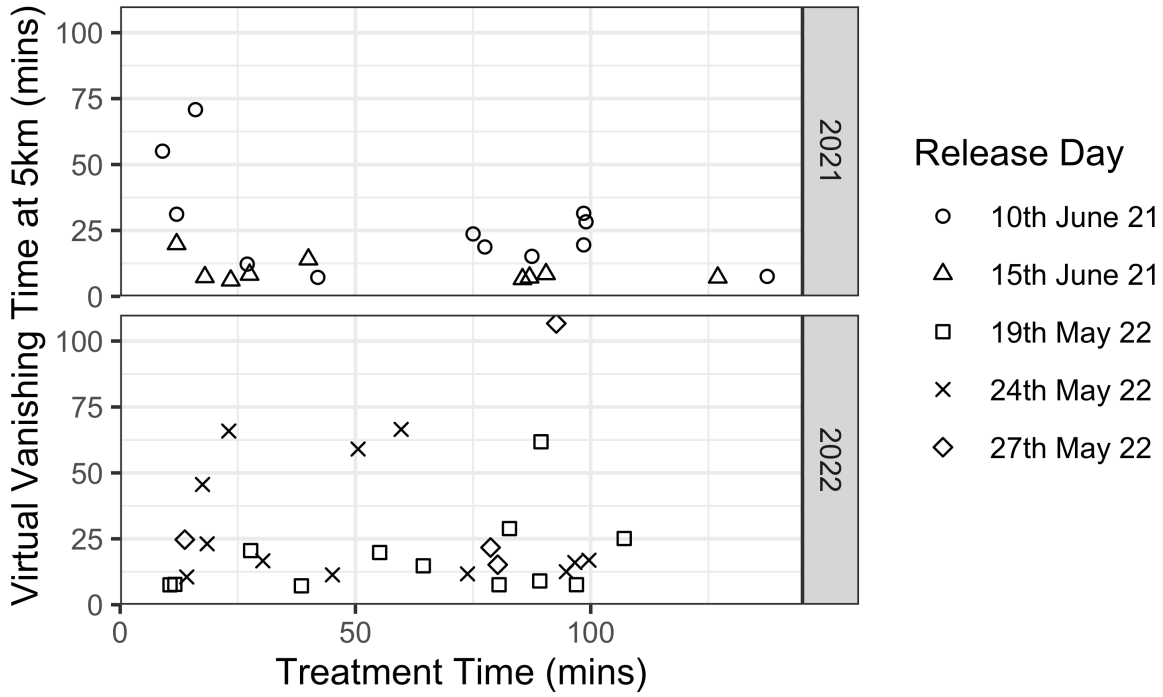


Figure 3.3. Virtual vanishing time at 5km. *The virtual vanishing times of birds and their treatment times are shown, with birds released in 2021 in the top panel, and 2022 in the bottom panel. A significant negative relationship was found in 2021, but this failed to replicate with a larger sample size in 2022.*

We found a significant positive relationship between the individual mean vector lengths of successive orientations and the treatment time in the first 2km section of the tracks (N = 21; effect size = 0.00094; confidence interval = (0.00021, 0.0017), P = 0.015), shown in the top panel of Fig. 3.4, but not the first 5km (N = 21; effect size = 0.0016; confidence interval = (-0.00022, 0.0035); P = 0.080), or 10km sections of the tracks (N = 21; effect size = -0.00053; confidence interval = (-0.0026, 0.0015); P = 0.59). Release day was not found to be a significant predictor of the individual mean vector lengths in the first 2km (P = 0.53), 5km (P = 0.22), or 10km track sections. (P = 0.89). The release time was found to be a significant predictor of the vector lengths in the first 10km track sections (P = 0.0097), but not in the first 2km (P = 0.34) or 5km sections (P = 0.11).

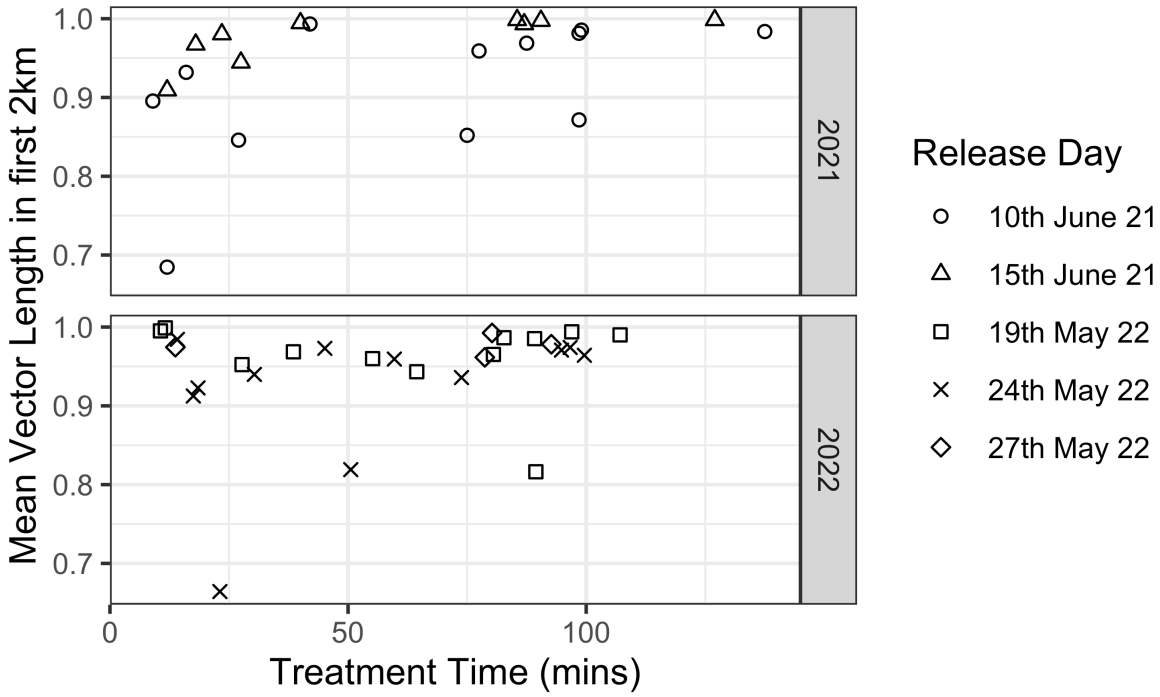


Figure 3.4. Mean Vector Lengths of Successive Orientations in first 2km. *The mean vector lengths of the successive orientations of birds and their treatment times are shown, with birds released in 2021 in the top panel, and 2022 in the bottom panel. A significant positive relationship was found in 2021, but this failed to replicate with a larger sample size in 2022.*

We found no significant relationships between the efficiency index and the treatment time in the first 2km (N = 21; effect size = 0.00017; confidence interval = (-0.000057, 0.00040); P = 0.13), 5km (N = 21; effect size = 0.0014; confidence interval = (-0.00026, 0.0031); *P* = 0.094), or 10km of the tracks (*N* = 21; effect size = -0.0017; confidence interval = (-0.0034, 0.000040); *P* = 0.055). We found release day to be a significant predictor of the efficiency index in the first 10km sections of the tracks (*P* = 0.0036), but not in the first 2km (P = 0.16), or 5km sections (*P* = 0.55). Release time was not found to be a significant predictor of the efficiency index in the first 2km (*P* = 0.84), 5km (*P* = 0.14), or 10km track sections (10km: *P* = 0.97).

Main analysis: 2022 tracks

Analysis of a greater number of tracks was undertaken in 2022 to attempt to replicate the relationships found between the treatment time and both the virtual vanishing time and the individual mean vector lengths in the 2021 tracks. However, these results did not replicate, with no significant relationships between the treatment time and any of the navigational metrics in 2022.

No significant relationship was found between virtual vanishing time and the time exposed to fresh air at the release site at 2km (N = 28; effect size = -0.0048; confidence interval = (-0.032, 0.023); P = 0.72), 5km (N = 28; effect size = 0.064; confidence interval = (-0.24, 0.37); P = 0.67), or 10km distances (N = 28; effect size = 0.14; confidence interval = (-0.32, 0.60); P = 0.54). We therefore failed to replicate the significant relationship found between the virtual vanishing time at 5km and the treatment time found in 2021; this result, from 2021 and 2022, is shown in Fig. 3.3. Neither did we find any relationship between the release day and the virtual vanishing time at these distances (2km: P = 0.22; 5km: P = 0.23; 10km: P = 0.11) nor between the release time and the virtual vanishing time (2km: P = 0.46; 5km: P = 0.99; 10km: P = 0.29).

We failed to replicate the relationship found in 2021 between individual mean vector length and treatment time in the first 2km track sections, with no significant relationship found in 2022 (N = 28; effect size = 0.00029; confidence interval = (-0.00059, 0.0012); P = 0.50); this is shown in Fig. 3.4. Additionally, we found no significant relationship between the individual mean vector lengths of successive orientations and the treatment time in the first 5km (N = 28; effect size = -0.00026; confidence interval = (-0.0031, 0.0026); P = 0.85), or 10km sections of the tracks (N = 28; effect size = -0.0014; confidence interval = (-0.0035, 0.00066); P = 0.17). We found a significant relationship between the vector lengths and the release day in the first 10km (10km: P = 0.036), but not in the first 2km (P = 0.54) or 5km track sections (P = 0.23) or between the vector lengths and the release times in those sections of the tracks (2km: P = 0.99; 5km: P = 0.063; 10km: P = 0.13).

Finally, we found no significant relationships between the efficiency index and the treatment time in the first 2km (N = 28; effect size = 0.000018; confidence interval = (-0.00044, 0.00048); P = 0.94), 5km (N = 28; effect size = -0.00022; confidence interval = (-0.0023, 0.0019); P = 0.83), or 10km of the site (N = 28; effect size = -0.00081; confidence interval = (-0.0028, 0.0012); P = 0.41). We found a significant relationship between efficiency index and release day in the first 10km section of the tracks (P = 0.011), but not in the first 2km or 5km sections of the tracks (2km: P = 0.67; 5km: P = 0.38). Finally, we found no significant relationships between the efficiency index and the release time in the first 2km, 5km or 10km sections of the tracks (2km: P = 0.19; 5km: P = 0.88; 10km: P = 0.87).

Discussion

Overall, we found no evidence that longer access to olfactants in the fresh air at a release site affects initial navigational performance, as none of the tested metrics showed significant results that replicated across both years of the study. While two of these metrics showed significant relationships with the treatment duration in the predicted direction in the 2021 pilot data, in 2022, with a larger sample size, there was no significant effect of treatment time on any of the tested metrics. We interpret that these contrasting results in the 2021 pilot analysis and the 2022 main analysis may be driven by chance, with 9 hypothesis tests in the 2021 pilot analysis turning up 2 significant results that could not be replicated with a larger sample size in 2022. Therefore, we found no clear evidence to suggest that olfactory cues underlie the navigational map of Manx shearwaters. There are multiple possible explanations for the lack of any consistently significant effect found in this study.

First, the sample size of 21 GPS tracks in the pilot study in 2021 and 28 tracks in the main study in 2022 may have been insufficient to detect a small effect on the initial homing navigation of the Manx shearwaters. This sample size is much smaller than the analogous experiment in homing pigeons, in which Wallraff showed differences in orientation between pigeons that had access to fresh air versus filtered air prior to release (Wallraff et al., 1984). However, Wallraff's study utilised observational vanishing metrics to analyse orientation, as it predated the use of miniaturised onboard GPS technology to provide much greater temporal and spatial resolution on the movements of birds post-release. In more recent work, the pre-release manipulation of access to visual cues was detectable in the differences in GPS track efficiencies of homing pigeons between treatments (Biro et al., 2002), with a sample size of pigeons at each release site smaller than the number of birds in the current study. Additionally, all of the previous studies on olfactory navigation in *Calonectris* shearwaters, in which differences were detected between the homing navigation of control and anosmic birds, had smaller overall sample sizes than the

sample size used in the current study (Gagliardo et al., 2013; Padget et al., 2017; Pollonara et al., 2015). However, the method used in those experiments, in which the birds' access to olfactory cues was disrupted during their homing navigation, likely generated a much larger effect of treatment than any potential effect induced in this study. In our experiment, access to olfactory cues was only manipulated pre-release, and hence any effect would only be expected in the initial portion of the track. In general therefore, it is difficult to necessarily conclude whether the sample size used in this experiment should have been large enough to detect an effect of pre-release access to olfactory cues. This is because of the lack of directly comparable previous experiments, and so it is not possible to rule out that the sample size used in this experiment was insufficient to detect an effect of duration with pre-release access to olfactory cues on the navigation of the shearwaters.

A second possible explanation for the lack of a detectable relationship between treatment time and initial navigation performance in this study is that the experimental design was inappropriate for detecting the use of an olfactory navigational map in shearwaters. While we know that homing pigeons attend to both visual and olfactory cues before release and that this can be detected in their homing trajectories (Baldaccini et al., 1982; Benvenuti and Wallraff, 1985; Biro et al., 2002; Braithwaite and Guilford, 1991; Dall'Antonia et al., 1999; Gagliardo et al., 2001b; Kiepenheuer, 1985; Papi et al., 1984; Wallraff et al., 1984), this might not be the case in other birds, potentially because, unlike homing pigeons, they are not accustomed to displacement and release. Additionally, it is possible that pre-release manipulations were negated by the access of all birds to olfactory cues after release, given that the birds were not made anosmic in this experiment. However, differences in access to olfactory cues prior to release were sufficient to generate orientation differences between groups of pigeons in Wallraff's experiment despite both groups having access to olfactory cues immediately after release. Either of these possibilities could have prevented this experiment from being able to detect a relationship between treatment time and initial navigational performance, even if Manx shearwaters do use an olfactory navigational map.

It is also possible that, unlike *Calonectris* shearwaters, Manx shearwaters might not use olfactory map cues. Both a previous experiment manipulating their sun compass (Padget et al., 2018) and a correlational study showing they navigate according to the beeline distance and direction of their colonies both indicate that they use map and compass navigation when homing (Padget et al., 2019). However, they may use other map cues in combination with their time-compensated sun compass to perform map and compass navigation, such as visual or magnetic map cues. The topography of the British Isles may facilitate a role for the use of familiar visual landmark cues in their homing navigation. Visual cues play an important role in pigeon homing navigation, both providing map information to be used in combination with a compass (Gagliardo et al., 1999; Gagliardo et al., 2001b; Luschi and Dall'Antonia, 1993), and in facilitating route-following navigation (Biro et al., 2004; Guilford and Biro, 2014; Lau et al., 2006; Mann et al., 2014; Meade et al., 2006). Visual cues also appear to be used by *Calonectris* shearwaters after being made anosmic (Padget et al., 2017; Pollonara et al., 2015). The use of familiar visual cues may also explain the partial effect of clockshift in the previous experiment that demonstrated that Manx shearwaters use a time-compensated sun compass (Padget et al., 2018). The use of magnetic inclination has been implicated in the natal philopatry of Manx shearwaters on return from their first migration as a potential indicator of latitude (Wynn et al., 2020); this opens the possibility of the use of a magnetic map in Manx shearwaters. Hence, there is a range of possible map cues that Manx shearwaters might utilise in their map and compass navigation.

This experiment was unable to provide evidence to suggest that Manx shearwaters use olfactory cues as a navigational map; hence, what cues underlie their navigational map remains an open question. We believe that understanding the identity of the map cues of Manx shearwaters would represent a step change in our understanding of the navigational mechanisms of this model species, and hence experimental approaches should continue to address this question. Finally, we

hope that methodologies with relatively low invasiveness, like we employed here, continue to be developed to carry out these experiments on the navigation of wild birds.

Chapter 4

Homing pigeon, *Columba livia*, navigational ontogeny: no evidence that exposure to a novel release site is sufficient for learning

Joe Morford, Anna Gagliardo, Enrica Pollonara, Tim Guilford

Author contributions

Joe Morford: Conceptualisation, Methodology, Software, Formal analysis, Investigation, Writing – Original Draft, Writing – Review and Editing, Visualisation. Anna Gagliardo: Conceptualisation, Methodology, Investigation, Writing – Review and Editing, Supervision, Project Administration. Enrica Pollonara: Investigation, Writing – Review and Editing. Tim Guilford: Conceptualisation, Writing – Review and Editing, Supervision.



Joe Morford

Abstract

The navigational mechanisms of homing pigeons have been extensively studied and represent a useful model for the navigation of birds and other animals. Pigeons navigate with an olfactory map and sun compass from unfamiliar areas and, in familiar areas, are largely guided by visual landscape cues, following stereotyped and idiosyncratic routes. However, the mechanisms by which they gain familiarity, improve their navigation, and transition between navigational strategies during learning, are not fully understood. Addressing these outstanding questions in this navigational model will help to improve our understanding of navigational ontogeny. We sought to investigate whether passive exposure to the cues at a site, without release, was sufficient for navigational learning, given that pigeons can determine the home direction before taking off. We exposed pigeons to cues at a novel site before returning them to the site the next day and releasing them alongside controls. We found no differences in the directional distributions, mean vector lengths, virtual vanishing times, efficiency indices, or homing efficiency indices between birds that had and had not previously visited the site. We therefore found no evidence to suggest that passive exposure to the cues at a novel site was sufficient to facilitate a detectable improvement in navigational performance. There are three possible explanations for this result: first, a larger sample size would have detected a weak effect of learning; second, passive exposure to a release site is insufficient to generate navigational learning; and third, pigeons learn from passive exposure but do not rely upon this information, showing no difference in performance, despite learning. We discuss these three explanations with reference to previous findings on navigational learning in homing pigeons. We suggest that experiments should continue to examine navigational ontogeny in homing pigeons to help address this major problem for the field of navigation.

Introduction

Homing pigeons, *Columba livia*, represent an excellent model species to investigate questions relating to the navigation of birds and other animals. The mechanisms by which they navigate home in both familiar and unfamiliar areas have been extensively studied, and many of these findings have been highly applicable to animals across a range of contexts and taxa (Bonadonna and Gagliardo, 2021; Gagliardo et al., 2013; Padget et al., 2018; Padget et al., 2017; Perez et al., 1997; Pollonara et al., 2015; Safi et al., 2016; Wiltschko and Balda, 1989).

From unfamiliar areas, pigeons are able to navigate home through a 'map-and-compass' mechanism (Kramer, 1953), using a distributed map of environmental odour cues (Gagliardo, 2013; Gagliardo et al., 2011; Gagliardo et al., 2018; Papi et al., 1972; Wallraff, 2005b; Wallraff, 2014b) and a time-compensated sun compass (Guilford and Taylor, 2014; Schmidt-Koenig, 1990). Learning of an olfactory map occurs during the first months after fledging, when pigeons memorise the odours carried by winds blowing at their home loft in association with the wind's direction (Gagliardo et al., 2001a; Odetti et al., 2003). Then, upon displacement, pigeons can determine their direction of displacement from the loft by relying on local environmental odour cues at the release site and orient in that direction using their sun compass (Gagliardo, 2013).

Soon after release and during the entire homing flight, pigeons gain familiarity with the traversed areas, so that even after a single homing experience from a site, birds improve their navigational efficiency, with better homeward orientation and shorter flight paths (Gagliardo et al., 2020b). This improvement is likely driven by learning of both olfactory and visual features of the release site and subsequently overflown areas. With successive releases, they gradually develop fidelity to individual idiosyncratic routes (Biro et al., 2004; Guilford and Biro, 2014; Meade et al., 2005). This is presumably concomitant with a change in navigational strategy dominance from solely

using distributed odour cues in combination with the sun compass when the site is initially unfamiliar, to using visually guided mechanisms after both the site and the overflown landscape has become familiar.

A number of studies have shown that displaced pigeons are able to pick up navigational information before being released, and even make navigational decisions before taking off. For instance, exposure to local olfactory cues at an unfamiliar release site prior to release is necessary and sufficient for homeward orientation in pigeons released in anosmic condition (Gagliardo et al., 2016; Wallraff et al., 1984). Consistently, an Immediate Early Genes study on pigeons showed activation of the piriform cortex, an associative telencephalic region involved in olfactory navigation, after exposure to environmental cues at the release site, even if not released (Gagliardo et al., 1997; Papi and Casini, 1990; Patzke et al., 2010). This observation, together with experiments showing homeward orientation in a circular arena before take-off (Chelazzi and Pardi, 1972; Gagliardo et al., 2001b; Mazzotto et al., 1999), suggests that pigeons start to process olfactory information before being released (Gagliardo et al., 2001b). Additionally, exposure to the visual cues of a familiar release site before release can affect homing performance (Biro et al., 2003; Braithwaite and Guilford, 1993; Braithwaite and Newman, 1994; Braithwaite, 1993; Braithwaite and Guilford, 1991), allowing pigeons to determine the home direction before they take off (Gagliardo et al., 2001b). These data raise the question of whether passive exposure to olfactory and visual cues at a novel release site might increase familiarity of pigeons to the site and facilitate navigational decisions, allowing faster vanishing times and lower uncertainty in taking an orientation decision upon subsequent release.

We designed an experiment to determine whether passive exposure to the environmental cues at a release site would be sufficient to improve navigational performance after release on a subsequent day. We exposed pigeons to the environmental cues, including visual and olfactory cues, at one of two sites, before returning them to their loft. On a subsequent day, the pigeons

were released either at the same site (the experimental treatment group) or at the other release site (the controls). We predicted that if passive exposure to the cues at a site would facilitate some navigational learning or increase in familiarity with the site, the vanishing metrics (individual mean directions, mean vector lengths, virtual vanishing times, efficiency indices, and homing efficiency indices) would differ between the two groups in the first kilometres from the release site.

Methods

Forty-nine first-year pigeons hatched at the Arnino field station (Latitude 43°39'26"N; Longitude 10°18'14"E), Pisa, Italy, were used in this study. The pigeons were housed in an aviary and had some experience free-flying and with local (<5km) training releases. At least 2 weeks prior to the experimental releases, all the birds were equipped with a PVC dummy mass, similar in dimension and mass to the GPS data logger they would be carrying, to accustom them to flying with a load. The dummy was attached to the pigeons' back by means of a Velcro strip glued on the feathers, which had been trimmed. For releases, the pigeons were tracked with Mobile Action IgotU GPS loggers (20 g; 44.5x28.5x13mm), with a sampling rate of 1Hz. The positional fixes stored by the loggers included latitude, longitude, date-time and speed.

On 10th August 2021, twelve pigeons were transported to a site in Castelfranco di Sotto (Site 1; bearing home 261°; distance 34.2 km), and twelve were transported to a site in Cecina (Site 2; bearing home 336°; distance 39.3km). At these sites, the pigeons were placed in cages on the roof of the car such that they could view the surrounding landscape. The cages had one open face and an open top and were turned through 90 degrees every half hour (three times). The pigeons therefore were exposed to the cues at the site for 2 hours and facing in all directions. On the subsequent day, all twenty-four birds were transported to the site 1 to be released. After arrival at the release site, the birds were kept inside an opaque airtight container ventilated by air that was filtered through an active charcoal filter. This removed most of the natural odourants contained in the air to ensure that those released last had not had much greater exposure to the olfactory cues at the release site than those released first. The birds were released individually, alternating between treatments, in sunny conditions, with light wind between 08.35 and 11.20 local time.

Similarly on 12th August, twelve pigeons were transported to site 1 and thirteen were transported to site 2 and exposed to the site for two hours using the procedure described above. The next day, these pigeons were released from site 2 between 08.35 and 10.50.

Half of the forty-nine birds had been exposed to the cues at their release site (experimental treatment; green in table below), and half had been exposed to the cues at a different, far-off release site (control treatment; yellow in table below). Summary of experimental design is shown in Table 4.1.

Table 4.1. Experimental design and sample sizes. *Pigeons in the experimental group, which were exposed to a release site and then released from the same site on a subsequent day, are shaded green; pigeons in the control group, which were exposed at one site and then released on a subsequent day at a different, far-off site, are shaded yellow.*

	Released at site 1	Released at site 2
Exposed at site 1	12	12
Exposed at site 2	12	13

Quantitative analyses and statistical procedure

To exclude data likely capturing an initial escape response immediately following release, the initial fixes of the track within a 500m radius of the release site were removed from all analyses. The initial sections of homing in which the pigeons left the release site were then analysed by

isolating the section of the tracks before they left a 2km radius of the release site for the final time. The track sections were visually inspected for instances in which the tracks of two or more birds closely followed each other for a period of time. The timings of these sections were manually checked to determine whether the birds flew together. Where this was identified, if the two or more birds flying together were of the same treatment group, one was randomly excluded from the analyses. However, if they were of different treatment groups, both were excluded, as it would not be possible to attribute any observed behaviours to either treatment group. Fixes with a recorded speed lower than 5km/h were excluded from the analyses to remove stops.

We tested for differences between the groups in their directional distributions of the successive orientations of birds between leaving a 500m radius of the release site and leaving a 2km radius for the last time. This was tested using Two-Sample Hotelling's T-Squared Tests.

Additionally, for each track, four metrics were calculated: the virtual vanishing time, the individual mean vector length, the homing efficiency index, and the efficiency index. The virtual vanishing time represents the time taken for the track to leave the 2km radius of the release site for the final time. To fit better the assumption that the residuals of the models were normally distributed (assessed with Q-Q plots), the virtual vanishing times were log-transformed (natural logarithm). The mean vector length was taken from the calculated individual mean vector averaging the directions, with respect to home, taken by the bird while moving from one point to the next. The homing efficiency index quantifies the efficiency with which the track approaches home (Gagliardo et al., 2016). It is equal to the difference between the distance to home from the release site and the distance to home from where the track leaves the 2km radius of the release site for the final time, divided by the path length. If the homing efficiency equals 1, the pigeon moved in a straight line from the release site in the direction of home. Finally, the efficiency index

was calculated; this is the distance between first and last points in these track sections, divided by the path length.

Differences in these metrics between the treatment groups were assessed with linear models, with the general formula:

Metric ~ Treatment group + Release site

These analyses were repeated with the section of the tracks before they leave a 5km radius of the release site for the final time. The effect sizes (with positive values signifying greater metric values in the experimental group than the treatment group, and in site 2 than site 1), along with the associated confidence intervals and p-values of the effects are reported.

Statistical analysis and graphical output was produced using R (R-Core-Team, 2018; RStudio-Team, 2020), using the R packages: circular (Agostinelli and Lund, 2022), geosphere (Hijmans, 2022), car (Fox and Weisberg, 2011), CircStats (Lund and Agostinelli, 2018), Hotelling (Curran and Hersh, 2021), scales (Wickham, 2018), useful (Lander 2018) and beeswarm (Eklund and Trimble, 2021).

Ethical note

The pigeons were bred and manipulated in accordance with the 57 EU Directive 2010/63/EU on the protection of animals used for scientific purposes. The experiment was approved by the Scientific Ethics Committee of the University of Pisa and by the Italian Ministry of Health (permit number 238/2020-PR).

After any manipulation (application of the Velcro strip) the birds were released in their aviary or in front of it. The opportunity to fly freely around is thought to diminish the stress due to the manipulation.

Results

The directional distributions of the different groups are shown in Figure 1. Each bird is represented by a mean direction of successive orientations with respect to home at 0 degrees. In all cases, the second order mean vectors of successive orientations were directed anticlockwise of the home direction, with longer vectors (indicating stronger orientation) observed in groups of pigeons released at site 1 than site 2. No differences were found in the directional distributions of the two treatment groups after leaving a 2km or 5km radius of the release site (Two-Sample Hotelling's T-Squared Tests; 2km radius: $N = 33$, test statistic = 1.5, $P = 0.49$; 5km radius: $N = 31$, test statistic = 2.8, $P = 0.27$). There was a significant difference in the directional distributions of the groups released at the two different sites after leaving a 2km radius of the release site and after leaving a 5km radius of the release site (Two-Sample Hotelling's T-Squared Tests; 2km radius: $N = 33$, test statistic = 11 $P = 0.012$; 5km: $N = 31$, test statistic = 9.7, $P = 0.018$).

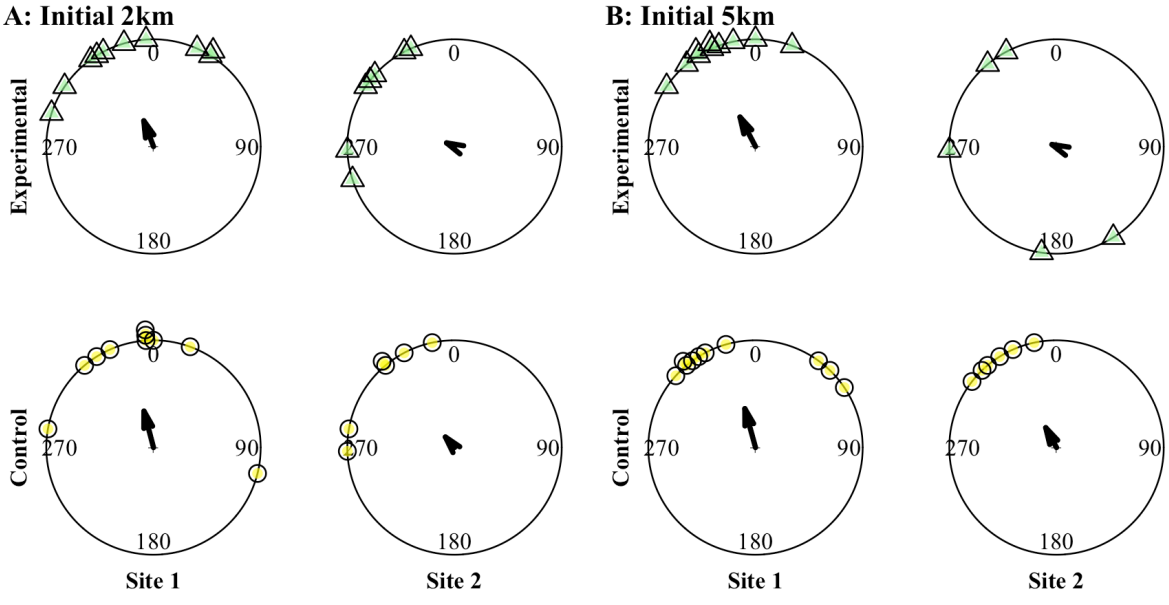


Figure 4.1. Directional distributions of initial orientations. The directions of the successive orientations of birds with respect to home (at 0 degrees), from release up to leaving a 2km radius of the release site for the final time (A), or a 5km radius of the release site (B). Each group is represented by a second order mean vector of successive orientations. The mean direction of successive orientations of birds from the experimental group are represented by green triangles, and the mean direction of birds from the control group are represented by yellow circles. Birds release from site 1 are in the left column of each panel, and those released from Site 2 are in the right column of each panel.

We found no significant difference in the mean vector length of successive orientations (Fig. 4.2) at a 2km or 5km radius between the treatment groups (linear models; 2km radius: N=33, effect size = -0.076; confidence interval = (-0.24, 0.091), p=0.36; 5km radius: N=31, effect size = -0.12, confidence interval = (-0.27, 0.036), p=0.13). There was a significantly greater mean vector length at site 1 than at site 2 at both a 2km and 5km radius (2km radius: effect size = -0.24, confidence interval = (-0.41, 0.069), p=0.0075; 5km radius: effect size = -0.24, confidence interval = (-0.40, -0.081), p=0.0046), indicating a stronger orientation of birds released at site 1 than site 2.

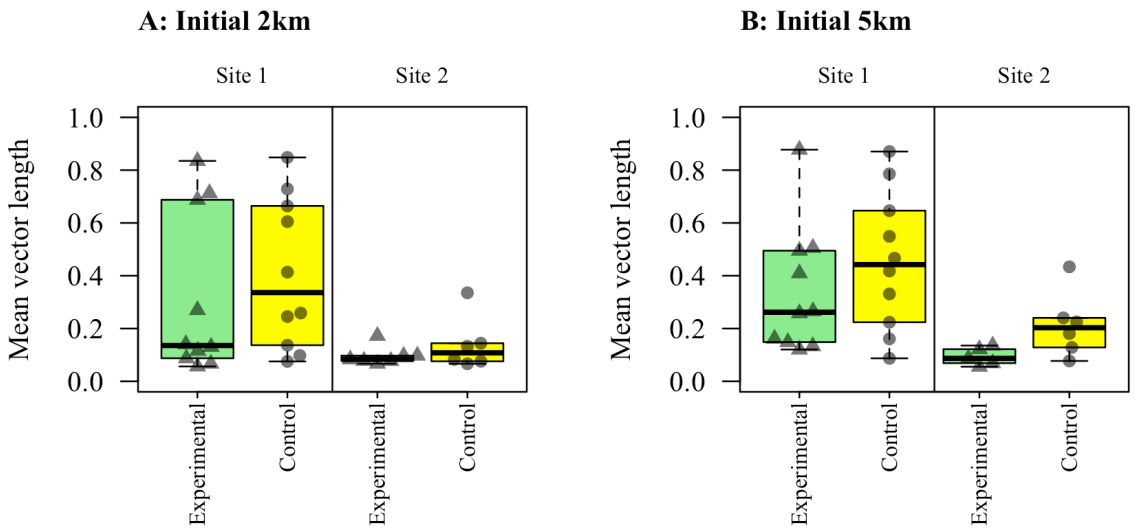


Figure 4.2. Mean vector lengths of successive orientations in initial homing paths. Boxplots are shown of the mean vector lengths of successive orientations of birds leaving 2km from the release site for the final time (A), or 5km from the release site for the final time (B). The datapoints of the mean vector lengths for the individual birds are also shown over the top of the boxplots. The experimental group is represented by green boxplots and triangular points, and the control group is represented by yellow boxplots and circular points.

We found no significant difference in the virtual vanishing time (log-transformed) of the tracks (Fig. 4.3) at a 2km or 5km radius between the treatment groups (linear models; 2km radius: N=34, effect size = 0.57, confidence interval = (-0.66, 1.8), p=0.35; 5km radius: N=32, effect size = 0.70, confidence interval = (-0.31, 1.7), p=0.17). There was a significantly greater virtual vanishing time in the birds released at site 2 than at site 1 at a 2km radius (effect size = 1.5, confidence interval = (0.22, 2.8), p=0.022) and a 5km radius (effect size = 1.7, confidence interval = (0.66, 2.8), p=0.002), indicating that birds released at site 1 were quicker to leave the vicinity of the release site than those released at site 2.

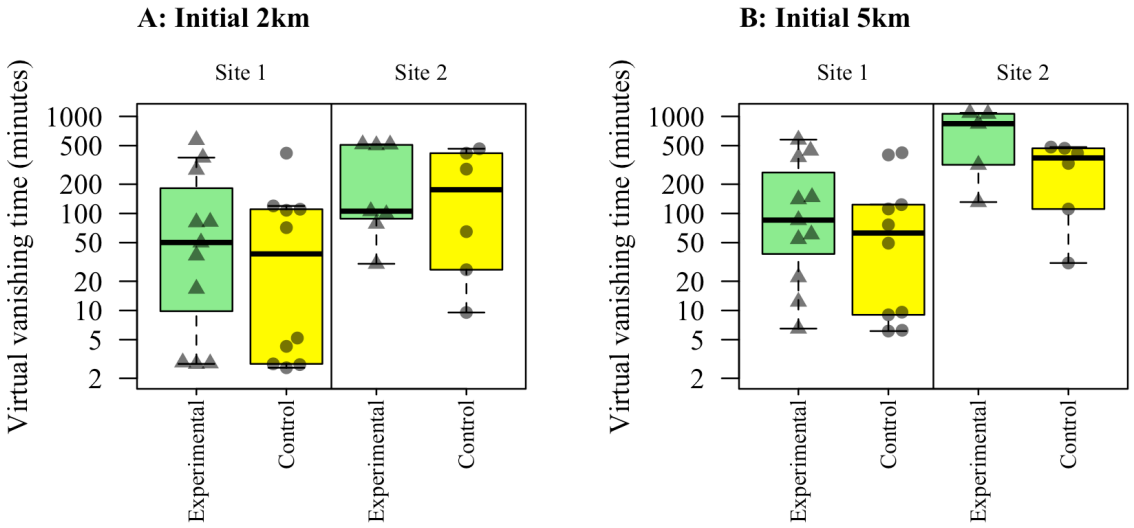


Figure 4.3. Virtual vanishing times. Boxplots are shown of the virtual vanishing time of birds leaving 2km from the release site for the final time (A), or 5km from the release site for the final time (B). The datapoints of the virtual vanishing times for the individual birds are also shown over the top of the boxplots. The experimental group is represented by green boxplots and triangular points, and the control group is represented by yellow boxplots and circular points. The virtual vanishing time is in minutes and shown on a logarithmic scale.

We found no significant difference in the homing efficiency index (Fig. 4.4) of the tracks at a 2km or 5km radius between the treatment groups (linear models; 2km radius: N=33, effect size = -0.0029, confidence interval = (-0.0096, 0.0037), p=0.37; 5km: N=31, effect size = -0.014, confidence interval = (-0.031, 0.0033), p=0.11). There was a significantly greater homing efficiency index at site 1 than at site 2 at both a 2km and 5km radius (2km radius: effect size = -0.012, confidence interval = (-0.019, -0.0050), p=0.0014; 5km radius: effect size = -0.033, confidence interval = (-0.051, -0.015), p=0.00078), indicating that birds released at site 1 initially approached home more efficiently than those released at site 2.

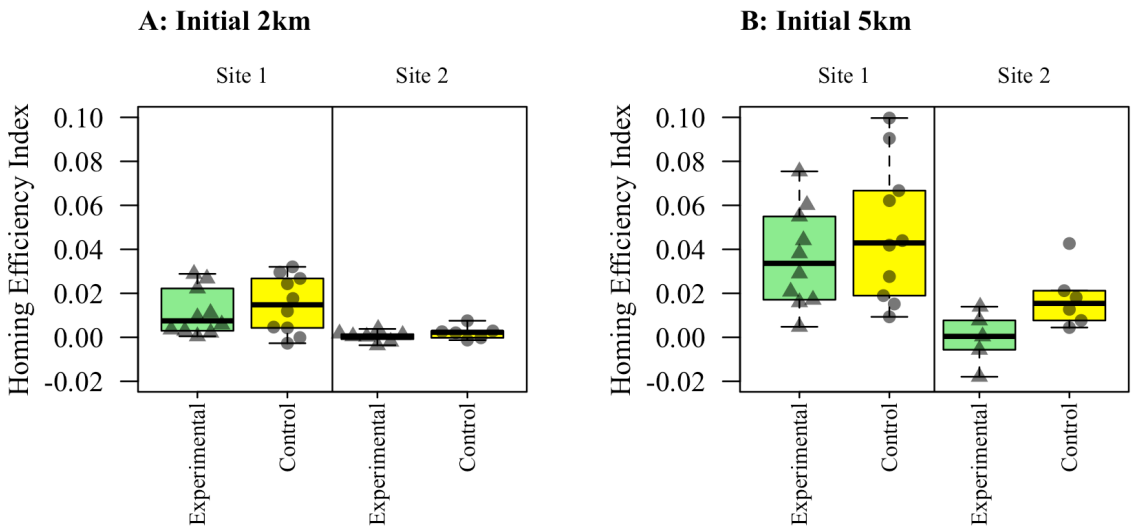


Figure 4.4. Initial homing efficiencies. *Boxplots are shown of the homing efficiency index of birds leaving 2km from the release site for the final time (A), or 5km from the release site for the final time (B). The datapoints for the individual birds are also shown over the top of the boxplots. The experimental group is represented by green boxplots and triangular points, and the control group is represented by yellow boxplots and circular points.*

Finally, we found no significant difference in the efficiency index of the tracks (Fig. 4.5) at a 2km or 5km radius between the treatment groups (linear models; 2km radius: N=33, effect size = -0.064, confidence interval = (-0.23, 0.10), p=0.44; 5km: N=31, effect size = -0.11, confidence interval = (-0.26, 0.050), p=0.17). There was a significantly greater efficiency index at site 1 than at site 2 at both a 2km and 5km radius (2km radius: effect size = -0.27, confidence interval = (-0.44, -0.10), p=0.003; 5km radius: effect size = -0.27, confidence interval = (-0.43, -0.10), p=0.0023), indicating that birds released at site 1 had more efficient initial trajectories than those released at site 2.

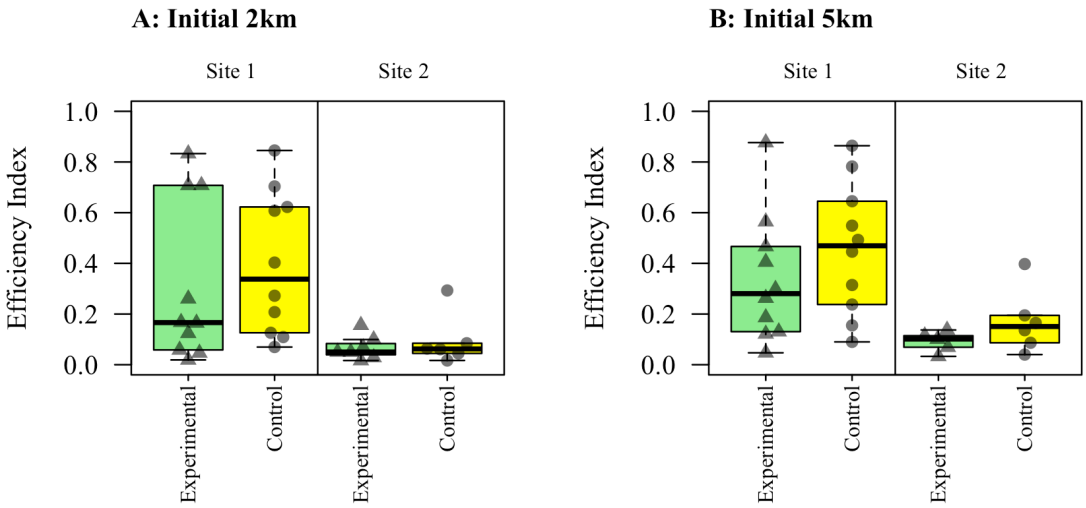


Figure 4.5. Initial efficiencies. *Boxplots are shown of the efficiency index of birds leaving 2km from the release site for the final time (A), or 5km from the release site for the final time (B). The datapoints for the individual birds are also shown over the top of the boxplots. The experimental group is represented by green boxplots and triangular points, and the control group is represented by yellow boxplots and circular points.*

Discussion

Overall, we found no differences in the initial homing performance of pigeons that had previously been passively exposed to a release site compared to those that had not, but a range of significant differences in the initial homing performance of pigeons released at different release sites. Release site specific effects on the initial homing performance of pigeons are well established (often termed release site bias) and are expected to play a larger role at unfamiliar release sites (Keeton, 1973; Kowalski and Wiltschko, 1987; Kramer, 1957; Wallraff, 1959). We found differences between release sites in the directional distribution of initial orientation and found that pigeons at site 1 left the vicinity of the release site more quickly and had a greater strength of orientation (mean vector length), a greater efficiency, and a greater efficiency of approaching home than pigeons released at site 2. Conversely, we found no differences between treatment groups in their directional distributions, their time taken to leave the release site, their initial strength of orientation, their efficiency, nor their efficiency of approaching home. Hence, we found no evidence to suggest that passive exposure to a release site was sufficient to generate any improvement in navigational performance. There are three possible explanations for this result: the first is that the sample size of the experiment was not large enough to detect a weak effect, but that it might have been detected with a larger sample size; the second is that passive exposure to a release site is insufficient to generate navigational learning, and hence pigeons cannot or do not learn from passive exposure to a novel site; the third is that pigeons learn from passive exposure to the release site, but do not rely upon what they have learned, showing no difference in performance, despite learning.

The first explanation for the lack of any detectable navigational learning generated by passive exposure to a release site is that some navigational learning does occur, but our experiment was

unable to detect it. This would be possible if the effect of learning after passive exposure to the release site were weak, especially given that some data had to be excluded from our analyses when pigeons followed each other after release. This left, in the analyses where the greatest number of birds had to be excluded, 15 in the experimental group and 16 in the control group, split across the two release sites. Nonetheless, the sample size of this study was sufficient to produce significant differences in the homing performance metrics between the two sites in this experiment. Additionally, a comparable study (Gagliardo et al., 2020b) found mean increases of 0.15, 0.26, and 0.22 in the efficiency index of (control) pigeons after a single release at three sites. Each of these increases was greater than our estimated upper bound of the confidence intervals for the improvements in efficiency indices (2km: 0.10; 5km: 0.050) and homing efficiency indices (2km: 0.0037; 5km: 0.0033) after passive exposure to the release site in this study (equivalent to effect size of the experimental treatment). This indicates that the sample size in our study was sufficient to distinguish biologically meaningful and relevant effect sizes, and that any increase in efficiency generated by passive exposure to a release site was less than the reported increases in efficiency generated by a single previous release in a similar experiment. Further experiments could include both passive exposure and single release at a novel release site as different treatments in the same experiment to directly compare the effect of these treatments on learning and subsequent homing. Hence, it is unlikely that a large effect of passive exposure, equivalent to the effect of a previous release at the site, on the subsequent homing of pigeons would not have been detected by this experiment. However, a weak effect of treatment and an insufficiently large sample size could potentially explain the lack of any detectable navigational learning in this experiment.

A second possibility is that passive exposure to a release site is insufficient for navigational learning. Previous experiments have shown that pigeons are able to determine the home direction at release sites before take-off (Chelazzi and Pardi, 1972; Gagliardo et al., 2001b; Mazzotto et

al., 1999), and that passive exposure to a release site activates a greater number of neurons than release in the vicinity of home in the piriform cortex (Patzke et al., 2010). However, neurons in the hippocampal formation are activated significantly less in pigeons after passive exposure to release sites than birds released and able to home from the same sites (Patzke et al., 2010). This is another important brain region for spatial learning in homing pigeons (Bingman et al., 2005), involved in developing route-following mechanisms from familiar sites, although not in developing site-specific compass orientation (Gagliardo et al., 1999; Gagliardo et al., 2009; Gagliardo et al., 2002; Gagliardo et al., 2020a). Similar results were recently reported for young domestic chicks, showing that hippocampal activation was significantly higher in chicks that could explore a novel environment, than in chicks that could only observe the same space without exploring it (Morandi-Raikova and Mayer, 2022). These Immediate Early Gene activation findings therefore fit with this explanation of our results that passive exposure to the cues of a release site may be insufficient to generate navigational learning, possibly because it fails to activate sufficiently their hippocampal formation and trigger learning about the visual cues at the site.

Therefore, one could hypothesise that flight, exploration and/or homing at a novel release site might be necessary for learning, whereas passive exposure is insufficient. This could explain why we found no effect of a single passive exposure to a site, despite a previous experiment showing that a single release from an unfamiliar site is sufficient for navigational learning using visual cues (Gagliardo et al., 2020b), with these cues relied upon more by pigeons subsequently released after made anosmic, than controls. However, the difference between anosmic and control pigeons in that experiment was observed in the 'en route navigation' rather than 'initial decision making' of the pigeons. It is therefore also unclear how much pigeons learn about the visual cues at a release site after a single release.

On the other hand, homing pigeons appear able to remember olfactory information after passive exposure to a novel release site for at least a few hours, as shown by 'site simulation experiments' (Benvenuti and Wallraff, 1985; Dall'Antonia et al., 1999). In these experiments, birds displayed orientations consistent with the home direction from the site where they had been exposed to environmental odours a few hours before. It is possible that exposure to the olfactory cues at a site in these experiments was sufficient for pigeons to make an orientation decision which is retained for some hours but would not be retained until a subsequent day, and hence not constitute navigational learning or an increase in familiarity with the site.

Finally, a third possible explanation of our results is that pigeons learn through passive exposure to a new release site, but nonetheless show no difference in subsequent navigational performance. This possibility is also demonstrated by the difference in reliance on visual cues after a single release from a site between pigeons released subsequently either anosmic or intact (Gagliardo et al., 2020b). This experiment demonstrates that pigeons can learn about various cues after release at a new site, but rely upon this information to different extents when subsequently released in different conditions (anosmic or intact), and hence that the transition between navigation mechanisms may not be limited by the rate of learning of visual landmarks. This highlights the distinction between learning and performance, and opens the possibility that the pigeons in our experiment might have learned about the cues at the release site, but not relied upon the information they had learned when subsequently released.

In summary, we found no evidence of an increase in navigational performance after exposure to the cues at a novel site without release or homing from the site. This suggests that any effect of learning generated by passive exposure to sites may be weak or not reflected in navigational performance upon subsequent release. We believe that further experiments should continue to

probe outstanding questions relating to navigational learning and ontogeny in homing pigeons and other animals, to better address this still outstanding major problem of ontogeny for the field of navigation, and ethology more generally (Tinbergen, 1963).

Chapter 5

Neural networks reveal emergent properties of collective learning in democratic but not despotic groups

Adapted from: Morford, J., Lewin, P., Biro, D., Guilford, T., Padget, O., & Collet, J. (2022). Neural networks reveal emergent properties of collective learning in democratic but not despotic groups. *Animal Behaviour, 194*, 151-159. https://doi.org/10.1016/j.anbehav.2022.09.020

Joe Morford, Patrick Lewin, Dora Biro, Tim Guilford, Oliver Padget, Julien Collet

Author contributions

Joe Morford: Conceptualisation, Methodology, Software, Formal analysis, Investigation, Writing – Original Draft, Writing – Review and Editing, Visualisation. **Patrick Lewin**: Methodology, Writing – Original Draft, Writing – Review and Editing, Visualisation. **Dora Biro**: Writing – Review and Editing, Supervision. **Tim Guilford**: Writing – Review and Editing, Supervision. **Oliver Padget**: Methodology, Supervision. **Julien Collet**: Conceptualisation, Investigation, Writing – Original Draft, Writing – Review and Editing, Supervision.



Biliana Todorova

Abstract

Collective learning, the improvement of behaviours through experience of collective actions, is an area of animal learning that has received little attention. We investigated how individual learning during collective actions could produce improvements in collective performance, and how collective decision-making processes, including leadership dynamics, could impact upon learning. We trained artificial neural networks, either solo or paired, at an orientation task, based upon collective navigation in animals. In pairs, we implemented two rules of collective decision making: 'democratic' (weighted average of individual propositions) or 'despotic' (one individual's proposition, determined randomly with weighted probabilities in each trial). Decision-making weightings were varied between pairs, but fixed for a given pair, with asymmetric weightings generating 'leaders' and 'followers'. We found nearly all pairs improved their orientation, but more slowly than solo learners. Within pairs, leaders learnt more quickly than followers ('the passenger-driver effect'). In democratic pairs, collective performance improved through individuals learning to compensate for partner error. This emergent process was not observed in pairs with despotic decision making, in which individuals learnt similarly to solo learners. Our model helps to clarify the links between individual learning, collective decision making and collective performance, in the context of collective navigation, and collective behaviour, more generally.

Introduction

Many animal species are capable of associative learning (Bouton, 2007; Dukas, 1998; Pearce, 2008), a process through which individuals can improve their performance over repeated executions of a task. In associative learning, rewards or costs received as a consequence of an individual's behaviour, feed back to improve its future decisions and thus increase its expected net reward. Yet many animals live in groups and take part in collective actions (for example, collective movements), which result from the integration of several and sometimes divergent individual propositions (Conradt and List, 2009; Couzin et al., 2005). Surprisingly though, we still know little about how associative learning processes at the individual level interact with collective decision-making processes in group-living animals (Biro et al., 2016; Kao et al., 2014).

First, it is unclear how collective contexts affect individual learning, with most empirical studies on animal learning focussing on individuals learning alone rather than while contributing to a collective decision (Biro et al., 2016; Kao et al., 2014). Even in social learning studies (focussed upon individual learning in group contexts), tests are generally individually based, investigating whether an animal can successfully copy the behaviour of conspecifics to solve the same task individually (Biro et al., 2016; Hoppitt and Laland, 2013). Yet it has been suggested that collective joint-action processes may fundamentally alter how and what individuals learn (Biro et al., 2016; Kao et al., 2014): reaching a consensus collective decision dilutes the relationship between an individual's behavioural preference and the action taken (Conradt and Roper, 2005). The outcome of this collective action may be rewarding or costly, and act to reinforce learning; hence, an individual's behavioural preference and the outcome of its behaviour are decoupled by the collective context, with potential implications for learning. Kao et al (2014) demonstrated this, showing that identical learning algorithms learned different solutions depending on whether they acted alone or within a cohesive group making collective decisions. However, it remains unclear how well their conclusions generalise to various contexts of animal collective learning, in

particular contexts in which the optimal solution does not depend on whether individuals act alone or in groups.

Second, even if individuals do learn effectively from experience during collective actions, we know little about how or whether this leads to improvements in collective performance. This is partly because most theoretical models of collective decision making in animal groups have so far assumed memory-less group members (Biro et al., 2016; Kao et al., 2014). For a number of reasons, simple associative processes at the individual level may not necessarily be sufficient to produce improvements in collective performance when a group repeats a collective task. For instance, within a group, individuals may not learn at the same rate or learn the same things (Burt de Perera and Guilford, 1999; Pettit et al., 2015); this may produce divergent actions between members of a group and so may not necessarily lead to improvements of collective performance (Conradt and List, 2009; Conradt and Roper, 2005; Couzin et al., 2005). Moreover, even if individuals do learn, this will not improve group performance unless these individuals also happen to be influential in the group decision-making process (Stroeymeyt et al., 2011). As a result, we may expect that in some cases the groups will perform less well than the most efficient member(s) would alone. In that regard, the rules by which individual preferences are combined to generate a collective decision (Biro et al., 2006; Conradt and Roper, 2005; Couzin et al., 2005) may be highly influential in whether and how individual learning generates improvements in collective performance.

On the other hand, we know empirically that at least some animal groups are capable of improving collective performance over repetitions of a collective task (homing pigeons, *Columba livia*, (Flack et al., 2013); predator avoidance by fish (Hansen et al., 2021); nest emigration by ants (Langridge et al., 2004); migratory green surfing in ungulates (Jesmer et al., 2018)), but the mechanisms underlying such collective learning have seldom been explored (Langridge et al., 2008). In theory, improvements in collective performance may be driven not merely by the

effects of each group member learning to complete the task individually, but perhaps also by emergent properties arising from increasingly efficient interactions between group members. For instance, if a group member learns to perform a task only partially, or with some systematic error, other members of the group may simultaneously learn to compensate for it. Forms of organisational learning like this have been demonstrated experimentally in humans playing a simple cooperative game without direct communication: some dyads spontaneously divided their contribution to the task in a systematic way to reach higher performance (Andrade-Lotero and Goldstone, 2021). In some cases, the group may thus perform better than any of its members would on their own, especially if members learn more about compensating for others than about completing the task itself (Kao et al., 2014). While a few theoretical simulations suggest that this is possible (Andrade-Lotero and Goldstone, 2021; Kao et al., 2014), we still know little about the conditions that will lead (or not) to such emergent collective learning processes.

We utilised a navigational paradigm to model collective learning. This provides a simple and easily quantifiable model of a task solvable both solo and collectively, to test the implications of the collective context on learning. Our model is based upon navigational learning at a single site, whereby, over repeated visits, a solo animal or group of animals improves its orientation towards a fixed target from the site, such that it navigates more efficiently (Fig. 5.1). In the model, each neural network proposes a direction (from 0 to 360°). Neural networks either learnt this task alone (solo learners, Fig. 5.1a), or within pairs (collective learners, Fig. 5.1b, c). Solo neural network learners generated an output direction and 'paid a cost' equal to the squared difference between its output and the 'correct' direction. This cost then fed into the learning of the network through backpropagation (Gulli and Pal, 2017). Within pairs, each neural network proposed a direction, and a single consensus direction of the pair was then determined through a collective decision-making function. The difference between the group (post-consensus) direction and the correct direction determined the cost for each individual member. As in solo learners, this cost

fed into the learning of each member's (pre-consensus) proposition. This coupled individual learning with the collective outcome, a crucial element of collective learning.

For pairs, we implemented two types of collective decision-making function: either a weighted average of the two proposed directions ('democratic'; Fig. 5.1b), or one of the individually proposed directions, determined randomly in accordance with weighted probabilities ('despotic'; Fig. 5.1c). We explored the effects of different dynamics of leadership/followership by varying between pairs the weightings of members' contributions to the consensus decision making. These two functions therefore allowed us to capture a wide range of consensus decision-making processes observed in animal groups and to vary both the extent to which decisions are shared between group members, and the consistency of leadership within groups (Biro et al., 2006; Conradt and Roper, 2005, 2007). We expected that leaders might learn more quickly than followers, a phenomenon which has previously been termed the 'passenger-driver' effect in relation to empirical research (Burt de Perera and Guilford, 1999). This is expected as leaders receive the most consistently appropriate reinforcement (cost) from the consequences of the collective action.

We assessed and compared the learning performance of pairs as a collective with different consensus rules and leader/follower weightings and made comparisons with the performance of solo learners. This allowed us to observe whether there was any 'collective intelligence' effect, with groups performing better than solo learners, and how this was affected by different decision-making processes. Within pairs, we examined what each individual member learnt to propose ('pre-consensus propositions'), to investigate how well individual members learnt the task within a collective, whether this depended on the leader-follower weighting (to test for the passenger-driver effect) and/or the type of collective decision rule (despotic or democratic). To test for emergent organisational forms of collective learning across different collective decision-making rules, we compared the performance of each individual's pre-consensus proposition

(individual preferred direction) with its performance after consensus (collective direction): 'collective membership gain' was observed if the individual performed better through the consensus than it would have without. This is highly related to the idea of 'consensus costs' (Conradt and Roper, 2005) that individuals pay by forgoing an optimal individual action in order to comply with the collective consensus. We qualitatively examined how our findings resemble empirical results on collective navigation, and collective behaviour more generally, focussing particularly on the collective navigation of homing pigeons, the best studied model species in relation to collective navigation.

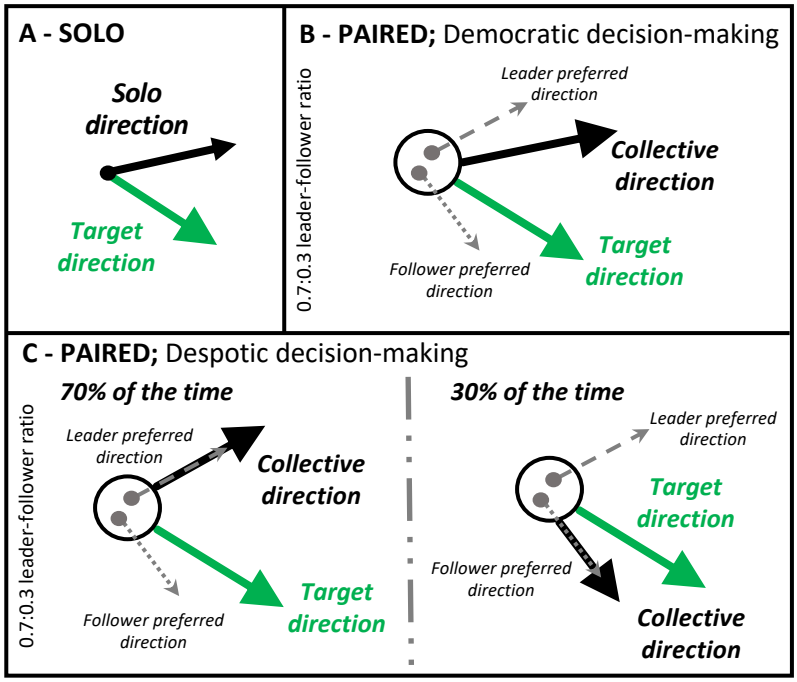


Figure 5.1. Model outline. *Our model is based upon an orientation decision towards a target from a single site in solo or collectively navigating animals. (a) Solo learners, with the output direction of the learner (Solo direction) and the correct direction (Target direction) shown. (b, c) Paired learners with 0.7:0.3 decision-making weightings, defining a leader and a follower. Their collective behavioural output is determined by a decision-making rule: either (b) democratic or (c) despotic. The individual output direction of each learner is shown (Leader preferred direction and Follower preferred direction), as well as the collective output (Collective direction). In all cases, learning relies on the 'cost paid', which feeds back into neural network learning and is*

determined by the difference between the overall output direction (Solo direction or Collective direction) and the correct direction (Target direction). Over repeated trials, the solo and paired learners could improve their output orientations, getting closer to the correct target direction, through learning.

Methods

Neural networks learnt the navigational task of returning an arbitrarily correct bearing either individually or collectively, in pairs. The neural network comprised multi-layer perceptrons of only 6 neurons and a single Dense hidden layer (4 neurons) with a Rectified Linear Unit (ReLU) activation function (Chollet, 2015; Gulli and Pal, 2017). In each task, neural networks were given a constant input of 1 and outputted a proposed direction between 0 and 360°, so that the task comprised simply the honing of the output, without changing the input. The output was generated with a linear activation function (units: degrees/360) and, in pairs, the two outputs were combined using a collective decision rule to generate a single consensus bearing. In each trial, the cost paid (the loss function) was equal to the squared error in orientation (0-180°) of the solo or consensus orientation. In pairs, this cost was applied equally to each member and in all neural networks, the cost was used to optimise the orientation in subsequent trials through standard gradient descent (learning rate = 0.05; momentum = 0; decay = 0). Training involved a single learning trial (training datapoint) at a time (batch size = 1, epochs = 1). The networks were implemented in Python (Van Rossum and Drake Jr, 1995), with libraries: keras (Chollet, 2015), sys, numpy (Harris et al., 2020), scipy (Virtanen et al., 2020), matplotlib (Hunter, 2007) and tensorflow (Abadi et al., 2016).

During collective learning, there were two consensus decision-making rules used: a democratic (averaging) decision-making rule and a despotic (probabilistic) decision-making rule. The democratic decision-making rule comprised a weighted circular mean of the two individual output directions. The despotic decision-making rule comprised randomly selecting one of the individual output directions using weighted probabilities. In the despotic instance, whether an individual led or followed on a given trial was not input into their learning process. The relative weightings in both democratic and despotic instances were set to 0.5:0.5, 0.7:0.3 or 0.9:0.1 for a given pair, and each individual retained its relative weighting throughout the learning process.

Individuals in a pair would therefore either input equally into consensus decision making (0.5:0.5) or would act as a leader and follower (0.7:0.3 and 0.9:0.1). Henceforth, 'leader' will be used to mean an individual with a weighting of greater than 0.5, and 'follower' will be used to mean an individual with a weighting less than 0.5.

250 neural networks were trained to complete the task solo, each learning over 25 learning trials (training datapoints). Similarly, for each consensus decision rule and each leadership ratio, 250 pairs of neural networks were trained over 25 trials. The networks were tested first after model initialisation but before any training, and then after every learning trial. Comparative tests of performance were made using pairwise MWU tests after 5 learning trials (to assess learning rates) and at the conclusion of learning, after 25 learning trials (to assess final asymptotic learning performance). Statistical analysis and graphical output was produced using R (R-Core-Team, 2018; RStudio-Team, 2020), including package scales (Wickham, 2018).

Results

Overall solo and collective performance

Over 25 learning trials, all of the solo learners ($N = 250$) improved at the navigational task, with better performance after the final learning trial than before the first learning trial. Median performance is shown in Fig. 5.2a.

Similarly, almost all (741 of 750) of the pairs of neural networks using the democratic decision-making rule improved in collective performance during training (performed better in the last trial than the first). Learning was quicker and final performance was better when pair members contributed less equally to decision making, such that one member was a clear leader and the other a clear follower (Fig. 5.2b). At the conclusion of training, performance was significantly better in pairs with a 0.9:0.1 decision-making weighting than in pairs with 0.7:0.3 and equal (0.5:0.5) decision-making weightings (Mann-Whitney U tests: $P < 0.0001$ in both cases); additionally, performance was significantly better in pairs with a 0.7:0.3 decision-making weighting than pairs with an equal decision-making weighting (Mann-Whitney U test: $P < 0.001$). These differences in performance between pairs with different leadership/followership ratios were already detectable after only 5 learning trials. Performance of solo learners was significantly better than the collective performance of paired learners with decision-making weightings of 0.5:0.5, 0.7:0.3 and 0.9:0.1 both after 5 learning trials (Mann-Whitney U tests: $P < 0.0001$, $P < 0.0001$ and $P = 0.024$, respectively) and at the conclusion of training (Mann-Whitney U tests: $P < 0.0001$ in all cases).

Of 750 pairs of learners using the despotic decision-making rule, 730 improved in collective performance during training (performed better in the last trial than the first). Again, learning was

quicker and final performance was better when pairs contributed less equally, with stronger leaders and followers. After 5 learning trials and at the conclusion of training, performance was significantly better in pairs with a 0.9:0.1 decision-making weighting than pairs with a 0.7:0.3 or 0.5:0.5 weighting (Mann-Whitney U tests: $P < 0.0001$, in all cases); however, there was no significant difference between pairs with 0.5:0.5 and 0.7:0.3 weightings (Mann-Whitney U tests: $P = 0.94$ after 5 trials; $P = 0.23$ at conclusion of training; Fig. 5.2c). Both after 5 trials and at the conclusion of training, performance by solo learners was significantly better than the collective performance of paired learners with all decision-making weightings (Mann-Whitney U tests: $P < 0.02$ in all cases).

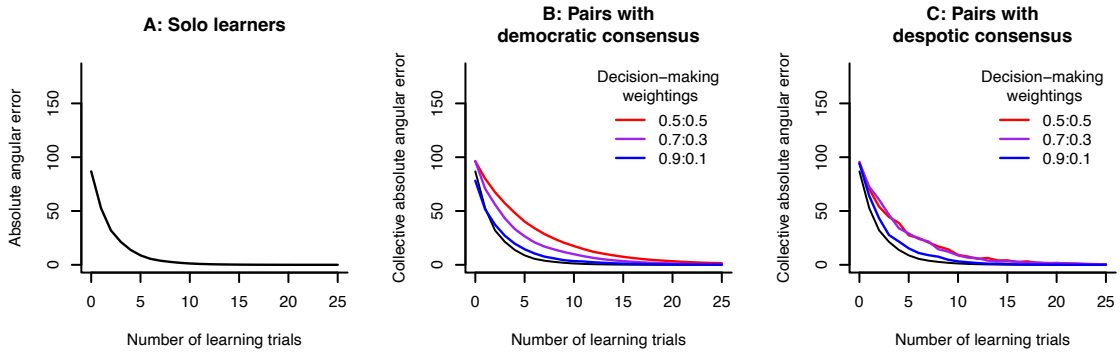


Figure 5.2. Overall performance of solo and paired learners. *Average learning curves are shown for (a) solo learners and pairs of networks learning collectively through (b) a democratic rule or (c) a despotic rule. (a) Median absolute angular error of 250 learners across trials (black curve); (b, c) Three median absolute angular errors of pairs after their consensus (collective performance), each of 250 pairs of neural networks. The average learning curve of solo learners (a) is also shown in panels (b) and (c) in black for comparison.*

Democratic decision making

In pairs of learners using a democratic decision-making rule, the error of each individual progressively reduced, but the median error appeared to quickly plateau at levels well above zero

(Fig. 5.3a). Individual error at the conclusion of learning was significantly greater in networks learning in pairs with democratic decision-making rules than in solo learners, irrespective of decision-making weighting (Mann-Whitney U tests: $P < 0.0001$ in all cases). Errors plateaued at a significantly higher level in learners more prone to follow than to lead (Mann-Whitney U tests: at final trial of learning, $P < 0.01$ for all pairwise combinations) but in neither leaders nor followers did the error appear to be approaching zero (Fig. 5.3a). On average, members of a pair did not learn to reduce the difference between their respective output angles ('pair difference'; Fig. 5.3b), with average pair difference remaining approximately level across trials, and no significant difference between the pair difference in the first and last trials, irrespective of the decision-making weightings of the pair (Mann-Whitney U tests: $P = 0.29$, $P = 0.16$ and $P = 0.71$ for pairs with 0.5:0.5, 0.7:0.3 and 0.9:0.1 leadership weightings, respectively). Hence, the increase in collective performance was not achieved by both members of a pair converging on the correct solution. This indicates that the collective context has changed the nature of the solution that individual learners are reaching.

The difference between an individual's error considered alone and the collective performance of its group is termed 'collective membership gain' if collective error is smaller than individual error, or 'collective membership loss' otherwise. During learning, there was an average increase in collective membership gain for democratic paired learners (Fig. 5.3c), with significantly greater collective membership gain in the final learning trial than in the first trial, whether they were leaders (Mann-Whitney U tests: $P < 0.0001$ for both pairs with 0.7:0.3 and 0.9:0.1 leadership weightings), followers (Mann-Whitney U tests: $P < 0.0001$ for both pairs with 0.7:0.3 and 0.9:0.1 leadership weightings), or individuals contributing equally to decision making (Mann-Whitney U test: $P < 0.0001$). Collective membership gain at the conclusion of learning was, on average, greater in individuals which contributed the least to decision making (Mann-Whitney U tests: $P < 0.0001$ for all pairwise comparisons). To understand how this collective membership gain emerged within pairs we quantified the correlation between the errors of the two individuals

within a pair. We predicted that if individuals were learning to compensate for the error of their partner, there would be negative correlations between the errors of the two individuals within a pair (e.g. a large anticlockwise error by one member of a 0.5:0.5 pair could be compensated by an equally large clockwise error by its partner). We therefore regressed the errors of the leaders on the errors of the followers at the conclusion of training, (or, in the case of the pairs with equally contributing members, split each pair randomly and performed the regression). We found negative relationships in each instance (linear regressions: $P < 0.0001$ in all cases). These correlations appeared to show excellent qualitative fit to the theoretical gradient expectations of -1, -3/7 and -1/9 in pairs with decision-making weightings of 0.5:0.5, 0.7:0.3 and 0.9:0.1, respectively, as shown in Fig. 5.3d.

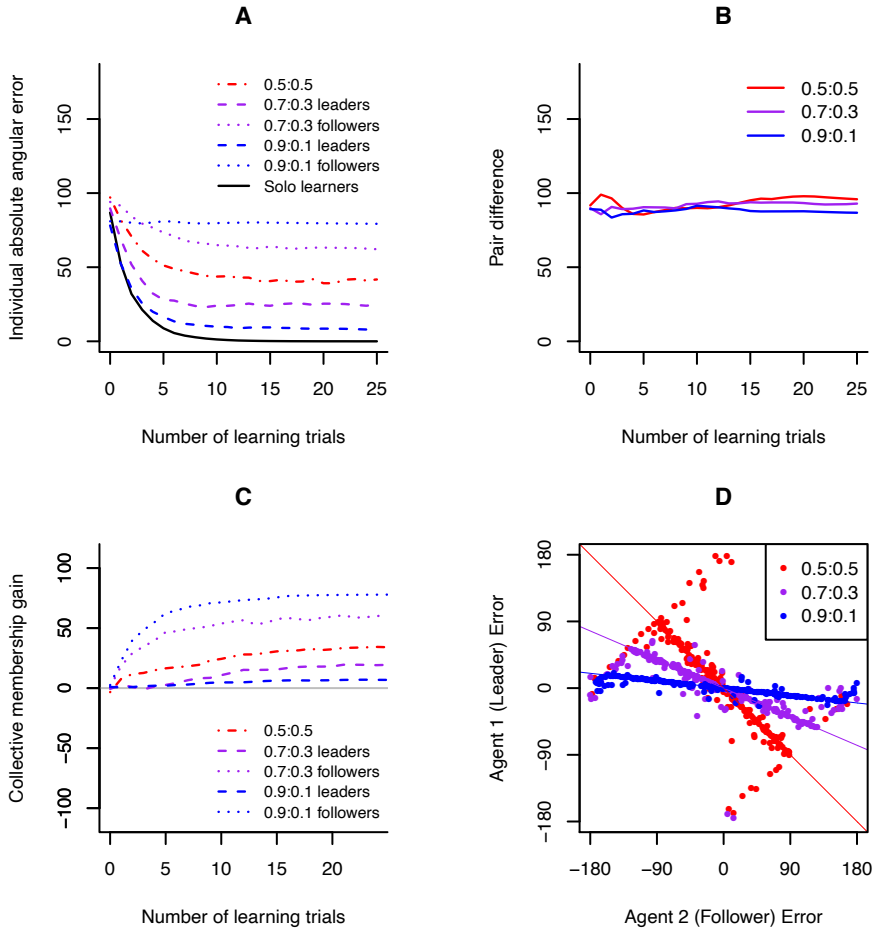


Figure 5.3. Democratic decision making: performance and contribution of each individual member. (a) Median absolute angular error of each pair member's output before consensus

(coloured curves), compared to median error observed in solo learners (black curve), across training trials. (b) Median within-pair difference between members' output directions before consensus, across training trials. (c) Collective membership gain across trials: the difference between the collective performance of a pair, and the performance of each of its members considered individually (individual error – collective error). (d) Points show the relationships between directions proposed by members of the same pair at the last (25th) learning trial; lines show the theoretical gradient expectations of -1, -3/7 and -1/9 in pairs with decision-making weightings of 0.5:0.5, 0.7:0.3 and 0.9:0.1, respectively

Despotic decision making

Conversely, in pairs using a despotic decision-making rule, the error of each individual appeared to approach zero across trials in all cases (Fig. 5.4a). Individual error at the conclusion of learning was significantly greater than in solo learners for followers (Mann-Whitney U tests: $P < 0.0001$ in both cases), equally contributing individuals (Mann-Whitney U test: $P < 0.0001$), and for leaders (Mann-Whitney U tests: $P < 0.0001$and $P = 0.027$ for pairs with 0.7:0.3 and 0.9:0.1 decision-making weightings, respectively). Individual error fell more quickly in leaders than in individuals contributing equally to decision making, and more slowly still in followers (Mann-Whitney U tests: $P < 0.02$ for all pairwise combinations after 5 learning trials). The pair difference (the difference in output between the members of a pair before consensus) decreased during learning (Fig. 5.4b), with significantly lower pair difference in the last trial than the first for pairs with all three decision-making weightings (Mann-Whitney U tests: $P < 0.0001$ in all three cases). During training, collective membership gain significantly increased in followers with 0.7:0.3 and 0.9:0.1 decision-making weightings (Mann-Whitney U tests: $P < 0.02$ and $P < 0.0001$, respectively), and decreased in leaders (Mann-Whitney U tests: $P < 0.01$ and $P < 0.0001$ for the two decision-making weightings, respectively). However, collective gain after training in the majority of individuals was zero, and hence these changes were not reflected by the median

collective membership gain (shown in Fig. 5.4c). There was no change in the collective membership gain during training for individuals in equally contributing pairs (Mann-Whitney U test: $P = 0.94$). Finally, no significant relationships were found between the errors of leaders and followers (linear regressions: $P = 0.50$ and $P = 0.99$ for pairs with 0.7:0.3 and 0.9:0.1 weightings, respectively), or randomly split pairs in equally contributing pairs (linear regression: $P = 0.57$), providing no evidence for organisational learning in pairs with probabilistic decision-making rules (Fig. 5.4d). Hence, learning in this collective context, with a despotic decision-making rule seemed to be qualitatively similar to learning in a solo context. In particular, the final solution reached by the learners converged upon the correct solution, like in a solo learning context, with the rate of learning determined by the decision-making weightings.

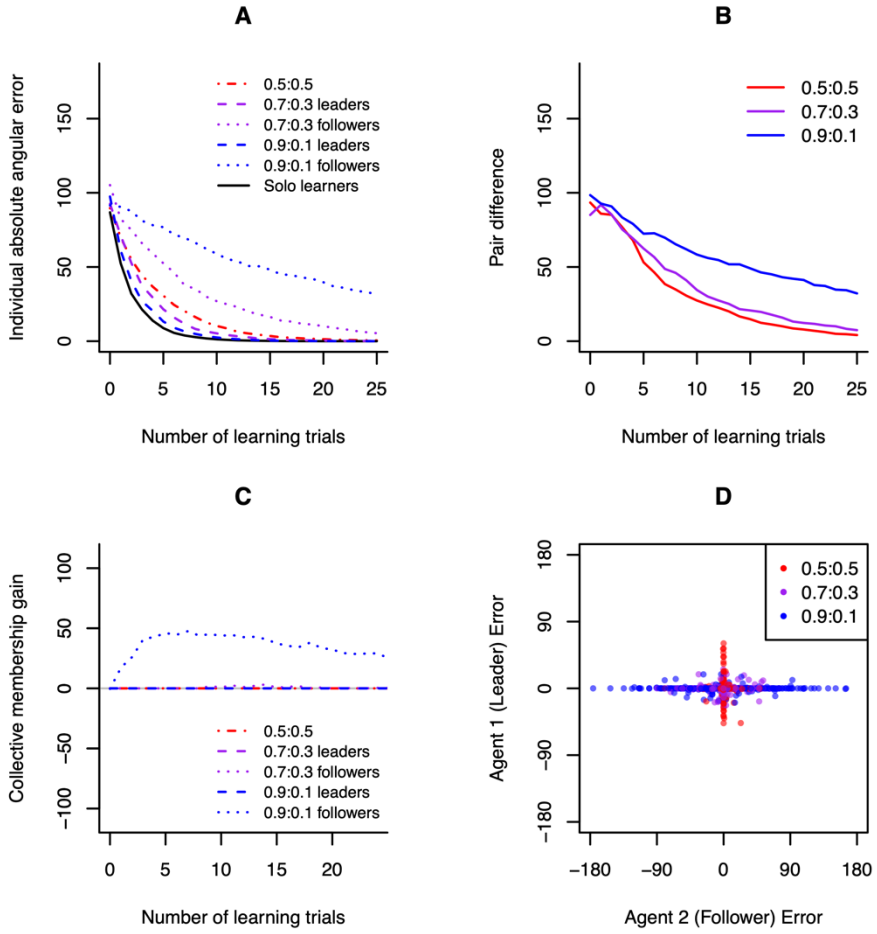


Figure 5.4. Despotic decision making: performance and contribution of each individual member. (a) Median absolute angular error of each pair member's output before consensus

(coloured dashed curves), compared to median error observed in solo learners (black curve), across training trials. (b) Median within-pair difference between members' output directions before consensus, across training trials. (c) Collective membership gain across trials: the difference between the collective performance of a pair, and the performance of each of its members considered individually (individual error – collective error). (d) Points show the relationships between directions proposed by members of the same pair at the last (25th) learning trial.

Discussion

Our artificial simulations of associative learning processes showed that most pairs of neural networks increased their performance through a repeated orientation task. However, the collective context altered the rate of learning and final performance of both the group itself and of its individual members. Overall, we found that pairs and their members learnt more slowly than solo learners. The type of consensus decision-making rule of a pair affected the processes through which they improved their collective performance. Democratic groups increased performance by improving the complementarity of their member's contributions, giving rise to an emergent form of collective learning; however, despotic groups improved entirely through individual improvements. The degree of leadership in pairs affected both the individual learning rate, with leaders learning faster under most circumstances, and the rate of collective learning (pairs with greater asymmetry in decision-making contribution tended to learn faster).

The unequal learning rates of leaders and followers can be termed the 'passenger-driver effect' (Burt de Perera and Guilford, 1999), in which individuals contributing more strongly to the collective decision learn more quickly. The passenger-driver effect has previously been observed in the individual navigational learning of pigeons within flocks (Pettit et al., 2015). Our model suggests that this can arise because individuals contributing most (leaders) to the collective decision receive the most consistently appropriate reinforcement (cost) from the consequences of the collective action. Here, this was true in both democratic and despotic groups through slightly different mechanisms. In democratic groups, the consensus collective action is determined through a weighted averaging of the propositions of the leader and follower. This generates noise in the relationship between an individual's proposition and the reinforcement it receives, which depends on the collective action. The noise in this relationship slows learning and slows the learning of followers to a greater extent than of leaders, as the leader's proposed direction is always closer to the collective action than the follower's proposition. Conversely, in

despotic groups, each individual determines the collective action with a given probability. In trials in which they lead, they learn as if performing the task solo whereas, when following, no learning takes place as there is no relationship between the individual proposition and the collective action. This effectively reduces the number of trials in which learning can take place, and leaders (individuals that lead more often) therefore learn more quickly than followers as they learn on a greater proportion of trials. Somewhat similarly, in the collective learning model of Kao et al (2014), individuals only learn about cues when they indicate the same discrete option as chosen by the group. This might be expected to slow learning in collective contexts relative to solo contexts, and to slow the learning of followers relative to leaders, by reducing the number of trials in which learning occurs.

The slower learning of individuals in both democratic and despotic groups in this model precluded the possibility of any 'collective intelligence' effect. Initially both solo learners and pairs performed equally well (orienting randomly), and solo learners outperformed pairs after learning, although would be expected to plateau at the same level, after sufficient trials. This contrasts the modelling results of Kao et al, (2014), in which groups could outperform individuals in various simulated scenarios by successfully exploiting cues with a low reliability for individuals, by averaging out the errors of group members. This is a manifestation of the 'many-wrongs principle' (Simons, 2004), a driver of collective intelligence. Further modelling work (Falcón-Cortés et al., 2019), shows how collective intelligence can emerge in foraging tasks through information transfer between individuals. Additionally, in empirical research, animal groups have often been observed to outperform solo individuals (Conradt and Roper, 2005; Simons, 2004), including in navigational contexts (Sasaki and Biro, 2017; Tamm, 1980), although not in all cases (Guilford and Chappell, 1996; Keeton, 1970). These collective intelligence effects may derive from perceptual errors or execution errors that are independent between individuals in a group and are not captured in our simple model.

The mechanism by which collective learning occurred was highly dependent on the collective decision-making rule. An organisational form of learning emerged in pairs adopting a democratic rule of weighted average between member propositions, but not in pairs adopting a despotic rule to determine which partner had total control in each trial. In democratic pairs, each member could learn to compensate for the error of its partner, proposing directions with error in the opposite direction to the error of its partner. With the rare exception of pairs not improving their collective performance, each democratic pair thus found its own idiosyncratic equilibrium between members (a form of 'convention' (Stephens and Heinen, 2018)), such that the average error of the collective approached zero. As a result, collective accuracy was, on average, better than the propositions of either individual member. Hence, if an individual which had learned as part of a group subsequently had to complete the task alone, their decision would, in almost all cases, be less accurate than the group's consensus decision. This is collective membership gain, with individuals performing better as members of a collective than alone. This represents an emergent property of collective learning: the collective context altered not only the learning rate of individual members, but also the nature of the solution upon which individuals converged (as in (Kao et al., 2014), but in a context where the optimal solution was independent of the social context). These results highlight the potentially complex relationship between individual and collective learning processes.

Our model includes a number of assumptions that may appear unrealistic of collective dynamics in navigating animals. First, for simplicity, we forced pairs to remain cohesive, even if they had highly divergent directional preferences. However, in animal groups, if there is a large conflict of interest and therefore 'consensus cost' (Conradt and Roper, 2005), then groups are less likely to come to a consensus decision, and may split. For instance, in pigeons, paired individuals often split, especially on first releases when partners are unfamiliar with the homing route (Flack et al., 2013; Guilford and Chappell, 1996), or when they have very divergent directional preferences (Biro et al., 2006). Nevertheless, once each bird, flying solo, converges towards the most direct

route, cohesion is often restored and so a phase of solo learning might be followed by collective learning in these instances. While such complications will have some effect upon the outcomes and processes of learning, they are not central to the interface between collective decision making and learning and hence were not included in our model. Second, we imposed a fixed ratio of leadership between paired individuals. In reality, this might itself change through learning as groups of individuals gain experience: leadership could vary randomly between trials, or some individuals may learn to lead more than others, and this could be contingent on the accuracy of each individual's proposition. In the latter case, there might be feedback between learning and leadership, whereby individuals which learn fastest become leaders and, once leaders, are able to learn faster still. In our model, learning and the accuracy of past decisions did not affect leadership and faster learning was only a consequence, not a cause of leadership. However, a stable leadership ratio appears relatively consistent with various examples of leadership in animal groups, in which stable individual attributes such as age, size and boldness (Beauchamp, 2000; Fischhoff et al., 2007; Pettit et al., 2015; Sasaki et al., 2018) have been shown to influence the level of contribution to collective decisions.

Third, one potential criticism of our model implementation is that the cost paid, feeding back into learning, is unrealistic: in an orientation task, an animal, or group of animals, could not possibly know its precise level of error without knowing the correct orientation. Furthermore, navigational tasks (and other behaviours) are more complex than a single orientation decision, so the reinforcement generated from completing the task (i.e. homing) will not relate perfectly to the error of the initial orientation. However, any reinforcement that an animal, or group of animals, could use to learn to improve an orientation task would have to show a strong relationship with the orientation error. For instance, an animal could use the length of time it took to reach a goal as a measure of its orientation performance. Providing that there is a relationship between this measure of performance, and its actual orientation error, learning will operate similarly in our model as in this more realistic potential scenario. We expect that the process of learning

reinforcement will be strongly related to task performance in solo and collective behavioural tasks more generally, and hence this simplifying assumption is unlikely to generate unrealistic modelling results.

A final limitation of our model may be that that the neural networks are relatively constrained in their learning in our modelling environment, and cannot, for instance, learn about or remember the collective action in previous training trials. In contrast, it might seem possible for individuals to simply remember and recapitulate behaviours previously executed within groups, and this is potentially true in homing pigeons (Pettit et al., 2013; Sasaki and Biro, 2017). Similarly, individuals could learn within groups through social learning mechanisms (Heyes, 1994; Hoppitt and Laland, 2013), for instance the follower within a pair observing and imitating the behaviour of the leader. Considering social learning within groups may complicate the predictions of our model. For instance, the passenger-driver effect could be lessened or disappear through the followers learning from leaders. Additionally, given that social learning can occur within groups and not in solo learners, social learning might contribute towards a collective intelligence effect, facilitating better performance in groups than in solo learners, contrary to the results of our model.

On the other hand, an improvement in the proposition of a group member at the individual-level through recapitulation of a previous collective output or imitation of another individual could counterintuitively worsen performance at the group level, through a failure to compensate for the errors of other group members. Furthermore, in many cases it may not be simple or even possible for an individual within a group to be able to remember and execute a collective behavioural output. This may be because collective behavioural outputs have many inputs from the propositions of group members themselves responding to various cues, making the behaviour difficult to perceive and replicate for an individual member of the group. Alternatively, complex cooperative collective behaviours such as group foraging behaviours (Stander, 1992) or the

biparental care of offspring may involve a spatiotemporal separation of cooperative individuals. Nonetheless, the collective performance (the number of prey caught by the group, or the condition of the chick) may feedback into the learning of the individual group members.

Overall, our model helps clarify the complex links between individual learning and collective decision making. Our results highlight that individual associative processes can lead to improvements in group level performance through experience, both through an individual increase in performance, and through organisational learning, where group members here learnt to compensate for the errors of others, even without explicit rules for them to learn about each other. Future research could explore in more depth how the collective and individual learning properties exposed in our study are affected by biologically realistic changes in model parameters, model complexity and/or model tasks. Additionally, empirical focus on the interaction between collective decision-making processes and individual learning would allow the assumptions and predictions of our model to be tested and would develop understanding of animal learning in collective contexts.

Chapter 6

General Discussion

Joe Morford, Tim Guilford

Author contributions

Joe Morford: Conceptualisation, Writing – Original Draft, Writing – Review and Editing. **Tim Guilford**: Writing – Review and Editing.

Overall, in this thesis, I have examined a range of questions relating to the mechanisms and ontogeny of navigational maps in animals. I broadly reviewed this area of animal behaviour, before focussing on a few specific questions with two general approaches, first employing artificial neural networks as computational models of animal learning, and second conducting experiments in two model species of animal navigation, Manx shearwaters and homing pigeons. In my conceptual review, "Map and compass navigation: the mechanism and ontogeny of animal maps", I introduced a framework setting out three interlinked components of animal maps in order to clarify the links between different findings on animal maps and to highlight outstanding questions relating to navigational mechanisms and ontogeny. These components were (1) cues, the nature of the environmental properties that animals use to determine goalward directions; (2) structure, the organisation of information used to determine goalward directions; and (3) strategy, the way in which animals approach their goals and combine multiple map cues. I went on to discuss the ontogeny of these three components of animal maps, showing that the ontogenetic mechanisms facilitating map and compass navigation over long distances are relatively little understood. I suggested that mechanisms implicated in the learning of maps over relatively small spatial scales in mammals, in particular involving using path integration to integrate changes in map cues with vectors of self-motion, could play a similar role in map learning in other taxa and over larger spatial scales.

The first general approach I used to investigate the mechanism and ontogeny of navigational maps in animals involved using artificial neural networks as simple computational models of learning in animals. This allowed me to generate predictions relating to the ontogeny of grid map navigation in Chapter 2, "Almost there: learning to navigate approximately with a grid map", and on learning in groups in Chapter 5, "Neural networks reveal emergent properties of collective learning in democratic but not despotic groups". While this type of approach has been used previously to model learning in animals (Ghirlanda and Enquist, 2007; Gluck, 1991; McClelland and Rumelhart, 1985; Peng and Chittka, 2017; Wisniewski et al., 2012), whether these models

sufficiently capture animal learning to make meaningful predictions that are not dependent on the specifics of implementation is an open question (Dawson, 2008; Franks and Ruxton, 2010). In Chapter 2, I used two different implementations of neural network output in order to confirm that these results were not specific to the implementation chosen and hence were general at least across two relatively different implementation of this modelling in neural networks. I trained neural networks at tasks analogous to navigation in environments comprising intersecting gradients. Then, at various stages of training, I tested the outputs of the neural networks against predictions of previously proposed models (Benhamou, 2003; Turner et al., 2016) of (a) linearly extrapolating gradient fields and (b) combining gradient fields. In relation to my framework on animal maps, these models respectively represent (a) the structure with which the neural networks' maps are organised and (b) the map navigation strategy which the neural networks employ to combine multiple sources of map information. In a range of simulated environments, and across both implementations, I consistently found that the neural networks initially adopted a strategy of combining the map cues by determining displacement vectors in each gradient field independently and summing these to approximate the goalward direction. This is termed the approximate model and this strategy produces predictable orientation errors in non-orthogonal grid environments (Benhamou, 2003; Turner et al., 2016). However, by the end of training, I found no evidence that the neural networks were utilising this strategy, and hence this strategy was only adopted for a period of training. In contrast, I found that the neural networks appeared to structure their maps with different linear extrapolations of the gradient fields depending on the simulated environment.

These results lend support to the idea that the approximate model may be simpler to adopt than a perfect solution to navigational tasks and show how animals might adopt this strategy during learning. I believe that this work lends nuance to the predicted signatures of mechanisms of grid map navigation in animals that could be crucial in testing for these mechanisms in animals. The accumulation of large tracking datasets of animal movements may enable the testing of these

predictions in the coming years through assessment of how well patterns of orientation error conform to the predictions of these models at various stages of development. However, these predictions will be difficult to test unless the cues, and the distribution of the cues, that animals use as a navigational map are already known as these are important in generating specific model predictions. Additionally, if animals use more than two map cues in combination or show patterns of orientation in response to other environmental features, such as obstacles or the wind, this may further complicate these predictions and make them difficult to test. Nonetheless, attempts to test these predictions would be potentially valuable in advancing our understanding of animal navigation and would facilitate answering outstanding questions relating to all three components of animal maps outlined in my framework.

In Chapter 5, I modelled individual learning within groups by pairing neural networks in completing a task inspired by homing pigeon navigation. The task was much simpler than that implemented in Chapter 2, and simply required outputting a single correct number that was invariant during learning. This model was loosely based on how homing pigeons might learn to orient in a homewards direction at a novel site. Flocks of homing pigeons navigate collectively, with compromises taken between the preferred directions of individuals (Biro et al., 2006; Flack et al., 2013) that can generate improvements in navigational performance in groups of larger sizes (Sasaki et al., 2022) and might affect navigational learning in various ways (Collet et al., 2023). In the modelling results, I found that the modelled collective decision-making process affected the learning of individual neural networks. 'Leader' neural networks, that had a greater input into collective decision making, approached the correct solution more quickly than 'followers'. This matches empirical findings in flocks of homing pigeons (Burt de Perera and Guilford, 1999). Additionally, I found that 'democratic' pairs of neural networks, in which an average/compromise was taken between individual outputs, learned to achieve the task differently to solo neural networks and those in 'despotic' pairs, in which one neural network took charge in each trial. In democratic pairs, individual neural networks learned to compensate for the error of their

partners, rather than each converging on the correct solution individually. There have been very few previous studies of how collective decision making impacts upon individual learning, and how this translates into collective performance (Collet et al., 2023; Kao et al., 2014). I suggest that the predictions of this model could be examined in groups of homing pigeons learning to collectively navigate using a similar procedure to the neural network training, by training pairs of pigeons to learn a new route together and then testing them individually. This would allow testing of whether the 'errors' of the pigeons during individual testing (where they deviate from the collectively learned route) negatively correlate between individuals of a pair and whether this is linked to the leadership hierarchy between the individuals. This type of empirical investigation would allow assessment of how well these neural network models capture dynamics of learning in a collective navigation system and help to bridge the link between theoretical and empirical understanding of collective learning.

I used experimental approaches in two model systems, on Manx shearwaters in Chapter 3 and homing pigeons in Chapter 4, to investigate the cues and the ontogeny of navigational maps, respectively. I designed an experiment to investigate a possible role of olfactory map cues in the homing navigation of Manx shearwaters by manipulating their access to olfactory cues before release. This was achieved through manipulating the duration of their access to olfactory cues in the fresh air before release, based upon an experiment on homing pigeons (Wallraff et al., 1984). I hypothesised that birds with longer access to olfactory cues prior to release would leave the vicinity of the release site more quickly and initially exhibit stronger orientation and more efficient navigation. After running this experiment in two years, I found that longer access to olfactory cues did not affect initial navigational performance, as none of the tested metrics showed significant results that replicated across both years of the study. I was therefore unable to conclude whether olfactory map cues play a role in the homing navigation of Manx shearwaters. Nonetheless, I believe that experimental approaches should continue to be employed to investigate the sensory basis of the navigational map of Manx shearwaters, and that

understanding the sensory basis of their map would represent a step change in our understanding of the navigational mechanisms of this model species. Additionally, this work would potentially be able to be integrated with correlational work on the map and compass navigation of Manx shearwaters (Padget et al., 2019) to attempt to link the spatial distribution of map cues with the navigational performance of the birds and probe further questions relating to the mechanisms that guide their navigation.

Unlike Manx shearwaters, which are currently very difficult to track in the years between their fledging and first breeding (Wynn et al., 2022a), homing pigeons represent a good model species for investigating the ontogeny, not only the mechanisms, of homing navigation. I investigated their navigational learning at novel release sites, seeking to determine whether passive exposure to the cues at a novel site, without flight or homing, would be sufficient for latent navigational learning. Previous experiments have shown that pigeons can determine the home direction before release (Gagliardo et al., 2016; Wallraff et al., 1984) and that they improve their navigational performance after a single release from a novel site (Gagliardo et al., 2020b). Additionally, latent learning of navigational cues has been demonstrated in pigeons, in studies showing that olfactory cues are learned in association with the wind direction even when pigeons are confined to their home loft (Gagliardo et al., 2001a; Odetti et al., 2003). I exposed pigeons to the cues at a novel site before releasing them from the same site on a subsequent day along with controls that had never previously visited the site. I predicted that the pigeons that had previously been exposed to the cues at the release site might show better navigational performance than controls through latent learning of cues at the release site. However, I found no significant differences between birds that had and had not previously visited and been exposed to the cues at the novel site, and therefore no evidence that this is sufficient for navigational learning. There are three possible explanations for the lack of a detectable difference in this experiment: first, the sample size may have been insufficient to detect a small learning effect; second, the pigeons may have learned but shown no difference in performance upon subsequent

release; finally, passive exposure to the cues at a novel release site may be insufficient for navigational learning. Further experiments which probe these possibilities would help to elucidate the precise mechanisms through which homing pigeons learn to navigate at novel sites and improve our understanding of navigational ontogeny in this important model system.

One of the limitations of the work completed in this thesis is the failure to bring together the theoretical and experimental approaches employed here to jointly advance our understanding of animal maps. I have not yet been able to test many of the predictions that I posed in my conceptual review, such as the potential role for path integration in navigational map learning, or the assumptions and predictions derived from my neural network models on grid map navigation and collective learning. However, I suggest that the predictions on grid map navigation might be possible to test in the future as large tracking datasets of animal movements accumulate. One of the challenges for testing these predictions is accumulating sufficient data in a system in which the map cues used by animals and their distribution are already relatively well understood. The predictions derived here from the collective learning modelling in Chapter 5 could be tested in groups of pigeons collectively learning to navigate. On the other hand, the experimental work carried out here has focussed upon somewhat different questions to those examined in my theoretical work. Understanding what environmental properties are utilised by animals as map cues, as my experiment on Manx shearwaters sought to do, is probably required as a precursor to understanding the ways in which animals extrapolate and combine cues, the focus of my modelling in Chapter 2.

Nonetheless, I have been able to generate a wide range of ideas, questions, and predictions both through my conceptual review of animal maps and my modelling with artificial neural networks. I hope that these contribute to navigational research going forward, as more of this work is published. Additionally, the experimental work on Manx shearwaters and homing pigeons represents an incremental step forward in our investigations on the mechanisms and ontogeny

of navigation in these two model systems. Moving forward, I believe that a combination of theoretical modelling of animal navigation with empirical testing for the predictions of those models in large tracking datasets of movements will advance our understanding of large-scale animal navigation. Further, developments on the methods in which we can experimentally manipulate how animals detect and perceive navigational cues as they navigate over long distances may be required to address many of the outstanding questions relating to the mechanisms and ontogeny of animal navigation. These approaches will be required to advance together in order to better identify and understand the proximate causes of the most impressive of the behaviours of animals, their long-distance navigation.

References

Abadi, M., P. Barham, J. M. Chen, Z. F. Chen, A. Davis, J. Dean, M. Devin, S. Ghemawat, G. Irving, M. Isard, M. Kudlur, J. Levenberg, R. Monga, S. Moore, D. G. Murray, B. Steiner, P. Tucker, V. Vasudevan, P. Warden, M. Wicke, Y. Yu, X. Q. Zheng, and U. Assoc, 2016, TensorFlow: A system for large-scale machine learning: Proceedings of OSDI'16: 12th USENIX Symposium on Operating Systems Design and Implementation, p. 265-283.

Able, K. P., 2001, The concepts and terminology of bird navigation: Journal of Avian Biology, v. 32, p. 174-183.

Abolaffio, M., A. M. Reynolds, J. G. Cecere, V. H. Paiva, and S. Focardi, 2018, Olfactory-cued navigation in shearwaters: linking movement patterns to mechanisms: Scientific Reports, v. 8, p. 11590.

Abrahms, B., C. S. Teitelbaum, T. Mueller, and S. J. Converse, 2021, Ontogenetic shifts from social to experiential learning drive avian migration timing: Nature Communications, v. 12, p. 7326.

Agostinelli, C., and U. Lund, 2022, R package 'circular': Circular Statistics (version 0.4-95).

Andrade-Lotero, E., and R. L. Goldstone, 2021, Self-organized division of cognitive labor: PLoS One, v. 16, p. e0254532.

Baker, R. R., 1978, The evolutionary ecology of animal migration: London, Hodder and Stoughton.

Baker, R. R., 1984, Bird navigation : the solution of a mystery?: London, Hodder & Stoughton.

Baldaccini, N., S. Benvenuti, V. Fiaschi, P. Ioalè, and F. Papi, 1982, Pigeon orientation: experiments on the role of olfactory stimuli perceived during the outward journey: Avian Navigation: International Symposium on Avian Navigation (ISAN) held at Tirrenia (Pisa), September 11–14, 1981, p. 160-169.

Baldaccini, N. E., S. Benvenuti, V. Fiaschi, and F. Papi, 1975, Pigeon navigation: effects of wind deflection at home cage on homing behavior: Journal of Comparative Physiology, v. 99, p. 177-186.

Bates, D., M. Mächler, B. Bolker, and S. Walker, 2015, Fitting Linear Mixed-Effects Models Using lme4: Journal of Statistical Software, v. 67, p. 1 - 48.

Batty, E. R., L. Hoban, M. L. Spetch, and C. T. Dickson, 2009, Rats' use of geometric, featural and orientation cues to locate a hidden goal: Behavioural Processes, v. 82, p. 327-334.

Beardsworth, C. E., E. Gobbens, F. van Maarseveen, B. Denissen, A. Dekinga, R. Nathan, S. Toledo, and A. I. Bijleveld, 2022, Validating ATLAS: A regional-scale high-throughput tracking system: Methods in Ecology and Evolution, v. 13, p. 1990-2004.

Beauchamp, G., 2000, Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches: Behaviour, v. 137, p. 301-314.

Benhamou, S., 2003, Bicoordinate navigation based on non-orthogonal gradient fields: Journal of Theoretical Biology, v. 225, p. 235-239.

Benhamou, S., and B. Poucet, 1998, Landmark use by navigating rats (Rattus norvegicus) contrasting geometric and featural information: Journal of Comparative Psychology, v. 112, p. 317.

Benhamou, S., J. Sudre, J. Bourjea, S. Ciccione, A. De Santis, and P. Luschi, 2011, The role of geomagnetic cues in green turtle open sea navigation: PLoS One, v. 6, p. e26672.

Benvenuti, S., P. Ioalè, and B. Massa, 1993, Olfactory experiments on Cory's shearwater (Calonectris diomedea): The effect of intranasal zinc sulphate treatment on short-range homing behaviour: Bollettino di zoologia, v. 60, p. 207-210.

Benvenuti, S., and H. G. Wallraff, 1985, Pigeon navigation: site simulation by means of atmospheric odours: Journal of Comparative Physiology A, v. 156, p. 737-746.

Berthold, P., 1996, Control of bird migration, Springer Science & Business Media.

Bingman, V. P., A. Gagliardo, G. E. Hough, P. Ioalè, M. C. Kahn, and J. J. Siegel, 2005, The avian hippocampus, homing in pigeons and the memory representation of large-scale space: Integrative and Comparative Biology, v. 45, p. 555-564.

Biro, D., R. Freeman, J. Meade, S. Roberts, and T. Guilford, 2007, Pigeons combine compass and landmark guidance in familiar route navigation: Proceedings of the National Academy of Sciences, v. 104, p. 7471-7476.

Biro, D., T. Guilford, and M. S. Dawkins, 2003, Mechanisms of visually mediated site recognition by the homing pigeon: Animal Behaviour, v. 65, p. 115-122.

Biro, D., T. Guilford, G. Dell'Omo, and H.-P. Lipp, 2002, How the viewing of familiar landscapes prior to release allows pigeons to home faster: evidence from GPS tracking: Journal of Experimental Biology, v. 205, p. 3833-3844.

Biro, D., J. Meade, and T. Guilford, 2004, Familiar route loyalty implies visual pilotage in the homing pigeon: Proceedings of the National Academy of Sciences, v. 101, p. 17440-17443.

Biro, D., T. Sasaki, and S. J. Portugal, 2016, Bringing a Time-Depth Perspective to Collective Animal Behaviour: Trends in Ecology & Evolution, v. 31, p. 550-562.

Biro, D., D. J. Sumpter, J. Meade, and T. Guilford, 2006, From compromise to leadership in pigeon homing: Current Biology, v. 16, p. 2123-8.

Blaser, N., G. Dell'Omo, G. Dell'Ariccia, D. P. Wolfer, and H.-P. Lipp, 2013, Testing cognitive navigation in unknown territories: homing pigeons choose different targets: Journal of Experimental Biology, v. 216, p. 3123-3131.

Blaser, N., S. I. Guskov, V. A. Entin, D. P. Wolfer, V. A. Kanevskyi, and H.-P. Lipp, 2014, Gravity anomalies without geomagnetic disturbances interfere with pigeon homing – a GPS tracking study: Journal of Experimental Biology, v. 217, p. 4057-4067.

Boles, L. C., and K. J. Lohmann, 2003, True navigation and magnetic maps in spiny lobsters: Nature, v. 421, p. 60-63.

Bonadonna, F., 2009, Olfaction in Petrels: Annals of the New York Academy of Sciences, v. 1170, p. 428-433.

Bonadonna, F., C. Bajzak, S. Benhamou, K. Igloi, P. Jouventin, H. P. Lipp, and G. Dell'Omo, 2005, Orientation in the wandering albatross: interfering with magnetic perception does not affect orientation performance: Proceedings of the Royal Society B: Biological Sciences, v. 272, p. 489-495.

Bonadonna, F., and V. Bretagnolle, 2002, Smelling home: a good solution for burrow-finding in nocturnal petrels?: Journal of Experimental Biology, v. 205, p. 2519-2523.

Bonadonna, F., and A. Gagliardo, 2021, Not only pigeons: avian olfactory navigation studied by satellite telemetry: Ethology Ecology & Evolution, v. 33, p. 273-289.

Bonadonna, F., J. Spaggiari, and H. Weimerskirch, 2001, Could osmotaxis explain the ability of blue petrels to return to their burrows at night?: Journal of Experimental Biology, v. 204, p. 1485-1489.

Bonadonna, F., M. Villafane, C. Bajzak, and P. Jouventin, 2004, Recognition of burrow's olfactory signature in blue petrels, Halobaena caerulea: an efficient discrimination mechanism in the dark: Animal Behaviour, v. 67, p. 893-898.

Bostrom, J. E., S. Akesson, and T. Alerstam, 2012, Where on earth can animals use a geomagnetic bi-coordinate map for navigation?: Ecography, v. 35, p. 1039-1047.

Bouton, M. E., 2007, Learning and behavior : a contemporary synthesis, Sunderland: Sinauer Associates.

Braithwaite, V., and T. Guilford, 1993, Recognition of familiar visual landmarks in homing pigeons: The Journal of Navigation, v. 46, p. 371-375.

Braithwaite, V., and J. Newman, 1994, Exposure to familiar visual landmarks allows pigeons to home faster: Animal Behaviour.

Braithwaite, V. A., 1993, When does previewing the landscape affect pigeon homing?: Ethology, v. 95, p. 141-151.

Braithwaite, V. A., and T. Guilford, 1991, Viewing familiar landscapes affects pigeon homing: Proceedings of the Royal Society of London. Series B: Biological Sciences, v. 245, p. 183-186.

Brooke, M., 2013, The Manx Shearwater, A&C Black.

Brothers, J. R., and Kenneth J. Lohmann, 2015, Evidence for Geomagnetic Imprinting and Magnetic Navigation in the Natal Homing of Sea Turtles: Current Biology, v. 25, p. 392-396.

Brothers, J. R., and K. J. Lohmann, 2018, Evidence that Magnetic Navigation and Geomagnetic Imprinting Shape Spatial Genetic Variation in Sea Turtles: Current Biology, v. 28, p. 1325-1329.e2.

Burt de Perera, T., and T. Guilford, 1999, The social transmission of spatial information in homing pigeons: Animal Behaviour, v. 57, p. 715-719.

Byholm, P., M. Beal, N. Isaksson, U. Lötberg, and S. Åkesson, 2022, Paternal transmission of migration knowledge in a long-distance bird migrant: Nature Communications, v. 13, p. 1566.

Cancalon, P., 1982, Degeneration and regeneration of olfactory cells induced by ZnSO4 and other chemicals: Tissue and Cell, v. 14, p. 717-733.

Chelazzi, G., and L. Pardi, 1972, Experiments on the homing behaviour of caged pigeons: Monitore Zoologico Italiano-Italian Journal of Zoology, v. 6, p. 63-73.

Cheng, K., 1986, A purely geometric module in the rat's spatial representation: Cognition, v. 23, p. 149-178.

Cheng, K., 2005, Reflections on geometry and navigation: Connection Science, v. 17, p. 5-21.

Chernetsov, N., D. Kishkinev, and H. Mouritsen, 2008, A Long-Distance Avian Migrant Compensates for Longitudinal Displacement during Spring Migration: Current Biology, v. 18, p. 188-190.

Chernetsov, N., A. Pakhomov, D. Kobylkov, D. Kishkinev, R. A. Holland, and H. Mouritsen, 2017, Migratory Eurasian Reed Warblers Can Use Magnetic Declination to Solve the Longitude Problem: Current Biology, v. 27, p. 2647-2651.e2.

Cheung, A., S. Zhang, C. Stricker, and M. V. Srinivasan, 2007, Animal navigation: the difficulty of moving in a straight line: Biological Cybernetics, v. 97, p. 47-61.

Cheung, A., S. Zhang, C. Stricker, and M. V. Srinivasan, 2008, Animal navigation: general properties of directed walks: Biological Cybernetics, v. 99, p. 197-217.

Chittka, L., J. Kunze, C. Shipman, and S. Buchmann, 1995, The significance of landmarks for path integration in homing honeybee foragers: Naturwissenschaften, v. 82, p. 341-343.

Chollet, F., 2015, Keras, GitHub, Github repository.

Collet, J., J. Morford, P. Lewin, A.-S. Bonnet-Lebrun, T. Sasaki, and D. Biro, 2023, Mechanisms of collective learning: how can animal groups improve collective performance when repeating a task?: Philosophical Transactions of the Royal Society B: Biological Sciences, v. 378, p. 20220060.

Collett, M., and T. S. Collett, 2000, How do insects use path integration for their navigation?: Biological Cybernetics, v. 83, p. 245-259.

Collett, T. S., 1987, The use of visual landmarks by gerbils: Reaching a goal when landmarks are displaced: Journal of Comparative Physiology A, v. 160, p. 109-113.

Collett, T. S., B. A. Cartwright, and B. A. Smith, 1986, Landmark learning and visuo-spatial memories in gerbils: Journal of Comparative Physiology A, v. 158, p. 835-851.

Collett, Thomas S., and M. Collett, 2011, Animal Navigation: Following Signposts in the Sea: Current Biology, v. 21, p. R843-R846.

Conradt, L., and C. List, 2009, Group decisions in humans and animals: a survey: Philosophical Transactions of the Royal Society B - Biological Sciences, v. 364, p. 719-42.

Conradt, L., and T. J. Roper, 2005, Consensus decision making in animals: Trends in Ecology & Evolution, v. 20, p. 449-56.

Conradt, L., and T. J. Roper, 2007, Democracy in animals: the evolution of shared group decisions: Proceedings of the Royal Society B, v. 274, p. 2317-26.

Couzin, I. D., and C. Heins, 2022, Emerging technologies for behavioral research in changing environments: Trends in Ecology & Evolution.

Couzin, I. D., J. Krause, N. R. Franks, and S. A. Levin, 2005, Effective leadership and decision-making in animal groups on the move: Nature, v. 433, p. 513-6.

Curran, J., and T. Hersh, 2021, Hotelling: Hotelling's T^2 Test and Variants.

Dall'Antonia, P., L. Dall'Antonia, A. Ribolini, P. Ioalè, and S. Benvenuti, 1999, Pigeon homing: site simulation experiments with bird-borne direction recorders: Behavioural Processes, v. 44, p. 331-339.

Dawson, M. R. W., 2008, Connectionism and classical conditioning, Comparative Cognition & Behavior Reviews, p. 1–115.

De León, A., E. Mínguez, and B. Belliure, 2003, Self-odour recognition in European storm-petrel chicks: Behaviour, v. 140, p. 925-933.

Dell'Ariccia, G., and F. Bonadonna, 2013, Back home at night or out until morning? Nycthemeral variations in homing of anosmic Cory's shearwaters in a diurnal colony: Journal of Experimental Biology, v. 216, p. 1430-1433.

Dell'Ariccia, G., A. Célérier, M. Gabirot, P. Palmas, B. Massa, and F. Bonadonna, 2014, Olfactory foraging in temperate waters: sensitivity to dimethylsulphide of shearwaters in the

Atlantic Ocean and Mediterranean Sea: Journal of Experimental Biology, v. 217, p. 1701-1709.

Dornfeldt, K., 1991, Pigeon homing in relation to geomagnetic, gravitational, topographical, and meteorological conditions: Behavioral Ecology and Sociobiology, v. 28, p. 107-123.

Dukas, R., 1998, Cognitive ecology: the evolutionary ecology of information processing and decision making: Chicago; London, University of Chicago Press.

Egevang, C., I. J. Stenhouse, R. A. Phillips, A. Petersen, J. W. Fox, and J. R. Silk, 2010, Tracking of Arctic terns Sterna paradisaea reveals longest animal migration: Proceedings of the National Academy of Sciences, v. 107, p. 2078-2081.

Eklund, A., and J. Trimble, 2021, beeswarm: The Bee Swarm Plot, an Alternative to Stripchart.

Emlen, S. T., 1967a, Migratory orientation in indigo bunting Passerina cyanea - Part I: evidence for use of celestial cues: Auk, v. 84, p. 309-&.

Emlen, S. T., 1967b, Migratory orientation in indigo bunting Passerina cyanea - Part II: Mechanism of celestial orientation: Auk, v. 84, p. 463-&.

Estandía, A., R. T. Chesser, H. F. James, M. A. Levy, J. F. Obiol, V. Bretagnolle, J. González-Solís, and A. J. Welch, 2021, Substitution rate variation in a robust Procellariiform seabird phylogeny is not solely explained by body mass, flight efficiency, population size or life history traits: BioRxiv, p. 2021.07. 27.453752.

Etienne, A. S., and K. J. Jeffery, 2004, Path integration in mammals: Hippocampus, v. 14, p. 180-192.

Etienne, A. S., R. Maurer, and F. Saucy, 1988, Limitations in the assessment of path dependent information: Behaviour, p. 81-111.

Falcón-Cortés, A., D. Boyer, and G. Ramos-Fernández, 2019, Collective learning from individual experiences and information transfer during group foraging: Journal of the Royal Society Interface, v. 16, p. 20180803.

Ferrer Obiol, J., H. F. James, R. T. Chesser, V. Bretagnolle, J. González-Solís, J. Rozas, A. J. Welch, and M. Riutort, 2022, Palaeoceanographic changes in the late Pliocene promoted rapid diversification in pelagic seabirds: Journal of Biogeography, v. 49, p. 171-188.

Fischhoff, I. R., S. R. Sundaresan, J. Cordingley, H. M. Larkin, M. J. Sellier, and D. I. Rubenstein, 2007, Social relationships and reproductive state influence leadership roles in movements of plains zebra, Equus burchellii: Animal Behaviour, v. 73, p. 825-831.

Fischler-Ruiz, W., D. G. Clark, N. R. Joshi, V. Devi-Chou, L. Kitch, M. Schnitzer, L. F. Abbott, and R. Axel, 2021, Olfactory landmarks and path integration converge to form a cognitive spatial map: Neuron, v. 109, p. 4036-4049. e5.

Flack, A., R. Freeman, T. Guilford, and D. Biro, 2013, Pairs of pigeons act as behavioural units during route learning and co-navigational leadership conflicts: Journal of Experimental Biology, v. 216, p. 1434-8.

Fox, J., and S. Weisberg, 2011, An R companion to applied regression, Sage publications.

Franks, D. W., and G. D. Ruxton, 2010, Robustness of Neural Network Models: Systems Biology for Signaling Networks, v. 1, p. 337-351.

Gagliardo, A., 2013, Forty years of olfactory navigation in birds: Journal of Experimental Biology, v. 216, p. 2165-2171.

Gagliardo, A., J. Bried, P. Lambardi, P. Luschi, M. Wikelski, and F. Bonadonna, 2013, Oceanic navigation in Cory's shearwaters: evidence for a crucial role of olfactory cues for homing after displacement: Journal of Experimental Biology, v. 216, p. 2798-805.

Gagliardo, A., P. Ioalè, and V. P. Bingman, 1999, Homing in pigeons: the role of the hippocampal formation in the representation of landmarks used for navigation: Journal of Neuroscience, v. 19, p. 311-315.

Gagliardo, A., P. Ioalè, C. Filannino, and M. Wikelski, 2011, Homing Pigeons Only Navigate in Air with Intact Environmental Odours: A Test of the Olfactory Activation Hypothesis with GPS Data Loggers: PLoS One, v. 6.

Gagliardo, A., P. Ioalè, F. Odetti, and V. P. Bingman, 2001a, The ontogeny of the homing pigeon navigational map: evidence for a sensitive learning period: Proceedings of the Royal Society B, v. 268, p. 197-202.

Gagliardo, A., P. Ioalè, M. Savini, G. Dell'Omo, and V. P. Bingman, 2009, Hippocampal-dependent familiar area map supports corrective re-orientation following navigational error during pigeon homing: a GPS-tracking study: European Journal of Neuroscience, v. 29, p. 2389-2400.

Gagliardo, A., M. Mazzotto, and V. P. Bingman, 1997, Piriform cortex ablations block navigational map learning in homing pigeons: Behavioural Brain Research, v. 86, p. 143-148.

Gagliardo, A., F. Odetti, and P. Ioalè, 2001b, Relevance of visual cues for orientation at familiar sites by homing pigeons: an experiment in a circular arena: Proceedings of the Royal Society of London. Series B: Biological Sciences, v. 268, p. 2065-2070.

Gagliardo, A., F. Odetti, P. Ioalè, V. P. Bingman, S. Tuttle, and G. Vallortigara, 2002, Bilateral participation of the hippocampus in familiar landmark navigation by homing pigeons: Behavioural Brain Research, v. 136, p. 201-209.

Gagliardo, A., E. Pollonara, G. Casini, M. G. Rossino, M. Wikelski, and V. P. Bingman, 2020a, Importance of the hippocampus for the learning of route fidelity in homing pigeons: Biology Letters, v. 16, p. 20200095.

Gagliardo, A., E. Pollonara, and M. Wikelski, 2016, Pigeon navigation: exposure to environmental odours prior to release is sufficient for homeward orientation, but not for homing: Journal of Experimental Biology, v. 219, p. 2475-80.

Gagliardo, A., E. Pollonara, and M. Wikelski, 2018, Only natural local odours allow homeward orientation in homing pigeons released at unfamiliar sites: Journal of Comparative Physiology A, v. 204, p. 761-771.

Gagliardo, A., E. Pollonara, and M. Wikelski, 2020b, Pigeons remember visual landmarks after one release and rely upon them more if they are anosmic: Animal Behaviour, v. 166, p. 85-94.

Gagliardo, A., E. Pollonara, and M. Wikelski, 2021, The homing pigeons' olfactory map is affected by geographical barriers: Ethology Ecology & Evolution, v. 33, p. 321-337.

Ghirlanda, S., and M. Enquist, 2007, How training and testing histories affect generalization: a test of simple neural networks: Philosophical Transactions of the Royal Society B-Biological Sciences, v. 362, p. 449-454.

Gluck, M. A., 1991, Stimulus-generalization and representation in adaptive network models of category learning: Psychological Science, v. 2, p. 50-55.

Gould, J. L., 1982, The map sense of pigeons: Nature, v. 296, p. 205-211.

Gould, J. L., 2008, Animal Navigation: The Longitude Problem: Current Biology, v. 18, p. R214-R216.

Greene, C. M., and R. G. Cook, 1997, Landmark geometry and identity controls spatial navigation in rats: Animal Learning & Behavior, v. 25, p. 312-323.

Griffin, D. R., 1952, Bird navigation: Biological Reviews, v. 27, p. 359-390.

Guilford, T., and D. Biro, 2014, Route following and the pigeon's familiar area map: Journal of Experimental Biology, v. 217, p. 169-179.

Guilford, T., and T. Burt de Perera, 2017, An associative account of avian navigation: Journal of Avian Biology, v. 48, p. 191-195.

Guilford, T., and J. Chappell, 1996, When pigeons home alone: Does flocking have a navigational function?: Proceedings of the Royal Society B-Biological Sciences, v. 263, p. 153-156.

Guilford, T., J. Meade, R. Freeman, T. J. Evans, D. Biro, F. Bonadonna, D. Boyle, S. Roberts, and C. Perrins, 2008, GPS tracking of the foraging movements of Manx Shearwaters Puffinus puffinus breeding on Skomer Island, Wales: Ibis, v. 150, p. 462-473.

Guilford, T., J. Meade, J. Willis, R. A. Phillips, D. Boyle, S. Roberts, M. Collett, R. Freeman, and C. Perrins, 2009, Migration and stopover in a small pelagic seabird, the Manx shearwater Puffinus puffinus: insights from machine learning: Proceedings of the Royal Society B: Biological Sciences, v. 276, p. 1215-1223.

Guilford, T., and G. K. Taylor, 2014, The sun compass revisited: Animal Behaviour, v. 97, p. 135-143.

Gulli, A., and S. Pal, 2017, Deep learning with Keras: Birmingham, UK, Packt Publishing.

Hagstrum, J. T., 2000, Infrasound and the avian navigational map: Journal of Experimental Biology, v. 203, p. 1103-1111.

Hansen, L. P., N. Jonsson, and B. Jonsson, 1993, Oceanic migration in homing Atlantic salmon: Animal behaviour, v. 45, p. 927-941.

Hansen, M. J., A. L. Burns, C. T. Monk, C. Schutz, J. T. Lizier, I. Ramnarine, A. J. W. Ward, and J. Krause, 2021, The effect of predation risk on group behaviour and information flow during repeated collective decisions: Animal Behaviour, v. 173, p. 215-239.

Harris, C. R., K. J. Millman, S. J. van der Walt, R. Gommers, P. Virtanen, D. Cournapeau, E. Wieser, J. Taylor, S. Berg, N. J. Smith, R. Kern, M. Picus, S. Hoyer, M. H. van Kerkwijk, M. Brett, A. Haldane, J. F. del Río, M. Wiebe, P. Peterson, P. Gérard-Marchant, K. Sheppard, T. Reddy, W. Weckesser, H. Abbasi, C. Gohlke, and T. E. Oliphant, 2020, Array programming with NumPy: Nature, v. 585, p. 357-362.

Harris, M., 1966, Age of return to the colony, age of breeding and adult survival of Manx Shearwaters: Bird Study, v. 13, p. 84-95.

Harten, L., A. Katz, A. Goldshtein, M. Handel, and Y. Yovel, 2020, The ontogeny of a mammalian cognitive map in the real world: Science, v. 369, p. 194-197.

Heyes, C. M., 1994, Social learning in animals: categories and mechanisms: Biological Reviews, v. 69, p. 207-31.

Hijmans, R. J., 2022, geosphere: Spherical Trigonometry.

Holland, R. A., 2014, True navigation in birds: from quantum physics to global migration: Journal of Zoology, v. 293, p. 1-15.

Hoppitt, W., and K. N. Laland, 2013, Social learning : an introduction to mechanisms, methods, and models: Princeton, Princeton University Press, ix, 307 pages p.

Hunter, J. D., 2007, Matplotlib: A 2D graphics environment: Computing in Science & Engineering, v. 9, p. 90-95.

Ioalè, P., F. Papi, V. Fiaschi, and N. E. Baldaccini, 1978, Pigeon navigation: Effects upon homing behaviour by reversing wind direction at the loft: Journal of Comparative Physiology A, v. 128, p. 285-295.

Jacobs, L. F., and F. Schenk, 2003, Unpacking the cognitive map: The parallel map theory of hippocampal function: Psychological Review, v. 110, p. 285-315.

Jesmer, B. R., J. A. Merkle, J. R. Goheen, E. O. Aikens, J. L. Beck, A. B. Courtemanch, M. A. Hurley, D. E. McWhirter, H. M. Miyasaki, K. L. Monteith, and M. J. Kauffman, 2018, Is ungulate

migration culturally transmitted? Evidence of social learning from translocated animals: Science, v. 361, p. 1023-1025.

Johnson, C. C., 1970, Triangulation Theory and Techniques: Navigation, v. 17, p. 308-324.

Jorge, P. E., A. E. Marques, and J. B. Phillips, 2009, Activational Rather Than Navigational Effects of Odors on Homing of Young Pigeons: Current Biology, v. 19, p. 650-654.

Jorge, P. E., P. A. Marques, and J. B. Phillips, 2010, Activational effects of odours on avian navigation: Proceedings of the Royal Society B, v. 277, p. 45-9.

Kano, F., T. Sasaki, and D. Biro, 2021, Collective attention in navigating homing pigeons: group size effect and individual differences: Animal Behaviour, v. 180, p. 63-80.

Kano, F., J. Walker, T. Sasaki, and D. Biro, 2018, Head-mounted sensors reveal visual attention of free-flying homing pigeons: Journal of Experimental Biology, v. 221.

Kao, A. B., N. Miller, C. Torney, A. Hartnett, and I. D. Couzin, 2014, Collective learning and optimal consensus decisions in social animal groups: PLoS Computational Biology, v. 10, p. e1003762.

Keeton, W. T., 1970, Comparative orientational and homing performances of single pigeons and small flocks: Auk, v. 87, p. 797-&.

Keeton, W. T., 1973, Release-site bias as a possible guide to the "map" component in pigeon homing: Journal of Comparative Physiology A, v. 86, p. 1-16.

Keeton, W. T., 1974, The Orientational and Navigational Basis of Homing in Birds, *in* D. S. Lehrman, J. S. Rosenblatt, R. A. Hinde, and E. Shaw, eds., Advances in the Study of Behavior, v. 5, Academic Press, p. 47-132.

Kelly, D. M., M. L. Spetch, and C. D. Heth, 1998, Pigeons' (Columba livia) encoding of geometric and featural properties of a spatial environment: Journal of Comparative Psychology, v. 112, p. 259.

Kiepenheuer, J., 1985, Can pigeons be fooled about the actual release site position by presenting them information from another site?: Behavioral Ecology and Sociobiology, v. 18, p. 75-82.

Kishkinev, D., A. Anashina, I. Ishchenko, and R. A. Holland, 2020, Anosmic migrating songbirds demonstrate a compensatory response following long-distance translocation: a radio-tracking study: Journal of Ornithology, v. 161, p. 47-57.

Kishkinev, D., N. Chernetsov, D. Heyers, and H. Mouritsen, 2013, Migratory reed warblers need intact trigeminal nerves to correct for a 1,000 km eastward displacement: PLoS One, v. 8, p. e65847.

Kishkinev, D., N. Chernetsov, and H. Mouritsen, 2010, A Double-Clock or Jetlag Mechanism is Unlikely to be Involved in Detection of East—West Displacements in a Long-Distance Avian Migrant: The Auk, v. 127, p. 773-780.

Kishkinev, D., N. Chernetsov, A. Pakhomov, D. Heyers, and H. Mouritsen, 2015, Eurasian reed warblers compensate for virtual magnetic displacement: Current Biology, v. 25, p. R822-R824.

Kishkinev, D., F. Packmor, T. Zechmeister, H.-C. Winkler, N. Chernetsov, H. Mouritsen, and R. A. Holland, 2021, Navigation by extrapolation of geomagnetic cues in a migratory songbird: Current Biology, v. 31, p. 1563-1569.e4.

Kowalski, U., and R. Wiltschko, 1987, Pigeon homing: familiarity with the release site reduces the release site bias: Journal of experimental biology, v. 133, p. 457-462.

Kramer, G., 1950, Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren: Naturwissenschaften, v. 37, p. 377-378.

Kramer, G., 1953, Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet?, Journal of Ornithology, p. 201–219.

Kramer, G., 1957, Experiments on bird orientation and their interpretation: Ibis, v. 99, p. 196-227.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen, 2017, lmerTest Package: Tests in Linear Mixed Effects Models: Journal of Statistical Software, v. 82, p. 1 - 26.

Lack, D., and R. Lockley, 1938, Skokholm bird observatory homing experiments: British Birds, v. 31, p. 242-248.

Lander , J. P., 2018, useful: A Collection of Handy, Useful Functions.

Langridge, E. A., N. R. Franks, and A. B. Sendova-Franks, 2004, Improvement in collective performance with experience in ants: Behavioral Ecology and Sociobiology, v. 56, p. 523-529.

Langridge, E. A., A. B. Sendova-Franks, and N. R. Franks, 2008, How experienced individuals contribute to an improvement in collective performance in ants: Behavioral Ecology and Sociobiology, v. 62, p. 447-456.

Lau, K.-K., S. Roberts, D. Biro, R. Freeman, J. Meade, and T. Guilford, 2006, An edge-detection approach to investigating pigeon navigation: Journal of Theoretical Biology, v. 239, p. 71-78.

Layne, J. E., W. J. P. Barnes, and L. M. Duncan, 2003, Mechanisms of homing in the fiddler crab Uca rapax 2. Information sources and frame of reference for a path integration system: Journal of Experimental Biology, v. 206, p. 4425-4442.

Lockley, R. M., 1942, Shearwaters: London, J. M. Dent and Sons.

Lohmann, K., J. Hester, and C. Lohmann, 1999, Long-distance navigation in sea turtles: Ethology Ecology & Evolution, v. 11, p. 1-23.

Lohmann, K., and C. Lohmann, 1994, Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude: Journal of Experimental Biology, v. 194, p. 23-32.

Lohmann, K. J., S. D. Cain, S. A. Dodge, and C. M. F. Lohmann, 2001, Regional magnetic fields as navigational markers for sea turtles: Science, v. 294, p. 364-366.

Lohmann, K. J., K. M. Goforth, A. G. Mackiewicz, D. S. Lim, and C. M. Lohmann, 2022, Magnetic maps in animal navigation: Journal of Comparative Physiology A, p. 1-27.

Lohmann, K. J., and C. M. Lohmann, 1996, Detection of magnetic field intensity by sea turtles: Nature, v. 380, p. 59-61.

Lohmann, K. J., and C. M. Lohmann, 2006, Sea turtles, lobsters, and oceanic magnetic maps: Marine and Freshwater Behaviour and Physiology, v. 39, p. 49-64.

Lohmann, K. J., and C. M. F. Lohmann, 2019, There and back again: natal homing by magnetic navigation in sea turtles and salmon: Journal of Experimental Biology, v. 222.

Lohmann, K. J., C. M. F. Lohmann, L. M. Ehrhart, D. A. Bagley, and T. Swing, 2004, Geomagnetic map used in sea-turtle navigation: Nature, v. 428, p. 909-910.

Lohmann, K. J., C. M. F. Lohmann, and N. F. Putman, 2007, Magnetic maps in animals: nature's GPS: Journal of Experimental Biology, v. 210, p. 3697-3705.

Lund, U., and C. Agostinelli, 2018, CircStats: Circular Statistics, from "Topics in Circular Statistics" (2001).

Luschi, P., S. Benhamou, C. Girard, S. Ciccione, D. Roos, J. Sudre, and S. Benvenuti, 2007, Marine Turtles Use Geomagnetic Cues during Open-Sea Homing: Current Biology, v. 17, p. 126-133.

Luschi, P., and P. Dall'Antonia, 1993, Anosmic pigeons orient from familiar sites by relying on the map-and-compass mechanism: Animal Behaviour, v. 46, p. 1195-1203.

Mann, R. P., C. Armstrong, J. Meade, R. Freeman, D. Biro, and T. Guilford, 2014, Landscape complexity influences route-memory formation in navigating pigeons: Biology letters, v. 10, p. 20130885.

Marhold, S., W. Wiltschko, and H. Burda, 1997, A magnetic polarity compass for direction finding in a subterranean mammal: Naturwissenschaften, v. 84, p. 421-423.

Massicotte, P., and A. South, 2023, rnaturalearth: World Map Data from Natural Earth.

Matthews, G., 1953a, Sun navigation in homing pigeons: Journal of Experimental Biology, v. 30, p. 243-267.

Matthews, G. V. T., 1951, The sensory basis of bird navigation: The Journal of Navigation, v. 4, p. 260-275.

Matthews, G. V. T., 1953b, Navigation in the Manx Shearwater: Journal of Experimental Biology, v. 30, p. 370-396.

Mayr, E., 1961, Cause and effect in biology: Kinds of causes, predictability, and teleology are viewed by a practicing biologist: Science, v. 134, p. 1501-1506.

Mazzotto, M., L. Nacci, and A. Gagliardo, 1999, Homeward orientation of pigeons confined in a circular arena: Behavioural processes, v. 46, p. 217-225.

McClelland, J. L., and D. E. Rumelhart, 1985, Distributed memory and the representation of general and specific information: Journal of Experimental Psychology-General, v. 114, p. 159-188.

McNaughton, B. L., C. A. Barnes, J. L. Gerrard, K. Gothard, M. W. Jung, J. J. Knierim, H. Kudrimoti, Y. Qin, W. Skaggs, and M. Suster, 1996, Deciphering the hippocampal polyglot: the hippocampus as a path integration system: Journal of Experimental Biology, v. 199, p. 173-185.

McNaughton, B. L., F. P. Battaglia, O. Jensen, E. I. Moser, and M. B. Moser, 2006, Path integration and the neural basis of the 'cognitive map': Nature Reviews Neuroscience, v. 7, p. 663-678.

Meade, J., D. Biro, and T. Guilford, 2005, Homing pigeons develop local route stereotypy: Proceedings of the Royal Society B: Biological Sciences, v. 272, p. 17-23.

Meade, J., D. Biro, and T. Guilford, 2006, Route recognition in the homing pigeon, Columba livia: Animal Behaviour, v. 72, p. 975-980.

Merkel, F., and W. Wiltschko, 1965, Magnetismus und richtungsfinden zugunruhiger rotkehlchen (Erithacus rubecula): Vogelwarte, v. 23, p. 71-77.

Minkoff, D., N. F. Putman, J. Atema, and W. R. Ardren, 2020, Nonanadromous and anadromous Atlantic salmon differ in orientation responses to magnetic displacements: Canadian Journal of Fisheries and Aquatic Sciences, v. 77, p. 1846-1852.

Mittelstaedt, M. L., and H. Mittelstaedt, 1980, Homing by path integration in a mammal: Naturwissenschaften, v. 67, p. 566-567.

Moller, P., and P. Görner, 1994, Homing by path integration in the spider Agelena labyrinthica Clerck: Journal of Comparative Physiology A, v. 174, p. 221-229.

Mooers, R. L., 1972, Finding your way in the outdoors: compass navigation, map reading, route finding, weather forecasting, Outdoor life.

Morandi-Raikova, A., and U. Mayer, 2022, Active exploration of an environment drives the activation of the hippocampus–amygdala complex of domestic chicks: Journal of Experimental Biology, v. 225.

Mouritsen, H., K. P. Huyvaert, B. J. Frost, and D. J. Anderson, 2003, Waved albatrosses can navigate with strong magnets attached to their head: Journal of Experimental Biology, v. 206, p. 4155-4166.

Mueller, T., R. B. O'Hara, S. J. Converse, R. P. Urbanek, and W. F. Fagan, 2013, Social Learning of Migratory Performance: Science, v. 341, p. 999-1002.

Müller, M., and R. Wehner, 1988, Path integration in desert ants, Cataglyphis fortis: Proceedings of the National Academy of Sciences, v. 85, p. 5287-5290.

Müller, M., and R. Wehner, 2010, Path Integration Provides a Scaffold for Landmark Learning in Desert Ants: Current Biology, v. 20, p. 1368-1371.

Neuser, K., T. Triphan, M. Mronz, B. Poeck, and R. Strauss, 2008, Analysis of a spatial orientation memory in Drosophila: Nature, v. 453, p. 1244-1247.

Nevitt, G. A., and F. Bonadonna, 2005, Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds: Biology Letters, v. 1, p. 303-305.

Nevitt, G. A., R. R. Veit, and P. Kareiva, 1995, Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds: Nature, v. 376, p. 680-682.

O'Keefe, J., and L. Nadel, 1978, The hippocampus as a cognitive map: Clarendon Press.

Odetti, F., P. Ioalè, and A. Gagliardo, 2003, Development of the navigational map in homing pigeons: effects of flight experience on orientation performance: Animal Behaviour, v. 66, p. 1093-1099.

Padget, O., S. L. Bond, M. M. Kavelaars, E. van Loon, M. Bolton, A. L. Fayet, M. Syposz, S. Roberts, and T. Guilford, 2018, In Situ Clock Shift Reveals that the Sun Compass Contributes to Orientation in a Pelagic Seabird: Current Biology, v. 28, p. 275-279 e2.

Padget, O., G. Dell'Ariccia, A. Gagliardo, J. Gonzalez-Solis, and T. Guilford, 2017, Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters: Scientific Reports, v. 7, p. 9668.

Padget, O., G. Stanley, J. K. Willis, A. L. Fayet, S. Bond, L. Maurice, A. Shoji, B. Dean, H. Kirk, I. Juarez-Martinez, R. Freeman, M. Bolton, and T. Guilford, 2019, Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips: Proceedings of the National Academy of Sciences of the United States of America, v. 116, p. 21629-21633.

Pakhomov, A., A. Anashina, D. Heyers, D. Kobylkov, H. Mouritsen, and N. Chernetsov, 2018, Magnetic map navigation in a migratory songbird requires trigeminal input: Scientific Reports, v. 8, p. 11975.

Papi, F., 1990, Homing phenomena: mechanisms and classifications: Ethology Ecology & Evolution, v. 2, p. 3-10.

Papi, F., and G. Casini, 1990, Pigeons with ablated pyriform cortex home from familiar but not from unfamiliar sites: Proceedings of the National Academy of Sciences, v. 87, p. 3783-3787.

Papi, F., L. Fiore, V. Fiaschi, and S. Benvenuti, 1971, The influence of olfactory nerve section on the homing capacity of carrier pigeons: Monitore Zoologico Italiano-Italian Journal of Zoology, v. 5, p. 265-267.

Papi, F., L. Fiore, V. Fiaschi, and S. Benvenuti, 1972, Olfaction and homing in pigeons: Monitore Zoologico Italiano-Italian Journal of Zoology, v. 6, p. 85-95.

Papi, F., P. Ioalè, V. Fiaschi, S. Benvenuti, and N. E. Baldaccini, 1974, Olfactory navigation of pigeons: The effect of treatment with odorous air currents: Journal of Comparative Physiology A, v. 94, p. 187-193.

Papi, F., P. Ioalè, V. Fiaschi, S. Benvenuti, and N. E. Baldaccini, 1984, Pigeon homing: the effect of outward-journey detours on orientation: Monitore Zoologico Italiano - Italian Journal of Zoology, v. 18, p. 53-87.

Patrick, S. C., J. D. Assink, M. Basille, S. Clusella-Trullas, T. A. Clay, O. F. C. den Ouden, R. Joo, J. N. Zeyl, S. Benhamou, J. Christensen-Dalsgaard, L. G. Evers, A. L. Fayet, C. Köppl, E. P. Malkemper, L. M. Martín López, O. Padget, R. A. Phillips, M. K. Prior, P. S. M. Smets, and E. E. van Loon, 2021, Infrasound as a Cue for Seabird Navigation: Frontiers in Ecology and Evolution, v. 9.

Patzke, N., M. Manns, O. Gunturkun, P. Ioalè, and A. Gagliardo, 2010, Navigation-induced ZENK expression in the olfactory system of pigeons (Columba livia): Eur J Neurosci, v. 31, p. 2062-72.

Pearce, J. M., 2008, Animal learning & cognition : an introduction: Hove ; New York, Psychology Press.

Peng, F., and L. Chittka, 2017, A Simple Computational Model of the Bee Mushroom Body Can Explain Seemingly Complex Forms of Olfactory Learning and Memory: Current Biology, v. 27, p. 224-230.

Perdeck, A. C., 1958, Two types of orientation in migrating starlings, Sturnus vulgaris L., and chaffinches, Fringilla coelebs L., as revealed by displacement experiments: Ardea, v. 46, p. 1-37.

Perez, S. M., O. R. Taylor, and R. Jander, 1997, A sun compass in monarch butterflies: Nature, v. 387, p. 29-29.

Perrins, C. M., M. P. Harris, and C. K. Britton, 1973, Survival of Manx shearwaters Puffins puffinus: Ibis, v. 115, p. 535-548.

Pettit, B., Z. Akos, T. Vicsek, and D. Biro, 2015, Speed Determines Leadership and Leadership Determines Learning during Pigeon Flocking: Current Biology, v. 25, p. 3132-7.

Pettit, B., A. Perna, D. Biro, and D. J. Sumpter, 2013, Interaction rules underlying group decisions in homing pigeons: Journal of the Royal Society Interface, v. 10, p. 20130529.

Phillips, J. B., and P. E. Jorge, 2014, Olfactory navigation: failure to attempt replication of critical experiments keeps controversy alive. Reply to Wallraff: Animal Behaviour, p. e7-e9.

Pollonara, E., P. Luschi, T. Guilford, M. Wikelski, F. Bonadonna, and A. Gagliardo, 2015, Olfaction and topography, but not magnetic cues, control navigation in a pelagic seabird: displacements with shearwaters in the Mediterranean Sea: Sci Rep, v. 5, p. 16486.

Putman, N. F., 2015, Inherited Magnetic Maps in Salmon and the Role of Geomagnetic Change: Integrative and Comparative Biology, v. 55, p. 396-405.

Putman, Nathan F., Courtney S. Endres, Catherine M. F. Lohmann, and Kenneth J. Lohmann, 2011, Longitude Perception and Bicoordinate Magnetic Maps in Sea Turtles: Current Biology, v. 21, p. 463-466.

Putman, N. F., E. S. Jenkins, C. G. J. Michielsens, and D. L. G. Noakes, 2014a, Geomagnetic imprinting predicts spatio-temporal variation in homing migration of pink and sockeye salmon: Journal of The Royal Society Interface, v. 11, p. 20140542.

Putman, Nathan F., Kenneth J. Lohmann, Emily M. Putman, Thomas P. Quinn, A. P. Klimley, and David L. G. Noakes, 2013, Evidence for Geomagnetic Imprinting as a Homing Mechanism in Pacific Salmon: Current Biology, v. 23, p. 312-316.

Putman, N. F., A. M. Meinke, and D. L. G. Noakes, 2014b, Rearing in a distorted magnetic field disrupts the 'map sense' of juvenile steelhead trout: Biology Letters, v. 10, p. 20140169.

Putman, N. F., M. M. Scanlan, E. J. Billman, J. P. O'Neil, R. B. Couture, T. P. Quinn, K. J. Lohmann, and D. L. G. Noakes, 2014c, An Inherited Magnetic Map Guides Ocean Navigation in Juvenile Pacific Salmon: Current Biology, v. 24, p. 446-450.

Putman, N. F., P. Verley, C. S. Endres, and K. J. Lohmann, 2015, Magnetic navigation behavior and the oceanic ecology of young loggerhead sea turtles: Journal of Experimental Biology, v. 218, p. 1044-1050.

Putman, N. F., C. R. Williams, E. P. Gallagher, and A. H. Dittman, 2020, A sense of place: pink salmon use a magnetic map for orientation: Journal of Experimental Biology, v. 223, p. jeb218735.

R-Core-Team, 2018, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, A. M., J. G. Cecere, V. H. Paiva, J. A. Ramos, and S. Focardi, 2015, Pelagic seabird flight patterns are consistent with a reliance on olfactory maps for oceanic navigation: Proceedings of the Royal Society B: Biological Sciences, v. 282, p. 20150468.

RStudio-Team, 2020, RStudio: Integrated Development for R, RStudio, PBC, Boston, MA.

Safi, K., A. Gagliardo, M. Wikelski, and B. Kranstauber, 2016, How Displaced Migratory Birds Could Use Volatile Atmospheric Compounds to Find Their Migratory Corridor: A Test Using a Particle Dispersion Model: Frontiers in Behavioral Neuroscience, v. 10.

Sankey, D. W., R. F. Storms, R. J. Musters, T. W. Russell, C. K. Hemelrijk, and S. J. Portugal, 2021, Absence of "selfish herd" dynamics in bird flocks under threat: Current Biology, v. 31, p. 3192-3198. e7.

Sasaki, T., and D. Biro, 2017, Cumulative culture can emerge from collective intelligence in animal groups: Nature Communications, v. 8, p. 15049.

Sasaki, T., R. P. Mann, K. N. Warren, T. Herbert, T. Wilson, and D. Biro, 2018, Personality and the collective: bold homing pigeons occupy higher leadership ranks in flocks: Philosophical Transactions of the Royal Society B - Biological Sciences, v. 373.

Sasaki, T., N. Masuda, R. P. Mann, and D. Biro, 2022, Empirical test of the many-wrongs hypothesis reveals weighted averaging of individual routes in pigeon flocks: Iscience, v. 25.

Satterthwaite, F. E., 1946, An Approximate Distribution of Estimates of Variance Components: Biometrics Bulletin, v. 2, p. 110-114.

Savelli, F., and J. J. Knierim, 2019, Origin and role of path integration in the cognitive representations of the hippocampus: computational insights into open questions: Journal of Experimental Biology, v. 222.

Scanlan, M. M., N. F. Putman, A. M. Pollock, and D. L. G. Noakes, 2018, Magnetic map in nonanadromous Atlantic salmon: Proceedings of the National Academy of Sciences, v. 115, p. 10995-10999.

Schmidt-Koenig, K., 1958, Der Einfluß experimentell veränderter Zeitschätzung auf das Heimfindevermögen bei Brieftauben: Naturwissenschaften, v. 45, p. 47-47.

Schmidt-Koenig, K., 1970, Ein Versuch, theoretisch mögliche Navigationsverfahren von Vögeln zu klassifizieren und relevante sinnesphysiologische Probleme zu umreißen: Verhandlungen der Deutschen Zoologischen Gesellschaft, v. 64, p. 243-244.

Schmidt-Koenig, K., 1975, Migration and homing in animals: Berlin, Springer.

Schmidt-Koenig, K., 1990, The sun compass: Experientia, v. 46, p. 336-342.

Simons, A. M., 2004, Many wrongs: the advantage of group navigation: Trends in Ecology & Evolution, v. 19, p. 453-455.

Stander, P. E., 1992, Cooperative hunting in lions - the role of the individual: Behavioral Ecology and Sociobiology, v. 29, p. 445-454.

Stephens, D. W., and V. K. Heinen, 2018, Modeling nonhuman conventions: the behavioral ecology of arbitrary action: Behavioral Ecology, v. 29, p. 598-608.

Stroeymeyt, N., N. R. Franks, and M. Giurfa, 2011, Knowledgeable individuals lead collective decisions in ants: Journal of Experimental Biology, v. 214, p. 3046-54.

Séguinot, V., J. Cattet, and S. Benhamou, 1998, Path integration in dogs: Animal Behaviour, v. 55, p. 787-797.

Tamm, S., 1980, Bird orientation - single homing pigeons compared with small flocks: Behavioral Ecology and Sociobiology, v. 7, p. 319-322.

The-MathWorks-Inc., 2021, MATLAB version: 9.11.0.1837725 (R2021b), Natick, Massachusetts, United States, The MathWorks Inc.

Tinbergen, N., 1963, On aims and methods of ethology: Zeitschrift für tierpsychologie, v. 20, p. 410-433.

Toledo, S., D. Shohami, I. Schiffner, E. Lourie, Y. Orchan, Y. Bartan, and R. Nathan, 2020, Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system: Science, v. 369, p. 188-193.

Tolman, E. C., 1948, Cognitive maps in rats and men: Psychological Review, v. 55, p. 189-208.

Tsoar, A., R. Nathan, Y. Bartan, A. Vyssotski, G. Dell'Omo, and N. Ulanovsky, 2011, Large-scale navigational map in a mammal: Proceedings of the National Academy of Sciences, v. 108, p. E718-E724.

Turner, R. M., M. M. Walker, and C. M. Postlethwaite, 2016, Literal grid map models for animal navigation: Assumptions and predictions: Journal of Theoretical Biology, v. 404, p. 169-181.

Van Rossum, G., and F. L. Drake Jr, 1995, Python reference manual, Centrum voor Wiskunde en Informatica Amsterdam.

Vickerstaff, R. J., and A. Cheung, 2010, Which coordinate system for modelling path integration?: Journal of Theoretical Biology, v. 263, p. 242-261.

Virtanen, P., R. Gommers, T. E. Oliphant, M. Haberland, T. Reddy, D. Cournapeau, E. Burovski, P. Peterson, W. Weckesser, J. Bright, S. J. van der Walt, M. Brett, J. Wilson, K. J. Millman, N. Mayorov, A. R. J. Nelson, E. Jones, R. Kern, E. Larson, C. J. Carey, I. Polat, Y. Feng, E. W. Moore, J. VanderPlas, D. Laxalde, J. Perktold, R. Cimrman, I. Henriksen, E. A. Quintero, C. R. Harris, A. M. Archibald, A. N. H. Ribeiro, F. Pedregosa, P. van Mulbregt, and C. SciPy, 2020, SciPy 1.0: fundamental algorithms for scientific computing in Python: Nature Methods, v. 17, p. 261-272.

von Saint Paul, U., 1982, Do Geese Use Path Integration for Walking Home?: Avian Navigation, p. 298-307.

Vyssotski, A. L., G. Dell'Omo, G. Dell'Ariccia, A. N. Abramchuk, A. N. Serkov, A. V. Latanov, A. Loizzo, D. P. Wolfer, and H.-P. Lipp, 2009, EEG responses to visual landmarks in flying pigeons: Current Biology, v. 19, p. 1159-1166.

Walcott, C., W. Wiltschko, R. Wiltschko, and G. K. H. Zupanc, 2018, Olfactory navigation versus olfactory activation: a controversy revisited: Journal of Comparative Physiology A, v. 204, p. 703-706.

Wall, P. L., L. C. Botly, C. K. Black, and S. J. Shettleworth, 2004, The geometric module in the rat: Independence of shape and feature learning in a food finding task: Animal Learning & Behavior, v. 32, p. 289-298.

Wallraff, H. G., 1959, Örtlich und zeitlich bedingte Variabilität des Heimkehrverhaltens von Brieftauben: Zeitschrift für Tierpsychologie, v. 16, p. 513-544.

Wallraff, H. G., 1970, Weitere Volierenversuche mit Brieftauben: Wahrscheinlicher Einfluß dynamischer Faktorens der Atmosphäre auf die Orientierung: Zeitschrift für vergleichende Physiologie, v. 68, p. 182-201.

Wallraff, H. G., 1974, Das Navigationssystem der Vögel : ein theoretischer Beitrag zur Analyse ungeklärter Orientierungsleistungen: Schriftenreihe Kybernetik: München, Oldenbourg.

Wallraff, H. G., 1988, Navigation mit Duftkarte und Sonnenkompaß: Das Heimfindevermögen der Brieftauben: Naturwissenschaften, v. 75, p. 380-392.

Wallraff, H. G., 2000, Simulated navigation based on observed gradients of atmospheric trace gases (models on pigeon homing, part 3): Journal of Theoretical Biology, v. 205, p. 133-145.

Wallraff, H. G., 2004, Avian olfactory navigation: its empirical foundation and conceptual state: Animal Behaviour, v. 67, p. 189-204.

Wallraff, H. G., 2005a, Avian navigation: pigeon homing as a paradigm, Springer Science & Business Media.

Wallraff, H. G., 2005b, Beyond familiar landmarks and integrated routes: goal-oriented navigation by birds: Connection Science, v. 17, p. 91-106.

Wallraff, H. G., 2013, Ratios among atmospheric trace gases together with winds imply exploitable information for bird navigation: a model elucidating experimental results: Biogeosciences, v. 10, p. 6929-6943.

Wallraff, H. G., 2014a, Do olfactory stimuli provide positional information for home-oriented avian navigation?: Animal Behaviour, p. e1-e6.

Wallraff, H. G., 2014b, Pigeon homing from unfamiliar areas: an alternative to olfactory navigation is not in sight: Communicative & Integrative Biology, v. 7, p. 6929-6943.

Wallraff, H. G., and M. O. Andreae, 2000, Spatial gradients in ratios of atmospheric trace gases: a study stimulated by experiments on bird navigation: Tellus B: Chemical and Physical Meteorology, v. 52, p. 1138-1157.

Wallraff, H. G., S. Benvenuti, and A. Fao, 1984, Pigeon navigation - time course of olfactory signal-processing and dependence on access to fresh environmental air: Journal of Comparative Physiology, v. 155, p. 139-150.

Wang, R. F., 2016, Building a cognitive map by assembling multiple path integration systems: Psychonomic Bulletin & Review, v. 23, p. 692-702.

Warrant, E., B. Frost, K. Green, H. Mouritsen, D. Dreyer, A. Adden, K. Brauburger, and S. Heinze, 2016, The Australian Bogong moth Agrotis infusa: a long-distance nocturnal navigator: Frontiers in Behavioral Neuroscience, v. 10, p. 77.

Wehner, R., 2008, The Desert Ant's Navigational Toolkit: Procedural Rather than Positional Knowledge: Navigation, v. 55, p. 101-114.

Whittington, J. C. R., D. McCaffary, J. J. W. Bakermans, and T. E. J. Behrens, 2022, How to build a cognitive map: Nature Neuroscience, v. 25, p. 1257-1272.

Wickham, H., 2011, The Split-Apply-Combine Strategy for Data Analysis: Journal of Statistical Software, v. 40, p. 1-29.

Wickham, H., 2016, ggplot2: Elegant Graphics for Data Analysis: New York, Springer-Verlag.

Wickham, H., 2018, scales: Scale Functions for Visualization.

Wickham, H., 2022, stringr: Simple, Consistent Wrappers for Common String Operations.

Wickham, H., L. Henry, and D. Vaughan, 2023, vctrs: Vector Helpers.

Wilke, C. O., 2020, cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'.

Wiltschko, R., and W. Wiltschko, 1995, Magnetic orientation in animals: New York ; London, Springer-Verlag.

Wiltschko, R., and W. Wiltschko, 2003, Avian navigation: from historical to modern concepts: Animal Behaviour, v. 65, p. 257-272.

Wiltschko, R., and W. Wiltschko, 2017a, Considerations on the role of olfactory input in avian navigation: Journal of Experimental Biology, v. 220, p. 4347-4350.

Wiltschko, W., and R. P. Balda, 1989, Sun compass orientation in seed-caching scrub jays (Aphelocoma coerulescens): Journal of Comparative Physiology A, v. 164, p. 717-721.

Wiltschko, W., and R. Wiltschko, 1972, Magnetic Compass of European Robins: Science, v. 176, p. 62-64.

Wiltschko, W., and R. Wiltschko, 2017b, Homing pigeons as a model for avian navigation?: Journal of Avian Biology, v. 48, p. 66-74.

Wiltschko, W., R. Wiltschko, and C. Walcott, 1987, Pigeon homing: Different effects of olfactory deprivation in different countries: Behavioral Ecology and Sociobiology, v. 21, p. 333-342.

Wisniewski, M. G., M. L. Radell, L. M. Guillette, C. B. Sturdy, and E. Mercado, 2012, Predicting shifts in generalization gradients with perceptrons: Learning & Behavior, v. 40, p. 128-144.

Wittlinger, M., R. d. Wehner, and H. Wolf, 2007, The desert ant odometer: a stride integrator that accounts for stride length and walking speed: Journal of experimental Biology, v. 210, p. 198-207.

Wynn, J., T. Guilford, O. Padget, C. M. Perrins, N. McKee, N. Gillies, C. Tyson, B. Dean, H. Kirk, and A. L. Fayet, 2022a, Early-life development of contrasting outbound and return migration routes in a long-lived seabird: Ibis, v. 164, p. 596-602.

Wynn, J., and M. Liedvogel, 2023, Lost: on what level should we aim to understand animal navigation?: Journal of Experimental Biology, v. 226, p. jeb245441.

Wynn, J., O. Padget, J. Morford, P. Jaggers, K. Davies, E. Borsier, and T. Guilford, 2022b, How might magnetic secular variation impact avian philopatry?: Journal of Comparative Physiology A, v. 208, p. 145-154.

Wynn, J., O. Padget, H. Mouritsen, J. Morford, P. Jaggers, and T. Guilford, 2022c, Magnetic stop signs signal a European songbird's arrival at the breeding site after migration: Science, v. 375, p. 446-449.

Wynn, J., O. Padget, H. Mouritsen, C. Perrins, and T. Guilford, 2020, Natal imprinting to the Earth's magnetic field in a pelagic seabird: Current Biology, v. 30, p. 2869-2873 e2.

Yeagley, H. L., 1947, A preliminary study of a physical basis of bird navigation: Journal of Applied Physics, v. 18, p. 1035-1063.

Yeagley, H. L., 1951, A preliminary study of a physical basis of bird navigation. Part II: Journal of Applied Physics, v. 22, p. 746-760.

Yeagley, H. L., and F. C. Whitmore, 1947, A Preliminary Study of a Physical Basis of Bird Navigation: Journal of Applied Physics, v. 18, p. 1035-1063.

Zannoni, N., M. Wikelski, A. Gagliardo, A. Raza, S. Kramer, C. Seghetti, N. Wang, A. Edtbauer, and J. Williams, 2020, Identifying volatile organic compounds used for olfactory navigation by homing pigeons: Scientific Reports, v. 10, p. 15879.

Zeil, J., 1998, Homing in fiddler crabs (Uca lactea annulipes and Uca vomeris: Ocypodidae): Journal of Comparative Physiology A, v. 183, p. 367-377.

Zidat, T., M. Gabirot, F. Bonadonna, and C. T. Müller, 2023, Homing and Nest Recognition in Nocturnal Blue Petrels: What Scent May Attract Birds to their Burrows?: Journal of Chemical Ecology.

Åkesson, S., and T. Alerstam, 1998, Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses?: Journal of Avian Biology, p. 618-625.