

Lost: on what level should we aim to understand animal navigation?

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ABSTRACT

Given that all interactions between an animal and its environment are mediated by movement, questions of how animals inherit, refine and execute trajectories through space are fundamental to our understanding of biology. As with any behavioural trait, navigation can be thought of on many conceptual levels – from the mechanistic to the functional, and from the static to the dynamic – as laid out by Niko Tinbergen in his four questions of animal behaviour. Here, we use a navigation-centric interpretation of Tinbergen's questions to summarise and critique advances in the field of animal navigation. We discuss the 'state of the art'; consider how a proximal/mechanistic understanding of navigation is not a prerequisite to understanding ultimate questions of evolutionary/adaptive importance; propose that certain aspects of animal navigation research – and certain taxa – are being neglected; and suggest that extreme experimental manipulations might lead to the mischaracterisation of non-adaptive 'spandrels' as functional navigational mechanisms. More generally, we highlight pressing questions within the field, the answers to which we believe are within reach, and highlight the important role that novel methods will have in helping us elucidate them.

KEY WORDS: Tinbergen, Experimental science, Learning, Navigation, Orientation

Introduction

The ability to orient efficiently through space – at any scale – is at the heart of how any animal interacts with the environment, and how the environment influences their evolution. As such, it is perhaps of little surprise that animal navigation and orientation has formed an important part of experimental biology for more than a century. Through this Commentary, we intend to outline briefly what progress has been made, highlighting the contribution of experimental biology to these advances, before critically dissecting the extant state of the field and discussing what goals might be set in the study of animal navigation going forward.

Although the mechanisms by which animals navigate are by no means perfectly understood, there is general consensus around the approximate progression of navigational ability occurring through an individual's life. Among long-distance migratory taxa, it is thought that genetic inheritance allows migratory information to be passed between generations, with this information thought to comprise an orientational 'vector' (i.e. a 'clock and compass' distance and direction to the goal; Perdeck, 1958; Thorup et al., 2007; Yoda et al., 2017) in birds, or a series of directional responses elicited at specific positions

along the migratory pathway in sea turtles and fish (Lohmann and Lohmann, 1994, 1996; Lohmann et al., 2001). How direction is genetically partitioned, regulated and encoded – how three-dimensional space can be represented on a genome – remains to be characterised. Although candidate genomic regions have been identified that seemingly predict migratory behaviour (e.g. Caballero-López et al., 2022; Delmore et al., 2016, 2020; Sokolovskis et al., 2023; Toews et al., 2019), there appears to be very little consensus on where these genomic regions are.

Asocial learning is thought to augment any genetically inherited orientation abilities through imprinting (see Glossary; Baker, 1978) to specific navigational cues (Brothers and Lohmann, 2015, 2018; Putman et al., 2014a, 2013; Wynn et al., 2022c, 2020b); associative learning through trial-and-error ('exploration-refinement'; Guilford and Burt de Perera, 2017; Guilford et al., 2011b; Wynn et al., 2020a); or even through the parameterisation of some pre-formed cognitive structure (as might be the case in topographic representations of space within the brain; e.g. Fyhn et al., 2004; O'Keefe and Dostrovsky, 1971). Although many migratory animals apparently make their first migrations unaided (e.g. Wynn et al., 2022a), additional navigational information is also thought to be imparted by social learning from experienced conspecifics in some species (Abrahms et al., 2021; Byholm et al., 2022; Chernetsov et al., 2004; Mueller et al., 2013).

Irrespective of the precise mechanism, it is perhaps within the context of positional information that learning is most crucial. Typically, positional information is often considered within the context of a 'map' (see Glossary). This term is hard to define, and probably deserves a commentary piece in its own right; here, we use it to simply mean a way of computing position relative to the goal relative to some sort of 'frame of reference' (see Box 1). This is thought, at least in birds, to comprise either a series of (visual) landmarks – the locations of which are known from experience (e.g. Biro et al., 2004; Braithwaite and Guilford, 1995; Capaldi et al., 2000) – or two or more learnt 'gradient cues', whose values together relate to position in space (e.g. Chernetsov et al., 2008b; Padgett et al., 2019). On a sensory level, olfactory cues (Baldaccini et al., 1975; Gagliardo, 2013; Padgett et al., 2017; Papi et al., 1972; Pollonara et al., 2015), or cues provided by the Earth's magnetic field (Boles and Lohmann, 2003; Chernetsov et al., 2017; Fransson et al., 2001; Kishkinev et al., 2015, 2021; Lohmann and Lohmann, 1994; Lohmann et al., 2001), are prime candidates for such gradients. Such maps are sometimes considered to rely upon a specific underlying neuronal architecture, perhaps analogous to the cognitive map seen in mammals (Fyhn et al., 2004; O'Keefe and Dostrovsky, 1971), though recent discussions have noted that evidence for map-type navigation is perhaps also consistent with simpler associative processes (Guilford and Burt de Perera, 2017). The cognitive underpinning of long-distance migration is, then, yet to be determined and is again likely to be worthy of an entire commentary piece in its own right.

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Box 1. What's in a word? The irony of analogy, and why semantics (regrettably) matter

Given that an investigator's view of the world is inherently subjective, we cannot take for granted that two people have the same understanding of any given concept. Although the level of consensus between scientists with regard to terminology is impressive, it is possible that progress is hindered because the understanding of key concepts is not absolute across all participants. This problem is perhaps particularly pronounced in animal navigation, where simplification through analogy and metaphor might, ironically, lead to misunderstanding.

As we have done throughout, we might consider the navigational 'map' as an example when exploring this problem. In lay conversation, a map is understood to be a topographic representation of space, usually displayed visually as a physical object. The phrase 'map', then, turns an abstract concept into something readily understood by most people. The same simplification presumably underpins the use of other terminology in navigation research: 'compass', 'stop sign' and 'signpost', to name but a few. Indeed, even the verb 'to navigate' was originally meant to describe driving a ship (Putman, 2021).

However, terminology based on analogy is hard to define. The map, as discussed above, appears to be well defined and even makes testable hypotheses. However, as discussed in the Glossary, it is apparent that the abilities thought to be conferred by a 'map' differ between authors. Within the last 10 years, maps have been described as being demonstrated by, on separate occasions, knowing the direction to the goal (Chernetsov et al., 2017; Kishkinev et al., 2021); knowing the distance and direction to the goal (Padget et al., 2019); or knowing neither, but instead giving 'uni-coordinate position' (e.g. latitude or longitude only; Wynn et al., 2022c).

Our aim here is not to define terminology, but rather to point out that – for all its utility – analogy might mask differences in understanding. Thus, the use of analogy should be underpinned by strong mechanistic and/or functional definitions, however pernickety such discussions might seem.

Maps are not, however, the only way in which animals might utilise sensory input to inform navigational decisions based on their position in space. Mechanisms that do not require an understanding of position relative to the goal might present an alternative solution. Indeed, instead of using gradient cues or landmarks to determine their specific position, some evidence exists that animals might use them as 'signposts' or 'stop signs' to denote when to either change direction or stop moving altogether (Chernetsov et al., 2008a; Holland, 2014; Liechti et al., 2012; Lohmann et al., 2001; Mouritsen, 2003; Wynn et al., 2023, 2022c). Such mechanisms do not necessitate an understanding of how a gradient varies through space, as a navigator would only need to know the cue value associated with discrete positions, which in turn might be less impacted by year-on-year variation in cue values (Putman and Lohmann, 2008; Wynn et al., 2022b).

When using positional information to direct goalward movement, a navigator needs a link between their egocentric direction (see Glossary) and their map-defined allocentric (or exocentric) position (see Glossary), a phenomenon referred to as a 'compass' (see Glossary). The necessity of a link between allocentric position and egocentric direction was first posited by Gustav Kramer in 1953, and over the past half-century the 'map and compass' theory of animal navigation has become a key concept in navigational investigation across all taxa and spatial scales. Four main sensory cues have been repeatedly implicated in compass systems in various taxa: the time-compensated position of the sun (e.g. Dacke et al., 2014; Padget et al., 2018; Perez et al., 1997; Schmidt-Koenig, 1958); the rotational pattern of night-time celestial cues (e.g. Emlen, 1967a,b; Michalik et al., 2014; Mouritsen and Larsen, 2001); the

Glossary

Compass

A device for determining heading direction within the same frame of reference as the map. This allows a navigator to link its egocentric direction to its allocentric position, which in turn allows for movement towards the goal (Kramer, 1950; Padget et al., 2018).

Egocentric

A frame of reference relative to the self (cf. exocentric/allocentric; Klatzky, 1998).

Emlen funnel

An assay in which a bird marks the sides of a funnel-shaped arena, in doing so expressing an orientation preference.

Exocentric/allocentric

An external frame of reference, often used interchangeably (Klatzky, 1998).

Imprinting

An evolutionarily primed mechanism through which animals become extremely sensitive to specific sensory information at a specific point in development.

Map

In the broadest sense, a map can be considered a means of determining direction to a goal at any point along a navigator's journey (Gould, 1998), suggesting that the navigator knows their longitudinal and latitudinal position relative to some external frame of reference (Holland, 2014; Mouritsen, 2001). This knowledge would allow a navigator to calculate a distance and direction to a known goal, which has been postulated as a functional definition of the phenomenon (Padget et al., 2019). Mechanistic definitions have also been postulated, and might refer to some form of topographic representation of space in the brain, though simpler systems of storing spatial information have also been referred to as 'maps' (Guilford and Burt de Perera, 2017; Walcott, 1996).

polarisation pattern of sunlight caused by the atmosphere (e.g. Dacke et al., 2003; Muheim et al., 2006; Wehner, 1990); and cues extracted from the Earth's magnetic field (e.g. Bottesch et al., 2016; Light et al., 1993; Lohmann et al., 1995; Wiltschko and Wiltschko, 1972).

Tinbergen's questions and animal navigation

Although our understanding of animal navigation has improved substantially over the past century, our knowledge is still imperfect and it is perhaps useful to consider a framework within which any remaining knowledge gaps can be addressed. For more than 50 years, Niko Tinbergen's 'four questions' have dominated discourse around animal behaviour (Tinbergen, 1963). These four questions are defined specifically as those of mechanism, function, ontogeny and phylogeny. Of these, the first two questions consider a 'static' perspective of observation on the individual, asking 'why' behaviours occur on an adaptive level (function) and 'how' these behaviours are executed on a mechanical level (mechanism; MacDougall-Shackleton, 2011). In contrast, the latter two questions deal with a historical or dynamic perspective, considering 'how' a behaviour develops over an individual's lifespan (ontogeny) and 'why' the behaviour has evolved through selection between generations (phylogeny and evolution). Although 'navigation' is clearly a complex trait with many underlying mechanisms, we assert that it, too, can be deconstructed using this umbrella (see Fig. 1).

Tinbergen's questions were set out as a direct response to a move away from the evolutionary study of ethology towards a more mechanistic understanding of behaviour (Tinbergen, 1963). By explicitly examining behaviour from different angles, the questions were designed specifically to promote a holistic view of behaviour,

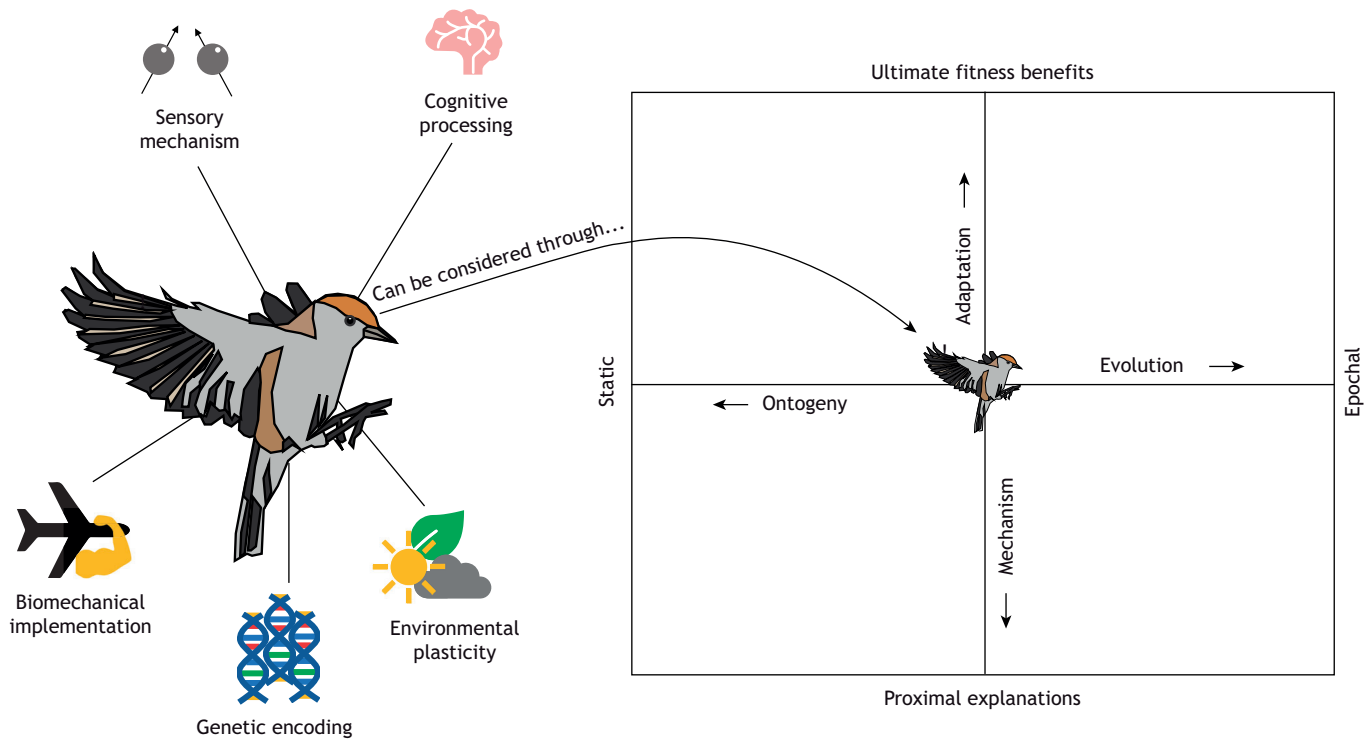


Fig. 1. A navigation-centric view of Tinbergen’s questions. Left: a complex trait such as navigation might be broken down into several facets, each of which can be considered using Tinbergen’s questions. Right: once an investigator has chosen a phenomenon, it can be considered mechanistically (by looking ‘down’ the conceptual levels for proximal explanations) or adaptively (by looking ‘up’ the conceptual levels for ultimate fitness benefits), and can be considered dynamically across different time scales (from the static through the ontogenetic to the evolutionary).

and address what Tinbergen described as a discipline moving towards being ‘overfed with the details of a type of comparative anatomy increasingly interested in mere homology’ which ‘has no interest in function’. It seems from the context that Tinbergen’s concerns extend to mechanistic interpretations of animal behaviour in a wider sense, and that he wished to retain a focus on the evolutionary implications of animal behaviour (Burkhardt, 2014).

One of the nuances of Tinbergen’s framework, noted by Tinbergen himself, is how strikingly similar questions of mechanism and adaptive function really are. At the most fundamental level, Tinbergen notes that all adaptations to the environment can be considered as the means by which fitness is achieved (i.e. as mechanisms). Conversely, the naturally selected mechanisms of animal behaviour must have some

adaptive advantage and, hence, might themselves be considered adaptations. This means that the difference between adaptation and mechanism is simply a question of perspective, with adaptation taking a question of phenomenon and looking ‘up’ – towards the ultimate questions of fitness and evolutionary advantage – and mechanism taking the same phenomenon and looking ‘down’ – towards proximal and atomical explanations.

This is considered in Fig. 2, where we have attempted to apply this rationale to the avian navigational map. Along the trajectory shown, we point to each step as the mechanism underlying the next; for example, magnetic inclination sensitivity is the mechanism by which positional information is acquired, which in turn is the mechanism facilitating migratory movement. Conversely, we can

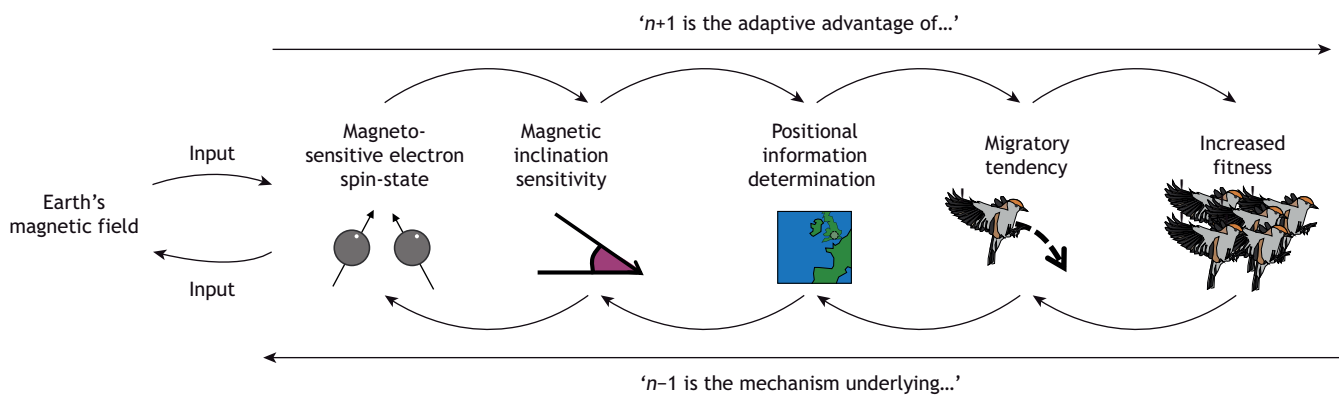


Fig. 2. The relationship between adaptation and mechanism in Tinbergen’s four questions. As noted by Tinbergen, the difference between mechanism and adaptation is dependent on whether we are looking ‘up’ the levels of abstraction towards ultimate evolutionary questions (‘why’ questions) or ‘down’ towards proximal explanations of phenomena (‘how’ questions).

also point to each step being an adaptation in its own right; the adaptation that allows for increased fitness is migratory navigation, and the adaptation that allows for migratory navigation is the ‘map’. Therefore, by shunting back-and-forth between an extremely proximal view of the mechanisms underlying an animal’s behaviour and ultimate questions of survival and fitness, the difference between function and mechanism might be seen simply as a question of which ‘end of the telescope’ the investigator chooses to look down.

However, an understanding of animal navigation is not complete without understanding how its underlying mechanisms change both across an individual’s lifespan (e.g. through learning) and across generations. This, in turn, suggests that there are scales, ranging from proximal to ultimate and from static (i.e. instantaneous) to dynamic (anything from second-by-second through to epoch-to-epoch changes), that can be used to characterise questions of animal navigation (see Fig. 1). These scales, however, are largely independent of the physical scaling of a given problem. For example, we can think of molecular details from an ultimate evolutionary perspective, and extremely long-distance migration can be considered from a proximal, mechanistic viewpoint. It would follow, then, that even investigation over a wide variety of contexts does not guarantee a full understanding of animal navigation.

Interestingly, it might be said that on the broadest and most specific levels we might already know the ‘answer to navigation’. On a proximal level, the universal constraint of physics necessarily means that everything is explainable in terms of Newtonian and quantum mechanics. Conversely, the ultimate answer to why behaviours occur has, to some extent, to be explainable using evolution through natural selection. The utility of Tinbergen’s framework is, then, to encourage the movement of information between conceptual levels of understanding, emphasising that a complete understanding of behaviour is an exercise in linking mechanism to adaptation across a variety of time scales.

The paintbrush dilemma: are ‘bottom up’ approaches in navigation feasible, or even desirable?

Given the intrinsic link between mechanism and adaptation, it is tempting to consider a ‘bottom up’ approach to the study of animal navigation: by addressing fundamental questions of mechanism, we will necessarily find answers to ultimate questions of evolution. This approach is perhaps best considered via an analogy – that of an artist painting a picture. If the artist wishes to save money, it would make sense to invest in the smallest possible paintbrush: the painter can paint large details using a small brush, but doing this in reverse

is challenging. However, in doing this, the painter will spend far longer painting than they otherwise would. Indeed, they may even be unable to finish the painting, or there might be techniques that cannot be replicated with the small brush. In much the same way, understanding the minute detail of a biological system is not the only way to understand it as a whole. Indeed, the most efficient way to make progress is rarely by investigation at the smallest possible scale, and certain phenomena are hard (or even impossible) to understand when observed in microscopic detail. By way of another analogy, this is akin to sitting far too close to the television when watching a film, and struggling to make sense of the plot when watching the seemingly random patterns of an individual pixel.

This phenomenon has been demonstrated across the life sciences, with perhaps the best example being the discovery of the process whereby natural selection drives changes in phenotype over time – evolution. Its discovery was not predicated on a mechanistic understanding of the functional unit of inheritance (Darwin, 1859) and it has even been argued that a focus on the mechanism of inheritance actively obfuscates the study of evolution. This has even led some to conclude that genomics’ contribution to genetics is minimal at best (Barton, 2022).

Although we can, then, suggest that a ‘myopic’ focus on proximal questions could lead to a less perfect understanding of the whole, it is hard to discern whether this problem persists specifically in animal navigation. To investigate this, we searched the abstracts of the bibliography maintained by the Animal Navigation Group (ANG), a Special Interest Group of the Royal Institute of Navigation (RIN). This bibliography comprises 10,036 publications spread across 75 journals on animal orientation and navigation. Specifically, we characterised research interest within navigation according to Tinbergen’s four questions (see Fig. 1; see also Table 1 for the search terms). Though admittedly not particularly nuanced, we reasoned that this approach was appropriate as we were interested in investigating both bias at the point of publication and bias at the point of dissemination. The RIN ANG citation list is, therefore, likely to inform more qualitatively on whether certain facets of navigation receive more attention than others.

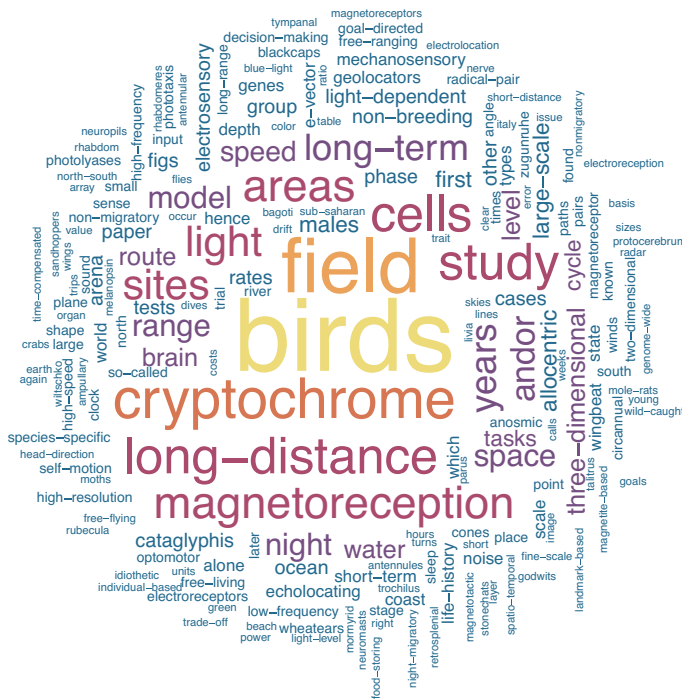
In total, 53% of abstracts contained detectable reference to one or more of Tinbergen’s questions (see Table 1). Of these, 40% of abstracts referred specifically to mechanism; 18% to adaptation; 25% to ontogeny; and 16% to evolution/phylogeny (see Fig. 3). It is possible that this pattern is skewed by reference to one question when the text sets out to answer another, though we think this is unlikely to drive the patterns observed, as this would imply that there was bias in the rate of irrelevant allusion to other questions. As

Table 1. Search terms used to characterise navigational literature with respect to Tinbergen’s four questions and to taxonomic diversity

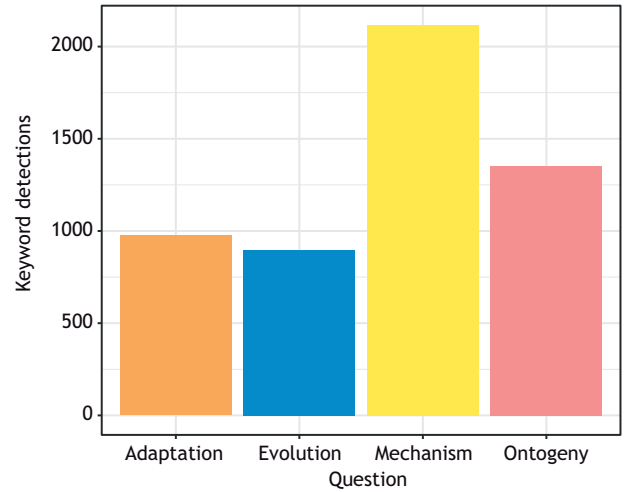
Analysis	Question	Search term 1	Search term 2	Search term 3	Search term 4	Search term 5
Tinbergen’s questions	Mechanism	‘Mechan-’				
	Adaptation	‘Adaptation’	‘Adaptive’	‘Function of’		
	Ontogeny	‘Ontogen-’	‘Developmental’	‘Learn-’	‘Inherit-’	
	Evolution	‘Evolution’	‘Phylogen-’			
Taxon	Amphibian	‘Amphibian’	‘Frog’	‘Toad’	‘Salamander’	
	Bird	‘-bird-’				
	Invertebrate	‘Invertebrate’	‘Insect’	‘Crustacean’	‘Moth’	‘Butterfly’
	Fish	‘Fish’	‘Teleost’	‘Shark’	‘Salmon-’	
	Mammal	‘Mammal’				
	Reptile	‘Reptile’	‘Turtle’			

The ‘str_detect’ function in R was used to determine whether a given term was present in each abstract, from which we tallied up total detections for each question. ‘Function of’ was used instead of ‘function’ singularly for questions of adaptation as the term ‘function’ could relate either to mechanism (e.g. ‘The magnetic compass is thought to function via a radial pair mechanism’) or adaptation (e.g. ‘The function of the magnetic compass is to provide egocentric directional information’). In the table ‘-’ is used in instances where the prefix/suffix of the word can vary and still register a positive hit with the search term.

A



B



C

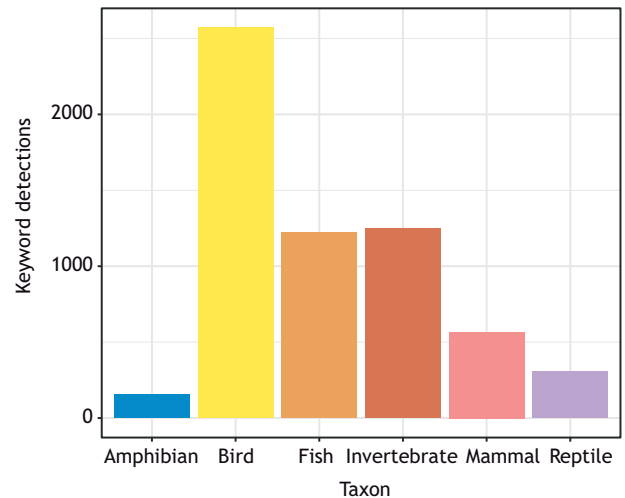


Fig. 3. Where does the focus of modern animal navigation lie? We analysed the Royal Institute of Navigation Animal Navigation Group’s weekly citation update, ranking words from the 10,036 abstracts based on the frequency of their use (A). For the sake of clarity, we removed words found in the top 100,000 words of the Corpus of Contemporary American English so that only those considered navigationally interesting were retained. We further searched each abstract for mentions of key terms relating to Tinbergen’s four questions (B) and to specific taxa (C). We found that the word ‘mechanism’ accounts for 44% of keyword detections (B), and that birds account for 43% of taxon-specific detections (C). We suggest that this reflects the importance placed upon ornithology and a mechanistic understanding of navigation in the 21st century. See Table 1 for the search criteria used to include/exclude terms.

such, these results would suggest a strong bias towards a mechanistic focus in the study of animal navigation. Beyond this, we further note that magnetoreception in particular is dominant: there are more abstracts that mention the ‘magnetic compass’ (5.1%) than mention the ‘sun compass’ (1.0%) and ‘star compass’ (2.7%) combined, and in total 13% of all animal navigation abstracts within the bibliography mention magnetoreception at least once at some point. We further found an imbalance regarding which animal clades receive the most attention. References to birds make up almost half of the total number of taxonomic identifiers (43%; see Fig. 3), more than double the references made to any other taxonomic group: insects (20%), fish (19%), mammals (10%), reptiles (5%) and amphibians (3%; see Table 1 for identifying terms). This suggests that much of our understanding of animal migration comes from a surprisingly ecologically and evolutionarily constrained subset of taxa.

It would seem, therefore, that the transduction and sensory modality of sensory information in a taxonomically limited subset

of animals dominates the animal navigation literature, and it is likely that this imbalance has implications for our understanding of animal navigation. We suggest, therefore, that it is important to recognise that a granular understanding of sensory modality does not equate to a complete understanding of an extremely complex trait like animal navigation, and that this has to change when considering research agendas going forward.

Is ‘progress’ a paradox in experimental science?

Although abstract discussion of where empirical study might be directed is fine in principle, the accumulation of scientific knowledge is limited by the available experimental paradigms. In turn, the utility of such paradigms can be expanded/refined over time, something perhaps best exemplified by considering the technological shifts that have revolutionised the study of animal navigation over the last century. To note a few examples: rapidly increasing computing power has allowed the contribution of simulation and complex multivariate statistics in animal

navigation to grow exponentially (e.g. Bates et al., 2015; McLaren et al., 2022; Padgett et al., 2018); the advent of tighter physical control in sensory manipulations (e.g. radio frequency generation in the study of magnetoreception) has yielded greater resolution in the investigation of sensory input (e.g. Chernetsov et al., 2017; Engels et al., 2014; Kobylkov et al., 2019); and more refined surgical techniques have allowed for increasingly ambitious neurosurgeries (e.g. Hayman et al., 2011; Takahashi et al., 2022).

Such improvements must be seen as ‘progress’; however, the utility of a given experimental paradigm is necessarily constrained by what it can be used for. For example, Emlen funnels (see Glossary) – a mainstay of ornithological research for more than 50 years – cannot be used to explore orientation in all birds, as the output of the assay requires that birds attempt to ‘fly’ in the correct direction (something that larger birds/gliding birds are unlikely to do in a confined space). If the detection of a given navigational ability (e.g. avian magnetoreception) was largely contingent on using a given assay (e.g. Emlen funnels), then the positive confirmation of that ability would be limited to certain species. This will, then, allow for profound insight into valuable model systems (e.g. the European robin, *Erithacus rubecula*), but may also lead to taxonomic bias in trait detection. This is because when a navigator cannot be tested in a given setting, it is difficult to conclude whether a negative result is indicative of a genuine lack of sensitivity or is simply caused by the unsuitability of the assay for that particular species. Indeed, in the case of avian magnetoreception, it appears that, in at least some species, the complete absence of other cues is a necessity for detection using a disorienting (rather than reorienting) stimulus (Packmor et al., 2021). Thus, if magnetoreception research were forever limited to Emlen funnel assays, it would follow that the true extent of magnetoreception across animal taxa would never be revealed.

The specific example discussed above illustrates a more general point: irrespective of any technical advances, it is possible to become over-reliant on a handful of workhorse experimental paradigms. This would make innovation within experimental paradigms insufficient when attempting to build a complete understanding of animal navigation. Instead, it would follow that either (a) the synthesis of new assays/approaches or (b) the assimilation of novel technologies from other fields is constantly required for a complete understanding of animal navigation.

The advent of biologging and tracking technology is one of the best available examples of this phenomenon, allowing for experimentation within a context of unparalleled biological realism (Guilford et al., 2011a). A similar revolution has occurred in high-throughput sequencing (Merlin and Liedvogel, 2019), which has allowed us not only to begin connecting migratory genotype to migratory phenotype (Caballero-López et al., 2022; Toews et al., 2019) but also to link navigational mechanism to population genetic structure (Brothers and Lohmann, 2018; Delmore et al., 2020). We suggest, then, that embracing new techniques and technologies is essential to animal navigation going forward.

Do experimental paradigms push us towards ‘experimental spandrels’?

Animal navigation experiments typically involve making some sort of intervention and measuring an animal’s understanding of distance or direction to a target. Most animal navigation experiments concerning distance/direction determination – including almost all experiments targeting map-and-compass navigation – revolve around one of two experimental paradigms: disorientation, where

the subject is expected not to move in the conventional direction/for the conventional distance (and all subjects are expected to move randomly with respect to each other; e.g. Engels et al., 2014; Gagliardo et al., 2013); and reorientation, where an *a priori* expected direction (e.g. Emlen, 1967b; Wiltschko and Wiltschko, 1972) or distance (e.g. Bulte et al., 2017; Fransson et al., 2001; Karlsson et al., 2022) of movement is specified in response to the manipulation.

Such experiments often rely on assays to measure a response, and the data obtained from these assays are often extremely noisy. For birds, an Emlen funnel is often used (see above; Emlen, 1967a,b), though similar paradigms exist in fish (e.g. Putman et al., 2014b), turtles (e.g. Lohmann and Lohmann, 1994), crustaceans (e.g. Boles and Lohmann, 2003) and insects (e.g. Dacke et al., 2014; Dreyer et al., 2018). Thus, in order to elicit an orientation response that is detectable in spite of assay noise, extreme sensory manipulations – those that seek to create extremely large effects through the use of biologically unrealistic stimuli – are often used. When investigating positional understanding (the ‘map sense’), this means that animals are often displaced (or virtually displaced via sensory manipulation) many thousands of kilometres (e.g. Chernetsov et al., 2008b; Lohmann et al., 2001; Putman et al., 2014b; Thorup et al., 2007, 2011), and when considering compass orientation, this often means compass rotations >90 deg (e.g. Cochran et al., 2004; Engels et al., 2014; Kobylkov et al., 2019). Such experiments have added remarkable detail to our understanding of animal navigation, and their impact cannot be overestimated. That said, drawing precise conclusions from extreme experimental manipulations is potentially dangerous; one might conclude that oxygen is lethal to humans if lower dosages are not explored. In much the same way, we suggest that extreme sensory manipulations may lead to ‘experimental spandrels’.

In their seminal paper, Stephen Jay Gould and Richard Lewontin invoke the idea of an evolutionary ‘spandrel’ to describe non-adaptive explanations for observed ‘adaptations’ (Gould and Lewontin, 1979). In architecture, a spandrel is the seemingly intentional structure formed when the arches holding up a pair of columns meet. In reality, however, the spandrel is simply a by-product of the arch. The argument therefore goes that structures exist within anatomy and behaviour that have no specific adaptive advantage, and that are simply a by-product of those that do. We wish to extend this historical idea of the spandrel to consider responses to extreme experimental stimuli that, although related to the phenomena examined, might not reflect the tasks that an animal performs in reality. In doing so, we propose that in pursuing an understanding of mechanistic nuances we might lose sight of the essential biology that the trait was adapted to perform.

This is, in essence, the difference between testing what animals can do – in an artificial and unnatural scenario – and what they actually do – in a biologically realistic context. Although these two responses appear to be intrinsically linked, this might not always be the case. For example, any navigational ability displayed by animals displaced far outside of their known range must, necessarily, be incidental (as it cannot have evolved for this specific task). Does a correct orientation response following trans-continental displacement (‘true’ navigation; Holland, 2014), then, really constitute evidence for an explicit understanding of bi-coordinate position relative to the goal at all points along a migratory trajectory (e.g. Chernetsov et al., 2017)? Or, alternatively, are birds just capable of guessing approximately the correct direction using a mechanism that must have evolved to do something else? Similarly: does an apparent deflection following twilight compass manipulation imply that birds update their compasses every night? Or, again, is this just what happens when

discrepancies in compass inputs are so large that some approximation of ‘common sense’ kicks in?

Although this conjecture is speculative, and the alternative explanations are outlandish, we suggest that when using extreme experimental paradigms it is impossible to rule out spandrel-like explanations of navigational phenomena. Indeed, we might even consider that the phenomena we wish to consider (such as the ‘true’ navigation discussed above) are, by definition, spandrels. Biological realism is, therefore, extremely important, and deviations from it highlight the importance of combining laboratory experimentation with *in situ* observation when planning future experiments and interpreting extant studies.

Conclusion: the shape of animal navigation to come

Within our Commentary we have submitted four main theses: (1) that understanding navigation involves understanding the adaptive advantage of every mechanism across a variety of time scales; (2) that a proximate understanding of mechanism cannot advance the subject as a whole; (3) that navigation has tended towards more mechanistic explanations in a confined taxonomic subset of animals; and (4) that the interpretation of experimental evidence – particularly that derived from unnatural sensory manipulation – must be considered carefully. Given this synthesis, we point to several areas within the study of animal navigation that warrant further attention.

First, we submit that certain areas of animal navigation research are under-investigated. Specifically, we suggest that the following require substantially more investigation: the proximal role of selection and its ultimate effects on navigational evolution; the roles of learning and senescence in determining navigational phenotype with age; and how navigational ability confers an adaptive advantage across taxa (see Fig. 3). Conversely, we might suggest that magnetoreception, and sensory transduction more generally, is over-represented in the navigational literature (see Fig. 3).

Second, we suggest that taxonomic diversity, and diversity in the life stages studied, is essential to navigational research going forward. Macroevolutionary questions of phylogeny, questions relating mechanism to ecology and questions of development necessarily require an understanding of navigational traits across a wide variety of species, contexts and ages. The wider this net is cast, therefore, the better our understanding of navigational ability and its flexibility across an individual’s lifespan, between generations and through space.

Third, we suggest that correlative studies and ‘natural experiments’ offer an opportunity to increase biological realism in studies of navigation. Correlative evidence is typically considered to be less reliable than experimental evidence, owing to an increased likelihood of confounding variables, but it offers much-needed biological realism. Thus, ‘natural experiments’ might bridge the gap between correlative and experimental science, combining the low-confirmed probability of experimental study with the inferential power of real-world data. Variation in the Earth’s magnetic field (e.g. Brothers and Lohmann, 2015, 2018; Wynn et al., 2022c,b), spatiotemporal variation in wind/speed direction (e.g. Thorup et al., 2003; Wynn et al., 2020a) and topographic differences across space (e.g. Padget et al., 2022, 2019) offer perhaps the best examples of such a paradigm, though biologging technology might also allow other navigational phenomena to be tackled using natural experiments.

Finally, we note that the trends of modern animal navigation are strikingly similar to those that Niko Tinbergen saw in the study of

animal behaviour in the 1960s. We suggest that we must be aware of the pitfalls associated with a primarily mechanistic understanding of navigation, and that redressing some of the observed imbalances discussed above will result in a more complete understanding of animal navigation. This will arise through the promotion of a diversity of opinion, which must be a key tenet of the field moving forward.

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Competing interests

The authors declare no competing or financial interests.

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ECR Spotlight

This article has an associated ECR Spotlight interview with Joe Wynn.

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