1 **An associative account of avian navigation**

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17 **Navigational concepts and mechanisms**

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19 Though many puzzles remain (e.g. Alerstam, 2006), the study of long-distance
20 orientation in birds has produced some astonishing biological discoveries, such
21 as innate vector control of migration (see Alerstam, 1990) or the magnetic sense
22 in animals (see Wiltschko & Wiltschko, 1995), and provided an enduring
23 framework for understanding animal movement behaviour through the
24 development of various navigational map and compass concepts (for a summary
25 see Wiltschko & Wiltschko, 2009). The conceptual approach to avian navigation
26 has generally if implicitly been to attempt to understand the sensory-
27 informational basis of these systems as if they were dedicated modules
28 adaptively designed to solve the navigational challenges that birds are thought to
29 face. But often discussion of these concepts has been silent on the issue of the
30 underlying learning mechanisms required to inform their effectiveness. Instead
31 we take a bottom-up approach, and try to outline the extent to which
32 navigational phenomena might be understood in terms of simple associative
33 learning mechanisms. We argue that whilst most concepts fit readily with what is
34 known about animal learning, some may need rethinking because they appear to
35 require significant departure from these known principles. We explore one issue
36 in detail, the apparent cognitive complexities required by extrapolated
37 navigational map concepts such as the gradient (or grid) map, suggesting a
38 potential refocus of attempts to understand the olfactory map in particular.

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40 Since much is now understood about how animals learn about the contingencies
41 in their environment through associative (and related) learning mechanisms
42 (e.g. Pearce, 2008), enabling them to operate adaptively in a wide variety of tasks
43 and contexts, we take the stance that we should expect the same mechanisms to
44 underlie animal navigation too. What we mean by ‘associative mechanisms’, at
45 the risk of caricaturing a huge and sophisticated body of knowledge and debate,
46 is the set of fundamental processes that enable the stable neural representation
47 by animals of the contingencies between perceived stimuli, events or actions, and
48 the apparent hedonic consequences of these. Put simply, actions become guided
49 (and here we mean significant movements) by the formation of links between
50 perceived stimuli, responses, and outcomes, that result from an animal’s direct
51 experience of the world. We contrast this with the idea that animals may employ
52 specific modules designed to be filled with specialized information to allow them
53 to operate adaptively in situations far outside of their direct experience. We
54 start by emphasizing that some phenomena in avian navigation (broadly
55 defined) do indeed owe their control to non-associative, highly specialized
56 mechanisms. For many first-time migration tasks, for example, especially those
57 performed by short-lived taxa, an innate toolbox for orienting may be needed
58 because the information required to make movements adaptive cannot be learnt
59 in time to be useful, and there is good evidence that birds in particular are
60 equipped with such a toolbox (e.g. Alerstam, 1990). So, associative mechanisms
61 cannot account for everything that controls long-distance movement in birds.
62 However, for much of what is considered to be navigation, the mechanisms of
63 control may more simply be the result of associative learning of the
64 contingencies between salient environmental cues and outcomes of importance

65 to the animal (such as getting out to and back home from the location of a
66 valuable resource, using the appearance or direction of a distant landmark close
67 to that location).

68

69 In this essay we develop briefly the idea that avian navigation might be
70 understood using a simple associative perspective. The intention is not to
71 diminish the impressive discoveries that have been made in the field over many
72 decades, instead it is to suggest that an associative perspective may help us
73 decide where we do and where we do not need distinct and separate conceptual
74 frameworks to account for these discoveries. At least, our approach may provide
75 a null-hypothesis for studies of navigation based on known mechanisms of
76 learning; a baseline against which the special abilities of birds, or lack thereof,
77 may be judged objectively.

78

79 **An associative account**

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81 Our premise is that as a consequence of needing to explore space to find
82 resources, and to return home (or to other places) efficiently, a bird will learn to
83 navigate using simple associative processes. As the bird moves about its
84 environment, it learns that certain stimuli or actions are associated with finding
85 resources or returning home (are rewarding) and that others may signal or lead
86 to delays or dangers (are punishing). These could be sequences of landmarks, or
87 they could be the following of directional cues associated with places. That could
88 lead simply to route following using the available visual landmarks (Guilford &
89 Biro, 2014), and it could lead to use of solar cues or magnetic cues to get home

from certain directions. See Figure 1 for simple schematic. The improvement of route efficiency may result as a consequence of slight deviations from a learnt route being rewarded by faster homing. Consistent reward for homing from a particular stable direction could lead to directional cues (compasses) controlling orientation even at very familiar sites (Fuller et al., 1983). In the extreme, as with the artefactual case of trained racing pigeons, directional control may come to dominate orientation from any location if the rewarding direction becomes the sole best predictor of homing.

The first expectation of our associative perspective is that birds will learn to navigate using whatever salient environmental cues are available. Because visual landscape cues are likely to be highly salient to such visual animals as birds, and because they are also often geographically stable and distinct, we may expect these to become important in guiding learnt goal orientation. Over larger distances, however, or where approximate directions provide the most efficient balance between information storage and navigational performance, more general cues from the environment might be more salient: cues such as olfactory gradients or parameters of the earth's magnetic field. Where the availability or suitability of different cue types varies then different navigational systems might be learnt by different individuals, or in different locations or environments.

Indeed, if this variation is itself predictable, depending for example on weather conditions, an associative perspective might also accommodate individuals learning multiple navigational cues and the ability to switch between them in a context dependent way. Both these possibilities might give the appearance of cue redundancy or a hierarchical navigational system (e.g. Wiltschko &

Wiltschko, 2009), as if these were somehow additional adaptive properties of a specialized navigational capacity in birds.

Thus, our associative approach can in principle account for the development of many commonly noted navigational behaviours, such as route-following behaviour, where birds pilot between known places features using the arrangement of landmark features (Guilford & Biro, 2014), or compass-dependent navigation where birds learn to associate homeward compass directions with places they have visited before (see Figure 1). Indeed, even the sun-compass itself might be seen as the product of an associative process connecting solar azimuthal position with temporal context through experience (Guilford and Taylor, 2014).

Descriptive versus extrapolated maps

So far, our proposal is that animals acquire maps or other spatially informative representations (e.g. compasses) that are descriptive of the environment through which they move, reinforced by actual contingencies encountered as a consequence of those movements. This seems uncontroversial. We have said little that cannot be found at least implicitly in previous theoretical treatments, such as that of Baker (1984). If we think about navigational abilities from a mechanistic learning perspective we find that most traditional concepts can be given a simple associative account. But not all. Some navigational concepts suppose that animals use maps that allow them to extrapolate their position to completely unfamiliar places, not just to describe their encountered

environment. And it is this distinction that concerns us for the rest of this essay because we think it potentially has profound implications for spatial learning in animals.

The most obvious of these extrapolated maps is the so-called gradient map, or grid map (for terms and concepts see Able, 2001), because it is hypothesized to consist of a representation of large scale (non-parallel) environmental gradients allowing position fixing from places never visited before (and without the integration of outward journey information). Many possible environmental cues have been investigated or considered, including the features of the sun's arc, gradients in magnetic intensity and dip angle, the Coriolis force and gravity (see Baker, 1984; Wiltschko & Wiltschko, 2009). Whilst past researchers have mainly concerned themselves with the nature of the cues themselves, our point here is that whatever the cues involved such a map is premised on the idea of extrapolation. It must involve the learning of environmental relationships to build a map whose adaptive purpose is to facilitate navigation from places not yet visited (and therefore in the absence of directly rewarding feedback). The potential power of a gradient map is precisely that it can be extrapolated far beyond the stimulus values perceived during its acquisition, but it is exactly this extrapolation that makes the idea problematic for a mechanistically simple associative account. At least some versions of the olfactory map hypothesis also have this extrapolation property (whether or not we choose to call them gradient maps). For example, Gagliardo (2013) provides a clear description of the olfactory hypothesis as it relates to studies of pigeon navigation especially. She makes explicit that the learning of relationships (at or around the home colony)

between odour signatures and geographic direction (deduced either directly from ranging in the familiar area or indirectly from the directions of the winds on which odour types arrive) functions to facilitate homeward orientation from completely unfamiliar places by interpretation of the up-gradient olfactory character of the novel site. At least in this version, the learnt olfactory map is designed to be extrapolated.

As was perhaps realized by Baker when he suggested that grid (gradient) maps, if they existed, would alone raise the phenomenon of bird navigation from the mundane to the mysterious (Baker, 1984), any extrapolated map provides a fundamental mechanistic challenge. This challenge is quite separate from that of determining which environmental factors are involved in the map - the usual concern of students of navigation. The challenge is to understand whether it is really the case that birds (say) are learning the details of their navigational map without directly rewarding feedback from the successful application of that map. Put simply, are navigators really capable of acquiring a map of unfamiliar places by learning its characteristics over familiar terrain? This is not impossible of course, but it is intriguing, and intriguing in a mechanistic way that was perhaps not recognized by the original proponents of such maps. It would, we argue, require the presence of a rather specific cognitive module primed to acquire memories about environmental contingencies that are inferred or predicted rather than actually experienced. Indeed, Jacobs (2012) has recently argued for just such a system driving the evolution of cognitive structures in general, and originating in the need for olfactory spatial learning which could extract and

represent bearing-related spatial information in both a descriptive and predictive way (i.e. at least partially involving extrapolation).

What, then, is the evidence that navigating animals use extrapolated maps, and therefore require mechanisms beyond simple associative learning for navigation? In his 1984 review, Baker concluded that the evidence for grid maps in birds was equivocal. 20 years later, Wallraff (2005) largely concurs with this view in his detailed review. On the other hand, evidence in support of some form of olfactory map in birds has accumulated steadily over the past 40 years (Papi, 1992; Gagliardo, 2013), even though challenges continue to be raised (e.g. Jorge et al., 2010) and countered (Gagliardo et al., 2011). Again, our aim here is not to review or take a position on the precise sensory nature of the navigational map in birds (where it has been best studied), but to ask whether there is robust evidence yet that it relies on extrapolation.

This question may at first seem puzzling, because it is almost axiomatic of navigational displacement experiments that subjects are transported to completely unfamiliar places and released, after some experimental manipulation of interest and often in the absence of outward journey information that might allow computation of the home direction through some form of path integration. Scores of experiments have shown that pigeons especially are capable of homeward orientation after such displacements, at least as long as their olfactory sense is intact (Gagliardo, 2013; Wallraff, 2005). Whilst such experiments do support the idea that birds have an olfactory map, we need to scrutinize more carefully whether they prove that the map is extrapolated in

light of the fact that this distinction has become mechanistically crucial. We do not think that the evidence for a genuinely extrapolated map is yet clear.

Homeward orientation at unfamiliar sites

The strongest claim for our proposal would be that the apparent ability to orient homeward from an unfamiliar location in displacement experiments may also arise as a product of generalization from an ability to navigate successfully in the familiar area, rather than providing unequivocal evidence for an extrapolated navigational map. To clarify this idea, we consider how it might work in the case of olfactory navigation (although in principle it applies with equal force to any navigational map that supposedly works by extrapolating from environmental gradients experienced by the navigator, magnetic gradients included).

Suppose that birds exploring their environment register that odour concentrations or ratios vary in different directions, so that olfactory gradients become learnt as distinctive of directional relationships within that expanding familiar environment. Thus, an olfactory map of the familiar environment emerges as a result of direct contact with it, and perhaps the directionally variable winds over it, during exploration. This learnt map then facilitates better goal orientation and more efficient movement within that familiar area. Perhaps olfactory cues lend themselves to such mapping because of their graded nature and spatial scale, with visual landmarks being learnt later or for more precise navigation because of their more local nature. So whilst it seems reasonable to suppose that relationships and contingencies involving olfactory cues may be

acquired for homeward guidance in the familiar area, in very few experiments has the efficacy of olfactory-based navigation been explicitly tested at familiar sites, although in those few the evidence shows that olfaction does indeed improve homeward orientation (e.g. Gagliardo et al., 2001b).

But why should olfactory navigation generate apparently sensible orientation from unfamiliar sites if, as we are here forced to argue, this is not its purpose? The argument (which we caricature in several forms in Figure 2) would be that a bird displaced artificially to an unfamiliar distant site is equipped only with memories of associations between cues and orientation in its familiar area, but that the bird may *generalize* to one or more of these if the stored representations of environmental cues are similar to those currently perceived at the unfamiliar site. In the absence of alternative sensible movement instructions, the animal may respond to that generalization (Case 2 in Figure 2). Generally we might expect that response to be weak. However, in some circumstances discrimination learning can in fact produce stronger than normal responses through a process known as peak shift (e.g. Weary et al., 1993), where a difficult discrimination between negative and positive stimuli on a dimension generates exaggerated response to stimuli displaced beyond the positive stimulus along the dimension away from the negative. If we imagine, then, that a bird has learnt in its familiar area to fly west to home when experiencing a particular odour ratio that is only apparently slightly different from that experienced at home, then experiencing a ratio that exaggerates the difference between these two might lead to a strong response in the correct direction to home (Case 4 in Figure 2).

This argument and our hypothetical odour ratio example appears to look more like a mechanism by which extrapolated navigation could be achieved through learning in the familiar area than an alternative account. So it is important to be clear about the differences. If sensible orientation appears at unfamiliar sites because the animal is accessing an extrapolatory navigation mechanism, then we would expect orientation and homing at such sites to be good because this is what must have provided the fitness feedback promoting the mechanism. On the other hand, if it is an artefact of familiar area orientation and without real ecological validity, then we might expect orientation and homing to be poor. Even if peak responding were to shift up the stimulus gradient away from values already experienced, it will not do so indefinitely so at some distance we would expect responding to become weak. These are perhaps not easy things to test, but crucially it would be reasonable to expect a mechanism for navigation from unfamiliar places to operate more effectively at unfamiliar sites than familiar ones. Since researchers have not generally considered that olfactory navigation, for example, might actually be a familiar area mechanism rather than an extrapolated navigational one, these kinds of data are not directly available. Indeed, the apparent efficacy of visual landscape cues in controlling orientation once places are familiar (for a review see Guilford & Biro, 2014) means that olfactorily-controlled orientation would probably be overshadowed in such releases, and the investigation of the relative efficacy of an olfactory association in familiar versus unfamiliar places would require special experimental considerations.

Nevertheless, some experiments do confirm that olfactory cues can exercise some control over navigation from familiar sites. Using an orientation cage design for pigeons which detected their directional preference before flying away from the site, Gagliardo et al (2001b) showed that olfactory cues can be used to orient at familiar sites when visual cues are blocked. Furthermore, Wallraff showed that homeward tendencies from novel sites within a broad familiar area were better in pigeons with their olfactory sense intact (in Wallraff, 2005). But of course the same argument that we have applied to the interpretation of releases from unfamiliar sites can apply in reverse to these examples. That is, if a bird has an olfactory map for the purpose of extrapolated navigation from completely unfamiliar sites, it might bleed into apparently sensible orientation at familiar sites as well especially in the absence of normal familiar area cues such as visual landmarks. These possibilities need to be carefully disentangled empirically.

At the other end of the spectrum, many experiments investigating the scale of pigeons' navigational ability showed that birds are capable of homeward orientation tendencies from remarkable distances (several hundred kilometres). Nevertheless, the homing performance of inexperienced (first flight) birds in particular when released at such distant sites is often surprisingly low, with only a small fraction ever arriving home, despite their homeward initial orientation (Wallraff, 2005). Although there are other ways to interpret this performance, it does seem surprising that the apparent ability to orient from such distances translates so poorly into actual homing.

313 An obvious objection to our alternative interpretation of apparent olfactory
314 navigation at unfamiliar release sites, and favouring the hypothesis that it may
315 rely on some form of special learning module, is that fact that young pigeons
316 appear able to learn to use olfactory cues from distant sites on first release even
317 when they have been bred confined in an aviary as long as they are allowed
318 access to environmental air from different wind directions (e.g. Gagliardo et al.,
319 2001a). They appear to have learnt inside the aviary what they will need to
320 navigate outside it. Indeed, this ability appears to show an early sensitive period.
321 Thus, if birds have simply learnt contingent relationships between odours and
322 wind directions inside their aviary, then our associative account would require
323 that they are literally orienting around their aviary using such information. We
324 accept that this may seem implausible, but suggest that the possibility that
325 directional odours may be used in combination with wind direction in very short
326 range orientation might be investigated further. It should also be said that even
327 though pigeons respond sensibly to odour directions apparently learnt confined
328 within an aviary, navigational performance is generally improved in birds that
329 are allowed to range freely around their loft, suggesting that much more
330 information may be acquired when birds are indeed able to use that information
331 actively. But again, experiments relating the scale of exploratory movements
332 explicitly with the efficacy of the acquired map have not yet been done.

333

334 In short, given that navigation experiments have generally been designed to
335 investigate the sensory nature of navigational maps rather than their
336 representational or associative structure, these experiments do not robustly
337 inform us as to whether the extrapolated navigational abilities reported are core

to the nature of the map (and hence indicative of a specialized spatial learning module of some sort), or peripheral artefacts of experimental design and consistent with a simple and general associative mechanism.

A null hypothesis for navigation

We argue that much of what we know about bird navigation may be founded in simple underlying associative mechanisms. However, thinking about navigation from an associative perspective has also clarified that some concepts commonly referred to in the navigation literature would require the existence of more complex underlying mechanisms, re-focussing the need for scrutiny of their empirical basis. In particular, we consider that maps requiring extrapolation of learnt spatial relationships rather than just descriptions of them, appear to conflict with this associative perspective. Gradient (or grid) maps, and some forms of olfactory map, appear to have this extrapolated property. Since there is now considerable empirical evidence in support of an avian olfactory map the question of the extent to which it genuinely functions as an extrapolated map adapted for navigation from unfamiliar places when birds have no access to familiar cues or outward journey information becomes critical. Here we have suggested ways in which a key outcome of navigational displacement experiments, homeward orientation from unfamiliar sites, could be generated artefactually by generalization from associations learnt for familiar area navigation. This emphasizes, for example, the need to study the relative functionality of olfactory navigation within and beyond the bird's familiar area.

Thus, we hope that our associative account may at least act as a principled null-hypothesis for future studies of avian navigation.

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