

## Animal Navigation – A Synthesis

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### ABSTRACT

Navigation, the ability to organize behavior adaptively to move from one place to another, appeared early in the evolution of animals and occurs in all mobile species. At the simplest level navigation may require only movement towards or away from a stimulus, but at the most sophisticated level it involves the formation of complex internal representations of the environment, the subject's position within it, the location of goals, the various routes from current position to goal and possible obstacles along the way. The vast array of navigational capabilities in various species has made it challenging for students of comparative cognition to formulate unifying frameworks to describe and understand these capabilities, although the variety also confers an exciting opportunity for asking comparative questions that are hypothesis-driven. Here, we propose a unifying framework which we call the *navigation toolbox*, to provide a way of formulating common underlying principles operating across many different taxa. The toolbox contains a hierarchy of representations and processes, ranging in complexity from simple and phylogenetically old sensorimotor processes, through the formation of navigational "primitives" such as orientation or landmark recognition, up to complex cognitive constructs such as cognitive maps, and finally culminating in the human capacity for symbolic representation and language. Each element in the hierarchy is positioned at a given level by virtue of (a) being constructed from elements in the lower levels, and (b) having newly synthesized spatial semantic contents in the representations that was not present in the lower levels. The challenge in studying individual species is to determine how given elements are implemented in that species, given its particular behavioral and anatomical constraints. The challenge for the field as a whole is to understand the semantic structure of spatial representations in general, which ultimately entails understanding the behavioral and neural mechanisms by which semantic content is synthesized from sensory inputs, stored, and used to generate behavior.

## INTRODUCTION

Navigation is one of the most fundamental problems that animals and humans confront. It is based on a complex interplay of a large number of different processes and components, and requires the integration of spatially-relevant information across sensory modalities, the formation and retrieval of memories and the selective activation of task-specific representations. Thus, navigation comprises a paradigmatic case of cognitive functions operating across several levels of complexity ranging from sensorimotor loops to higher forms of cognitive processing.

Because navigational tasks are performed by most animal species, taking place in a wide variety of environmental conditions and over very different spatial scales and using a variety of sensorimotor systems, the analysis of navigation poses an exciting but difficult challenge for comparative cognition. That such a variety of sensory inputs and motor outputs could all be subserved by the same general mechanisms seems *a priori* unlikely. Nevertheless, some fundamental processes may have been conserved by evolution, and others may have evolved convergently in different taxa.

Comparison of animal species and their associated environmental adaptations provides us with vital information about the potential representations and processes involved in navigation, and is a key strategy in identifying both the general and the task- and species-specific components.

Comparative studies of navigation in a wide range of species have revealed certain processes that seem to be fundamental, inasmuch as they appeared early in evolution and have persisted, and other processes that seem to be more recent, and more complex. Furthermore, evidence, some of it reviewed in this chapter, suggests that the more complex and recent processes are, in many (if not all) cases, synthesized from the older and simpler processes. This can be concluded not only from behavioral studies looking at the different abilities displayed by different animals, but also by studies of the underlying neurobiology and of how these processes are organized in the brain. These considerations have led us to propose a taxonomy of navigational processes, organized hierarchically, to try and capture the elements of this synthetic process. The following text presents this taxonomy, which we call the “navigation toolbox”, and which forms the basis for organizing the subsequent discussion of what we know, and what we have yet to discover, about how animals and humans navigate. Having outlined the processes in the toolbox, we then use it as the basis to explore the synthetic processes that gave rise to the higher-level elements, before concluding with an examination of how these tools may be used in decision-making and planning.

## THE NAVIGATION TOOLBOX

1  
2 The toolbox we propose (Figure 1) was compiled by considering findings in the literature on animal  
3 behavior and neuroscience concerning navigation and its building blocks. It comprises a collection  
4 of processes and representations (“tools”) that have been identified by various research enterprises  
5 as contributing to navigation in species of different kinds. Each species has access to a subset of the  
6 tools in the toolbox, and it uses these tools to construct navigational behaviors. We acknowledge  
7 that alternative typologies and vocabularies exist in other disciplines, such as the spatial ontologies  
8 proposed by computer scientists (e.g., Kuipers, 1978, 2000), the space syntax developed by  
9 architects (Hillier and Hanson, 1984), the concepts employed by geographers and used in applied  
10 sciences that rely critically on the analysis of spatial relationships such as geographic information  
11 science (GIS) and cartography, the formulations of mathematicians working in metric geometry or  
12 topology, and even the long-standing philosophical debate about absolute and relative space.  
13 Ultimately, intensive cross-disciplinary discussion is needed to delineate the points of  
14 correspondence and difference among these approaches. Many of the differences may derive from  
15 the different data types considered, as well as differing assumptions and goals in the various fields.  
16 The toolbox is organized hierarchically, distinguishing between lower-level sensory processes and  
17 higher-level processes thought to operate on the lower-level components. This is, inevitably, an  
18 artificial and hence imperfect hierarchy, because for convenience we have made it discrete, whereas  
19 in reality there is no clear dividing line between simpler and more complex processing capabilities.  
20 However, we hope the organization of the toolbox may be useful for students of navigation in  
21 thinking about how complex behaviors are synthesized from more elemental processes in the  
22 nervous system.

23 Navigational elements (representation or processes) are assigned to different levels of the hierarchy  
24 according to two principles:

- 25 (a) Elements at a given level are synthesized by integration of elements at lower levels;
- 26 (b) Elements at a given level possess new spatial semantic content not present in the lower  
27 levels.

28 While the first principle is intuitively obvious, the second requires some explanation. By “spatial  
29 semantic content” is meant the “meaning”, in spatial terms, of the given element: in other words,  
30 how the content of that element relates to some real-world parameter. Examples could be heading,  
31 distance, or “place”. An example of “new spatial semantic content” might be construction of a  
32 position vector by integrating information about distance with information about direction. Not only

1 is the new representation synthesized by integration of elements at lower levels, it also contains  
2 additional spatial information. With this new, semantically richer representation, it is possible to  
3 perform more sophisticated navigational feats, such as homing, or shortcutting. Thus, the hallmark  
4 of navigational complexity is the synthesis of internal representations. We shall return to this point  
5 in the discussion of cognitive mapping.

6 The navigation toolbox has four levels:

7 **Level 1: The sensorimotor toolbox**, comprising different sensory modalities such as vision,  
8 olfaction etc., together with simple motor processes such as approach and avoidance, that provide  
9 information relevant for locomotion and navigation. In mammals, these processes take place in, or  
10 near, primary sensory or motor cortices. The elements of the sensorimotor toolbox are involved also  
11 in other, non-spatial behaviors, such as mating, predator avoidance, tool use, or social interaction.

12 **Level 2: Spatial primitives**, a set of representations that animals build, using the sensorimotor  
13 tools in Level 1. For example, an animal may combine the pattern of optic flow, computed in the  
14 visual system, together with linear acceleration signals extracted from the otolith organs in the inner  
15 ear, to help construct a representation of velocity. Velocity is a spatial primitive in the sense that  
16 while it is metric, being a measure of distance travelled per unit time, it does not in itself contain  
17 positional information. It can, however, be used to *compute* position, a Level 3 representation.  
18 Another example is landmark identification, another higher order process that may make use of  
19 several sensory modalities. Again, landmarks in themselves do not contain positional information,  
20 but can be used to compute position if the animal can determine their relative distances and  
21 directions with respect to itself. These navigational building blocks are formed using integrative  
22 processes that are discussed in detail later in the chapter.

23 **Level 3: Spatial constructs** are even higher level, more complex, spatial representations that are  
24 constructed from the spatial primitives (level 2). An example could be position, calculated by  
25 identifying landmarks and determining their distances and directions – all Level 2 processes in our  
26 hierarchy – and using these to create a representation of current location by a process known as  
27 piloting. In a complementary manner, velocity signals computed using Level 2 processes can be  
28 used to update a positional calculation, by interaction with the piloting process. Moreover, by  
29 relating such positional calculations with landmarks an integrated representation of space can be  
30 formed at Level 3. As with Level 2, the underlying integrative processes in Level 3 are explored  
31 later.

1 **Level 4: Spatial symbols**, including human language and graphic representations, that allow for  
 2 external storage and inter-individual communication of Level 3 spatial constructs.

3

Level	Level 1 Sensorimotor toolbox	Level 2 Spatial primitives	Level 3 Spatial constructs	Level 4 Spatial symbols (uniquely human)
Elements	Vision Audition Olfaction Touch Kinaesthetic Proprioception Magnetic cues Thermoreception ...	Landmarks Terrain slope Compass heading Local heading Panorama Boundaries Posture Speed Acceleration ...	Cognitive Map Self localization Goal localization Frames of reference	External maps Wayfinding signage Human language
		Contextual Information (e.g., motivations, odor)		
	▼	▼	▼	▼
Behaviour supported	e.g. Taxes, Kineses	e.g. View-matching Beacon navigation	e.g. Cogn. mapping Path planning	Communicating spatial information

4

5

Figure 1: The navigation toolbox.

6 **Generating behavior with the navigational tools**

7 A given organism does not need all of the tools, or even all of the levels in the toolbox, in order to  
 8 generate navigational behavior. Spatial behavior can be supported by any or all four levels of the  
 9 navigation toolbox, as follows:

- 10 • The *sensorimotor toolbox* can support spatial behavior that is based purely on sensory  
 11 processes, or sensorimotor loops. Examples of such behavior are taxes and kineses (e.g.,  
 12 positive phototaxis in flies) that do not require forming representations of space or spatial  
 13 concepts, as may occur in the higher levels of the navigation toolbox. All that is required is

1 simple detection of a stimulus, such as light or odour, and then organisation of movement  
2 either proportional in its intensity (kinesis) or towards or away from that stimulus (taxis).

- 3 • At the level of the *spatial primitives*, information from the sensory toolbox has been  
4 integrated to form simple representations that may lack positional information, but which  
5 are useful in some kinds of navigation, and are used to build complex spatial  
6 representations. At this level, simple locomotion and navigational behavior such as centering  
7 by keeping optic flow equal on the two visual hemispheres, beacon navigation or view  
8 matching is supported (see Shettleworth, 2010, Chapter 8), but the assembly of more  
9 spatially complex internal representations is not yet implied.
- 10 • The third level of the navigation toolbox, *spatial constructs*, consists of representations that  
11 are built from the spatial primitives. At its more sophisticated level, integration of primitive  
12 non-spatial processes, such as landmark identification, together with primitive relational  
13 information, such as the relative distances and directions of landmarks, can result in a spatial  
14 memory structure (an internal representation of space) that is in many ways map-like, and  
15 often referred to as a “cognitive map”. The extent to which animals of various kinds do or  
16 do not possess a memory organized like a cognitive map has been the source of lively debate  
17 over many years, and we discuss the debate at greater length later in the chapter.
- 18 • The fourth level of the toolbox, the *spatial symbols*, allows, of course, for unique behavioral  
19 feats in humans, such as navigating to an arbitrary place given a street address anywhere  
20 around the world. However, more importantly, humans exhibit the ability to communicate  
21 their navigational computations, to a high level of sophistication, to other humans, via maps,  
22 language and mathematics. Map-drawing exists to a very restricted degree in other species  
23 (e.g., bees) and vocal communication likewise, but the level attained by humans far  
24 surpasses anything seen in the rest of the animal kingdom in its flexibility and productive  
25 power.

26 Spatial behavior supported by Level 2 (spatial primitives) and Level 3 (spatial constructs) of the  
27 navigation toolbox is of particular interest for comparative cognition: at these levels we are able to  
28 move away from species-specific mechanisms and towards general principles of navigation. For  
29 example, migrating birds may have access to magneto-reception while insects are capable of  
30 perceiving polarization patterns in the sky. Despite these differences on the sensory level (Level 1),  
31 both sources of information are utilized or integrated to derive semantically equivalent information  
32 about space – a compass heading (Level 2). Similarly, honeybees and desert ants rely primarily on

1 different sensory cues (optic flow and proprioception) in order to estimate the distance that the  
2 animal has travelled (odometry). Bees flying over a large range of local cues and following long  
3 ranging landmarks, however, are equipped with the capacity to integrate these spatial structures in  
4 such a way that they localize themselves, and navigate to the intended goal by novel shortcuts (see  
5 Chapter xx by Menzel, this volume). Differences occur not just on the sensory but also the motor  
6 side. An example is the navigation behavior of the desert ant *Cataglyphis* which, when running over  
7 a featureless landscape seems to primarily rely on **an elementary form of** path integration, while  
8 ants navigating in a landscape rich in local cues, such as *Melophorus bagoti* in contrast, **appear to**  
9 learn sequences of turns in **relating measures of path integration with** these cues in their rather  
10 stereotypical foraging routes. These examples illustrate that the processes operating during  
11 navigation are heavily constrained by the animal's action space.

12 One might think of these higher level representations (compass heading, or distance) as being  
13 *supramodal* – that is, independent of, or “lying above” specific sensory modality – and of having  
14 meaning (semantic content) independent of the neural implementation. Such abstractions allow not  
15 only comparison across species, but also for interactions between students of natural and artificial  
16 navigational agents. We will return to this issue in the section on integration.

17 The navigation toolbox thus provides an organisational framework that allows for more systematic  
18 cross species comparisons of higher-level principles supporting spatial navigation, independent of  
19 species-specific implementations. We suggest that by attempting to fit the diversity of navigational  
20 inputs and outputs seen among species to this proposed framework, we will make significant  
21 progress in understanding the similarities and differences in their navigational (and cognitive)  
22 abilities. However, having extracted general principles, it is then important to consider whether and  
23 how species-specific constraints influence information processing. For example, does an animal's  
24 action space and complexity of neural integration determine the set of spatial primitives that are  
25 used by the animal? And, what is the influence of the animal's navigation range and how do the  
26 properties of its habitat influence how it uses the spatial primitives and spatial constructs available  
27 (Level 2 and Level 3 in Figure 1)?

28 Below, we consider the four levels in the toolbox in more detail, before examining the integrative  
29 processes that lie behind the construction of these navigational elements.

## LEVEL 1: SENSORIMOTOR PROCESSES

The simplest level of the navigation toolbox contains a set of sensory and motor processes that can support simple navigational processes, such as taxes. These sensory processes are used to build higher-order tools in the toolbox and will not be considered further here. Increasing evidence supports the notion of top-down modulation of sensory processing and it may be that some kinds of simple navigational process, such as template-matching for view-based navigation, might occur at very early stages of neural processing such as primary sensory cortical areas.

## LEVEL 2: SPATIAL PRIMITIVES

Many navigational phenomena, particularly those seen in laboratory settings using small scale environments, can be explained by one or more mechanisms that are more sophisticated than simple sensory-driven Level 1 processes such as taxes, but are nevertheless spatially still relatively unsophisticated (i.e., belonging to Level 2 of the navigation toolbox). Spatial primitives are considered to exist at a level of complexity above sensorimotor elements for two reasons: (a) they are synthesized *from* Level 1 elements, and (b) they have spatial (or proto-spatial) semantic content not present in those elements.

An example of a spatial primitive is landmark recognition. The majority of species that have been studied to date rely on landmarks, at least some of the time, to help organize their spatial behavior, and so this competence seems to be phylogenetically old (although landmark recognition may require different levels of processing sophistication: an ant may simply recognize a landmark as being a particular retinal pattern as part of a panorama (Collet & Collet, 2002); in this case, the “snapshot” is a code of the place or view-point from which it has been taken. In addition to this snapshot memory, primates might have a multimodal, viewpoint-independent representation built using object-processing capabilities in the perirhinal cortex. In this case, one landmark memory may be used in the recognition of more than one place and the places recognized may be remote from the actual landmark position. Landmark identity, being (usually) multimodal, is a semantically different category from a simple stimulus pattern impinging on a sense organ. Note, however, that the simplest forms of recognition, such as odor detection, or the ant landmark recognition example above, could be considered as bordering on Level 1 processes, reinforcing that this is not a hierarchy to be taken too rigidly. However, while a landmark may be necessary for spatial navigation, it is not sufficient, inasmuch as it contains no spatial information – unless the goal is *at* the landmark, the animal needs other information in order to navigate. In this sense, the landmark,

1 being space-free, is a spatial primitive. If the goal is at the landmark then a simple kind of  
2 navigation, beacon homing, is supported, and evidence suggests that many species can do this.

3 Spatial primitives can support behavior that looks remarkably complex to an observer. Navigation  
4 by view-matching is an example: it requires a representation of the goal (a standard, e.g. a snapshot  
5 or a panorama recorded at the home location), and a record of the current location. According to the  
6 snapshot model (Cartwright and Collett, 1982) the difference between the standard and the current  
7 record is computed by a comparator, resulting in an error. This error is thought to drive the  
8 movement of the navigator and in this way the error is reduced. View-matching can thus be  
9 conceptualized as a servomechanism (Cheng, XYZ). Beacon navigation requires landmark  
10 identification, which may be a higher order object recognition process, but the behavior that follows  
11 is simple approach or avoidance. At a more sophisticated level, a turning movement could be  
12 organized to left or right on the basis of a perceived stimulus – this introduces the beginnings of  
13 true spatial (i.e., relational) processing and such behavior lies on the boundary between Levels 2  
14 and 3.

15 Navigating along a well known route is another example of behavior supported at level 2, allowing  
16 animals to reach distant destinations even if these are beyond the current sensory horizon. It can be  
17 explained assuming spatial primitives such as a string of beacons or landmarks to identify the place  
18 at which a particular turn has to be carried out. These turns can be informed by motor responses  
19 associated to the place. A series of such recognition-triggered responses therefore is sufficient for  
20 explaining route navigation. Importantly, such processes do not require the operation of a cognitive  
21 map, although this does not in itself rule out that some animal species use a map, even in route-  
22 following, if one is available.

23 Heading calculation is another well known example of what we call here a spatial primitive. Many  
24 species are able to extract Earth-relative directional information from either magnetic or celestial  
25 compass cues. Behavioral and neurobiological studies in the laboratory have additionally revealed  
26 the existence of local orientational reference frames that are conferred by local cues such as distal  
27 landmarks. Heading calculation is an interesting process from a theoretical point of view because it  
28 may require the bringing together of very different sensory information streams (directional cues  
29 e.g. with respect to a compass, landmarks and multimodal self-motion cues) in order to synthesize a  
30 semantically new, supramodal representation (such integration processes are discussed in more  
31 detail below). As with landmarks, heading alone is of limited use in navigation but is of very great  
32 use when combined with other spatial primitives such as distance leading to an integration of

1 traversed path – i.e. path integration – for example in the formation of goal or homing vectors. In its  
2 basic form, path integration integrates rotational and distance information (both spatial primitives)  
3 resulting in a home vector, i.e. a working memory representation of the distance and direction to the  
4 home or to other places encountered during travel. When heading home, the animal moves such as  
5 to reduce this home-vector to zero. It may be debated whether such a home vector represents a  
6 spatial primitive or a spatial construct (see next section). If, however, the status of the path  
7 integration measure is associated with other spatial primitives such as landmarks this would allow  
8 forming long term representations of metric relationships between different places in the  
9 environment. In this case path integration undoubtedly becomes part of a spatial construct.

### 11 LEVEL 3: SPATIAL CONSTRUCTS

12 Having established a collection of relatively primitive tools that animals may have access to for  
13 navigational purposes, we focus now on Level 3, the spatial constructs. As with the previous levels,  
14 the elements in this level are characterized by having been synthesized from lower-level elements,  
15 and by having new semantic content. An important new semantic category is that of *position*, a  
16 relational term that implies specification of a subject, or an object, by means of adjacencies or  
17 neighborhoods, distances or bearings to other memory items. We will call such relations a frame of  
18 reference without implying that it has to take the form of a metrical coordinate system. In this light,  
19 one of the most interesting and contentious issues has been the extent to which it is appropriate to  
20 place, in this level, a representation that could be called map-like. We return to this issue, below.

21 A good example of a spatial construct is the local vector (Collett and Collett, 2002). In executing a  
22 local vector operation, contextual cues, such as a view, are associated with path integration to  
23 enable travel in a particular compass direction. A view of the surrounding scene, one spatial  
24 primitive, serves as the trigger to execute a behavior that relies on another spatial primitive, a  
25 compass upon which a direction of travel is derived. Local vectors based on the current state of path  
26 integration have been well demonstrated in desert ants (*Cataglyphis*: Collett et al. 1998;  
27 *Melophorus*: Legge et al. 2010). It is possible that route following behavior consists of a string of  
28 such local vectors, with the end of one local vector providing the initial conditions (e.g., the  
29 appropriate view) to trigger the next (Trullier et al., 1997; Cheng, 2006). If such associations  
30 between places and local vectors are spread in the vicinity of a goal, they can support homing from

1 an area exceeding the sensory horizon, or catchment area, of a single snapshot marking the home  
2 (Cartwright & Collett, 1987).

3 A closely related example is that of path integration. As discussed in the last section, it can be  
4 viewed as a spatial primitive combining velocity and heading over the course of a journey so as to  
5 maintain a constant, ongoing representation, or when combined with landmark information it can be  
6 seen as an example of a spatial construct including relational information of landmarks. The exact  
7 nature of this representation has not been fully elucidated and may be different for different species  
8 or in different settings: it could be a vector, as for example the distance and direction back to a  
9 home base at a particular location, or to another known position, or it could be a location in a  
10 cognitive map (see below). If the path integrator transiently fails, or if the animal has just arrived in  
11 the environment, it can undertake a position fix using a different set of spatial primitives: namely,  
12 available landmarks together with their computed distances and directions. The process of taking a  
13 position fix from familiar landmarks is, as mentioned earlier, known as piloting.

14 The sophistication of Level 3 constructs also allows for navigation towards unseen goals. Insofar as  
15 a given species uses such relational spatial constructs, goals can be defined as attractive locations in  
16 the spatial reference system, and the task for the animal is to reach the goal from its current  
17 location. For spatial behavior at level 3 it is assumed that the goal cannot be approached simply by  
18 steering towards a beacon at the goal, or executing a set of landmark-stimulated responses or a  
19 learned sequence of body turns. Rather, Level 3 constructs are relational, whereby more than one  
20 spatial primitive is required to be integrated to solve the spatial problem.

### 21 **The cognitive map**

22 In the section on spatial primitives, we explored navigational behaviors that can be achieved with  
23 relatively simple processes, such as view-matching and beacon homing. Other navigation behaviors,  
24 in contrast, cannot be explained without reference to a spatial memory in which places are related to  
25 one another in a common reference frame. It is usual to call such a reference-frame-based spatial  
26 memory system a *cognitive map*. This is an interesting class of spatial semantic information that is  
27 likely possessed by humans (Gillner & Mallot, 1998; Hartley et al., 2003), and for which the  
28 existence in other animals has been disputed (Bennett, 1996; Shettleworth, 2010).

29 The strongest evidence for the operation of a cognitive map, in the sense of a connected allocentric  
30 representation of familiar space, has been seen as the ability to take a shortcut or a novel route  
31 under conditions in which path integration, view-matching and beacon orientation can be excluded.  
32 While the exclusion of these processes is difficult to achieve experimentally, this can, for example,

1 be demonstrated when an animal is displaced from a goal-oriented route and needs first to self-  
2 localise, on the basis of local cues, and then to correct for its displacement in order to re-orient  
3 towards a goal. What kind of memory structure would allow an animal to relocate its position  
4 relative to the goal and subsequently compute a corrective direction to the goal? It can be argued  
5 that only a spatial representation with features that resemble a map could enable such corrective  
6 reorientations. The critical feature of this representation that makes it map-like is its ability to  
7 support spatially relational processes: in this case of (1) self-localization, and (2) vector calculation.  
8 Thus, the term “cognitive map” has frequently been used to refer to internal spatial representations  
9 that organize spatial knowledge about different locations in the world by relating them to one  
10 another either by adjacencies or in a common reference frame. The term originated in experimental  
11 psychology with Tolman (1948) and was memorably utilized in a widely cited book by O’Keefe  
12 and Nadel (1978). While the concept of cognitive maps has been criticized, in that it has been used  
13 too often as a metaphor without reference to mechanisms, researchers working on navigation in the  
14 field where the animal is allowed to navigate in an open space find a *map* a useful concept and see  
15 evidence for *cognitive maps* in several species and settings (see Menzel and Bingman, this volume).  
16 The organization of spatial information in the mammalian (rat) brain can also be seen in terms of  
17 mapping. In fact, the place and grid cell system in rats constitute a neural substrate of metric  
18 information/coordinate system (see Jeffery, this volume, Hafting et al., 2005). Similarly, functional  
19 brain imaging studies in humans navigating large scale virtual environments demonstrate that novel  
20 shortcutting/route planning behavior recruits a different cortical network than route following  
21 behavior (e.g., Hartley et al., 2003); the “map-task” used in this and similar studies can be solved  
22 with a memory based on place adjacencies, leaving the possibility that the underlying “map” is not  
23 using metric coordinates but only a simpler graph structure (Gillner & Mallot 1998).  
24 As discussed above, cognitive maps do need to encode spatial relations between locations in the  
25 environment – either as a graph of adjacent places or via an allocentric reference frame. Spatial  
26 behavior specified in Level 3 of the Navigation Toolbox (see above) such as self localization, goal  
27 localization, and the formation of a plan designed to get to the goal (cf., definition of spatial  
28 planning in Section 3) require such relational knowledge. While spatial relations between places can  
29 be encoded in a topological (i.e., non-metric) graph-like format, in which places are represented as  
30 nodes and transitions between places are represented as edges (graph-theoretic representation), the  
31 inclusion of metric information appears to be crucial to explain a number of behavioral findings  
32 (see Menzel, this volume).

1 In humans, evidence of metric information in spatial long term memory is debatable (but see,  
2 Schinazi et al., 2009). For example, Foo et al. (2005) trained subjects to walk two straight paths  
3 from a starting point, thereby acquiring clear knowledge of distances and directions of each path.  
4 When released at the end of one path, shortcutting to the end of the other path was poor (for an  
5 analogous study in dogs, see Chapuis and Varlet, 1987). Note that this shortcutting is not a type of  
6 path-integration but requires metric recombination of local distance and angle information from  
7 long term memory. The question about the amount of metric information encoded in the cognitive  
8 map remains controversial. A challenge for the future will be to answer a number of questions that  
9 are related to this point: 1. Is metric knowledge a prerequisite for cognitive maps? 2. Is metric  
10 knowledge equivalent to cognitive maps? 3. How do local and global metric information relate to  
11 the concept of the cognitive map?

12 A different notion of the map has been suggested for birds. Often discussed in the context of bird  
13 navigation is a map, referred to as the “navigational map”, formed by intersecting stimulus  
14 gradients that form a bi-coordinate system by which any point in space is characterized by a unique  
15 combination of coordinates (Wallraff, 2005). These coordinate values could provide a global  
16 allocentric reference frame with respect to which items of spatial long term memory (places,  
17 landmarks, “home”) could be represented (for a fuller discussion of this issue, see Bingman chapter  
18 in this volume).

19 Some of the controversy on the nature of the cognitive map may arise from a confounding of  
20 separable functions that must be integrated for novel shortcutting but that may be used  
21 independently. For example, it may be necessary to separately analyze the cognitive map  
22 component derived from distributed cues, such as compass bearings and gradients, from those  
23 derived from discrete cues, as done by the parallel map model for the integration of such cues  
24 (Jacobs & Schenk, 2003; reviewed in Menzel, this volume). Because of the necessity of an  
25 underlying distributed cue representation (i.e., a bearing map) for shortcutting, it may be difficult to  
26 demonstrate true cognitive map shortcutting in small laboratory settings. In the notable exceptions  
27 (e.g., Roberts, 2007), the experimental space is characterized by an extreme paucity of discrete  
28 cues, which may force the animal to rely on bearing-map function, even in the relatively small  
29 space of a laboratory maze. In contrast, free-flying birds and insects may naturally recruit a strategy  
30 based on such distributed cues, which would enable them to flexibly shortcut. One of the challenges  
31 for future navigation research therefore is the development of well controlled laboratory  
32 experimental paradigms that allow to distinguishing spatial behaviors supported by Level 2  
33 processes and Level 3 processes.

## LEVEL 4: SPATIAL SYMBOLS

The final class of navigational elements in our hypothetical navigation toolbox is an almost-  
uniquely human capacity, the ability to use external symbols to represent space, thereby allowing  
the development of semantic information that goes beyond what can be achieved by the neural  
navigation systems embedded in the brain. Two classes of symbolic manipulation are particularly  
important in this regard, language and mathematics. We mostly focus here on language, because its  
role in ordinary day-to-day spatial navigation processes has been the focus of intensive recent study.

### **Are there uniquely human navigational strategies? Is there a role of language?**

Humans have a distinctive, and arguably unique, capacity for symbolic representation and  
communication that form Level 4 of the navigation toolbox (see Figure 1). Symbolic systems  
include language, of course, but also encompass more spatial systems such as gesture, sketching,  
drawing, and external maps. In the context of comparative cognition, we need to consider two  
questions. First, to what extent does the availability of Level 4 have a top-down influence on the  
prior levels? This is the classic issue of to what extent language (as well as other symbolic systems)  
influences thought. Second, to what extent, does the availability of Level 4 extend or augment the  
capabilities available in species that only have access to the first three levels? That is, are symbolic  
systems powerful tools for augmenting spatial functioning?

### **To what extent does the availability of Level 4 have a top-down influence on the prior levels?**

Thinking about this question has concentrated almost exclusively on spatial language, so we will  
begin our discussion there. It is interesting that there are some notable design mismatches between  
space and language. Space is continuous while language is categorical, and multiple spatial  
relations are available simultaneously in the world, but must be discussed sequentially in language.  
Given these considerations, one might suspect that spatial language can be helpful in spatial  
functioning to some extent, but perhaps to a limited extent.

However, there have been strong claims recently that spatial language *shapes* spatial thought (e.g.,  
Levinson, 2003). A prominent and often-cited example of such shaping concerns languages that  
require the use of compass-referenced coordinates to describe spatial relations, e.g., the cup is to the  
NORTH of the plate. By contrast, many other languages describe this spatial relation in a relative  
fashion, e.g., the cup is to the RIGHT of the plate. Experiments have been done in which speakers  
of these contrasting kinds of languages have been asked to view objects arranged in a line on one  
table, and then to place them in the same way on a second table after rotating 180 degrees. In many

1 studies, as reviewed in Levinson (2003), speakers of absolute languages maintain the correct  
2 compass directions in their reproductions on the second table, while speakers of relative languages  
3 use a relative coding internal to the array. However, Li and Gleitman (2002) have shown these  
4 results can be altered by small environmental manipulations, so that, for example, speakers of  
5 relative languages will produce absolute reproductions when a landmark is available (e.g., a pond at  
6 one end of the table). They suggest that there is a great deal of flexibility in spatial representations  
7 and thought, so that language picks out certain systems of spatial coding but does not preclude the  
8 existence of others (see also Gallistel, 2002; Newcombe, 2005).

9 The issue of the uses of spatial language has special resonance in terms of thinking about human  
10 development, since of course children begin life without having a language, and acquire language(s)  
11 over the first few years of life. Two lines of research have been important in recent thinking about  
12 how spatial language affects spatial development. First, it has been argued that the spatial language  
13 infants hear structures their acquisition of spatial concepts (e.g., Bowerman, 1996). For example,  
14 Korean children hearing a language in which a distinction between “tight fit” and “loose fit” is an  
15 important semantic contrast acquire the perceptual and conceptual basis for the distinction, while  
16 English children do not. A contrasting position is that infants begin with an array of spatial concepts  
17 (either innately specified or acquired in the first year), and subsequently map certain of those  
18 concepts to the language they hear around them (e.g., Mandler, 1996). Data gathered on this issue  
19 seem to favor the position that spatial concepts exist before spatial language, but that spatial  
20 language draws attention to some of these concepts and dampens others, making the concepts used  
21 frequently more available and the ones not used more difficult to activate (see review by Göksun,  
22 Hirsh-Pasek & Golinkoff, 2010).

23 Second, Spelke and her co-workers have claimed that language (specifically productive control of  
24 the terms “left” and “right”) is essential to being able to use features for reorientation in the  
25 geometric module paradigm introduced by Cheng (1986) and reviewed by Cheng and Newcombe  
26 (2005). This group has claimed that children younger than 6 years behave like non-linguistic non-  
27 human animals in using geometric information alone to reorient, ignoring useful featural  
28 information. They also report a transition to a uniquely human use of features as well as geometry at  
29 the age of 6 years (with the advent of the productive use of the words “left” and “right”). However,  
30 toddlers’ failure to use features turns out to be specific to the use of extremely small spaces of  
31 limited ecological validity (Learmonth, Nadel & Newcombe, 2002). Twyman and Newcombe  
32 (2010) have recently reviewed the extensive literature that has accumulated on this issue, arguing  
33 that there is a variety of evidence that feature use is far more flexible than the Spelke group has

1 argued, and that language is not necessary to the development that does occur (although it could be  
2 helpful, as could other kinds of experience).

3 What about symbolic systems other than language? There have been few, if any, strong Whorfian  
4 positions taken on the topic of how maps (or other visuo-spatial systems) might mold spatial  
5 thinking. Uttal (2000) reviewed how maps affect spatial development, arguing that they are helpful  
6 in the acquisition of abstract spatial concepts and in systematizing spatial thinking. However, this  
7 position is an “augmentation” one (related to our second question), not a determinist one. In fact,  
8 Dehaene, Izard, Pica and Spelke (2006) claim that the basic geometry of maps is innately available  
9 without experience with them, a nativist position that would suggest that maps merely capture  
10 knowledge rather than molding it. However, their data do show development in Western cultures in  
11 the use of some map-relevant concepts that does not occur in their Amazonian population,  
12 suggesting a role of cultural input (Newcombe & Uttal, 2006).

13 **Does the availability of Level 4 extend or augment the capabilities available in species that**  
14 **only have access to the first three levels?**

15 Spatial language and other spatial symbolic systems seem to aid spatial thought in a powerful way,  
16 even if they do not have a strictly determinative effect. For example, babies learn spatial concepts  
17 better when the concepts are labeled (Casola, Bhagwat & Burke, 2009), and, similarly, teaching  
18 children a particular spatial word (such as “middle”) seems to support their learning of the  
19 corresponding spatial concept (Simms & Gentner, 2010). Preschool children whose parents use  
20 more spatial words (such as “outside” or “corner”) show stronger spatial growth than children who  
21 do not hear as much language of this kind (Pruden et al., 2010). Spatial thinking in adults is also  
22 clearly affected by spatial language (Boroditsky, 2001; Casasanto, 2008)—although some studies of  
23 this kind take a turn back in the Whorfian direction.

24 Maps may be as important as or more important than language in giving human navigation a  
25 distinctive quality (Uttal, 2000). Maps have been used by humans for millennia (possibly up to  
26 8,000 years), though there have been notable technical advances over the past centuries, e.g., the  
27 discovery of a means of measuring longitude and navigation assistant systems that guide navigators  
28 to the destination. External maps offload memory and cognitive processing demands, allow for  
29 communication and social interaction towards a spatial goal, and also highlight areas of ignorance –  
30 territories not explored or separate territories that are known internally but whose relation needs to  
31 be determined (cf. discussion of cognitive maps in the last section).

1 While maps are very elaborate external navigation aids, humans also design and utilize less  
2 complex tools to communicate spatial information, for example signposts. Such simpler means of  
3 communicating spatial information are not unique to humans but are also found in animals. Many  
4 animal species, for example, mark their territories with “scent posts” which could be seen as aids to  
5 conspecifics in detecting territory boundaries. The most famous example of spatial communication  
6 in animals is the waggle dance of honey bees (von Frisch, 1965). In fact, bees use symbolic  
7 communication to convey distance and direction information to food locations. However, this  
8 system is a closed one lacking the productivity and flexibility found in a true language.

## 9 SYNTHESIS AND THE NAVIGATION TOOLBOX

10 The navigation toolbox identifies several sets of processes and representational structures, some  
11 taxon-specific and some more general, that can be integrated in the service of navigation. Such  
12 integration is useful for two reasons. One is simply that for a given type of information, two sensors  
13 carrying information of the same semantic content are better than one: the accuracy of detection can  
14 always be improved by increasing the number of detectors. The other is that, as discussed in the  
15 first part of this chapter, integration of information streams having different semantic content allows  
16 the formation of higher order representations that allow computations not possible at the lower  
17 levels. These two types of integration are discussed in turn.

### 18 **Integration of information streams having similar semantic content**

19 In many cases it is advantageous to combine semantically equivalent information sources in order to  
20 derive maximum advantage from all the information available. Homing pigeons, for example, may  
21 use both sun compass information and magnetic compass information (both Level 2 primitives, and  
22 both belonging to the semantic category of “heading”) to compute the direction towards the home.  
23 The information sources may even come from the *same* sensory modality: for example, from two  
24 visual landmarks both intermittently visible in foggy conditions. Cue integration presents an  
25 interesting problem, however: what should the brain do with these two sources of information –  
26 average them, or choose one or the other? If the former, should all sources be given equal weight or  
27 should some count more towards the average than others? And if the latter, how to decide which  
28 one to prefer?

29 Bayesian approaches provide a normative framework for modeling how and whether animals  
30 should combine vs. select information from multiple cues, in order to make inferences or  
31 judgments. The importance of the Bayesian approach is its reliance on the existence of “priors”,

1 which comprise pre-configured knowledge about the nature of the incoming information. An  
2 example of a Bayesian prior would be the past experience that a landmark is positionally unstable.  
3 Prior knowledge allows a decision-maker to discount information known to be unreliable, or at least  
4 to rely more heavily on sources known to be trustworthy. Specifically, the Bayesian framework  
5 suggests that the available sources of information should be weighted in inverse proportion to their  
6 reliability, as measured in terms of variance in the estimate. The principle applies when the animal  
7 has multiple sources of information (such as Level 2 primitives) that may be combined, and the  
8 animal has a past history of relevant experiences (the Bayesian prior) that may be used to weight the  
9 current information sources. While Bayesian probability theory has been extensively used in human  
10 spatial perception, it has also been proposed for the integration of spatial information in other  
11 species (see Cheng, Shettleworth, Huttenlocher and Rieser 2007). However, it is important to note  
12 that controversy remains concerning the value of the Bayesian approach for the explanation of  
13 animal navigation behavior. This is, first, because at present there is little evidence for Bayesian  
14 integration outside of humans, and second, because the Bayesian approach provides a formalism  
15 that deals with the statistics of information sources rather than with animals' responses to these  
16 sources. While Bayesian approaches are often accepted as useful for hypothesis generation, the  
17 direct relation between the formalism and actual behavior is arguable (Jones & Love, in press).

18 While it is advantageous to combine semantically equivalent information sources in many cases, it  
19 sometimes makes more sense to choose one or the other in a winner-take-all (or "first past the  
20 post") manner. The question then arises as to how to determine which approach to take. Cheng and  
21 colleagues (Cheng et al., 2007) and Körding and colleagues (Körding et al., 2007) argue that the  
22 Bayesian framework predicts the integration of different sources of spatial information only if these  
23 sources indicate directions near to each other. If, however, the two sources indicate directions very  
24 different from each other, integrating and thus averaging will result in a direction that is indicated  
25 by neither of the two sources which makes integration unreasonable. In cue-conflict experiments  
26 this lack of integration is often exploited to compare the behavioral relevance of different  
27 information sources such as different Level 2 primitives. For example, phase- or clock-shift  
28 experiments in homing pigeons result in a large difference (conflict) in the indicated compass  
29 direction to the home between the sun compass and magnetic compass; a situation where  
30 integration, in the Bayesian view described above, should be unlikely. Indeed, under phase-shift  
31 conditions, homing pigeons almost exclusively rely on the sun compass with very little integration  
32 of magnetic information in the final behavioral output [REF needed].

1 Similarly, studies of place neurons in the rat hippocampus have found that the ensemble location-  
2 specific activity will rotate to follow small shifts (10-20 degrees) of a landmark, but will fail to  
3 follow large shifts (180 degrees) which introduce a large discrepancy between the landmark and the  
4 animal's internal sense of direction (Rotenberg and Muller 1996). Prior history of the landmark also  
5 influences how the neurons respond: they will tolerate reasonably large angular rotations of the  
6 landmark if the animal did not see these occur, but will not follow the landmark if the animal saw it  
7 moved (Jeffery & O'Keefe, 1999). An interesting and unresolved question concerns whether the  
8 place system is able to re-weight the reliability of various cues based on the animal's own internal  
9 state. For example, if an animal has been deprived of vision for some time, allowing time for its  
10 path integrator to drift, it may be more inclined to tolerate large discrepancies between external and  
11 internal cues than if its path integrator was recently re-set and hence more reliable.

## 12 **Integration of information streams having different semantic content**

13 As well as simply improving detection accuracy for information of a single semantic category,  
14 integration can occur when streams of semantically different information converge to form  
15 semantically new kinds of information. A prototypical example of integration to form a semantically  
16 new representation is the head direction system in rats, in which vestibular, proprioceptive, motor  
17 efferent, and visual signals are combined to form a representation of the orientation of the animal's  
18 head. The incoming sensory information is semantically different in nature: vestibular signals, for  
19 example, code for accelerations of the animal's head, while visual information conveys the presence  
20 and/or location of static landmarks. The Level 2 primitive resulting from integrating these Level 1  
21 sensory inputs, the head direction signal, is a supramodal representation because it is not anchored  
22 to a particular sensory modality, nor a particular information type, but arises through the  
23 convergence of several different kinds. Supramodal representations allow an organism to make use  
24 of different kinds of information having different properties. In the case of the head direction signal,  
25 the self-motion cues are imprecise but always present, whereas landmarks are very precise but only  
26 available sporadically (e.g., when the animal is looking in their direction). By using both, the  
27 organism derives an adaptive advantage. Indeed, it can be speculated that the great enlargement of  
28 the cerebral cortex during vertebrate evolution derives from the development of multiple  
29 supramodal representations in many different domains.

30 Even more importantly than simply exploiting the advantages of different cue types, the resulting  
31 representation is of a semantically different class: "heading", which was not present in the original  
32 inputs. This allows the brain to construct signals with new properties, which allow an organism

1 greater flexibility in its behavior. In the head direction cell example, the construction of a heading  
2 signal allows an animal to navigate even in directions in which there is no specific cue present.  
3 Furthermore, it is one of the building blocks to formation of yet another semantically new class of  
4 information, the cognitive map, which in turn allows an animal to perform such feats as  
5 navigational planning.

6 Bayesian rules can be used to model integration of semantically different information, just as they  
7 can be used to integrate cues of the same “sort”. Warren et al. (2001), for example, using head-  
8 mounted virtual displays, found that humans integrated two kinds of information, both providing a  
9 heading direction towards an object (beacon). Subjects used both the focus of expansion in optic  
10 flow, in which the optic flow pattern expands from the point towards which we face, and the  
11 identified beacon object. This was shown by dissociating the two cues in virtual reality. In human  
12 path integration, both visual cues (optic flow) and cues from the body senses (kinaesthetic and  
13 proprioceptive senses) are used (Kearns et al., 2002; Nico et al., 2002).

14 Bayesian priors might affect not just whether cue combination or choice occurs, but also the  
15 hierarchy of cue preference in cases when choice is necessary. Cue-conflict experiments have been  
16 a classic method for examining the hierarchy of cue use in spatial problems (e.g. Brodbeck 1994).  
17 The hierarchy appears to be dependent on the species, their ontogenetic experience, and on  
18 reliability of the cues. For example, when solving spatial problems in the field, free-living  
19 hummingbirds use information in a context-dependent manner: they will use the color of a flower  
20 but only if spatial information is not relevant (Hurly & Healy, 2002). They will learn the location  
21 of a flower relative to other flowers if those others are relatively close (up to 40cm) but will ignore  
22 the information from those other flowers once they are further away (>40cm ; Healy & Hurly  
23 1998). In squirrels, the use of a hierarchy or a majority strategy appears to change by season under  
24 natural conditions, suggesting that physiological changes induced by photoperiod and/or experience  
25 may constrain or mould the attentional resources available for spatial mapping and hence the final  
26 strategy used for orientation (Waisman & Jakobs, 2008). In adult humans, the choice of a geometric  
27 or a featural cue depends on the size of the enclosure (Ratliff & Newcombe, 2008). Geometric cues  
28 seem to be preferred in smaller spaces, while featural cues are followed in larger ones.

29 In summary, therefore, cue integration has the advantage of allowing an animal to maximize its use  
30 of information: it can choose the most reliable cues and discount the less reliable, it can use  
31 different cues in different ways depending on their characteristics, and it can combine them to form  
32 supramodal, semantically new representations that allow more sophisticated calculations. For some  
33 navigation behavior Bayesian approaches appear to describe how information can be combined.

1 Determining how general Bayes' rule is in navigation, and how it is implemented at the neural  
2 level, remains a challenge for the future.

### 3 **Cue integration and cognitive mapping**

4 Integrating spatial primitives (Level 2) into spatial constructs (Level 3) is a crucial feature of  
5 cognitive mapping. Essentially, different Level 2 primitives such as landmarks that may define  
6 particular locations in space are related to one another either by adjacency or in a global reference  
7 frame (see the section on "The Cognitive Map"). One proposal is a common coding system that  
8 integrates location on a coordinate map constructed from distributed cues (the bearing map) with  
9 the topological relations of discrete objects (the sketch map) that are encoded in relation to their  
10 location on the coordinate map (the integrated, i.e., cognitive map; Jacobs & Schenk, 2003).

11 Localization, whether it be of self, other, goal etc. is a central process of Level 3 of the Navigation  
12 toolbox either requiring a representation of that place (see discussion above) which may be  
13 recognized from landmarks or some context in the neighborhood or it requires a specification of  
14 what the locality is being specified with respect to – that is, the frame of reference. It is usual in the  
15 field of spatial cognition to distinguish between egocentric and allocentric frames of reference (both  
16 Level 3 constructs), where egocentric is self-referred and allocentric (literally: "other-centred") is  
17 referenced to the external world. Egocentric frames of reference follow the animal around, as it  
18 were, and neurobiological studies in mammals indicate that there are many such reference frames,  
19 at least in this taxon, encoded in parietal cortex. The mammalian frames are anchored variously to  
20 the eye, head, arm etc, and need to be integrated in order for actions to be coordinated. Likewise,  
21 there are probably many different allocentric reference frames. At least three have so far been  
22 identified: object-centered, in which encoding is specified relative to an object, earth-centered, in  
23 which encoding is specified with respect to global latitude/longitude and north/south, and encoding  
24 referenced to the local environment (as delineated by boundaries, landmark arrays etc). These  
25 allocentric frames have been identified in a variety of taxa, including insects, birds and mammals.

26 An open question in navigation concerns whether and/or how integration across allocentric  
27 reference frames might take place. This can be examined at the level of the neural substrate and/or  
28 at level of behavior. In the literature on egocentric integration it has been proposed that interactions  
29 between reference frames occur whereby neurons encoding one frame modulate the activity of  
30 those in another by a process known as gain field modulation (Andersen et al., 1985). For example,  
31 in monkeys, neurons in parietal cortex that respond to the position of a visual stimulus on the retina  
32 are modulated by how the head is oriented with respect to the torso, and their activity thus reflects

1 both parameters. An analogy in the allocentric domain might be found in rodent hippocampal place  
2 cells whose response to a boundary is modulated by how that boundary is oriented with respect to  
3 direction (Jeffery, this volume).

4 At the behavioral level, we often see examples of choice rather than integration. Cue dissociation  
5 experiments suggest that animals can plan navigational trajectories in more than one reference  
6 frame. There are several strategies to utilize the memory of a location that has been encoded by  
7 multiple reference frames. The animal could simply pick one frame from the list of remembered  
8 frames or it could orient to frames in a fixed hierarchy of preferences, as seen in juncos and black-  
9 capped chickadees, respectively (Brodbeck, 1994). The animal could also construct a majority  
10 strategy, where the animal chooses the location indicated by the majority (2 of 3) of the  
11 remembered frames of reference, with no preference for one frame over another, as has been shown  
12 in squirrels (Gibbs, Lea & Jacobs, 2007; Waisman & Jacobs, 2008).

13 Animals that undertake long-range migration often use an earth-centered allocentric reference  
14 frame, but animals with local ranges may have reference frames that are defined by local  
15 environmental features. In rodents, data from single neuron recordings suggest that encoding of  
16 local environments is metric – that is, contains information about distances and directions (Jeffery,  
17 this volume). An unknown question concerns how independent local reference frames (such as  
18 patches in a heterogeneous foraging environment or, as in humans, different rooms in an office  
19 block) can be related to each other, and whether these between-room relationships are metric or  
20 whether they are simply topological (reflecting adjacency relations only). An open question  
21 concerns whether animals are able to represent environments they are not currently in and whether  
22 – if so – they do this in a strictly metric way. Very recently, research has begun on how spatial maps  
23 at local levels can be interconnected and coordinated to allow for navigation in large and complex  
24 (and changing) natural environments (Derdikman & Moser, 2010), and pursuing this issue is a clear  
25 challenge for the future.

26 Efficient navigation in three dimensional space requires computing and integrating both horizontal  
27 and vertical position. The computation of position in two dimensions requires integration of  
28 distance and direction, or (equivalently) distance in two orthogonal directions, in a trigonometric-  
29 like fashion. How this is done remained mysterious until recently when studies of the neural  
30 representation of space in mammals revealed the existence of grid cells and so-called conjunctive  
31 cells, whose activity seems to combine distance and direction in the horizontal plane (Fyhn et al.,  
32 2004; Sargolini et al., 2006). The next question concerns whether the third dimension – i.e. the  
33 vertical dimension – is integrated in a similar fashion, using neurons sensitive to distances in all

1 three dimensions. Up to now, there are very few experimental data on this. Ecological  
2 considerations suggest many species – those that swim, glide, fly or climb – would benefit from an  
3 integrated three-dimensional representation because they move freely in volumetric space. On the  
4 other hand, the theoretical considerations outlined by Jeffery (this Volume) suggest this would be  
5 computationally expensive and that a modified two-dimensional representation might have to  
6 suffice. This is a matter for future research and comparative studies will be particularly important  
7 here.

## 8 USING THE NAVIGATION TOOLBOX: DECISION, PLANNING AND MEMORY 9 PROCESSES IN NAVIGATION

10 As well as self-localization (a sensory process) and orchestration of movement (a motor process),  
11 navigation requires decision-making, planning and memory, because there may be more than one  
12 way to navigate to a goal, or more than one goal, or the usual route to a goal may be blocked. In  
13 cognitive science, planning is usually conceptualized as searching for a path (i.e., a solution) in a  
14 problem space. A problem space is a mental representation of the problem containing knowledge of  
15 the initial state and goal state as well as possible intermediate states. The discussion below centers  
16 on the questions of how to define decision making and planning in the context of animal navigation.  
17 We consider these processes in light of the contributions made by elements in the navigation  
18 toolbox.

### 19 **Decision-making vs. planning**

20 It is useful to distinguish between decision-making and planning, although these are often conflated  
21 in discussion. Decision-making can be defined as choosing between alternative options, and,  
22 depending on the exact definition, may not require any form of internal representation at its simplest  
23 level (*for more detailed discussions on definitions of decision making, cf. Group report of Group 2,*  
24 *this Volume*). Decision-making therefore could, in principle, be supported by simple processes in  
25 Levels 1 and 2 of the navigation toolbox. By contrast, planning occurs if this choice is informed by  
26 simulated future states of the system. In the context of navigation, this means that an animal has to  
27 form expectations about future pay-off if it makes a particular spatial choice. At its most  
28 sophisticated level, navigational planning could potentially involve expectation or simulation of  
29 future *location*. The operation of such simulations could be said to involve recruitment of spatial  
30 constructs (Level 3), e.g., of a map-like representation – the cognitive map – and the question of  
31 whether non-human animals can do this is so far unresolved (but see Menzel, this volume). Below,

1 we discuss what kinds of navigational decision-making could take place without the need for a map,  
2 and what kinds would need true map-dependent planning.

### 3 **Mapless navigational choices**

4 Many quite sophisticated navigational behaviors can be orchestrated without the need for activation  
5 of a cognitive map. Navigating along a well known route, for example, requires choosing between  
6 different options at intersection or choice points. These choices, however, can be informed solely by  
7 recognition-triggered responses or servomechanisms, mechanisms that do not require reference to a  
8 planning process as discussed here, nor to any kind of map-based representation. Navigation along a  
9 route can therefore be explained by only assuming spatial primitives (i.e. Level 2 of the navigation  
10 toolbox, see also “The concept of a cognitive map”) such as landmarks or panoramas to identify a  
11 specific choice point, together with an associated local heading to inform about the required  
12 movement direction. In the context of this discussion it is important to stress that such choices can  
13 therefore be explained without internal simulations of future states and as such, they constitute  
14 decision-making but not necessarily planning. When these decisions are automatic and not  
15 influenced by any representation of a goal, they are said to be *habits*.

16 Planning, in contrast, requires goal directed actions. Much of the traditional support for the  
17 distinction between habits and goal-directed actions discussed by Dickinson (this volume) comes  
18 from studies of rats in mazes and runways. Habits continue automatically even when their outcome  
19 is devalued, whereas goal directed behavior is sensitive to the value of its outcome. For example, if  
20 the animal is satiated on the food that it will find at the end of its trip, goal-directedness would mean  
21 not setting out, or setting out in search of a different goal. Good evidence that some small-scale  
22 spatial behavior has this property has been obtained in laboratory studies with a few species  
23 (Dickinson, this volume). To what extent does behavior of other species in more naturalistic spatial  
24 tasks provide evidence that it is goal-directed in the same sense? The behavior of honeybees, which  
25 routinely travel among multiple goals in a flexible way indicates that bees choose to fly either along  
26 novel shortcuts to one of the goals or to apply the memory for a flight direction that would have  
27 taken them to the intended goal if they had not been transported to an unexpected location.  
28 Honeybees also choose between the information they receive from dance communication and their  
29 own experience from former foraging flights. After they have made such a decision they can correct  
30 themselves if the outcome did not meet the expectations, and fly along a novel shortcut to the other  
31 location, a behavior that meets our definition of planning (see also Menzel, this volume, who  
32 interprets these findings as support for planning in relation to a cognitive map).

1 **Navigational planning requiring a cognitive map**

2 What are experimental paradigms in animal navigation research that address planning processes  
3 requiring a cognitive map? It is generally agreed that to confirm the operation of a cognitive map, it  
4 is necessary to demonstrate behavioral planning that has a spatial component: for example, showing  
5 that an animal can compute a novel shortest-path route to a goal.

6 An example of the minimal test of map-based planning is a route-planning experiment in vervet  
7 monkeys (Gallistel and Cramer 1996) in which baited locations were arranged in a diamond shape.  
8 When starting from the lower corner, the shortest possible path depends on whether the animals are  
9 required to return to the start. The most efficient path to the upper corner is a zigzag route. If,  
10 however, a monkey intended to return to the starting position, because it was baited after the  
11 monkey left it, a different route is optimal, resembling a diamond in this travelling salesman task.  
12 The choice at one of the baited locations was reportedly influenced in a flexible way by options that  
13 were present only later in the navigation task (i.e. the absence or presence of a food reward at the  
14 start location). In other words, the animals used memory of the options and information about their  
15 current state to take different paths according to the circumstances (for a related paradigm in  
16 humans, see Wiener et al, 2008).

17 Experiments like these certainly seem suggestive of the operation of map-like planning processes.  
18 However, in situations requiring training about each possible path, as in many experiments on small  
19 spatial scales (such as in the experiments described above), it seems difficult to provide cognitive-  
20 map like knowledge without conditional discrimination training, e.g., that in the presence of cue A,  
21 path A is the most profitable, in the presence of cue B, path B is, and so on. If the animal then  
22 chooses appropriately depending on whether A or B is present at the start, one need not assume it is  
23 planning. Because Gallistel and Cramer did not describe how their monkeys were trained, their  
24 experiment is potentially subject to this objection.

25 Experiments like these, in which animals can be shown to make decisions informed by activation of  
26 internal spatial representations, will be needed to demonstrate the operation of cognitive maps  
27 convincingly. The difficulty is that such demonstrations must take place in a single probe trial,  
28 because from the second trial onwards, rapidly acquired associative reinforcement processes could,  
29 in principle, explain successful navigation. However, one-trial processing is difficult to show in  
30 animals, because novelty responses often override their goal-directed inclinations on the first probe  
31 trial. Thus the question of whether non-human animals use map-based planning in navigation is still  
32 not fully resolved.

1 An alternative approach is to observe internal cognitive representations directly, and indeed, some  
2 neurobiological studies are beginning to provide evidence suggestive of spatial simulation  
3 processes. Van der Meer and Redish (van der Meer & Redish, 2009, 2010) recently provided  
4 evidence from electrophysiological experiments investigating decision making and planning in  
5 navigating rats. The animals were trained to run loops on an elevated track in order to receive food  
6 reward. Between sessions, the rewarded side is varied such that at the beginning of each session rats  
7 were uncertain about the correct choice. During this period of relative uncertainty, rats paused  
8 longer at the critical choice points than at other choice points. Moreover, while pausing at the  
9 choice points, sequential activation of place cells with place fields around the choice point may be  
10 observed (Johnson and Redish, 2007). Van der Meer and Redish interpret these findings as rats  
11 representing future locations – i.e. simulating the outcome of a spatial decision – which is a crucial  
12 aspect of spatial planning. The rats' behavior here seems to be an example of the classic  
13 phenomenon of “vicarious trial and error” (VTE), in which animals spend time sampling the cues  
14 associated with the options in a difficult discrimination. As discussed in the chapter by Group 2, one  
15 criterion for true decision-making is that the latency to choose between options is greater than that  
16 to accept either one alone. Evidence for behavioral and/or neurological “VTE” suggest that  
17 observations of spatial behavior may provide evidence for decision making by this criterion.

18 Because of the difficulties of convincingly demonstrating cognitive mapping in small-scale  
19 laboratory settings, it has been suggested that navigation experiments in large scale spaces such as  
20 the animal's natural habitat (or a city-like environment in the human case) may be a more promising  
21 arena for collecting planning relevant data. Wiener and colleagues (Wiener & Mallot, 2003; Wiener  
22 et al., 2004), for example, used large scale virtual environments to investigate route planning  
23 behavior in humans. They demonstrated that the hierarchical organization of spatial memory  
24 influenced participants' route choice behavior and proposed a planning mechanism that uses spatial  
25 information at different levels of detail simultaneously. Analogous data might in principle be  
26 obtained from observations of how the paths animals take through their familiar home ranges  
27 change across days and seasons. Short-term changes in routes may appear to reflect planning, for  
28 instance to visit certain kinds of trees when their fruits are available. However, it may be difficult to  
29 infer anything about spatial knowledge and plans from such data, typically gathered without  
30 experimentally manipulating the animals' knowledge or goals (see Janson and Byrne, 2007).

31 In summary, then, one of the challenges for future navigation research is to develop controlled  
32 experiments to investigate spatial planning. According to the definition introduced above, planning  
33 requires the animal to form internal representations of simulated future states, given a particular

1 movement decision scenario. Spatial (i.e., map-based) planning requires, furthermore, that these  
2 simulated states incorporate spatial information, as shown, for example, in the ability to calculate  
3 shortest or least-effort paths, or to find novel detours that reveal a knowledge about the spatial  
4 relations of connected spaces. One possible way to demonstrate that animals/humans do, in fact,  
5 form such representations might be to demonstrate behavioral or physiological responses to the  
6 violation of their expectations (which may be conceptualized as “surprise”). An alternative  
7 approach, which is just beginning, is to observe the underlying neural processes directly. It may be  
8 easier to see future simulations (sometimes called “preplay”) in neural activity, although  
9 interventional studies would be needed to show that these processes are causally related to  
10 navigational behavior. Emerging technologies, such as optogenetic manipulation of neural circuits,  
11 will be very exciting in this regard.

## 12 **CONCLUDING REMARKS AND FUTURE DIRECTIONS**

13 This chapter has reviewed the current status of animal navigation research, focusing on overarching  
14 principles that arise independent of a given animal substrate. Comparing across a range of species  
15 whose navigational competence ranges from simple to sophisticated, we note that complex and  
16 more phylogenetically recent abilities appear to be synthesized from simple, phylogenetically older  
17 ones. Using this observation as a starting point, we have loosely organized the panoply of  
18 navigational behaviors into a hierarchical framework that we call the navigation toolbox, which is a  
19 collection of processes that can support, either alone or collectively, navigational behaviors of  
20 varying complexity. This collection is organized such that elements in higher levels are synthesized  
21 from elements in lower levels, acquiring new semantic content in the process. We argue that it is  
22 this ability to integrate across sensory modalities and semantic classes, to generate semantically new  
23 information (such as “position”) that expanded during brain evolution. It reaches a peak in the  
24 human ability to represent spatial information symbolically, using language and mathematics,  
25 deriving entirely new semantic content in the process (e.g., multidimensional space, non-Euclidean  
26 space, complex space).

27 The task now, in comparative cognition, is twofold. First, at the level of individual taxa we need to  
28 know how a given element in the navigation toolbox is implemented: in route-following or beacon  
29 homing, for example, what sensory modalities, and what spatial primitives, are recruited to enable  
30 decision-making? Second, more broadly, we need to know the underlying neural principles behind  
31 certain types of spatial computation. For example, how does the brain do “trigonometry”, and is this  
32 process the same across all taxa or have multiple solutions evolved independently? And finally,

1 there remains the as-yet-unanswered question of whether any animals other than humans make use  
2 of the complex internal representation of spatial relations that is sometimes called a “cognitive  
3 map”, and even to what extent humans do so. This will require a combination of both more  
4 sophisticated behavioral experiments, controlling for the possibly occult operation of more  
5 primitive processes, and also neurobiological studies that can probe the existence of putative  
6 simulation phenomena such as neural sequence “preplay”. Answering these questions  
7 unequivocally will require the ability to undertake sophisticated interventional experiments to  
8 disable the processes in question and test hypotheses about spatial representation.

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