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Edited by Francine L. Dolins and Robert W. Mitchell
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Linking spatial cognition and spatial perception

> A boundary is that which is an extremity of anything.
>
> Euclid's *Elements*: Book 1

Space is not a "final frontier" despite the familiar phrase heard on television. In fact, a frontier depicts a barrier of sorts, a wall, the opposite of space. Without borders, space, as in Gertrude Stein's (1937, p. 289) statement, can be defined as "*there is no there there*." That is, space is defined only by what encloses it, the boundaries imposed on space. Thus, the study of organisms that move through space is the study of their perception of boundaries and landmarks, and what lies within those distances.

Boundaries can be physically continuous or a few discrete points (landmarks). However, even discrete points can be perceived in gestalt-like fashion as continuous, as encompassing or imposing a shape on space; the perception is often relative to visual overview, near or far (Poucet, 1993). Knowledge of boundaries and landmarks is not trivial in survival terms. Localizing route and place are essential for fulfilling adaptive behaviors, such as goal-directed navigation to sleeping and foraging sites, locating mates, and avoiding predators. The capacity for spatial perception and cognition underlies the necessity for spatial updating and referencing of past and present locations during movement.

Navigating organisms respond to actual space through behavioral strategies based on what they perceive as space. There may not exist a one-to-one correspondence between their internal representation and the physical world. Representations encoding the distance, angle and direction between perceived landmarks may be skewed subjectively, where the absolute symmetry and metric organization required

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for Euclidean spatial understanding is not necessarily maintained. The question is, how do these intermediary internal representations or even external, two-dimensional symbolic representations of space (e.g., map-form) function to generate spatial behavior (Golledge, 1999)? Perception and use of boundary and landmark information reflect the experience, knowledge, goals and motivation of the organism. Thus, we can examine spatial perception and cognition according to how spatial knowledge is accrued, accounting for: (1) the attention and perception of salient spatial information from which subsequent strategies emerge; (2) changes during lifespan development and from experience affecting the processes of attention and perception of spatial information and subsequent spatial strategies; and (3) the emergence of spatial strategies and behaviors in response to environmental information derived from understanding the body's location and movement in space.

Spatial Cognition, Spatial Perception: Mapping the Self and Space examines the topic of spatial cognition from two different yet closely related perspectives: the encoding in representations of both external and internally perceived stimuli, and subsequently their effects on behavior. In this volume we integrate the study of spatial perception and spatial cognition to more fully understand how visual and other types of perception incorporate spatial knowledge at multiple levels, enabling complex spatial strategies and behaviors to emerge. The emergence of these behaviors involves the perception and encoding of spatial boundaries and location of objects relationally, as well as the body's relationship to those boundaries and landmarks in space, that is, shifts between egocentric and non-egocentric perspectives of the environment. Methodologically, we will examine the study of spatial perception and cognition from behavioral, cognitive, developmental, evolutionary, neuroanatomical, and neurophysiological perspectives.

What are the origins of spatial behavior? We address this question by examining the processes of deriving externally perceived stimuli (e.g., landmarks and sensory perception of environmental stimuli) in relation to internally generated perceptions (e.g., kinesthesis, visual imagery, etc.), translated into internal representations. Our goal is to elucidate what spatial-perceptual information derived from the physical movement and placement of the self within the environment informs and relates to cognitively understanding the surrounding environment itself. A broad question arising from this idea is how spatial cognition, and perhaps all cognition, might be derived from and/or influenced by perceptual processes. To this end, there is an

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in-depth examination in this book of representations of the self and of cross-modal spatial information (e.g., between vision and kinesthesis).

In this volume we examine the components of spatial cognition, exploring the bases of internal spatial representations, what kinds of information populate different kinds of representations, and how these representations determine behavior and cognitive abilities and strategies. We also explore the foundations of the self and the body underlying the development of spatial understanding and skills through how these are mapped onto representations of the body and the body in space.

We have organized this book into conceptual divisions to present a scope of the current body of research and theoretical debates in how spatial knowledge is accrued, as well as to identify questions for future research. The divisions of this volume address the five following topic areas:

1. What do animals know and how do they represent external space?
2. Perception and memory of landmarks: implications for spatial cognition and behavior.
3. Evolutionary perspectives of cognitive capacities in spatial perception and object recognition.
4. Does mapping of the body generate understanding of external space?
5. Comparisons of human and non-human primate spatial cognitive abilities.

Contributing authors discuss within their chapters spatial cognition and perception from multiple perspectives, for example, the perception of extant boundaries and landmarks and how these influence behavior and cognitive processes; how encoded spatial information is organized and applied to navigate toward specific goals; and the organism's understanding of external space as defined by understanding of the body's movement and position in space.

Part I examines the kinds of information required for animals when navigating or solving spatial problems. Chapter 2 by Mitchell and Dolins discusses the historical trajectory of spatial cognitive and perceptual research. Chapter 3 by Cheng elucidates diverse models of spatial cognition and details underlying commonalities between spatial and other forms of cognition, between spatial cognition and perception. It addresses the question of where spatial cognition falls within cognition as a learning and encoding process overall and what

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is unique about spatial learning and cognition. A discussion of the geometry of space and the use of discrete or grouped landmarks forms the basis of the implications for spatial cognitive abilities in animals. Chapter 4 by Emil Menzel introduces some of the major questions of the book and identifies important topics related to spatial cognition and perception, discussing major philosophical questions raised by attempting to understand other species' spatial knowledge and subsequent differences in spatial strategies and navigation.

The translation from what is "actual" in the physical world to what is "perceived" is fundamental to cognitive processing and encoding in representations. From a strict Euclidean framework, perceptual and spatial information from the external world would necessarily be encoded veridically. However, it is clear that our perceptions, and therefore our representations of space, are skewed toward subjectivity (Golledge, 1999). However, a system coding for spatial relations of the environmental features must by necessity have evolved for relative spatial accuracy, as a system consistently coding spatial misperceptions would have been selected against (Rozin, 1976). The question is, how accurately and how much of the veridical world do we actually perceive and encode? How is this difference between accuracy and subjectivity negotiated in perceptual, cognitive, and behavioral outcomes?

In Part II, the initial chapter discusses the use of landmarks, geometry of space and vision in navigation (see Chapter 5). Specifically, an argument is presented for understanding spatial learning and representations through differentiating the geometric encoding of spatial information compared to that of discrete elements in the environment. In Chapter 5, Thinus-Blanc *et al.* present distinctions in performance of species for the capacity to be able to abstractly process spatial information, i.e., processing geometric and local cues, to compute novel information about their environment.

Environments afford animals perceptual information dependent on their species-specific sensory and learning capabilities and ecological and dietary requirements (see Chapters 7 and 9, this volume; also Gibson, 1986; Greeno, 1994; Wells, 2002). It is essential for most animals to forage for food, find mates, and locate secure places for rest and sleep. The environment can provide numerous potential cues to achieve these goals. Small South American tamarin monkeys, for example, rely on "visual, olfactory, and auditory cues (i.e., landmarks, smell of fruits or flowers, calls of birds or other primates) [which] undoubtedly play a role in spatial orientation and the exploitation of

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nearby feeding trees" (Garber, 1989, p. 212). The role of experience permits "learning associated with food acquisition and sensitivity to changes in the location, orientation, and presence of objects in the environment" (Garber, 1989, p. 212).

In examining the navigational strategies of an animal very different from primates, Collett and Graham (see Chapter 6) present experimental and ecological evidence of ant species' recognition and knowledge of routes and local environmental information. What is fascinating, as illustrated in this chapter, is that the spatial learning mechanisms animals rely upon are based on some fundamentally shared principles, such as route following using path integration and based on a sequence of perceptual cues. In the case of some ant species, these are often pheromone/olfactory-based, but can also be visual (e.g., in the case of the giant tropical ant). By distinguishing between innate mechanisms and learning processes, Collett and Graham address questions about how the ants learn routes, what information these routes are based on, and how that information is used in navigation.

In Chapter 7, differences in landmark use and memory in small-scale and large-scale space across multiple species (e.g., birds, deer, bees, etc.) are compared, providing a comprehensive overview of the types of spatial strategies used by animals under free-ranging conditions (also see Chapter 4). Spatial learning in small- and large-scale space involves distinguishing cues that are available short- and long-term, near and far. Short-term cues such as changes in the color of ripening fruit or placement of rocks or sticks may provide more precise spatial information in small-scale, local space (Poucet, 1993). However, as these are not stable over time, global, distal cues such as trees, streams and rocky outcroppings that are relatively permanent may provide more dependable although less precise spatial information in large-scale space (see Chapters 3, 6, 8 and 9, this volume; also, Spetch and Edwards, 1988; Garber and Dolins, 1996). In a prescient (1949) statement, D. O. Hebb wrote, "Now it happens that the visual activity of lower species is dominated by the perception of place. This turns out experimentally to mean a dominance of cues from remote objects instead of near ones; and remote objects provide the most stable and constant stimulation of the animal's environment" (p. 47).

Chapters 8 and 9 address questions about (1) whether animals' spatial cognitive and behavioral strategies differ when they are afforded a simultaneous overview of the entire array of salient spatial-perceptual information as compared to a subset of landmarks; (2) how

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spatial memory functions in differing spatial contexts (e.g., small or large, simple, complex, etc); and (3) whether these strategies are parsed for emerging spatial behaviors from the same or different types of spatial representations.

Part III explores spatial perception, object recognition and emergent spatial strategies from evolutionary and neurophysiological perspectives. With objects as the basis of landmark arrays and spatial representations, these chapters examine how landmark information is organized and the functional and evolutionary importance of optimizing navigational and spatial behavior in relation to environmental context.

The question of how perceptual and cognitive representations of space are generated leads us to examine the way in which information is perceived and encoded, and what motivates an organism to explore its environment. One interpretation posits that as the physical world is a dynamic place, an organism's perceptual and cognitive processes have to adapt accordingly on an ongoing basis (Krechevsky, 1932; Tolman, 1948; Gibson, 1986). This presupposes that organisms are either active seekers or passive recipients of information, both consequences for developing animal's spatial behavior (see Chapters 21 and 23). The degree to which learning is active also has implications for understanding an organism's attention and response to internally-dervied input from kinesthesia and proprioception in combination with that from external environmentally-based information (see Chapters 3, 4, and 5).

Each of the four chapters in Part III reflects contributions from the authors' diverse disciplines. In Chapter 10, Wynn examines the evolution of modern human's visuo-spatial cognitive capacities necessary for recognizing constructed objects such as tools, and the combined cognitive and eye-hand coordination process required for creating these objects. Constructing objects such as tools requires use of egocentric and allocentric frames of reference by the individual creating the tool. Wynn discusses how object-centered spatial information about tools (and other objects), such as details of their size and shape, are linked to a perceptual frame of reference which includes the self and external stimuli. This information is typically perceived visually (Paillard, 1991) but can be also perceived by echolocation (see Chapter 12, this volume; Altringham, 1996; Price *et al.*, 2004) or haptic (tactile) perception (see Chapters 2 and 14). Haptic, auditory, as well as olfactory perceptions can translate into visual expectations that can be spatial, providing information of distance, angle and direction for localizing cues. These perceptual modalities provide bases that can be translated into behavioral

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strategies and offer animals means for understanding and taking action in the external world (see Chapter 12, this volume; also Garber and Dolins, 1996).

Species' perceptual modalities are constructed within the constraints of morphological and species-specific requirements and capabilities, and are often hierarchically organized in relation to the saliency of the perceptual cues (see Chapters 4 and 8, this volume; also Garber and Dolins, 1996). For instance, microchiropteran bat species as well as some birds (e.g., swiflets) navigate via echolocation and are therefore highly dependent upon their sense of hearing, while others such as the Megachiroptera rely principally on sight and smell (for bats, see Altringham, 1996; for birds, see Price *et al.*, 2004; see Chapter 12 on cetacean echolocation). Some sensory perceptual systems will be more relevant than others in allowing an animal to respond behaviorally to environmental contexts. For example, while rats use vestibular, auditory, olfactory and tactile sensory information to navigate, rats are highly reliant upon visual information even with their limited visual acuity (see Chapter 23, this volume; Zoladek and Roberts, 1978; Leonard and McNaughton, 1990). Visual information permits distance estimations whereas tactile and olfactory information enable only non-localized gradient estimations to be performed (see Chapter 6). There is also an inherent hierarchy and interplay of information derived internally and externally about space. Visual information and kinesthesis usually work in tandem, but can also be conflicting. The result leads to a prioritization in attentional capacities (see Chapter 15).

Both the integration of sensory systems for localization of cues and navigation in a species relying on perception of a different kind than that used by humans (i.e., cetaceans) is discussed in Chapter 12. For terrestrial animals, a cue may be a single distal landmark, such as the sun, or multiple landmarks, as in a constellation of stars or a mountain range. Across species and environments, cues can be obscured or hidden from direct perception. Learning about obvious or hidden cues involves generating a landmark-to-desired-object representation. Tasks evaluating understanding of object permanence in relation to cue/object localization can be used to show development of different forms of spatial learning. In this chapter, object permanence and cue localization are also discussed in relation to the hierarchy of some sensory systems over others for different species.

Areas of neural processing of spatial information are distributed corresponding to the type of spatial responses employed by an animal. Evidence shows that the hippocampus and related structures are

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selectively activated when animals are engaged in different types of spatial strategies (Holdstock *et al.*, 1999; Maguire *et al.*, 2000). In rats the CA1 of the hippocampus is more active for a response strategy, whereas CA3 and dentate gyrus are activated for a place strategy (Miranda *et al.*, 2005). Spatial experience also alters the neural areas responsible for processing spatial challenges encountered in the environment. Maguire *et al.* (2000) found that London taxi drivers with extensive navigational experience had a significantly larger posterior hippocampus than non-taxi driver controls. Moreover, the navigational performance of experienced taxi drivers was more efficient and optimal around a virtual London, indicating that experience modifies the hippocampal region responsible for place learning, resulting in greater behavioral flexibility and enhanced navigational skills and spatial memory. The authors write that, “differential changes in posterior and anterior hippocampus may represent two separate processes . . . our findings reflect an overall internal reorganization of hippocampal circuitry in response to a need to store an increasingly detailed spatial representation, where changes in one hippocampal region are very likely to affect others” (p. 4402).

The role of the hippocampus in relational as well as associative learning observed in the spatial domain extends more generally (Hartley *et al.*, 2003). Animals and humans with hippocampal damage show selective deficits in both the spatial and nonspatial domains in the ability to form associations between previously unrelated items or between items and context, even though the ability to learn single items in isolation is relatively spared (Gaffan *et al.*, 2002; Henke *et al.*, 2003). In addition, the processing in the hippocampus also incorporates temporal information into memory, thus contributing to the formation of memories of the sequence of events, a foundation for relational learning (Fortin *et al.*, 2002). Evidence from a radial maze task suggests that damage to the hippocampus impairs an animal’s ability for sequential spatial learning (DeCotaeu and Kesner, 2000). For example, rats with hippocampal damage were selectively impaired on learning sequential orderings of odors despite their intact ability to recognize recently encountered odors (Dusek and Eichenbaum, 1997; see also Alvarez *et al.*, 2002).

Forming associations of objects and events in spatial and temporal contexts are two component abilities of relational learning. While lesions to the hippocampus are known to impair relational learning in spatial tasks (e.g., Aggleton and Brown, 2005), evidence also indicates that the hippocampus plays an important role in the

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formation of episodic memory. Episodic memory can be considered a foundation for relational memory in that it invokes associations of objects and events in spatial and temporal contexts, linking them into a large-scale framework that allows for inferences and generalizations from organized relations to new situations (Eichenbaum, 2004). Consistent with this idea, damage to the hippocampus has been shown to impair function of episodic memory despite largely spared semantic memory and simple recognition memory, which does not involve associations (Vargha-Khadem *et al.*, 1997; Holdstock *et al.*, 2004). In a study of sequential learning, hippocampal-damaged rats failed to make transitive inferences applicable to normal novel stimuli, which indicates that episodic relational memory is also impaired due to hippocampal lesions (Dusek and Eichenbaum, 1997).

In rats trained to perform identical olfactory recognition tasks in different spatial locations, the neural activity of most of the hippocampal cells was selective to particular combinations of spatial locations and nonspatial events (e.g., perceptual, behavioral, cognitive) (Wood *et al.*, 1999). The evidence suggests that the hippocampus is capable of encoding discrete episodes at the same time as representing features common/overlapping in different episodes and environments.

Thus, the hippocampus' role in associative, sequential and relational memory in the spatial domain seems to generalize to memory in general (Eichenbaum, 2000a). In producing more complex spatial strategies, the hippocampus is crucial for encoding relational information and for place learning. The hippocampus plays a role in forming associations between spatially present stimuli and the incorporation of temporal information in relational episodic memory. However, although accumulating evidence suggests the involvement of the hippocampus in general episodic memory, the precise degree to which it makes contributions is still not clear (Burgess *et al.*, 2002; Eichenbaum, 2004). For instance, Kumaran and Maguire (2005) showed that the hippocampus was selectively activated by a spatial navigation task but not by an equivalent navigation task in the nonspatial, social domain (see also Kumaran and Maguire, 2006). Nevertheless, the hippocampus does provide links between discrete objects and events in their spatial and temporal contexts. These links aid in the unification of spatial–temporal information into a relational representation in the spatial domain, fundamental for coherent and goal-oriented complex spatial behaviors to be performed.

In their discussion of the significant role of the hippocampus in spatial learning, Rehbein *et al.* (Chapter 11) present evidence based on investigations of nonhuman primates' spatial processing from a comparative perspective. Recent studies have added layers of understanding about the specificity of neural processing pathways for spatial learning, spatial cognition, and memory in various cortical regions and, in particular, in the hippocampus (e.g., Eichenbaum, 2000b; Ekstrom *et al.*, 2003; Maguire *et al.*, 2003). Processing of spatial information and generation of spatial representations in neuroanatomical structures appears to be specific to the type of spatial learning, with each area processing and contributing input for different types of spatial behaviors, such as in route, place or response learning. For example, in response to dynamic changes in an environment, separate neural pathways are activated when an individual plans a new route than when following one previously known (Spiers and Maguire, 2006).

Using neural processing as the basis for robotic spatial cognition, Arleo and Rondi-Reig (Chapter 13) present an excellent review and highlight the integration of sensory processes comparing real and artificial organisms in generating navigational strategies. These authors provide evidence of spatial learning in neuro-mimetic robots in a series of experiments in which visual cues were constant while the route to the goal was randomized within the familiar environment. They demonstrate that neuro-mimetic robots learned to distinguish between idiothetic and allothetic signals, thereby computing novel allocentric routes to known locations. Additional experiments with variations on origination points and landmarks are also discussed, with the implication of disorientation emerging from the de-coupling of the idiothetic and allothetic signals, interrupting the mapped representation of these landmark relations. The results from the neuro-mimetic robots are compared with biological models and ethological and neurophysiological evidence.

Part IV presents research and discussion about how humans and animals use their own interpretation of bodily space to understand their position in space and body movements (internal stimulus mapping). A relevant question is whether or not an individual's internal experience of their own body movements provides a developmental basis for their ability to learn about external space. This question is explored in developmental contexts in the next and final section of the book.

Gibson (1986) proposed that perception is not created through an individual's static picture of the environment and translated through the construct of an abstract notion of space; instead the environment is where the individual dynamically samples points in its world to create