MIDDLE-SCALE NAVIGATION: THE VERTEBRATE CASE

DAVID F. SHERRY

Department of Psychology, University of Western Ontario, London, Ontario, Canada N6A 5C2

Few ideas have had a greater impact on the study of navigation at the middle scale than the theory of the cognitive map. As papers in this section show, current views of the cognitive map range from complete rejection of the idea (Bennett, 1996) to new proposals for the behavioural and neural bases of the cognitive map (Gallistel and Cramer, 1996; McNaughton *et al.* 1996). The papers in this section also make it clear that path integration has taken centre stage in theorizing about navigation at the middle scale. Path integration is the use of information generated by locomotion to determine the current distance and direction to the origin of the path. Etienne (1980) provided one of the first experimental demonstrations of path integration by a vertebrate, and in this section Etienne *et al.* (1996) describe recent research with animals and humans on the interaction between path integration and landmark information. Path integration is also the fundamental means of navigation in the model described by Gallistel and Cramer (1996). McNaughton *et al.* (1996) suggest that the neural basis of path integration is found in the place cells and head direction cells of the hippocampus and associated brain regions.

The theory of the cognitive map, developed by O'Keefe and Nadel (1978) from an earlier more informal idea of Tolman's (1948), proposed that animals have at their disposal a rich representation of the spatial relationships among places in their environment. This representation goes beyond learned routes and responses to landmarks to include inferred relationships among places. O'Keefe and Nadel (1978), in addition, placed the neural implementation of the cognitive map in the hippocampus.

One test of whether an animal possessed a cognitive map was whether it could derive from its map a novel short cut: the most direct route between places that were familiar but had never been visited successively. Many published experiments show the use of novel short cuts, but Bennett (1996) makes the strong claim that none of these is unequivocal evidence for a cognitive map. Path integration and orientation to familiar landmarks have never been satisfactorily eliminated as alternative explanations, according to Bennett (1996).

Because there are alternative explanations for the data used to demonstrate the use of a cognitive map, and because the idea has come to be used in ways that are contradictory and sometimes untestable, Bennett (1996) concludes that it is time to abandon the cognitive map and to move on to more precise models of the representation of space.

One such model is the proposal by Gallistel and Cramer (1996) that cognitive maps consist of landmarks placed on a geocentric frame of reference by vector addition. Addition of a geocentric vector, giving the current location of the animal, to an egocentric vector, giving the location of a landmark relative to the animal, yields a geocentric vector for the landmark. In this way, maps of the geocentric positions of landmarks can be assembled. Animals determine their geocentric position by path integration and take positional fixes on known landmarks, according to Gallistel and Cramer (1996), to deal with the error accumulation of path integration.

O'Keefe and Nadel (1978) and Tolman (1948) both stressed the contrast between the cognitive map and navigation by learned responses to stimuli. Biegler and Morris (1996) describe experiments that explicitly compare cognitive mapping with associative models of landmark learning. Increasing the contingency between a landmark and a goal, while decreasing the contingency between context and a goal, would be expected to increase associative learning. These procedures, in fact, reduce landmark learning according to Biegler and Morris (1996).

Finally, Galea *et al.* (1996) and Sherry and Duff (1996) describe navigation at the middle scale in two rather different ecological contexts that illustrate the diversity of behavioural and neural processes of navigation by vertebrates. Sex differences in navigation have been described in a number of rodents, usually favouring males and sometimes appearing and disappearing seasonally. Galea *et al.* (1996) examine the relationship between navigational ability, development and seasonal reproductive behaviour. Navigation in the water maze is adversely affected by an increase in oestradiol in female deer mice, while pre-natal exposure to androgens improves navigation in both male and female meadow voles. Identifying the neural targets and the cognitive effects of these hormonal manipulations may help to specify the mechanisms of navigation used by rodents.

Sherry and Duff (1996) describe navigation by food-storing birds that remember the locations of large numbers of concealed food caches. These birds use visual landmarks and the sun compass for navigation, and show specializations of the hippocampus that are not found in non-storing birds. Lesions of the hippocampus disrupt cache retrieval in food-storing birds and produce dissociations between spatial and non-spatial cognitive abilities. Understanding how animals outside the laboratory integrate the representation of landmarks into a frame of reference, such as that provided by the sun compass, may provide further clues to the mechanisms of navigation used by vertebrates.

References

Bennett, A. T. D. (1996). Assessing models of spatial memory: the cognitive map. *J. exp. Biol.* **199**, 219–224.

Biegler, R. and Morris, R. G. M. (1996). Landmark stability: studies exploring whether the perceived stability of the environment influences spatial representation. *J. exp. Biol.* **199**, 187–193.

Etienne, A. S. (1980). The orientation of the golden hamster to its nest-site after elimination of various sensory cues. *Experientia* **36**, 1048–1050.

Etienne, A. S., Maurer, R. and Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *J. exp. Biol.* **199**, 201–209.

Galea, L. A. M., Kavaliers, M. and Ossenkopp, K.-P. (1996). Sexually dimorphic spatial learning in meadow voles *Microtus pennsylvanicus* and deer mice *Peromyscus maniculatus. J. exp. Biol.* **199**, 195–200.

Gallistel, C. R. and Cramer, A. E. (1996). Computations on metric maps in mammals: getting oriented and choosing a multi-destination route. *J. exp. Biol.* **199**, 211–217.

McNaughton, B. L., Barnes, C. A., Gerrard, J. L., Gothard, K., Jung, M. W., Knierim, J. J., Kudrimoti, H., Qin, Y., Skaggs, W. E., Suster, M. and Weaver, K. L. (1996). Deciphering the hippocampal polyglot: the hippocampus as a path integration system. *J. exp. Biol.* **199**, 173–185.

O'Keefe, J. and Nadel, L. (1978). *The Hippocampus as a Cognitive Map.* Oxford: Oxford University Press.

Sherry, D. F. and Duff, S. J. (1996). Behavioural and neural bases of navigation in food-storing birds. *J. exp. Biol.* **199**, 165–171.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psych. Rev.* **55**, 189–208.