Available online at www.sciencedirect.com

SCIENCE DIRECT®

Behavioural Processes 68 (2005) 51–67

BEHAVIOURAL PROCESSES

www.elsevier.com/locate/behavproc

Route finding by rats in an open arena

Rebecca A. Reid[a], Alliston K. Reid[b,*]

[a] South Carolina Governor's School for Science and Mathematics and Wofford College, USA
[b] Department of Psychology, Wofford College, 429 N. Church Street, Spartanburg, SC 29303, USA

Received 11 August 2004; accepted 6 November 2004

Abstract

Rats were repeatedly exposed to an open arena containing two depletable food sources in a discrete-trials procedure. Their movement patterns were recorded and compared to adaptive foraging tactics such as minimizing distance or energy expenditure, thigmotaxis, and trail following. They were also compared to the predictions of the associative route-finder model of Reid and Staddon [Reid, A.K., Staddon, J.E.R., 1998. A dynamic route finder for the cognitive map. Psychol. Rev. 105 (3), 585–601]. We manipulated the presence/absence of food, goal cups, and a wooden runway to determine the influence of local and distal stimuli (visual, olfactory, and tactile) on movement patterns. Increased experience in the arena produced decreases in travel distance and time to the food sources. Local and distal stimuli influenced movement patterns in ways compatible with visual beacons and trail following. The route-finder model accurately predicted movement patterns except those that were influenced by local and distal stimuli. These results show how certain stimuli influence movement and provide a guide for the incorporation of local and distal stimuli in a future version of the dynamic route-finder model.

Keywords: Cognitive map; Computer simulation; Foraging; Generalization; Route; Spatial navigation

1. Introduction

In the last few decades, spatial navigation has stimulated substantial research, especially following O'Keefe and Nadel (1978) classic work proposing the hippocampus as a cognitive map. Biegler (2003) identifies three current approaches to the study of spatial navigation that have different assumptions and goals: (a) The ethological or adaptationist approach tends to concentrate on species-specific adaptations, whereas the (b) cognitive approach and the (c) associative approach aim to discover general principles underlying behavior. Biegler argues that the cognitive approach assumes that different species may perform qualitatively different types of computation during spatial navigation, whereas the associative approach generally assumes that the computations are only quantitatively different across species and task domains. The main goal of the current study was to contrast explanations of spatial foraging patterns based on species-specific adaptations

---

* Corresponding author. Tel.: +1 864 597 4642;
fax: +1 864 597 4649.
E-mail address: alliston.reid@wofford.edu (A.K. Reid).

0376-6357/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.beproc.2004.11.004

with the predictions of the Reid and Staddon (1998) associative route-finder model.

Reid and Staddon (1998) point out that spatial orientation has two logical parts, knowledge and action. Their route-finder model was designed to explain action — it was not intended to explain how the organism acquired spatial knowledge, or how the animal knows where it is. Nevertheless, most recent research in spatial navigation has centered on the mechanisms that permit the acquisition of spatial knowledge. Such knowledge includes learning the location of a goal in relation to landmarks or beacons (e.g., Benhamou and Poucet, 1998; Mackintosh, 2002; Poucet, 1993; Roberts and Pearce, 1998), computation of position based on path integration (e.g., Etienne, 2003; Gallistel, 1990; Wallace et al., 2003; Wehner and Srinivasan, 2003) or the geometric properties of the environment (e.g., Cheng, 1986), the creation of a cognitive map (e.g., O'Keefe and Nadel, 1978), and various other processes. The current debate about the existence of a cognitive map is centered on the knowledge that enables spatial orientation. For the interested reader, the various chapters in Jeffrey (2003), Healy (1998) and Wang and Spelke (2002) provide comprehensive overviews of the acquisition of spatial knowledge and discussions of the various systems or modules (including species-specific adaptations) involved in acquiring spatial knowledge.

The Reid and Staddon (1998) route-finder focuses on action — the means by which spatial knowledge is used to produce movement patterns, such as when animals forage for food in a well-learned environment. It simply assumes the existence of an orientation process sufficient to locate the animal in space. The underlying "map" could be quite detailed, or it could be rudimentary and incomplete, and it could change dynamically as the animal forages or encounters barriers. By "map" Reid and Staddon mean only that for every spatial location, there must be one and only one node (which will have a defined state) and adjacent locations in space would be represented by a connection between nodes. This model promises, "If you can provide certain details of the animal's knowledge of space, the model will show how the animal's history of reward and nonreward in that space will produce dynamic step-by-step movement patterns as the animal forages."

Just as systems and modules have been proposed for acquiring spatial knowledge (e.g., Cheng, 1986; Gallistel, 1990; Rodrigo, 2002; Wang and Spelke, 2002, 2003), modules have also been proposed for action. The most well-known approach, represented extensively in the ethology and adaptationist literature, is the assumption that different movement patterns represent different adaptive behavioral modules, or search tactics, that may combine to produce elaborate movement patterns. Examples of these tactics in rats are thigmotaxis, distance minimization, trail following, detour avoidance, central-place foraging, area-restricted (focal) search, and other win-shift or win-stay strategies compatible with the maximization of net rate of energy gain (e.g., Hoffman et al., 1999; Krebs and McCleery, 1984; Olton and Samuelson, 1976; Rodrigo, 2002; Stephens and Krebs, 1986; Timberlake et al., 1999). This conceptual approach has considerable appeal because these behavioral tactics are normally assumed to be independent of each other, yet they may be simultaneously expressed in many environments. It is easy to imagine evolutionary selection pressures that would favor or suppress each of these foraging strategies in a known environment, eventually resulting in highly adaptive foraging patterns. This conceptual approach implies that: (a) the separate behavioral modules may have evolved independently of one another; (b) they may represent the interactions of multiple motivational systems (such as foraging and predator avoidance); and (c) they may be influenced by different characteristics of the environment (such as distance, walls, trails, sounds, and odors).

Surprisingly, the Reid and Staddon (1998) route-finder model produces most of these behavioral tactics in a single one-parameter model, based on the well-known process of diffusion, without the need of additional modules. Their goal was to identify the most parsimonious mechanism that would generate movement patterns consistent with those observed in a variety of species in the open field and in mazes, such as area-restricted search, avoiding barriers, finding shortcuts, and radial maze behavior. Thus, their model fits squarely within the associative approach. Their dynamic model is based on stimulus generalization in which an elementary diffusion process produces a landscape of reward expectancy, and the simplest hill-climbing algorithm produces movement toward areas of higher expected reward (see Reid and Staddon, 1998; Staddon, 2001; Staddon and Reid, 1990 for additional details). Thus, the model has only two parts: the diffusion of reward expectancy along adjacent nodes