Journal of Theoretical Biology 263 (2010) 242–261

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Which coordinate system for modelling path integration?

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ARTICLE INFO

Article history:
Received 1 September 2009
Received in revised form
19 November 2009
Accepted 22 November 2009
Available online 3 December 2009

Keywords:
Navigation
Geocentric
Egocentric
Allothetic
Idiothetic

ABSTRACT

Path integration is a navigation strategy widely observed in nature where an animal maintains a running estimate, called the home vector, of its location during an excursion. Evidence suggests it is both ancient and ubiquitous in nature, and has been studied for over a century. In that time, canonical and neural network models have flourished, based on a wide range of assumptions, justifications and supporting data. Despite the importance of the phenomenon, consensus and unifying principles appear lacking. A fundamental issue is the neural representation of space needed for biological path integration. This paper presents a scheme to classify path integration systems on the basis of the way the home vector records and updates the spatial relationship between the animal and its home location. Four extended classes of coordinate systems are used to unify and review both canonical and neural network models of path integration, from the arthropod and mammalian literature. This scheme demonstrates analytical equivalence between models which may otherwise appear unrelated, and distinguishes between models which may superficially appear similar. A thorough analysis is carried out of the equational forms of important facets of path integration including updating, steering, searching and systematic errors, using each of the four coordinate systems. The type of available directional cue, namely allothetic or idiothetic, is also considered. It is shown that on balance, the class of home vectors which includes the geocentric Cartesian coordinate system, appears to be the most robust for biological systems. A key conclusion is that deducing computational structure from behavioural data alone will be difficult or impossible, at least in the absence of an analysis of random errors. Consequently it is likely that further theoretical insights into path integration will require an in-depth study of the effect of noise on the four classes of home vectors.

1. Introduction

Path integration (PI) (Mittelstaedt and Mittelstaedt, 1980; Mittelstaedt, 1983b) is a navigation strategy many animals are capable of using, including ants (Cheng et al., 2009; Müller and Wehner, 1988; Wehner and Srinivasan, 2003), bees (von Frisch, 1967), spiders (Moller and Görner, 1994), birds (von Saint Paul, 1982), crabs (Layne et al., 2003a, b; Zeil, 1998), rodents (Mittelstaedt and Mittelstaedt, 1980) and humans (Mittelstaedt and Glasauer, 1991), whereby the animal maintains an estimate of its location as it moves around, by integrating its velocity over time. The animal's estimate of its location is referred to as the home vector (HV), since it can be thought of as a vector connecting the animal's current location to the starting point of its journey, and allows it to return directly to the starting point. For reviews introducing this behaviour see Collett and Collett (2000), Gallistel (1990), Redish (1999), and Wehner and Srinivasan (2003).

This paper undertakes a systematic comparison of several alternative ways of describing PI, based on the coordinate system in which the HV is expressed to define the spatial relationship between the animal and its home location. Previous mathematical models of PI have generally chosen a single coordinate system or frame of reference, often on the basis of incomplete or implicit assumptions. The only previous attempt to translate models between the alternative coordinate systems (Benhamou and Séguinot, 1995) made a weakly justified assumption that PI should only be thought of using one specific reference frame. To complicate matters, most published neural network models of PI were not defined using the standard coordinate nomenclature. This has resulted in a wide range of seemingly inconsistent, even contradictory opinions concerning the necessary properties of a biological PI system. At various times, some version of each of the standard coordinate systems have been proposed to be the foundation of the correct model of PI in the arthropod literature.

In systematically comparing multiple coordinate systems, we explore and attempt to resolve several important questions. For example, the HV, being a vector, is suggestive of a polar representation. On the other hand, once near home, polar

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doi:10.1016/j.jtbi.2009.11.021

representations have significant drawbacks. An egocentric representation seems most intuitive for heading home. However, the egocentric position of home moves with every turn, even without displacement. Are these types of issues peculiar to specific coordinate systems? Do they persist following coordinate transforms? Can all major aspects of PI be represented equivalently in all coordinates systems? Are there theoretical clues as to which might be favoured biologically? It is important to recognise at the outset that there are intervening steps between the maintenance of a HV and its utilisation for finding home. For example, the HV could theoretically be represented in a geocentric framework (for definitions see below) but the motor commands needed to follow that HV may be more suitably transformed into an egocentric framework. This and related issues will be discussed later.

This paper covers the four standard coordinate systems within which PI has previously been modelled, and provides equations for translating HV values between them. It also introduces a scheme for classifying PI models into four extended families of coordinate systems for those models which do not easily fit into any of the four standard systems, allowing the classification of virtually any conceivable PI system. Based on the analytical results, a critique is given of the usage of particular coordinate systems in existing models. Equational models of biologically important aspects of PI are introduced in all four of the standard coordinate systems. These include HV updating, steering, searching, and systematic errors. This forms the basis for an objective analytical comparison of the properties of the coordinate systems. This paper considers PI in the absence of noise, and lays the foundation for later work which will incorporate the effects of random errors on PI to compare the noise tolerance of different classes of HV. Specifically, the definitions of the four extended families of coordinate systems were chosen to be suitable both for the present paper and for the study of noise tolerance.

The general conclusion reached is that, mathematically speaking, we confirm that all the coordinate systems can adequately and usefully *describe* PI (in the sense of documenting or giving insights into navigation behaviour). However, geocentric Cartesian-like systems (see below for definition) appear the most robust solution for *implementing* a full PI system (in the sense of modelling the way in which an animal's nervous system needs to process and update information), particularly when an allothetic compass is available.

2. Classification of coordinate systems for path integration

Before considering which coordinate systems are most suitable for describing or implementing PI, it is essential to be able to classify the system which a given model uses. This section begins with four well known, standard coordinate schemes, and generalises them into four extended classes which can be used to classify virtually any conceivable model which can carry out accurate PI.

Most existing equational models of PI can be directly assigned to one of four 'standard' coordinate systems according to the type of HV used. The class depends on whether the animal's position is given in Cartesian or polar form and whether the journey's starting point (the geocentric case) or the animal's body (the egocentric case) is used as the origin of the system. This leads to the four standard coordinate systems: geocentric Cartesian (GC), geocentric polar (GP), egocentric Cartesian (EC) and egocentric polar (EP). This paper considers only PI on a flat two-dimensional plane, hence the simplest complete HV contains two values. Such a system can be extended to include PI on a non-flat surface by taking account of the local gradient, without the need for a full three-dimensional HV. Desert ants appear to use such an approach, where an essentially two-dimensional PI system is made to cope with uneven ground (Grah et al., 2005, 2007). This paper will use the following symbols to express the four standard types of HV: GC as (x, y), GP as (r, θ), EC as (x', y') and EP as (r', θ'). The symbol ϕ will be used to indicate the animal's compass heading measured anti-clockwise from the direction of the x-axis. Fig. 1 shows the meaning of the four types of HV diagrammatically. Table 1 gives the equations needed for converting any standard HV into any other. Table 2 summarises all the abbreviations used in this paper.

Geocentric coordinates express the animal's position relative to the ground, with the origin corresponding to the starting point of the outbound journey and the direction of the axes corresponding to fixed directions with respect to the ground. The geocentric frame of reference is a special case of an 'allocentric' or 'exocentric' one: allo- or exocentric coordinates are those defined relative to something external to the animal's body, but in this paper the external reference used is always assumed to be the ground (for example the model animal is never on a table-top which can be rotated relative to the ground), making geo-synonymous with allo- and exocentric. Egocentric coordinates express the home position relative to the animal's current position and orientation. The origin in this case is the centre of the animal's body, the x'- axis corresponds to the forward direction along its body axis and the y'- axis to a perpendicular axis pointing to the left from the animal's point of view.

This paper presents equational PI models from the four standard classes of coordinate systems, because they encapsulate the essence of the majority of existing models, and they are mathematically convenient for analysis. However, to properly classify all the neural network models reviewed below (except

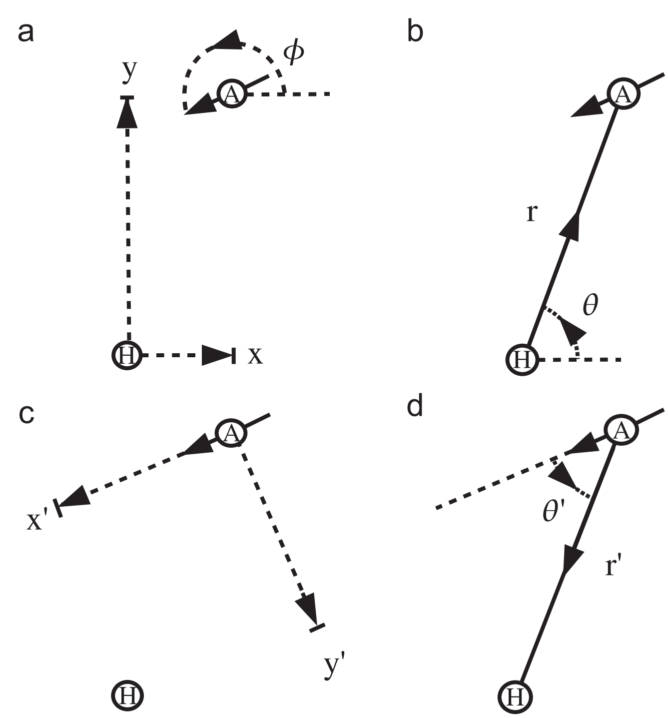

Fig. 1. Four ways to represent the same spatial relationship between animal and home. 'A' is the animal's location, the associated arrow shows the orientation of its body axis. 'H' shows the home location. Shown are HVs for each of the four 'standard' coordinate systems considered in this paper: (a) geocentric Cartesian (GC), (b) geocentric polar (GP), (c) egocentric Cartesian (EC), (d) egocentric polar (EP). The angle ϕ (shown only for the GC case, but relevant for all cases) is the absolute compass heading, and is not part of the HV. The angles θ, θ' and ϕ are measured positive in the anti-clockwise direction in radians.