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# Animal path integration: A model of positional uncertainty along tortuous paths

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## HIGHLIGHTS

- Cumulative noise leads to uncertainty during the navigation by path integration (PI).
- Uncertainty is quantified exactly using a general trajectory and noise model.
- Path and noise properties both affect PI error, often nonlinearly.
- Highly tortuous paths reduce uncertainty during PI, with or without a compass.
- PI using a compass depends mainly on linear noise, without a compass on angular noise.

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## ABSTRACT

Exact closed form mathematical solutions are reported which quantify the dynamic uncertainty resulting from path integration (PI) along tortuous paths. Based on a correlated random walk model, the derived results quantify positional estimation error moments with and without a compass, in discrete and continuous time. Consistent with earlier studies on attempted straight-line navigation, using a compass significantly reduces the uncertainty during PI, making purely idiothetic PI biologically implausible except over short distances. Examples are used to illustrate the contributions of angular noise, linear noise and path tortuosity, under different conditions. Linear noise is shown to be relatively more important with a compass while angular noise is more important without. It is shown that increasing path tortuosity decreases positional uncertainty, true for long and short journeys, irrespective of whether a compass is used, or the level of noise. In contrast, reducing angular noise also reduces uncertainty, but only below some critical level of noise. Using canonical equations of PI, it is shown that polar PI using a compass accumulates uncertainty in a manner similar to Cartesian PI without a compass. Issues of data sampling bias and intermittent use of a compass are also considered for PI along tortuous paths.

## 1. Introduction

Effective spatial navigation is crucial to the survival of most animal species. Path integration (PI) (Mittelstaedt, 1983; Mittelstaedt and Mittelstaedt, 1980) is one of the most important and ubiquitous navigation strategies used in the animal kingdom. Its use has been reported in ants (Cheng et al., 2009; Muller and Wehner, 1988; Wehner and Srinivasan, 2003), bees (Chittka et al., 1995; von Frisch, 1967), flies (Neuser et al., 2008), spiders (Moller and Görner, 1994), crabs (Layne et al., 2003a, 2003b; Zeil, 1998), birds (von Saint Paul, 1982), rodents (Etienne et al., 1988; Kimchi et al., 2004; Mittelstaedt and Mittelstaedt, 1980), dogs (Séguinot et al., 1998) and humans (Mittelstaedt and Glasauer, 1991). Converging experimental and theoretical evidence points to PI as the scaffold on which other navigation processes, including landmark navigation, are built (Cheung et al., 2012b; Collett et al., 2003; McNaughton et al., 2006; Milford et al., 2010; Muller and Wehner, 2010).

PI (also called dead reckoning or vector navigation) is the process whereby an animal maintains an estimate of its position relative to its starting point, as it moves around, by integrating its velocity or displacements over time (Collett and Collett, 2000; Mittelstaedt and Mittelstaedt, 1980; Vickerstaff and Cheung, 2010). In the absence of noise or error, velocity or displacement information from allothetic or idiothetic cues are equivalent, and PI using any spatial reference frame leads to perfect accuracy (Vickerstaff and Cheung, 2010). Without uncertainty, accurate PI is straightforward from a computational standpoint.

The presence of uncertainty, especially when cumulative, fundamentally alters the performance and requirements of a navigation system. Uncertainty is recognized as a key constraint

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on the type of sensory information (Benhamou et al., 1990; Cheung et al., 2007b, 2008), search strategy (Cheung et al., 2012a; Vickerstaff and Merkle, 2012) and even the neural representation of space (Cheung and Vickerstaff, 2010; Cheung et al., 2012b) which may be effective for animal spatial navigation, particularly when PI is involved. For instance, allothetic path integration (aPI) involves the use of a stable absolute directional reference, i.e., some sort of compass cue, which results in low uncertainty and no systematic underestimation of net positional displacement. In contrast, idiothetic path integration (iPI) uses estimates of angular displacement, e.g., via idiothetic cues, integrated over time to provide an approximation of the true heading at any time. The latter results in cumulative angular errors which result in gross nonlinearities in the estimation of net displacement during PI, as well as high levels of uncertainty, making its use biologically implausible for long journeys (Cheung et al., 2007a, 2007b, 2008).

The origin of uncertainty may include noise or error in the sensory input, motor output, and neural processing (Faisal et al., 2008). In turn, errors may accumulate during spatial navigation tasks such as PI (Benhamou et al., 1990; Cheung and Vickerstaff, 2010; Cheung et al., 2007b, 2008; Vickerstaff and Cheung, 2010). There are observable behavioral and neural correlates of navigational uncertainty, which depend on the duration and/or distance of the journey. For example, when ants search for a fictive nest position (Merkle et al., 2006), or bees search for a fictive reward location (Cheng et al., 1999), the spatial variance of their search initiation points increases with the distance of the outbound journey. Another example is the gradual increase in directional drift in tuning functions of the rodent head direction cells when visual information is not available (Clark and Taube, 2010; Goodridge et al., 1998). The latter was shown to have implications on the degree of information fusion required for maintaining a stable representation of place without vision (Cheung et al., 2012b). It is possible to simultaneously record the neuronal activity from over a hundred place cells (Wilson and McNaughton, 1993) and grid cells (Stensola et al., 2012), allowing an ensemble neural code to be used to infer the animal's estimate of current position (Brown et al., 1998; Jensen and Lisman, 2000; Wilson and McNaughton, 1993). It is therefore feasible that an animal's estimate of position during navigation tasks such as PI may be compared to its true position in order to test hypotheses about sensory information usage and underlying computational processes.

However, exact analytic solutions to model PI errors are only available for true trajectories which are perfectly linear (Cheung and Vickerstaff, 2010; Cheung et al., 2007b, 2008). It was found recently through empirical simulations that the tortuosity of the underlying path may impact on the magnitude of positional uncertainty during PI (Cheung et al., 2012b). Comparing simulations of straight-line navigation against navigation in an enclosed space, there was a decrease in the magnitude of positional uncertainty following a more tortuous path during iPI. However, the generality of these findings was unclear. Issues such as the relative contributions of linear and angular noise, long-term behaviors of uncertainty, dependence on error distributions, and the role of path tortuosity itself were not studied in detail, and cannot be readily generalized through empirical simulations alone.

To address these issues, exact mathematical results are reported in this paper which quantifies the growth of positional uncertainty during a class of intentionally tortuous paths during PI, either with or without a compass (aPI and iPI, respectively), in discrete or continuous time. Exact closed form solutions are given for the first and the second error moments of PI given a tortuous trajectory model, both with and without a compass. Continuous time solutions are included where there is a direct mechanistic analog with the discrete time model. Examples are used to illustrate some important insights and some potential challenges arising from the analytic solutions.

In Section 2, the tortuous path and noise models are described, with and without a compass, in discrete and continuous time. A published rodent path and noise model is briefly described, which is used to illustrate important path and PI error results used in Section 3. Comprehensive derivations of all relevant path and PI error moments are included in Appendix B. Key results are tabulated in Tables 3 and 4. In Section 3, a selection of important path and PI error results are described and discussed. These include comparisons of discrete and continuous time descriptions of paths, the relative contributions of linear and angular noise to PI error, and the effect of path tortuosity on PI error. In addition, practical issues of path and noise parameter corrections, and extensions of current results to include PI update errors, are discussed. Finally, the effects of intermittent use of a compass on PI errors are found (derivations in Appendix C) and discussed.

## 2. Path and noise models

The general path and noise models used for the derivations and simulation examples are described below. See Appendix B for further details.

### 2.1. Tortuous path model

For simplicity and consistent with previous work, spatial uncertainty is considered here in two mathematically equivalent ways. Firstly, it may be considered as a discrepancy between an estimate of position (Fig. 1A and B, red lines) and the true position (Fig. 1A and B, back lines) following a given number of steps (or time). Alternatively, it may be considered as the discrepancy between the intended position (Fig. 1A and B, black lines) and the actual realized position (Fig. 1A and B, red lines). For simplicity, only the former interpretation is used unless otherwise specified.

The axis of initial locomotion is used to provide a reference direction and is defined as the $X$-axis without the loss of generality (Fig. 1A and B). In earlier work (Cheung et al., 2007b, 2008), this was the path which would have been taken in the absence of all noise, i.e., the ideal path was a straight line without tortuosity. In the current work, the $X$-axis is the directed path which would have been taken, in the absence of all noise and without path tortuosity (Fig. 1A and B). In the absence of all noise, the tortuous path is modeled as a correlated random walk (CRW), also known as a persistent random walk (PRW), or a simple idiothetic directed walk (IDW), and will be denoted herein as a CRW. CRWs have been used extensively and successfully to model the tortuous trajectories of both large and small organisms (Berg, 1983; Codling et al., 2008).

For clarity, the particular version of the CRW model used for the derivations in Table 3 and Appendix B is outlined below (definitions summarized in Table 1). Each step is modeled as the indexed pair $(\theta_i, l_i^{path})$ which denotes the independent rotation and the forward displacement of step $i$ relative to the previous orientation and position. By convention, the random turn $\theta$ is realized prior to the random forward step $l^{path}$. Following $n$ steps, the true total displacement $(X_T, Y_T)$ along and perpendicular to the $X$-axis, respectively, is given by

$$(X_T, Y_T) = \left(\sum_{i=1}^{n} X_i, \sum_{i=1}^{n} Y_i\right) = \left(\sum_{i=1}^{n} l_i^{path} \cos\left(\sum_{j=1}^{i} \theta_j\right), \sum_{i=1}^{n} l_i^{path} \sin\left(\sum_{j=1}^{i} \theta_j\right)\right) \quad (1)$$

Note that the upper case subscript $T$ is used specifically to denote the total displacement accumulated over $n$ steps (or elapsed time $t$ in continuous time). Lower case subscripts denote the step