

Animal navigation: general properties of directed walks

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Abstract The ability to locomote is a defining characteristic of all animals. Yet, all but the most trivial forms of navigation are poorly understood. Here we report and discuss the analytical results of an in-depth study of a simple navigation problem. In principle, there are two strategies for navigating a straight course. One is to use an external directional reference and to continually reorient with reference to it. The other is to monitor body rotations from internal sensory information only. We showed previously that, at least for simple representations of locomotion, the first strategy will enable an animal or mobile agent to move arbitrarily far away from its starting point, but the second strategy will not do so, even after an infinite number of steps. This paper extends and generalizes the earlier results by demonstrating that these findings are true even when a very general model of locomotion is used. In this general model, error components within individual steps are not independent, and directional errors may be biased. In the

absence of a compass, the expected path of a directed walk in general approximates a logarithmic spiral. Some examples are given to illustrate potential applications of the quantitative results derived here. Motivated by the analytical results developed in this work, a nomenclature for *directed walks* is proposed and discussed. Issues related to path integration in mammals and robots, and measuring the curvature of a noisy path are also addressed using directed walk theory.

Keywords Navigation · Compass · Cumulative errors · Sensory noise · Motor noise · Directed walk · Elementary step · General · Simple · Bias · Path integration · Straightness · Curvature · Correlated random walk · Persistent random walk · Logarithmic spiral · Dead reckoning · Vectorial navigation · Central limit theorem · Positional moments · Mean position · Expected position · Positional variance · Axis of intended locomotion

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1 Introduction

Noise is ubiquitous in biological systems. From stochastic openings of ion channels to variability in muscular force, there are ample sources from which noise can arise intrinsically in any biological control system. Concurrently, there may be non-ideal environmental conditions causing difficulties in acquiring precise sensory information, and/or difficulties in executing precise motor output. It is well recognized that cumulative noise/errors occurring during navigation will lead to uncertainties in the final position of any navigating agent. Furthermore, there is an intuitive agreement amongst most people who study animal navigation that the use of an external direction reference, i.e., a compass, would reduce that final uncertainty, although this has never been proven rigorously until recently. Cheung et al. (2007) provided this

proof, at least for a simplified model of locomotion in which angular and linear displacement errors were statistically independent, and turning errors were unbiased. Here we show that the proof holds even when the simplifying assumptions are removed, and a very general model is used to characterize locomotion and the properties of the sensory and motor errors. To carry out the generalization, we compare analytically two strategies for navigating a straight course; i.e., performing a directed walk. The first strategy is to use an external directional reference, which in practice may be the earth's magnetic field (recently reviewed by [Wiltshko and Wiltshko 2005](#)), the position of the sun or moon, or of the polarization pattern that it generates in the sky ([Wehner 1992, 1994; Dacke et al. 2003](#)), or distant landmarks ([Collett and Rees 1997](#)). The second strategy is to infer body rotations from egocentrically based information, such as from limb motions, or from vestibular or optokinetic signals, and to use this information to prevent or compensate for unwanted deviations.

This study generalizes the quantitative theory developed in [Cheung et al. \(2007\)](#). In particular, the analysis will demonstrate the navigational consequences of cumulative errors in the presence and absence of a compass, for general locomotion. Some examples of performance, predicted by theory, will be illustrated and verified through computer simulation.

2 General elementary step

We wish to uncover general characteristics of the positional distribution during navigation without making specific assumptions about the locomotion (details of which may not always be available). To do this, it is necessary to develop a mathematical description of the elementary step (the basic repeating unit of locomotion), that is completely general.

It is clear that an accurate description of an animal's general elementary step must be more complex than a turn and a step. What is the simplest mathematical description of a completely general elementary step? We need to preserve both qualitatively and quantitatively the features of locomotion which affect the position of an animal during navigational tasks. The corollary is that only the components of the general elementary step which actually change the net position and/or orientation of the animal need to be considered. It should be noted that this does not in any way imply that other movements are unimportant for navigation, but merely that they do not affect the position of the animal. For example, an animal which stops occasionally to scan its environment may move its eyes, head, even limbs, without causing body displacement. Sometimes, perhaps a higher level command causes a brief excursion away from the current path, but with perfect recovery of the current path at the point of deviation, i.e., zero net displacement. Multiple contiguous rotations may

be summed and expressed as a net rotation mathematically, without knowing the details of the component rotations. It is clear that in these and similar examples, from the perspective of the directed walk, the analytical treatment would be equivalent even though there are clear behavioural differences. Therefore, movements which do not alter the net displacement or net rotations of the navigating agent will be considered as being outside of the scope of the current work.

Vectors are convenient for representing the positional change associated with each movement of an animal, allowing the geometrically correct addition of the component movements. Moreover, this procedure allows the breakdown of individual components into any spatial and/or temporal resolution, which is practical for measurement and/or analysis. For instance, a hypothetical quadruped may have a gait such that movement of each of the four limbs generates some positional change of the animal, in some sort of sequence. Hence, it may be prudent to represent the positional change due to each limb as a single vector, with some joint probability function for the distribution of possible (egocentric) angular and linear displacements. This hypothetical animal's general elementary step will therefore be built up of four component vectors—one for the movement produced by each limb—and their associated probability distributions (Fig. 1).

Suppose in another context it is necessary to have a description with much higher spatiotemporal resolution e.g. a description of the movements of an animal resulting from the activation of each muscle of each limb, or even each motor unit of each muscle. Again, all the movements may be represented as a sequence of vectors, with some associated joint probability distributions describing the angular and linear errors.

Careful consideration reveals that the basic repeating unit of locomotion can be modelled as consisting of $m + 1$ angular and of m linear components, in an alternating sequence, where m can be an arbitrarily large integer. There is no intrinsic reason why locomotion cannot include rotations before and after displacements. Although the rotation at the end of the chain of displacements will not cause another displacement per se, it will affect the starting orientation for the subsequent step. Note that without loss of generality, all contiguous angular or linear components are assumed to be summed. A simple example illustrates the significance of the three fundamental components of displacement (angular, linear, angular). Suppose a flying insect such as a wasp is attempting to move forward along a straight trajectory. We may consider every wing beat cycle as a "step." During each step of its flight trajectory, the wasp attempts to move forward through the air, but inevitably makes some error, so that its actual displacement deviates slightly from the true forward direction at the start of the step. Furthermore, due to random inequalities in torque, its orientation would also have deviated slightly, but not necessarily by the same amount of

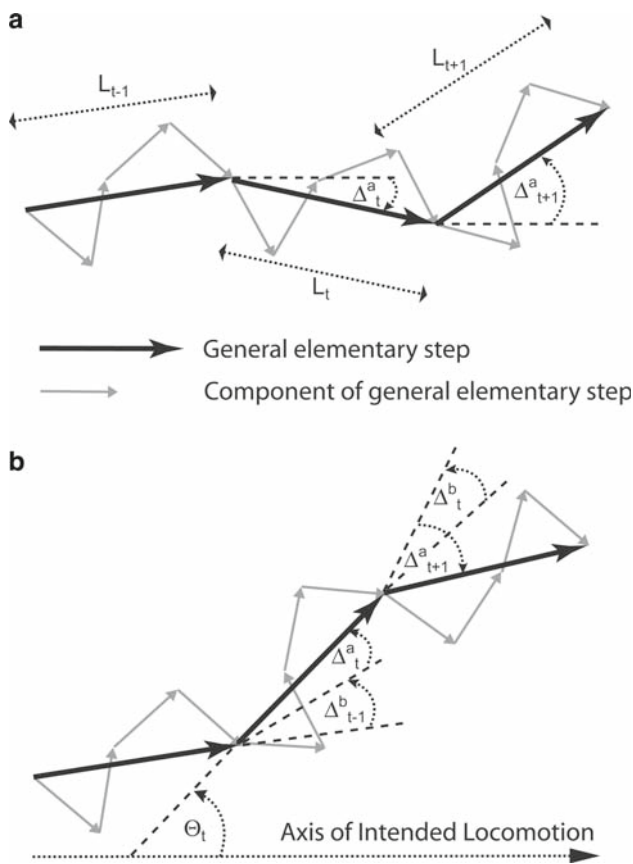


Fig. 1 Diagrammatic representation of a general elementary step (in 2-D space) during an allothetic directed walk (a), and an idiothetic directed walk (b). The *small black arrows* represent the reduced, statistically dependent, component vectors making up each elementary, repeating step unit (*large gray arrows*). L_t is the length of the general elementary step at time t . Δ_t^a is the angular displacement error resulting in the angular discrepancy between the heading of the last component of the $t - 1$ th general elementary step, and the t th general elementary step. Δ_t^b is the angular displacement error resulting in the angular discrepancy between the t th general elementary step and the heading of its last component. This particular example shows four component vectors per elementary step, but this number is completely arbitrary and depends on the complexity of the locomotor biomechanics of the animal. Note that angular displacement bias terms have been omitted for clarity

deviation as the net displacement. In other words, the directions of heading and displacement may be misaligned. Hence, at the end of the flight cycle, the wasp’s forward direction would, in general, be slightly different from the displacement direction which brought it there. To account for this discrepancy, one must incorporate a second rotational error term. Then at the next flight cycle, the wasp again tries to move forward, unintentionally making another set of displacement and heading errors, and so forth.

In general, any of the above components of motion may be statistically dependent on any other. Using the example of the hypothetical quadruped (Fig. 1), factors such as anatomical asymmetry may cause each limb to contribute differently to

the elementary step. Indeed, it would be difficult to imagine that the four limbs can move (displace) the animal totally independently of each other.

From the preceding analysis, it is clear that the net positional displacement can be represented by a single vector (sum of all m component vectors). Unfortunately, the net vector cannot simultaneously account for both the angular displacement before and the angular displacement after the net positional displacement (see Fig. 1b). The reason is that the allocentric direction of the vectorial sum is generally different to the allocentric direction of the last component of movement. Mechanistically, it is the last component of the $t - 1$ th step which directly precedes the first component of the t th step. Hence the allocentric direction of the last component of the $t - 1$ th step must be used as the reference direction to measure the angular displacement, Δ_t^a , of the t th step. The actual heading of the t th step, Θ_t , will be the sum of the reference direction and the displacement Δ_t^a . The reference direction of the $t + 1$ th step is $\Theta_t + \Delta_t^b$. Hence combining the two results, it becomes clear that a complete description of the general elementary step requires *two* angular displacements¹ and one linear displacement (see Fig. 1b). This is consistent with empirically derived descriptions of locomotion in the robotics navigation literature (for example see Milford et al. 2006). For completeness, it should be noted that the second angular component Δ_t^b is effectively removed when a compass is used to reset heading (see Fig. 1a).

3 Dealing with biased angular error distributions

To simplify the derivation of first and second positional moments, it is advantageous to define the following:

$$E \left[\sin \left(\Delta^a + \Delta^b \right) \right] = 0.$$

In essence, the above definition implies that one must shift the angular error distributions until the above equation is satisfied. This is achieved by incorporating bias terms. All subsequent derivations and indeed valid applications of the results require that this step has been performed correctly. However, this definition does not in any way constrain the error distribution(s) allowed in the description of locomotion. The reason is that a constant bias term may be added to either or both distributions to ensure generality. Thus for an error $\Delta^{a'} + \Delta^{b'}$ following any finite distribution there must exist a constant Δ_{bias} such that:

$$E \left[\sin \left(\Delta^{a'} + \Delta^{b'} - \Delta_{\text{bias}} \right) \right] = 0.$$

¹ There is no distinction at this stage between biased and unbiased general elementary steps. However, it should be clear that any systematic bias may be incorporated into the angular displacement terms. The distinction does become important for the derivation of the analytical results.

Proof Suppose there exist random variables $\Delta^{a'} + \Delta^{b'}$ distributed such that

$$E \left[\sin \left(\Delta^{a'} + \Delta^{b'} \right) \right] = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sin \left(\Delta^{a'} + \Delta^{b'} \right) P \left(\Delta^{a'}, \Delta^{b'} \right) d\Delta^{a'} d\Delta^{b'} < 0$$

then

$$\begin{aligned} E \left[\sin \left(\Delta^{a'} + \Delta^{b'} - \pi \right) \right] &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sin \left(\Delta^{a'} + \Delta^{b'} - \pi \right) P \left(\Delta^{a'}, \Delta^{b'} \right) d\Delta^{a'} d\Delta^{b'} \\ &= - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sin \left(\Delta^{a'} + \Delta^{b'} \right) P \left(\Delta^{a'}, \Delta^{b'} \right) d\Delta^{a'} d\Delta^{b'} \\ &> 0. \end{aligned}$$

Since the expectation changes sign during the phase shift, by Bolzano’s theorem (a special case of the Intermediate Value Theorem) or by an argument of continuity of the sine function, there must have been some intermediate value, call it Δ_{bias} , which satisfied the original equality (Kreyszig 1993). So a new variable can be defined:

$$\Delta^a + \Delta^b = \Delta^{a'} + \Delta^{b'} - \Delta_{\text{bias}}$$

whereby

$$E \left[\sin \left(\Delta^a + \Delta^b \right) \right] = E \left[\sin \left(\Delta^{a'} + \Delta^{b'} - \Delta_{\text{bias}} \right) \right] = 0.$$

Clearly an analogous argument applies if $E \left[\sin \left(\Delta^{a'} + \Delta^{b'} \right) \right] > 0$.

This result guarantees that within the mathematical derivation for the first and second positional moments, it is possible to decompose the angular displacement errors into a zero bias distribution, plus a bias term, without loss of generality. The significance of this will become apparent later.

Every general elementary step for a navigating agent which used purely idiothetic cues; i.e., carrying out an idiothetic directed walk (see Sect. 4), regardless of error distribution(s), can be written as a sequence of:

- (a) turn 1 ($\Delta^a + \Delta_{\text{bias}}^a$),
- (b) forward step (L), and
- (c) turn 2 ($\Delta^b + \Delta_{\text{bias}}^b$).

Without correction, the allocentric heading Θ at step t would be:

$$\Theta_t = \sum_{j=1}^t \Delta_j^a + t \Delta_{\text{bias}}^a + \sum_{j=1}^{t-1} \Delta_j^b + (t - 1) \Delta_{\text{bias}}^b.$$

As shown already, it is clear that without loss of generality, the two bias terms may be set such that $E \left[\sin \left(\Delta^a + \Delta^b \right) \right] = 0$. It will be demonstrated later that the bias terms may be

separated via trigonometric identities to simplify the final derivation of the positional moments.

In contrast, for a navigating agent which reset its heading using an allothetic directional reference; i.e., carrying out an allothetic directed walk (see Sect. 4), the general elementary step reduces to:

- (a) turn 1 ($\Delta^a + \Delta_{\text{bias}}^a$), and
- (b) forward step (L).

By resetting the current heading at every step using the compass, the allocentric heading Θ at step t would be:

$$\Theta_t = \Delta_t^a + \Delta_{\text{bias}}^a.$$

□

4 Nomenclature of walks

The idea of using “random walks” (RWs) to describe biological phenomena, including animal movements, is not new (see for example Berg 1983; Wu et al. 2000; Byers 2001). However, from the perspective of animal navigation, the terminology excludes important, related types of walks. Furthermore, it will be shown through the subsequent mathematical derivations that the nomenclature of RWs do not have the necessary emphasis on the directed nature of useful navigation. There is also a tendency to make simplifying assumptions about the elementary step (see Sects. 2, 3). In short, the RW nomenclature does partially overlap with directed walks. However, even where there is overlap, the existing results from the RW literature are insufficient to properly quantify directed walks, particularly from a navigation perspective. This motivates a new nomenclature which we define here. A more detailed justification will be provided in Sect. 7.

We introduce here an intuitive yet mathematically rigorous nomenclature for *directed walks* (DWs), which may better serve the study of animal navigation than the traditional RW nomenclature. At this time, the nomenclature includes two independent sets of descriptors. The first type of descriptor denotes the nature of the directional cue used to guide navigation. The nature of the directional cue was shown to be critical in determining the properties of the directed walk (Cheung et al. 2007). Hence a logical subdivision of directed walks would be *idiothetic directed walks* (IDWs) and *allothetic directed walks* (ADWs). As their names suggest, during an IDW, only internal directional cues are used, i.e. no compass, while during an ADW a compass is used to directly reset heading during every elementary step. For clarity, we emphasize that a “compass” here refers to any cue which gives stable allocentric directional information, and includes global geomagnetic information, distant landmarks, and celestial cues (perhaps with ephemeris corrections). Intuitively, this definition can be considered to imply that a true directional pointer, behaving much like a geomagnetic compass

Table 1 Classification of directed walks

Sensory data	Idiothetic	Allothetic	
Examples	Vestibular Proprioceptive	^a Optic flow ^b Estimation of rotation using allothetic reference	Geomagnetic Distant landmark Corrected celestial cue
Processing	Neurally integrated (internal)		-
Angular error	Cumulative		Non-cumulative
Directional cue	Idiothetic (IDW)		Allothetic (ADW)

^a Optic flow uses spatial and/or temporal changes in light intensity recorded by the motion detectors of the visual system. Even though it is thought that the estimation of optic flow occurs in the motion detector apparatus, the light signal itself has an allothetic origin

^b For example, a navigating agent could take two bearings of an allothetic cue (such as the solar azimuth or a distant landmark), one before and one after a rotation. The angular displacement of the agent could be estimated from the observed angular displacement of the allothetic cue

needle, is always available to the navigating agent throughout the navigation task.

For example, consider a navigating agent attempting to move along a straight line using purely optic flow information to correct for estimated deviations off course. In the same way that differential wheel-based odometry may be used to estimate rotations in a robot, differential optic flow may be used as a surrogate measure of rotation. Is this an IDW or ADW? The principle of the classification is based on the source of the estimate of absolute heading (rather than rotation rate or rotation per step). If the optic flow is measured through an analysis of local spatiotemporal changes in the image, as described, for example, in Barlow and Levick (1965), Reichardt (1961), Horn and Schunck (1981) or Srinivasan (1990, 1994), then the navigating agent would still have to internally sum or integrate rotations in order to obtain an estimate of absolute heading, leading to cumulative angular errors. Consequently, the behaviour would be no different, at least in principle, to using inertial or proprioceptive information. If optic flow is measured in this way, it would lead to an IDW. Table 1 summarizes the conditions under which IDWs and ADWs are obtained.

The second set of descriptors refers to the complexity of the locomotory unit, i.e., the type of elementary step. We define a *simple DW* (IDW or ADW) as locomotion with a simple elementary step; i.e., one step consists of a linear displacement and an angular displacement that are statistically independent of each other and the distribution of the angular error is unbiased. Thus, the examples in Cheung et al. (2007) would all be classified as simple directed walks. A *general DW* is defined as locomotion with a general elementary step (see Sect. 2), of which *simple DWs* are a subset.

To give an example using this nomenclature, a *general unbiased IDW* denotes a compassless directed walk, where

the unit of locomotion is a general elementary step but with bias terms set to zero.

It is important to remember that a DW may be used to describe an animal’s displacement through real or neurally represented space. The former is best imagined as an actual animal attempting to travel along some ideal path. Due to cumulative sensorimotor errors, locomotion is imperfect and deviates from the ideal path. The latter may be thought of as an imperfect neural record of actual movements, again due to noise. Both interpretations are mathematically equivalent.

5 Methods

Important principles and definitions are described below, which are used during the derivation of analytical and numerical results.

5.1 Mathematical derivations, substitutions and definitions

Most of the detailed steps required to derive the results listed in the text are omitted, due to space constraints. However, the fundamental principles of all the derivations are explained. For example, it is well understood that the second central moment, otherwise referred to as the variance, is readily obtained from the first and second raw moments of a distribution i.e.,

$$V(X) = E(X^2) - E(X)^2,$$

and the variance of the linear combination of two variables is given by

$$V(aX + bY) = a^2V(X) + b^2V(Y) - 2abCov(X, Y).$$

Repeated applications of trigonometric identities and sums of geometric series, standard algebraic manipulations, and

in some instances basic integral calculus yield all the results listed in the text. More detailed derivations are available in the supplementary section.

A range of symbols is used to represent quantities which could not be further simplified without losing generality. Other symbols are used to make complicated expressions more succinct. Symbols used in the text include the following:

$$\mu_2 = E(L^2)$$

$$\omega_a = E(L^2 \cos \Delta^a \sin \Delta^a)$$

$$\varphi_a = E(L^2 \cos^2 \Delta^a)$$

$$\gamma_{a,b} = E(\cos^2(\Delta^a + \Delta^b))$$

$$\rho_a = E(L \cos \Delta^a)$$

$$\varepsilon_a = E(L \sin \Delta^a)$$

$$\eta_{a,b} = E(L \cos \Delta^a \cos(\Delta^a + \Delta^b))$$

$$\iota_{a,b} = E(L \sin \Delta^a \sin(\Delta^a + \Delta^b))$$

$$\varpi_{cs} = E(L \cos \Delta^a \sin(\Delta^a + \Delta^b))$$

$$\varpi_{sc} = E(L \sin \Delta^a \cos(\Delta^a + \Delta^b))$$

$$\chi_{a,b} = E(\cos(\Delta^a + \Delta^b) \sin(\Delta^a + \Delta^b))$$

$$\beta_{a,b} = E(\cos(\Delta^a + \Delta^b))$$

$$\mathbf{p}_1 = [\varepsilon_a \ \rho_a] = [E(L \sin \Delta^a) \ E(L \cos \Delta^a)]$$

$$\mathbf{p}_2^a = \begin{bmatrix} -\sin(\Delta_{\text{bias}}^a) \\ \cos(\Delta_{\text{bias}}^a) \end{bmatrix} \quad \mathbf{p}_2^b = \begin{bmatrix} \cos(\Delta_{\text{bias}}^a) \\ \sin(\Delta_{\text{bias}}^a) \end{bmatrix}$$

$$\mathbf{m}_0^a = \begin{bmatrix} \eta_{a,b} + \iota_{a,b} \\ \varpi_{sc} - \varpi_{cs} \end{bmatrix} = \begin{bmatrix} E(L \cos \Delta^a \cos(\Delta^a + \Delta^b)) \\ + E(L \sin \Delta^a \sin(\Delta^a + \Delta^b)) \\ E(L \sin \Delta^a \cos(\Delta^a + \Delta^b)) \\ - E(L \cos \Delta^a \sin(\Delta^a + \Delta^b)) \end{bmatrix}$$

$$\mathbf{m}_0^b = \begin{bmatrix} \varpi_{sc} - \varpi_{cs} \\ -\eta_{a,b} - \iota_{a,b} \end{bmatrix} = \begin{bmatrix} E(L \sin \Delta^a \cos(\Delta^a + \Delta^b)) \\ - E(L \cos \Delta^a \sin(\Delta^a + \Delta^b)) \\ - E(L \cos \Delta^a \cos(\Delta^a + \Delta^b)) \\ - E(L \sin \Delta^a \sin(\Delta^a + \Delta^b)) \end{bmatrix}$$

$$\mathbf{m}_1 = [\rho_a \ \varepsilon_a] = [E(L \cos \Delta^a) \ E(L \sin \Delta^a)]$$

$$\mathbf{m}_2^a = \begin{bmatrix} \cos(2\Delta_{\text{bias}}^a) \\ \sin(2\Delta_{\text{bias}}^a) \end{bmatrix} \quad \mathbf{m}_2^b = \begin{bmatrix} -\sin(2\Delta_{\text{bias}}^a) \\ \cos(2\Delta_{\text{bias}}^a) \end{bmatrix}$$

$$\mathbf{m}_3^a = [\eta_{a,b} - \iota_{a,b} \ -\varpi_{cs} - \varpi_{sc}] = \begin{bmatrix} E(L \cos \Delta^a \cos(\Delta^a + \Delta^b)) \\ - E(L \sin \Delta^a \sin(\Delta^a + \Delta^b)) \\ - E(L \cos \Delta^a \sin(\Delta^a + \Delta^b)) \\ - E(L \sin \Delta^a \cos(\Delta^a + \Delta^b)) \end{bmatrix}^T$$

$$\mathbf{m}_3^b = [\varpi_{cs} + \varpi_{sc} \ \eta_{a,b} - \iota_{a,b}] = \begin{bmatrix} E(L \cos \Delta^a \sin(\Delta^a + \Delta^b)) \\ + E(L \sin \Delta^a \cos(\Delta^a + \Delta^b)) \\ E(L \cos \Delta^a \cos(\Delta^a + \Delta^b)) \\ - E(L \sin \Delta^a \sin(\Delta^a + \Delta^b)) \end{bmatrix}^T$$

$$\mathbf{m}_4 = [\varphi_a - \frac{\mu_2}{2} \ \omega_a] = [E(L^2 \cos^2 \Delta^a) - \frac{E(L^2)}{2} \ E(L^2 \cos \Delta^a \sin \Delta^a)]$$

To allow terms with trigonometric functions of multiple angles to be expressed as powers, the following substitution is made.

$$\Upsilon = \cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) + i \sin(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) \quad \text{where } i = \sqrt{-1},$$

which means that

$$\begin{aligned} \cos(m(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b)) &= \frac{\Upsilon^m + \Upsilon^{-m}}{2} \quad \text{and} \quad \sin(m(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b)) \\ &= \frac{\Upsilon^m - \Upsilon^{-m}}{2i}. \end{aligned}$$

Using complex representations of the cosine and sine of multiple angles is convenient for the subsequent derivations but it should be noted that in the final results, all the imaginary components cancel when evaluated (which of course must be the case, given the positional moments are real).

5.2 Hypothetical example

An hypothetical example of a general elementary step was generated consisting of a turn Δ^a , a step L , and another turn Δ^b , with statistical dependence between error terms, and with biases.

$$\text{pdf}(\Delta^a) = \begin{cases} 2(a+1 - \Delta^a) & a < \Delta^a < a+1 \\ 0 & \text{otherwise} \end{cases}$$

$$\Delta^b = \frac{1}{2}\Delta^a$$

$$L = 2\Delta^a + 1$$

$$\Delta_{\text{bias}}^a = -0.1 \text{ rad}$$

$$\Delta_{\text{bias}}^b = +0.05 \text{ rad}$$

As explained earlier, the bias terms must be adjusted such that

$$E\left(\sin\left[\Delta^a + \Delta^b\right]\right) = \frac{8}{9}\left[-\sin\left(\frac{3}{2}a\right)\cos\left(\frac{3}{2}\right) - \cos\left(\frac{3}{2}a\right)\sin\left(\frac{3}{2}\right) + \sin\left[\frac{3}{2}a\right] + \frac{3}{2}\cos\left[\frac{3}{2}a\right]\right] = 0.$$

In this example, the parameter a can then be evaluated

$$a = \frac{2}{3} \tan^{-1}\left(\frac{\sin\left(\frac{3}{2}\right) - \frac{3}{2}}{1 - \cos\left(\frac{3}{2}\right)}\right).$$

All other relevant parameters for the first and second positional moments can be expressed as functions of a as follows (derivations are found in supplementary Sect. A5):

$$\beta_{a,b} = 2\left[-\frac{4}{9}\cos\left(\frac{3}{2}(a+1)\right) - \frac{2}{3}\sin\left(\frac{3}{2}a\right) + \frac{4}{9}\left(\frac{3}{2}a\right)\right]$$

$$\gamma_{a,b} = \frac{1}{2} - \frac{1}{9}\cos(3(a+1)) - \frac{1}{3}\sin(3a) + \frac{1}{9}\cos(3a)$$

$$\varphi_{a,b} = \left[(a+1)\left(\frac{3}{2} + \frac{17}{6}a + \frac{5}{3}a^2 + \frac{1}{3}a^3\right) - \left(\frac{19}{27} + \frac{4}{3}a + \frac{4}{9}a^2\right) \times \cos(3(a+1)) + \left(\frac{8}{9} + \frac{16}{27}a\right)\sin(3(a+1)) - \left[a\left(1 + \frac{5}{2}a + 2a^2 + \frac{1}{3}a^3\right) + \left(\frac{17}{27} + \frac{4}{9}a - \frac{4}{9}a^2\right) \times \cos(3a) + \left(\frac{1}{3} + \frac{52}{27}a + \frac{4}{3}a^2\right)\sin(3a)\right]$$

$$\chi_{a,b} = -\frac{1}{9}\sin(3a+3) + \frac{1}{3}\cos(3a) + \frac{1}{9}\sin(3a)$$

$$\omega_{a,b} = \frac{1}{27} \begin{bmatrix} -(24 + 16a)\cos(3(a+1)) \\ -(19 + 36a + 12a^2)\sin(3(a+1)) \\ +(9 + 52a + 36a^2)\cos(3a) \\ -(17 + 12a - 12a^2)\sin(3a) \end{bmatrix}$$

$$\eta_{a,b} = 2 \begin{bmatrix} 16\sin\frac{(a+1)}{2} - (4a+6)\cos\frac{(a+1)}{2} \\ + 0.128\sin\frac{5(a+1)}{2} - (0.24+0.16a)\cos\frac{5(a+1)}{2} \\ -(2a+17)\sin\frac{a}{2} - (2-4a)\cos\frac{a}{2} \\ -(0.4a+0.328)\sin\frac{5a}{2} - (-0.16a+0.08)\cos\frac{5a}{2} \end{bmatrix}$$

$$\iota_{a,b} = 2 \begin{bmatrix} 16\sin\frac{(a+1)}{2} - (4a+6)\cos\frac{(a+1)}{2} \\ - 0.128\sin\frac{5(a+1)}{2} + (0.24+0.16a)\cos\frac{5(a+1)}{2} \\ -(2a+17)\sin\frac{a}{2} - (2-4a)\cos\frac{a}{2} \\ + (0.4a+0.328)\sin\frac{5a}{2} + (-0.16a+0.08)\cos\frac{5a}{2} \end{bmatrix}$$

$$\varpi_{cs} = 2 \begin{bmatrix} -16\cos\frac{(a+1)}{2} - (4a+6)\sin\frac{(a+1)}{2} \\ -0.128\cos\frac{5(a+1)}{2} - (0.24+0.16a)\sin\frac{5(a+1)}{2} \\ +(2a+17)\cos\frac{a}{2} - (2-4a)\sin\frac{a}{2} \\ +(0.4a+0.328)\cos\frac{5a}{2} - (-0.16a+0.08)\sin\frac{5a}{2} \end{bmatrix}$$

$$\varpi_{sc} = 2 \begin{bmatrix} 16\cos\frac{(a+1)}{2} + (4a+6)\sin\frac{(a+1)}{2} \\ - 0.128\cos\frac{5(a+1)}{2} - (0.24+0.16a)\sin\frac{5(a+1)}{2} \\ -(2a+17)\cos\frac{a}{2} + (2-4a)\sin\frac{a}{2} \\ +(0.4a+0.328)\cos\frac{5a}{2} - (-0.16a+0.08)\sin\frac{5a}{2} \end{bmatrix}$$

5.3 Computer simulations

Monte Carlo simulations of attempted straight line navigation were carried out in MATLAB 6.5 for 500 steps, both with and without a compass. Locomotion was assumed to be described by the general elementary step defined above. At each iteration, 20,000 random floating point numbers were generated by using the inverse of the cumulative distribution function of the first angular displacement error

$$\Delta^a = \text{cdf}^{-1}(r) = a + 1 - \sqrt{1-r},$$

where r was a random value drawn from the interval $[0, 1]$ using MATLAB’s standard random number generator. Note that the probability density function was defined in the previous section. The linear and second angular displacement errors were functionally dependent on this first randomly distributed value as explained previously. For compass-based navigation, the heading direction was reset to zero following each step, whilst for the case without a compass, the heading errors were accumulated. Each iteration represented a single general elementary step. For each of the 20,000 runs, the positions were recorded following 1, 2, 5, 20, 100 and 500 steps (iterations) to show how the distribution of positions evolved with step number during attempted straight-line navigation with and without a compass.

6 Results

Subsequently, we will derive the properties of the four different directed walks, namely the general unbiased ADW, the general ADW, the general unbiased IDW and the general IDW. Then the effect of large systematic bias during IDWs is examined, and lastly, the shape of the general IDW is derived.

6.1 A general unbiased allothetic directed walk

It is straightforward to derive the first and second positional moments of the directed walk using a compass. The results are:

$$E(X_{\text{total}}) = nE(L \cos \Delta^a) = n\rho_a$$

$$E(Y_{\text{total}}) = nE(L \sin \Delta^a) = n\varepsilon_a$$

$$V(X_{\text{total}}) = n(\varphi_a - \rho_a^2)$$

$$V(Y_{\text{total}}) = n(\mu_2 - \varphi_a - \varepsilon_a^2)$$

Like the results of a directed walk with a simple elementary step (Cheung et al. 2007), all of the above four quantities increase linearly with step number n . However, due to the statistical dependence between linear and angular errors, even in the absence of bias, it is possible for the step to be asymmetrical and lead to a net drift away from the axis of intended locomotion. Furthermore, the asymmetry may lead to an asymptotic distribution asymmetrical about any line parallel to the axis of intended locomotion (see next section for more details). This is in contrast to the simple elementary step where the expected path would follow the axis of intended locomotion for either an idiothetic or allothetic directed walk (Cheung et al. 2007). Table 2 provides a comparison of some important properties of various forms of directed walks.

6.2 A general allothetic directed walk

The positional expectations and variances for the completely general elementary step whilst using a compass are as

follows.

$$E(X_{\text{total}}) = nE(L \cos(\Delta^a + \Delta_{\text{bias}}^a)) = \dots = n\mathbf{p}_1\mathbf{p}_2^a$$

$$E(Y_{\text{total}}) = nE(L \sin(\Delta^a + \Delta_{\text{bias}}^a)) = \dots = n\mathbf{p}_1\mathbf{p}_2^b$$

The positional variances are proportional to the step number so since

$$\begin{aligned} V(X_1) &= E(L^2 \cos^2(\Delta^a + \Delta_{\text{bias}}^a)) \\ &\quad - E(L \cos(\Delta^a + \Delta_{\text{bias}}^a))^2 \\ &= \dots = \varphi_a \cos(2\Delta_{\text{bias}}^a) - \omega_a \sin(2\Delta_{\text{bias}}^a) \\ &\quad + \mu_2 \sin^2 \Delta_{\text{bias}}^a - (\mathbf{p}_1\mathbf{p}_2^a)^2 \end{aligned}$$

then

$$\begin{aligned} V(X_{\text{total}}) &= n[\varphi_a \cos(2\Delta_{\text{bias}}^a) - \omega_a \sin(2\Delta_{\text{bias}}^a) \\ &\quad + \mu_2 \sin^2 \Delta_{\text{bias}}^a - (\mathbf{p}_1\mathbf{p}_2^a)^2]. \end{aligned}$$

Similarly, in the perpendicular direction,

$$\begin{aligned} V(Y_1) &= E(L^2 \sin^2(\Delta^a + \Delta_{\text{bias}}^a)) \\ &\quad - E(L \sin(\Delta^a + \Delta_{\text{bias}}^a))^2 \\ &= \dots = -\varphi_a \cos(2\Delta_{\text{bias}}^a) \\ &\quad + \omega_a \sin(2\Delta_{\text{bias}}^a) + \mu_2 \cos^2 \Delta_{\text{bias}}^a - (\mathbf{p}_1\mathbf{p}_2^b)^2 \end{aligned}$$

which becomes

$$\begin{aligned} V(Y_{\text{total}}) &= n\left[-\varphi_a \cos(2\Delta_{\text{bias}}^a) + \omega_a \sin(2\Delta_{\text{bias}}^a) \right. \\ &\quad \left. + \mu_2 \cos^2 \Delta_{\text{bias}}^a - (\mathbf{p}_1\mathbf{p}_2^b)^2\right] \end{aligned}$$

The analysis above and the computer simulation example shown in Fig. 2a show that the average distance travelled along the intended direction increases in direct proportion to the number of steps taken. Thus, with the use of a compass, the animal can travel arbitrarily far away from its starting point.

The results derived above are completely valid for the general elementary step. In fact, applying the Central Limit

Table 2 Comparison of various types of directed walks

Properties of directed walks	Expected path shape	Deviation from axis of intended locomotion	Theoretical limit to expected path length
Simple ADW	Straight	No	No
Simple IDW	Straight	No	Yes
General unbiased ADW	Straight	Yes	No
General unbiased IDW	Straight	Yes	Yes
General ADW	Straight	Yes	No
General IDW	Logarithmic spiral	Yes	Yes

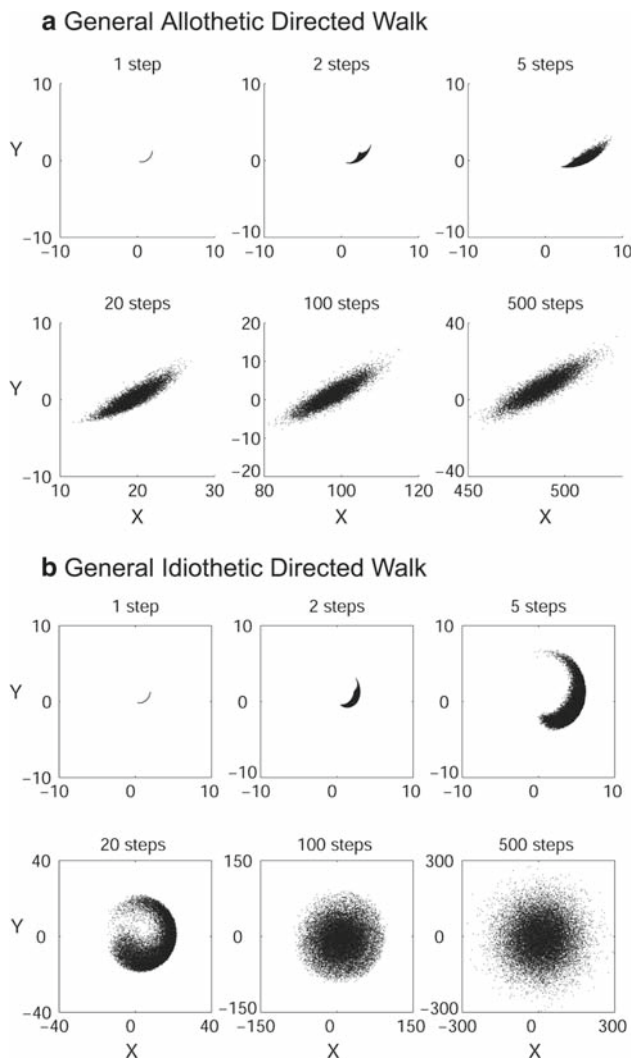


Fig. 2 **a** Computer simulations of the results of general compass-based navigation, showing the end points of 20,000 simulated journeys after 1 step, 2 steps, 5 steps, 20 steps, 100 steps and 500 steps. At every step, the axis of intended locomotion is along the abscissa. All 20,000 simulated journeys began at the origin (0,0). The hypothetical locomotory unit was described in detail in Sect. 5. Note the change in scale of positions of the simulated agents. **b** Computer simulations of the results of general navigation without a compass, showing the end points of 20,000 simulated journeys (other parameters as in part **a**)

Theorem, it is possible to show that the asymptotic positional distribution will be a bivariate Gaussian (see supplementary Sect. A2.2 for further details). Although all bivariate Gaussian functions have elliptical isodensity curves, the axis of intended locomotion may not coincide with either the long (major) or short (minor) axis of the ellipse. In order to calculate the orientation of the elliptical axes, the covariance of the X and Y displacement is needed:

$$\begin{aligned} \text{Cov}(X_1, Y_1) &= E(X_1 Y_1) - E(X_1) E(Y_1) \\ &= E\left(L^2 \cos(\Delta^a + \Delta_{\text{bias}}^a) \sin(\Delta^a + \Delta_{\text{bias}}^a)\right) \end{aligned}$$

$$\begin{aligned} &-E\left(L \cos(\Delta^a + \Delta_{\text{bias}}^a)\right) \\ &E\left(L \sin(\Delta^a + \Delta_{\text{bias}}^a)\right) \\ &= \dots = \cos(2\Delta_{\text{bias}}^a) \omega_a + \sin(2\Delta_{\text{bias}}^a) \\ &(\varphi_a - \mu_2/2) - (\mathbf{p}_1 \mathbf{p}_2^a) (\mathbf{p}_1 \mathbf{p}_2^b). \end{aligned}$$

Suppose the original Cartesian axes are called X_0 and Y_0 , and that the short (minor) and long (major) axes of the elliptical bivariate Gaussian are X and Y. The transformation between the two coordinate systems may be written in matrix form as follows:

$$\begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \cos \phi & -\sin \phi \\ \sin \phi & \cos \phi \end{bmatrix} \begin{bmatrix} x_0 \\ y_0 \end{bmatrix}$$

Thus the positional variances along the rotated axes would be

$$\begin{aligned} V(X) &= V(X_0 \cos \phi - Y_0 \sin \phi) \\ &= (\cos^2 \phi) V(X_0) + (\sin^2 \phi) V(Y_0) \\ &\quad - 2(\cos \phi)(\sin \phi) \text{Cov}(X_0, Y_0) \end{aligned}$$

$$\begin{aligned} V(Y) &= V(X_0 \sin \theta + Y_0 \cos \theta) \\ &= (\sin^2 \theta) V(X_0) + (\cos^2 \theta) V(Y_0) \\ &\quad + 2(\cos \theta)(\sin \theta) \text{Cov}(X_0, Y_0) \end{aligned}$$

The rotational angle ϕ , which minimizes/maximizes the respective positional variances can be found through differentiation. The value is given by

$$\phi = \frac{1}{2} \tan^{-1} \left(\frac{2\text{Cov}(X_0, Y_0)}{V(Y_0) - V(X_0)} \right) \pm k\pi \quad \text{where } k \in \{\mathbb{Z} > 0\}.$$

Thus the asymptotic positional probability density function would be

$$\begin{aligned} \text{pdf}(x_0, y_0) &= \frac{1}{2\pi \sigma_x \sigma_y} \\ &\times e^{-\frac{1}{2} \left(\frac{(x_0 \cos \phi - y_0 \sin \phi - n\mathbf{p}_1 \mathbf{p}_2^a)^2}{\sigma_x^2} + \frac{(x_0 \sin \phi + y_0 \cos \phi - n\mathbf{p}_1 \mathbf{p}_2^b)^2}{\sigma_y^2} \right)}, \end{aligned}$$

where

$$\begin{aligned} \sigma_x &= \sqrt{(\cos^2 \phi) V(X_0) + (\sin^2 \phi) V(Y_0) - 2(\cos \phi)(\sin \phi) \text{Cov}(X_0, Y_0)}, \\ \sigma_y &= \sqrt{(\sin^2 \phi) V(X_0) + (\cos^2 \phi) V(Y_0) + 2(\cos \phi)(\sin \phi) \text{Cov}(X_0, Y_0)}, \\ \text{Cov}(X_0, Y_0) &= n \left[\cos(2\Delta_{\text{bias}}^a) \omega_a + \sin(2\Delta_{\text{bias}}^a) (\varphi_a - \mu_2/2) \right. \\ &\quad \left. - (\mathbf{p}_1 \mathbf{p}_2^a) (\mathbf{p}_1 \mathbf{p}_2^b) \right], \end{aligned}$$

$$V(X_0) = V(X_{\text{total}}) \quad \text{and} \quad V(Y_0) = V(Y_{\text{total}}).$$

This form of the density function effectively rotates the frame of reference to coincide with the major and minor axes of the elliptical bivariate Gaussian. Figure 3a shows the rotational transformation graphically.

A more conventional method would be to account for the rotation directly through the covariance matrix. The general multivariate normal distribution can be written as

$$\text{pdf}(\mathbf{z}) = \frac{1}{(2\pi)^{N/2} \sqrt{|\Sigma|}} e^{-\frac{1}{2}(\mathbf{z}-\boldsymbol{\mu})^T \Sigma^{-1}(\mathbf{z}-\boldsymbol{\mu})}.$$

For the current example, $N=2$

$$\mathbf{z} = \begin{bmatrix} x \\ y \end{bmatrix} \text{ and } \boldsymbol{\mu} = \begin{bmatrix} \mu_X \\ \mu_Y \end{bmatrix}.$$

$$\begin{aligned} E(X_{\text{total}}^2) &= (\varphi_a - \frac{\mu_2}{2}) \frac{(2\gamma_{a,b}-1)^{n-1}}{2\gamma_{a,b}-2} + \frac{n\mu_2}{2} - \frac{\omega\chi_{a,b}}{\gamma_{a,b}-1} \\ &\times \left[(n-1)(2\gamma_{a,b}-1)^{n-1} - \frac{(2\gamma_{a,b}-1)^{n-1}-1}{2\gamma_{a,b}-2} \right] + \frac{1}{\beta_{a,b}-1} \\ &\times \left\{ \left[\rho_a(\eta_{a,b} + \iota_{a,b}) - \varepsilon_a(\varpi_{cs} - \varpi_{sc}) \right] \left(\frac{\beta_{a,b}^n - \beta_{a,b}}{\beta_{a,b}-1} - n + 1 \right) + \left[\rho_a(\eta_{a,b} - \iota_{a,b}) - \varepsilon_a(\varpi_{cs} + \varpi_{sc}) \right] \left[\frac{\beta_{a,b}(2\gamma_{a,b}-1)^{n-1} - \beta_{a,b}^n}{(2\gamma_{a,b}-1) - \beta_{a,b}} - \frac{(2\gamma_{a,b}-1)^{n-1}-1}{2\gamma_{a,b}-2} \right] \right. \\ &\left. - 2\chi_{a,b} \left(\rho_a(\varpi_{cs} + \varpi_{sc}) + \varepsilon_a(\eta_{a,b} - \iota_{a,b}) \right) \left[\frac{(n-2)\beta_{a,b}(2\gamma_{a,b}-1)^{n-2}}{2\gamma_{a,b}-1-\beta_{a,b}} - \frac{\beta_{a,b}^2((2\gamma_{a,b}-1)^{n-2} - \beta_{a,b}^{n-2})}{(2\gamma_{a,b}-1-\beta_{a,b})^2} - \frac{(n-2)}{2\gamma_{a,b}-2} (2\gamma_{a,b}-1)^{n-2} + \frac{(2\gamma_{a,b}-1)^{n-2}-1}{(2\gamma_{a,b}-2)^2} \right] \right\}. \\ E(Y_{\text{total}}^2) &= (\frac{\mu_2}{2} - \varphi_a) \frac{(2\gamma_{a,b}-1)^{n-1}}{2\gamma_{a,b}-2} + \frac{n\mu_2}{2} + \frac{\omega\chi_{a,b}}{\gamma_{a,b}-1} \left[(n-1)(2\gamma_{a,b}-1)^{n-1} - \frac{(2\gamma_{a,b}-1)^{n-1}-1}{2\gamma_{a,b}-2} \right] + \frac{1}{\beta_{a,b}-1} \\ &\times \left\{ \left[\rho_a(\eta_{a,b} + \iota_{a,b}) - \varepsilon_a(\varpi_{cs} - \varpi_{sc}) \right] \left(\frac{\beta_{a,b}^n - \beta_{a,b}}{\beta_{a,b}-1} - n + 1 \right) - \left[\rho_a(\eta_{a,b} - \iota_{a,b}) - \varepsilon_a(\varpi_{cs} + \varpi_{sc}) \right] \left[\frac{\beta_{a,b}(2\gamma_{a,b}-1)^{n-1} - \beta_{a,b}^n}{(2\gamma_{a,b}-1) - \beta_{a,b}} - \frac{(2\gamma_{a,b}-1)^{n-1}-1}{2\gamma_{a,b}-2} \right] \right. \\ &\left. + 2\chi_{a,b} \left(\rho_a(\varpi_{cs} + \varpi_{sc}) + \varepsilon_a(\eta_{a,b} - \iota_{a,b}) \right) \left[\frac{(n-2)\beta_{a,b}(2\gamma_{a,b}-1)^{n-2}}{2\gamma_{a,b}-1-\beta_{a,b}} - \frac{\beta_{a,b}^2((2\gamma_{a,b}-1)^{n-2} - \beta_{a,b}^{n-2})}{(2\gamma_{a,b}-1-\beta_{a,b})^2} - \frac{(n-2)}{2\gamma_{a,b}-2} (2\gamma_{a,b}-1)^{n-2} + \frac{(2\gamma_{a,b}-1)^{n-2}-1}{(2\gamma_{a,b}-2)^2} \right] \right\}. \end{aligned}$$

The covariance matrix is

$$\Sigma = \begin{bmatrix} V(X_0) & \text{Cov}(X_0, Y_0) \\ \text{Cov}(Y_0, X_0) & V(Y_0) \end{bmatrix}.$$

The resulting probability density function is of course identical to the previous, but expressed in a different reference frame.

6.3 A general unbiased idiotic directed walk

Consider now the case where the animal attempts to travel along a straight line *without* the use of an external direction reference, i.e., no compass (an IDW using the current nomenclature). The derivations for a generalized step are similar in approach to the case of the simple elementary step (Cheung et al. 2007) but yield slightly different results. The most significant difference between a simple IDW and a general unbiased IDW is that, in the latter case, the component of displacement perpendicular to the axis of intended locomotion is, in general, not zero. In other words, the expected path drifts away from the axis of intended locomotion much

like the case with a compass (general ADW). As before, the cause is an (unbiased) asymmetry in locomotion due to the way in which angular and linear displacement are statistically interdependent in the mathematically general case.

$$E(X_{\text{total}}) = \sum_{t=1}^n \rho_a \beta_{a,b}^{t-1} = \rho_a \frac{\beta_{a,b}^n - 1}{\beta_{a,b} - 1}$$

$$E(Y_{\text{total}}) = \sum_{t=1}^n \varepsilon_a \beta_{a,b}^{t-1} = \varepsilon_a \frac{\beta_{a,b}^n - 1}{\beta_{a,b} - 1}$$

The second positional moments are more complicated than for the simple elementary step but the resemblance in form is evident. For clarity, only the second raw positional moments are listed here.

6.4 A general idiotic directed walk

In the presence of bias, the derivation of the expected path is more complicated than for the case without bias. Note that the first step is identical to the case with a compass (e.g. first panel of Fig. 2a, b). The first positional moments for the general IDW are reported below. Details of the derivations are found in supplementary Sects. A3.1 and A3.2.

$$E(X_{\text{total}}) = \left(\frac{\mathbf{p}_1 \mathbf{p}_2^a + i \mathbf{p}_1 \mathbf{p}_2^b}{2} \right) \left(\frac{1 - \beta_{a,b}^n \gamma^n}{1 - \beta_{a,b}^n \gamma} \right) + \left(\frac{\mathbf{p}_1 \mathbf{p}_2^a - i \mathbf{p}_1 \mathbf{p}_2^b}{2} \right) \left(\frac{1 - \beta_{a,b}^n \gamma^{-n}}{1 - \beta_{a,b}^n \gamma^{-1}} \right)$$

$$E(Y_{\text{total}}) = \left(\frac{\mathbf{p}_1 \mathbf{p}_2^b - i \mathbf{p}_1 \mathbf{p}_2^a}{2} \right) \left(\frac{1 - \beta_{a,b}^n \gamma^n}{1 - \beta_{a,b}^n \gamma} \right) + \left(\frac{\mathbf{p}_1 \mathbf{p}_2^b + i \mathbf{p}_1 \mathbf{p}_2^a}{2} \right) \left(\frac{1 - \beta_{a,b}^n \gamma^{-n}}{1 - \beta_{a,b}^n \gamma^{-1}} \right)$$

Despite the increased complexity in form, the results bear resemblance to the simple elementary step without a compass

(Cheung et al. 2007). Not surprisingly, there is also an asymptotic expected displacement along and perpendicular to the axis of intended locomotion, as the number of steps increases.

$$\begin{aligned} \lim_{n \rightarrow \infty} E(X_{\text{total}}) &= \left(\frac{\mathbf{p}_1 \mathbf{p}_2^a + i \mathbf{p}_1 \mathbf{p}_2^b}{2} \right) \left(\frac{1}{1 - \beta_{a,b} \gamma} \right) \\ &+ \left(\frac{\mathbf{p}_1 \mathbf{p}_2^a - i \mathbf{p}_1 \mathbf{p}_2^b}{2} \right) \left(\frac{1}{1 - \beta_{a,b} \gamma^{-1}} \right) \\ &= \mathbf{p}_1 \mathbf{p}_2^a \left(\frac{1 - \beta_{a,b} \cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b)}{1 - 2\beta_{a,b} \cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) + \beta_{a,b}^2} \right) - \mathbf{p}_1 \mathbf{p}_2^b \\ &\times \left(\frac{\beta_{a,b} \sin(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b)}{1 - 2\beta_{a,b} \cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) + \beta_{a,b}^2} \right) \\ \lim_{n \rightarrow \infty} E(Y_{\text{total}}) &= \left(\frac{\mathbf{p}_1 \mathbf{p}_2^b - i \mathbf{p}_1 \mathbf{p}_2^a}{2} \right) \left(\frac{1}{1 - \beta_{a,b} \gamma} \right) \\ &+ \left(\frac{\mathbf{p}_1 \mathbf{p}_2^b + i \mathbf{p}_1 \mathbf{p}_2^a}{2} \right) \left(\frac{1}{1 - \beta_{a,b} \gamma^{-1}} \right) \\ &= \mathbf{p}_1 \mathbf{p}_2^b \left(\frac{1 - \beta_{a,b} \cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b)}{1 - 2\beta_{a,b} \cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) + \beta_{a,b}^2} \right) \\ &+ \mathbf{p}_1 \mathbf{p}_2^a \left(\frac{\beta_{a,b} \sin(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b)}{1 - 2\beta_{a,b} \cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) + \beta_{a,b}^2} \right) \end{aligned}$$

Given the curvature of the expected path, the asymptotic expected position may not be the maximum expected displacement. For example, it is clear from Fig 3c that the mean position following 500 steps was not the furthest reached during the journey either along or perpendicular to the axis of intended locomotion. Section 6.5 provides details of the expected path itself.

As for the simple IDW of Cheung et al. (2007), the second positional moments for the general IDW are much more complicated in form than those of the first positional moments. For the general elementary step, the complexity is compounded by the fact that error components are no longer assumed to be statistically independent. Consequently, there are many more irreducible terms (whose definitions were listed in Sect. 5.1).

The second positional raw moments for the general IDW are reported below. Details of the derivations are found in supplementary Sects. A3.3 and A3.4.

$$\begin{aligned} E(X_{\text{total}}^2) &= \frac{n\mu_2}{2} + \left(\frac{\mathbf{m}_4 \mathbf{m}_2^a + i \mathbf{m}_4 \mathbf{m}_2^b}{2} \right) \left(\frac{\gamma^2 - \gamma^{2n} (2\gamma_{a,b} - 1)^n}{1 - \gamma^2 (2\gamma_{a,b} - 1)} \right) \\ &+ \left(\frac{\mathbf{m}_4 \mathbf{m}_2^a - i \mathbf{m}_4 \mathbf{m}_2^b}{2} \right) \left(\frac{\gamma^{-2} - \gamma^{-2n} (2\gamma_{a,b} - 1)^n}{1 - \gamma^{-2} (2\gamma_{a,b} - 1)} \right) \\ &- \chi_{a,b} (\mathbf{m}_4 \mathbf{m}_2^b - i \mathbf{m}_4 \mathbf{m}_2^a) \\ &\times \left(\frac{\gamma^4 - n \gamma^{2n-2} (2\gamma_{a,b} - 1)^{n-1} + (n-1) \gamma^{2n} (2\gamma_{a,b} - 1)^n}{(1 - \gamma^2 (2\gamma_{a,b} - 1))^2} \right) \end{aligned}$$

$$\begin{aligned} &- \chi_{a,b} (\mathbf{m}_4 \mathbf{m}_2^b + i \mathbf{m}_4 \mathbf{m}_2^a) \\ &\times \left(\frac{\gamma^{-4} - n \gamma^{2-2n} (2\gamma_{a,b} - 1)^{n-1} + (n-1) \gamma^{-2n} (2\gamma_{a,b} - 1)^n}{(1 - \gamma^{-2} (2\gamma_{a,b} - 1))^2} \right) \\ &+ \frac{\mathbf{m}_1 \mathbf{m}_0^a - i \mathbf{m}_1 \mathbf{m}_0^b}{2(1 - \gamma \beta_{a,b})} \left((n-1) \gamma - \frac{\gamma^2 \beta_{a,b} - \gamma^{n+1} \beta_{a,b}^n}{1 - \gamma \beta_{a,b}} \right) \\ &+ \frac{\mathbf{m}_1 \mathbf{m}_0^a + i \mathbf{m}_1 \mathbf{m}_0^b}{2(1 - \gamma^{-1} \beta_{a,b})} \left((n-1) \gamma^{-1} - \frac{\gamma^{-2} \beta_{a,b} - \gamma^{-n-1} \beta_{a,b}^n}{1 - \gamma^{-1} \beta_{a,b}} \right) \\ &+ \frac{\mathbf{m}_3^a [\mathbf{m}_1 \mathbf{m}_2^a \mathbf{m}_1 \mathbf{m}_2^b]^T - i \mathbf{m}_3^a [-\mathbf{m}_1 \mathbf{m}_2^b \mathbf{m}_1 \mathbf{m}_2^a]^T}{2(1 - \gamma \beta_{a,b})} \\ &\times \left(\frac{\gamma^3 - \gamma^{2n+1} (2\gamma_{a,b} - 1)^{n-1}}{1 - \gamma^2 (2\gamma_{a,b} - 1)} \right) \\ &- \frac{\gamma^{n+2} \beta_{a,b}^n - \gamma^{2n+1} (2\gamma_{a,b} - 1)^{n-1} \beta_{a,b}}{\beta_{a,b} - \gamma (2\gamma_{a,b} - 1)} \\ &\chi_{a,b} \left\{ \mathbf{m}_3^b [\mathbf{m}_1 \mathbf{m}_2^a \mathbf{m}_1 \mathbf{m}_2^b]^T - i \mathbf{m}_3^b [-\mathbf{m}_1 \mathbf{m}_2^b \mathbf{m}_1 \mathbf{m}_2^a]^T \right\} \\ &\frac{1 - \gamma \beta_{a,b}}{\left(\frac{\gamma^5 - \gamma^{2n+1} (2\gamma_{a,b} - 1)^{n-2}}{(1 - \gamma^2 (2\gamma_{a,b} - 1))^2} - \frac{(n-2) \gamma^{2n+1} (2\gamma_{a,b} - 1)^{n-2}}{1 - \gamma^2 (2\gamma_{a,b} - 1)} \right)} \\ &\times \left(\frac{\gamma^{n+3} \beta_{a,b}^n - \gamma^{2n+1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}^2 + (n-2) \gamma^{2n+1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}}{(\beta_{a,b} - \gamma (2\gamma_{a,b} - 1))^2} + \frac{(n-2) \gamma^{2n+1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}}{\beta_{a,b} - \gamma (2\gamma_{a,b} - 1)} \right) \\ &+ \frac{\mathbf{m}_3^a [\mathbf{m}_1 \mathbf{m}_2^a \mathbf{m}_1 \mathbf{m}_2^b]^T + i \mathbf{m}_3^a [-\mathbf{m}_1 \mathbf{m}_2^b \mathbf{m}_1 \mathbf{m}_2^a]^T}{2(1 - \gamma^{-1} \beta_{a,b})} \\ &\times \left(\frac{\gamma^{-3} - \gamma^{-2n-1} (2\gamma_{a,b} - 1)^{n-1}}{1 - \gamma^{-2} (2\gamma_{a,b} - 1)} \right) \\ &- \frac{\gamma^{-n-2} \beta_{a,b}^n - \gamma^{-2n-1} (2\gamma_{a,b} - 1)^{n-1} \beta_{a,b}}{\beta_{a,b} - \gamma^{-1} (2\gamma_{a,b} - 1)} \\ &\chi_{a,b} \left\{ \mathbf{m}_3^b [\mathbf{m}_1 \mathbf{m}_2^a \mathbf{m}_1 \mathbf{m}_2^b]^T + i \mathbf{m}_3^b [-\mathbf{m}_1 \mathbf{m}_2^b \mathbf{m}_1 \mathbf{m}_2^a]^T \right\} \\ &\frac{1 - \gamma^{-1} \beta_{a,b}}{\left(\frac{\gamma^{-5} - \gamma^{-2n-1} (2\gamma_{a,b} - 1)^{n-2}}{(1 - \gamma^{-2} (2\gamma_{a,b} - 1))^2} - \frac{(n-2) \gamma^{-2n-1} (2\gamma_{a,b} - 1)^{n-2}}{1 - \gamma^{-2} (2\gamma_{a,b} - 1)} \right)} \\ &\times \left(\frac{\gamma^{-n-3} \beta_{a,b}^n - \gamma^{-2n-1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}^2 + (n-2) \gamma^{-2n-1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}}{(\beta_{a,b} - \gamma^{-1} (2\gamma_{a,b} - 1))^2} + \frac{(n-2) \gamma^{-2n-1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}}{\beta_{a,b} - \gamma^{-1} (2\gamma_{a,b} - 1)} \right) \end{aligned}$$

$$\begin{aligned} E(Y_{\text{total}}^2) &= \frac{n\mu_2}{2} - \left(\frac{\mathbf{m}_4 \mathbf{m}_2^a + i \mathbf{m}_4 \mathbf{m}_2^b}{2} \right) \\ &\times \left(\frac{\gamma^2 - \gamma^{2n} (2\gamma_{a,b} - 1)^n}{1 - \gamma^2 (2\gamma_{a,b} - 1)} \right) - \left(\frac{\mathbf{m}_4 \mathbf{m}_2^a - i \mathbf{m}_4 \mathbf{m}_2^b}{2} \right) \\ &\times \left(\frac{\gamma^{-2} - \gamma^{-2n} (2\gamma_{a,b} - 1)^n}{1 - \gamma^{-2} (2\gamma_{a,b} - 1)} \right) + \chi_{a,b} (\mathbf{m}_4 \mathbf{m}_2^b - i \mathbf{m}_4 \mathbf{m}_2^a) \\ &\times \left(\frac{\gamma^4 - n \gamma^{2n-2} (2\gamma_{a,b} - 1)^{n-1} + (n-1) \gamma^{2n} (2\gamma_{a,b} - 1)^n}{(1 - \gamma^2 (2\gamma_{a,b} - 1))^2} \right) \\ &+ \chi_{a,b} (\mathbf{m}_4 \mathbf{m}_2^b + i \mathbf{m}_4 \mathbf{m}_2^a) \\ &\times \left(\frac{\gamma^{-4} - n \gamma^{2-2n} (2\gamma_{a,b} - 1)^{n-1} + (n-1) \gamma^{-2n} (2\gamma_{a,b} - 1)^n}{(1 - \gamma^{-2} (2\gamma_{a,b} - 1))^2} \right) \\ &+ \frac{\mathbf{m}_1 \mathbf{m}_0^a - i \mathbf{m}_1 \mathbf{m}_0^b}{2(1 - \gamma \beta_{a,b})} \left((n-1) \gamma - \frac{\gamma^2 \beta_{a,b} - \gamma^{n+1} \beta_{a,b}^n}{1 - \gamma \beta_{a,b}} \right) \end{aligned}$$

$$\begin{aligned}
 & + \frac{\mathbf{m}_1 \mathbf{m}_0^a + i \mathbf{m}_1 \mathbf{m}_0^b}{2(1 - \Upsilon^{-1} \beta_{a,b})} \left((n-1) \Upsilon^{-1} - \frac{\Upsilon^{-2} \beta_{a,b} - \Upsilon^{-n-1} \beta_{a,b}^n}{1 - \Upsilon^{-1} \beta_{a,b}} \right) \\
 & - \frac{\mathbf{m}_3^a [\mathbf{m}_1 \mathbf{m}_2^a \mathbf{m}_1 \mathbf{m}_2^a]^T - i \mathbf{m}_3^a [-\mathbf{m}_1 \mathbf{m}_2^b \mathbf{m}_1 \mathbf{m}_2^a]^T}{2(1 - \Upsilon \beta_{a,b})} \\
 & \times \left(\frac{\Upsilon^3 - \Upsilon^{2n+1} (2\gamma_{a,b} - 1)^{n-1}}{1 - \Upsilon^2 (2\gamma_{a,b} - 1)} \right. \\
 & \left. - \frac{\Upsilon^{n+2} \beta_{a,b}^n - \Upsilon^{2n+1} (2\gamma_{a,b} - 1)^{n-1} \beta_{a,b}}{\beta_{a,b} - \Upsilon (2\gamma_{a,b} - 1)} \right) \\
 & + \frac{\chi_{a,b} \left\{ \mathbf{m}_3^b [\mathbf{m}_1 \mathbf{m}_2^a \mathbf{m}_1 \mathbf{m}_2^b]^T - i \mathbf{m}_3^b [-\mathbf{m}_1 \mathbf{m}_2^b \mathbf{m}_1 \mathbf{m}_2^a]^T \right\}}{1 - \Upsilon \beta_{a,b}} \\
 & \times \left(\frac{\Upsilon^5 - \Upsilon^{2n+1} (2\gamma_{a,b} - 1)^{n-2}}{(1 - \Upsilon^2 (2\gamma_{a,b} - 1))^2} - \frac{(n-2) \Upsilon^{2n+1} (2\gamma_{a,b} - 1)^{n-2}}{1 - \Upsilon^2 (2\gamma_{a,b} - 1)} \right. \\
 & \left. - \frac{\Upsilon^{n+3} \beta_{a,b}^n - \Upsilon^{2n+1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}^2}{(\beta_{a,b} - \Upsilon (2\gamma_{a,b} - 1))^2} + \frac{(n-2) \Upsilon^{2n+1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}}{\beta_{a,b} - \Upsilon (2\gamma_{a,b} - 1)} \right) \\
 & - \frac{\mathbf{m}_3^a [\mathbf{m}_1 \mathbf{m}_2^a \mathbf{m}_1 \mathbf{m}_2^b]^T + i \mathbf{m}_3^a [-\mathbf{m}_1 \mathbf{m}_2^b \mathbf{m}_1 \mathbf{m}_2^a]^T}{2(1 - \Upsilon^{-1} \beta_{a,b})} \\
 & \times \left(\frac{\Upsilon^{-3} - \Upsilon^{-2n-1} (2\gamma_{a,b} - 1)^{n-1}}{1 - \Upsilon^{-2} (2\gamma_{a,b} - 1)} \right. \\
 & \left. - \frac{\Upsilon^{-n-2} \beta_{a,b}^n - \Upsilon^{-2n-1} (2\gamma_{a,b} - 1)^{n-1} \beta_{a,b}}{\beta_{a,b} - \Upsilon^{-1} (2\gamma_{a,b} - 1)} \right) \\
 & + \frac{\chi_{a,b} \left\{ \mathbf{m}_3^b [\mathbf{m}_1 \mathbf{m}_2^a \mathbf{m}_1 \mathbf{m}_2^b]^T + i \mathbf{m}_3^b [-\mathbf{m}_1 \mathbf{m}_2^b \mathbf{m}_1 \mathbf{m}_2^a]^T \right\}}{1 - \Upsilon^{-1} \beta_{a,b}} \\
 & \times \left(\frac{\Upsilon^{-5} - \Upsilon^{-2n-1} (2\gamma_{a,b} - 1)^{n-2}}{(1 - \Upsilon^{-2} (2\gamma_{a,b} - 1))^2} - \frac{(n-2) \Upsilon^{-2n-1} (2\gamma_{a,b} - 1)^{n-2}}{1 - \Upsilon^{-2} (2\gamma_{a,b} - 1)} \right. \\
 & \left. - \frac{\Upsilon^{-n-3} \beta_{a,b}^n - \Upsilon^{-2n-1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}^2}{(\beta_{a,b} - \Upsilon^{-1} (2\gamma_{a,b} - 1))^2} + \frac{(n-2) \Upsilon^{-2n-1} (2\gamma_{a,b} - 1)^{n-2} \beta_{a,b}}{\beta_{a,b} - \Upsilon^{-1} (2\gamma_{a,b} - 1)} \right).
 \end{aligned}$$

Given the prevalence of usage of the correlated random walk as a model of animal dispersal, it is pertinent to write the measure of dispersal, $E(R^2)$, for the general elementary step. It is more complicated than for a simple elementary step (Kareiva and Shigesada 1983) but is considerably simpler in form than the second positional moment either along or perpendicular to the axis of intended locomotion.

$$\begin{aligned}
 E(R_{\text{total}}^2) &= E(X_{\text{total}}^2 + Y_{\text{total}}^2) = E(X_{\text{total}}^2) + E(Y_{\text{total}}^2) \\
 &= n\mu_2 + \frac{\mathbf{m}_1 \mathbf{m}_0^a - i \mathbf{m}_1 \mathbf{m}_0^b}{(1 - \Upsilon \beta_{a,b})} \left((n-1) \Upsilon - \frac{\Upsilon^2 \beta_{a,b} - \Upsilon^{n+1} \beta_{a,b}^n}{1 - \Upsilon \beta_{a,b}} \right) \\
 &+ \frac{\mathbf{m}_1 \mathbf{m}_0^a + i \mathbf{m}_1 \mathbf{m}_0^b}{(1 - \Upsilon^{-1} \beta_{a,b})} \left((n-1) \Upsilon^{-1} - \frac{\Upsilon^{-2} \beta_{a,b} - \Upsilon^{-n-1} \beta_{a,b}^n}{1 - \Upsilon^{-1} \beta_{a,b}} \right) \\
 &= n \left(\mu_2 + \Upsilon \frac{\mathbf{m}_1 \mathbf{m}_0^a - i \mathbf{m}_1 \mathbf{m}_0^b}{(1 - \Upsilon \beta_{a,b})} + \Upsilon^{-1} \frac{\mathbf{m}_1 \mathbf{m}_0^a + i \mathbf{m}_1 \mathbf{m}_0^b}{(1 - \Upsilon^{-1} \beta_{a,b})} \right) \\
 &- \frac{\mathbf{m}_1 \mathbf{m}_0^a - i \mathbf{m}_1 \mathbf{m}_0^b}{(1 - \Upsilon \beta_{a,b})} \left(\Upsilon + \frac{\Upsilon^2 \beta_{a,b} - \Upsilon^{n+1} \beta_{a,b}^n}{1 - \Upsilon \beta_{a,b}} \right) \\
 &- \frac{\mathbf{m}_1 \mathbf{m}_0^a + i \mathbf{m}_1 \mathbf{m}_0^b}{(1 - \Upsilon^{-1} \beta_{a,b})} \left(\Upsilon^{-1} + \frac{\Upsilon^{-2} \beta_{a,b} - \Upsilon^{-n-1} \beta_{a,b}^n}{1 - \Upsilon^{-1} \beta_{a,b}} \right).
 \end{aligned}$$

Figure 5b shows how the two variance functions of the example IDW increase with the step number. This is in contrast to Fig. 5a which shows the equivalent ADW. Like the results of Cheung et al. (2007), the lack of an allothetic directional cue (i.e. a compass) tends to lead to larger variances (noisier navigation), but although both functions asymptotically tend to parallel linear functions, in the case of general elementary steps, they may cross those linear functions and even each other (see Fig. 5b).

As alluded to already, the probability density function for the location of the end point will approach a circularly-symmetric Gaussian distribution, as evident in the lower right-hand panel of Fig. 2b and also in Fig. 4c.

Careful examination of the variance functions show that asymptotic gradients can be found by setting all terms with n in the index to zero, and all terms which do not possess n form the constants. Therefore, the variance functions asymptote to the same linear function of the step number n so that

$$\begin{aligned}
 \lim_{n \rightarrow \infty} \frac{dV(X_{\text{total}})}{dn} &= \lim_{n \rightarrow \infty} \frac{dV(Y_{\text{total}})}{dn} = \frac{\mu_2}{2} \\
 &+ \frac{\mathbf{m}_1 \mathbf{m}_0^a (\cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) - \beta_{a,b}) + \mathbf{m}_1 \mathbf{m}_0^b \sin(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b)}{1 - 2\beta_{a,b} \cos(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) + \beta_{a,b}^2}.
 \end{aligned}$$

Similar to the asymptotic case of the compassless directed walk with a simple elementary step (Cheung et al. 2007), the variance functions are again essentially stationary and bounded above and below by linear functions, satisfying the strongly-mixing (α -mixing) condition (Rosenblatt 1956). Hence, the central limit theorem may be applied and we conclude that in the limit as the number of steps becomes large, the variables X_{total} and Y_{total} will be (approximately) normally distributed, i.e.,

$$\lim_{n \rightarrow \infty} \frac{X_{\text{total}} - E(X_{\text{total}})}{\sqrt{V(X_{\text{total}})}} \sim N(0, 1)$$

and

$$\lim_{n \rightarrow \infty} \frac{Y_{\text{total}} - E(Y_{\text{total}})}{\sqrt{V(Y_{\text{total}})}} \sim N(0, 1).$$

Furthermore, we note that the asymptotic gradients of the variance functions are identical. This means that the ratio of the two variances will approach unity as the number of steps n increases. Since the angular error distribution approaches a flat distribution in the limit (radially symmetric), the covariance of the X and Y displacements asymptotically goes to zero, i.e.,

$$\lim_{n \rightarrow \infty} \text{Cov}(X_{\text{total}}, Y_{\text{total}}) = 0.$$

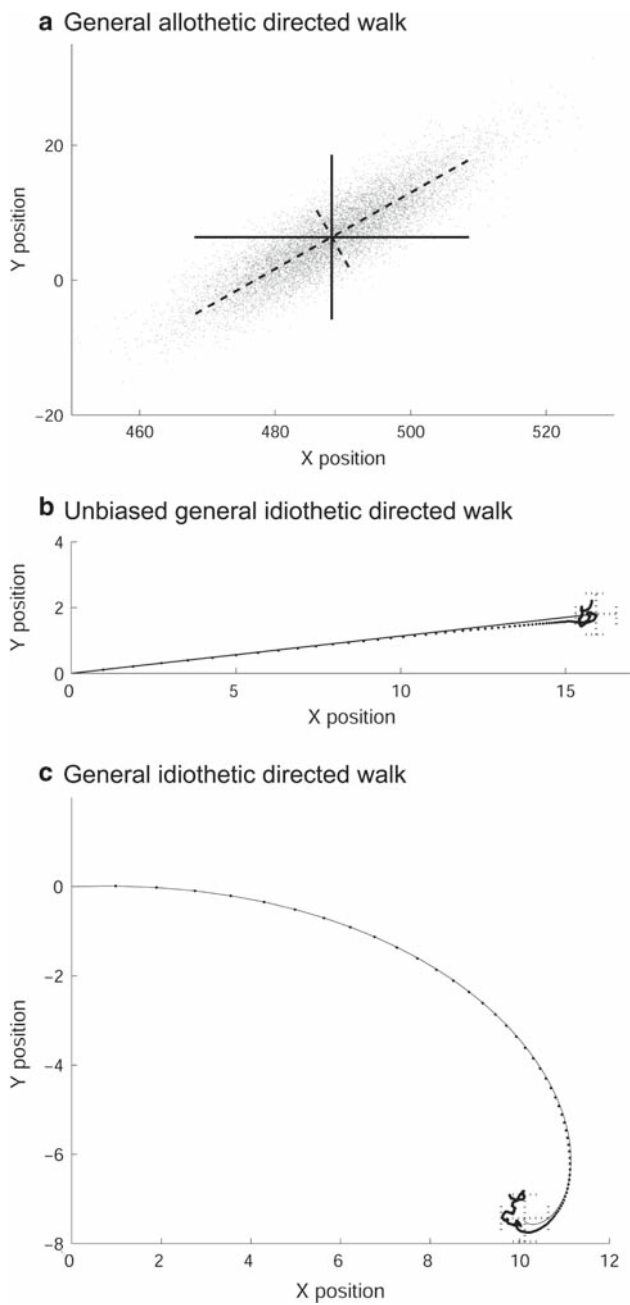


Fig. 3 Comparing simulation and derived results. **a** The distribution of 20,000 agents following 500 steps of directed walk with a compass is shown. This corresponds to the last panel of Fig. 2a. Two pairs of derived axes are shown. The first represents \pm two standard deviations either side of the mean along and perpendicular to the axis of intended locomotion. The second represents \pm two standard deviations either side of the mean along the long and short axes of the elliptical distribution. **b** The expected path for an unbiased directed walk without a compass (black line) and mean path from simulation (black dots). The whiskers shown at the end of the expected path correspond to one standard error of the mean. **c** As per **b** except bias is present. Details of the locomotor unit are described in methods (Sect. 5.2)

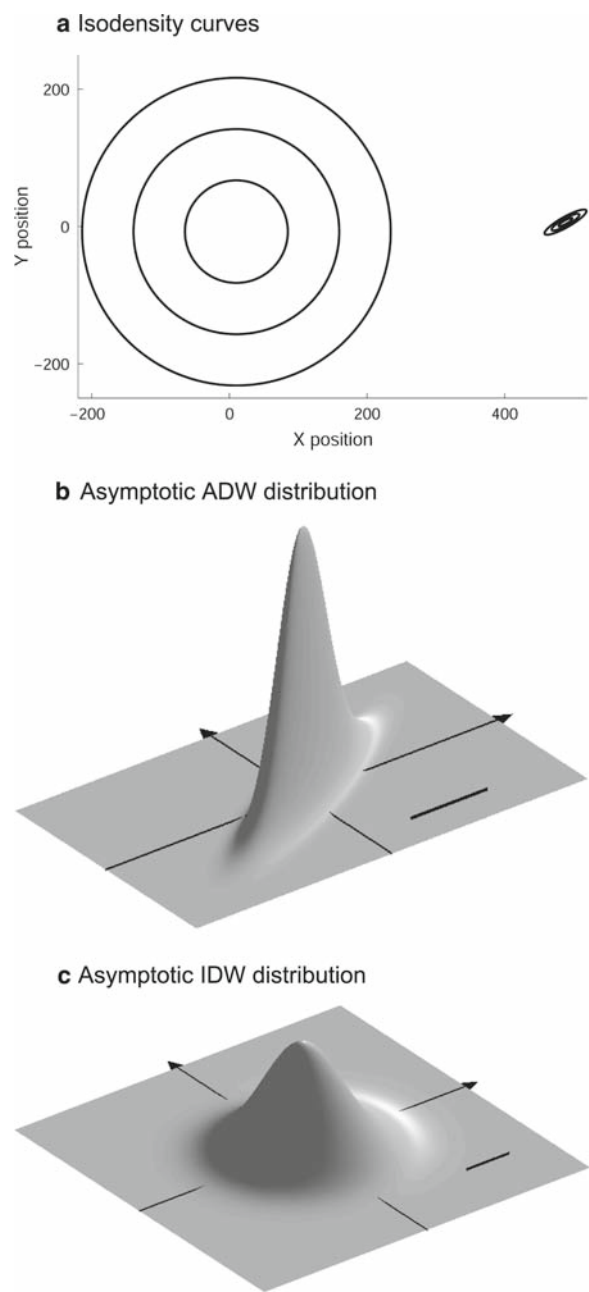


Fig. 4 Comparison of probability density functions following a 500 step directed walk in the presence and absence of a compass. Locomotion was assumed to be described by the hypothetical general elementary step described in the text. **a** The isodensity functions for 1, 2 and 3 standard deviations from the final expected position are shown for the two probability density functions. **b** The positional probability density function, using a compass. The scale bar represents 20 linear units. **c** The positional probability density function without the use of a compass. The locomotor assumptions are otherwise the same as in **b**. The scale bar represents 100 linear units. Both the 2-dimensional ($X - Y$) spatial domains shown represent 5 standard deviations from the centre of each distribution along and perpendicular to the axis of intended locomotion. The maximum probability density of each distribution is 2.6×10^{-3} (linear units) $^{-2}$ and 2.9×10^{-5} (linear units) $^{-2}$, respectively, for panels **b** and **c**

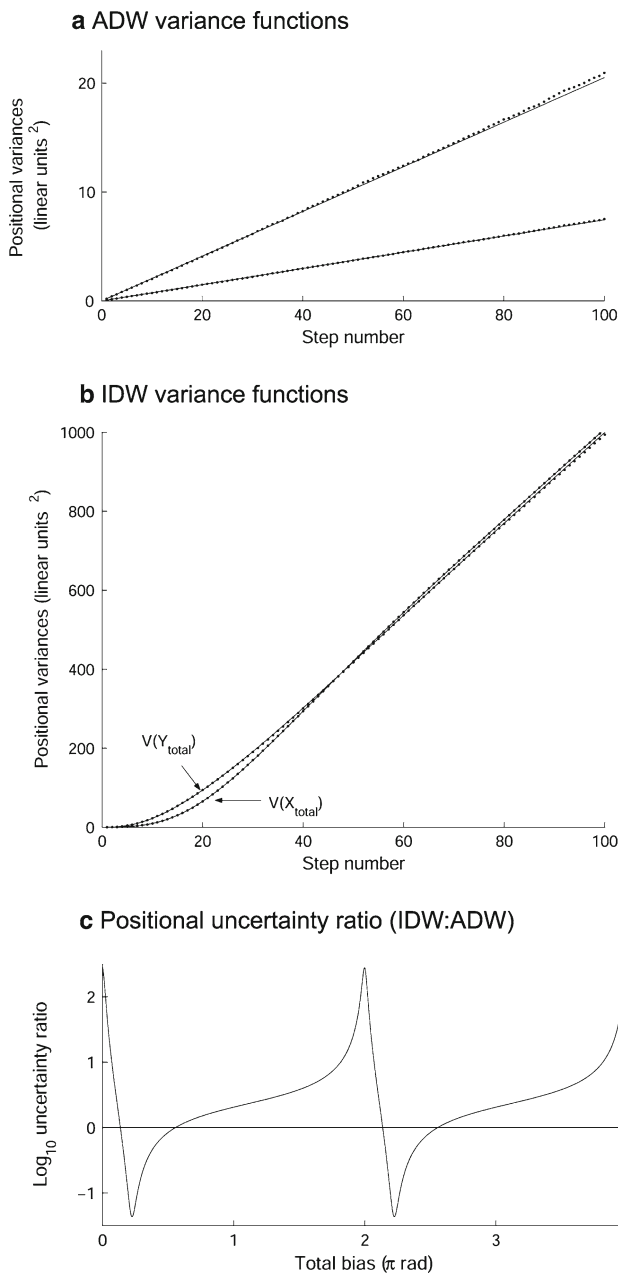


Fig. 5 **a** How the variances along and perpendicular to the axis of intended locomotion increases with the number of steps, when using a compass at every step. The variances from derivation (*line*) and simulation (*dots*) are shown. **b** The same without a compass. **c** The ratio of the positional uncertainty between an IDW (no compass) and an ADW (compass), as a function of the total angular bias. The asymptotic gradient for the IDW was used as the measure of rate of increase of positional uncertainty without a compass. The product of the standard deviations along the elliptical axes was used to calculate an equivalent rate of increase of positional uncertainty for the ADW. Due to the large differences in positional uncertainties, the ratio is more conveniently displayed on a logarithmic scale. A log₁₀ uncertainty ratio of 0 implies equal rate of increase of positional uncertainty. The locomotor unit was otherwise the same as that described in methods (Sect. 5.2), except for the variable bias as shown

This implies a joint probability density function which reduces to

$$\lim_{n \rightarrow \infty} \text{pdf}(X_{\text{total}}, Y_{\text{total}}) = \frac{1}{2\pi \sqrt{V(X_{\text{total}}) V(Y_{\text{total}})}} \times e^{-\frac{1}{2} \left[\frac{(X_{\text{total}} - E(X_{\text{total}}))^2}{V(X_{\text{total}})} + \frac{(Y_{\text{total}} - E(Y_{\text{total}}))^2}{V(Y_{\text{total}})} \right]}$$

Given the theoretical usefulness of Lévy flights or Lévy walks (Viswanathan et al. 1999), and a growing body of evidence for their use by animals (Viswanathan et al. 1996, 1999; Atkinson et al. 2002; Bartumeus et al. 2003; Ramos-Fernández et al. 2004; Reynolds et al. 2007) and even by humans (Brown et al. 2007), we discuss them briefly below.

Cheung et al. (2007) detailed the justifications for assuming step length distributions had finite means and variances. It was also acknowledged that a truncated Lévy distribution would have a finite mean and variance, and could theoretically be a biologically plausible distribution of step length in an arbitrarily complex unit of locomotion. As before, the central limit theorem would still apply (Mantegna and Stanley 1994) but the rate of convergence to Gaussian would be slower (Shlesinger 1995). Nevertheless, the general conclusions of this work would remain valid.

6.5 A general idiothetic directed walk follows a logarithmic spiral

It is clear from Figs. 2b and 3c that the expected path of a general IDW appears to be more complex than for the general ADW (compare with Figs. 2a and 3b). What is the expected path of a completely general directed walk? To answer this question, the expected displacements are derived again using integral approximations of series sums (see supplementary Sects. A3.1 and A3.2 for details). In this way, a parametric continuous approximation of the discrete path is obtained.

$$\begin{aligned} E(X_{\text{total}}) &\approx \frac{\rho_a \ln \beta_{a,b} + \varepsilon_a [\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b]}{[\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b]^2 + [\ln \beta_{a,b}]^2} \\ &\times \left[\begin{aligned} &\beta_{a,b}^{n-1/2} \cos([\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b](n + 1/2) - \Delta_{\text{bias}}^b) \\ & - \beta_{a,b}^{-1/2} \cos([\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b](1/2) - \Delta_{\text{bias}}^b) \end{aligned} \right] \\ &+ \frac{\rho_a [\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b] - \varepsilon_a \ln \beta_{a,b}}{[\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b]^2 + [\ln \beta_{a,b}]^2} \\ &\times \left[\begin{aligned} &\beta_{a,b}^{n-1/2} \sin([\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b](n + 1/2) - \Delta_{\text{bias}}^b) \\ & - \beta_{a,b}^{-1/2} \sin([\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b](1/2) - \Delta_{\text{bias}}^b) \end{aligned} \right] \\ &= r_0 e^{\alpha \theta} \cos(\theta + \tau) \end{aligned}$$

and

$$\begin{aligned}
 E(Y_{\text{total}}) &\approx \frac{\varepsilon_a \ln \beta_{a,b} - \rho_a [\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b]}{[\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b]^2 + [\ln \beta_{a,b}]^2} \\
 &\times \left[\begin{aligned} &\beta_{a,b}^{n-1/2} \cos([\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b](n + 1/2) - \Delta_{\text{bias}}^b) \\ &-\beta_{a,b}^{-1/2} \cos([\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b](1/2) - \Delta_{\text{bias}}^b) \end{aligned} \right] \\
 &+ \frac{\varepsilon_a [\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b] + \rho_a \ln \beta_{a,b}}{[\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b]^2 + [\ln \beta_{a,b}]^2} \\
 &\times \left[\begin{aligned} &\beta_{a,b}^{n-1/2} \sin([\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b](n + 1/2) - \Delta_{\text{bias}}^b) \\ &-\beta_{a,b}^{-1/2} \sin([\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b](1/2) - \Delta_{\text{bias}}^b) \end{aligned} \right] \\
 &= r_0 e^{\alpha \theta} \sin(\theta + \tau)
 \end{aligned}$$

where

$$\begin{aligned}
 \alpha &= \frac{\ln \beta_{a,b}}{\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b}, \quad \theta = n (\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b), \\
 \tau &= \frac{\Delta_{\text{bias}}^a - \Delta_{\text{bias}}^b}{2} + \tan^{-1} \left(\frac{\varepsilon_a \ln \beta_{a,b} - (\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) \rho_a}{(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b) \varepsilon_a + \rho_a \ln \beta_{a,b}} \right), \\
 \text{and } r_0 &= \sqrt{\frac{\rho_a^2 + \varepsilon_a^2}{\beta_{a,b} ((\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b)^2 + (\ln \beta_{a,b})^2)}}.
 \end{aligned}$$

In fact, the expected path is well approximated by parametric equations of a logarithmic spiral. The seventeenth century Italian mathematician/physicist Evangelista Toricelli showed that in fact the total inward path of a logarithmic spiral (starting from a fixed point) is finite, irrespective of the number of revolutions travelled. In view of the current results, this is not surprising.

6.6 Systematic bias can reduce positional uncertainty

There is a curious phenomenon associated with a general directed walk without a compass. If there is no net bias i.e., $\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b = 0$, then the positional uncertainty behaves very much like that of the simple directed walk described in Cheung et al. (2007). In particular, we can see that the asymptotic rate of increase of positional uncertainty will be greater than for a purely random walk, under most realistic conditions. Specifically, the condition which needs to be met is

$$\begin{aligned}
 \mathbf{m}_1 \mathbf{m}_0^a &= E(L \cos \Delta^a) E(L \cos \Delta^b) \\
 &- E(L \sin \Delta^a) E(L \sin \Delta^b) \geq 0.
 \end{aligned}$$

Then

$$\begin{aligned}
 \lim_{n \rightarrow \infty} \frac{dV(X_{\text{total}})}{dn} &= \lim_{n \rightarrow \infty} \frac{dV(Y_{\text{total}})}{dn} \\
 &= \frac{\mu_2}{2} + \frac{\mathbf{m}_1 \mathbf{m}_0^a}{1 - \beta_{a,b}} \geq \frac{\mu_2}{2}.
 \end{aligned}$$

The condition is really a measure of the tendency to drift from the axis of intended locomotion due to the asymmetry in statistical dependence between angular and linear components of the general elementary step. Thus for most practical purposes, the inequality would hold for both equations. Indeed, the hypothetical example described earlier had asymptotic positional variances which increased more than 22 times faster than that of a random walk with equivalent step sizes!

However, in the presence of bias, the behaviour can be quite different. For instance, if the bias terms of the earlier example are changed to $\Delta_{\text{bias}}^a = \Delta_{\text{bias}}^b = +0.35$ rad, the asymptotic positional variances of the general directed walk only increase at a rate of 5.1×10^{-3} times that of a random walk. In fact, the equivalent directed walk with a compass yields larger positional variances. This is true for the major and minor elliptical axes.

It should be noted that the bias terms are treated as constants which superimpose onto the random angular error distributions. Therefore, the biases could be interpreted as unmeasured biases in the locomotor unit, or as a controlled movement pattern. This peculiar result suggests that if an agent had to continue moving in order to, say, escape from a pursuing predator, but loses access to a compass, its best strategy would be to make purposeful biased movements. At the conclusion of such a journey, its positional uncertainty would have increased less than if it tried to maintain a straight course. Unfortunately, the expected positional gain is also very limited. Hence an optimal escape strategy is likely to be one which balanced the risk of predation against the risk of getting lost.

7 General discussion

In Sect. 4, we introduced the nomenclature of “directed walks” (DWs) with brief justification. Here we discuss the use of traditional “random walks” (RWs) and their shortcomings in navigation theory, motivating the use of DWs.

RW and diffusion-reaction models have had a long history of finding applications in previously unexpected contexts. For example, random movements of pollen in aqueous suspensions (Brown 1828) led, eventually, to the first quantitatively testable predictions of molecular properties using kinetic theory (Einstein 1905). Karl Pearson first posed the problem of the drunkard’s random walk (Pearson 1905a) and was probably the first to describe any form of animal/human navigation in this way. Lord Rayleigh (1905) recognized

the problem was analogous to earlier works on the physics of sound wave propagation, to Pearson's surprise (Pearson 1905b). Since then, fields as apparently unrelated as economics (e.g. Malkiel 1973) have found RWs and their variants provide useful frameworks in which to describe and analyze problems.

In biology, the “correlated random walk” (CRW) has been used as a model of animal foraging (Bovet and Benhamou 1988), dispersion of animals and plants (McCulloch and Cain 1989; Byers 2001), surface locomotion of biological cells (Nossal and Weiss 1974), and insect movement (Kareiva and Shigesada 1983). In an apparently unrelated context (but see Wu et al. 2000), the “persistent random walk” (PRW) has been used to describe end-to-end lengths of polymers (Tchen 1952; Claes and Van den Broeck 1987; Bracher 2004). Chemical bonds along a polymer are assumed to have random but restricted bending, which gives rise to a distribution of the polymer's net length. In a 2D situation, the restricted bond angle's random deviation is actually analogous to the angular displacement error of a navigating agent during a simple IDW. Similarly, the bond lengths are analogous to the step sizes.

It turns out that Eqs. (4) and (5) from Bracher (2004) are exactly analogous to the expected displacement along the axis of intended locomotion, and E_{\max} , respectively, of Cheung et al. (2007). It should be noted that although CRWs (e.g. Bovet and Benhamou 1988) and PRWs (e.g. Grey 1989) are defined differently, their properties are very similar.

Despite the long history of RWs and some distinct similarities to DWs, there are several critical differences that justify keeping the DW nomenclature separate from RWs.

(1) Many variants of RWs begin by assuming a uniform heading distribution, implying that all allocentric directions are equally likely, at least for the first step. There is potential for confusion here because the description of a single animal attempting to head towards a particular goal should obviously begin with a biased heading direction, as the term “directed walk” intuitively suggests. From the analysis in Cheung et al. (2007), it is clear that even in the absence of a compass, the probability function of the agent has a distinct directed character at the early stages of the walk, and only later degenerates to what appears to be a CRW distribution. However, irrespective of the number of steps taken, the expected displacement is not zero. Thus, a distinct direction is maintained, unlike the classical (Pearson's) RW or the CRW. Furthermore, the rate at which the “directed” character of the walk degenerates and takes on more “random” character depends critically on the statistical magnitude of the angular errors that are made at each step. The angular errors are inversely related

to the allocentric correlation of headings of successive steps. Indeed, the greater the correlation, the slower the degeneration, implying the persistence of a directed character for a longer period. Only when the correlation between the headings of successive steps is negligible or very small, does the walk display a truly random character. Hence the degree of “correlation” and “randomness” are actually inversely related.

- (2) Adding a compass does not alter the intrinsic locomotor unit other than using the compass to reset the animal's heading direction at the beginning of each step (or end of the previous step). This is the “allothetic directed walk” (ADW). It is clear from the current work that the ADW behaves very differently to the IDW. Yet this very pertinent description of navigation would now fall outside the standard RW nomenclature. Marsh and Jones (1988) used the terms “oriented” models and “unoriented models” to describe using and not using a compass, respectively. This nomenclature is by itself consistent with the current work but is not used here for two reasons. Firstly, the term “unoriented” suggests no directionality exists at all which is not true even for the IDW. Indeed, for small idiothetic angular displacement errors, the directed nature of the IDW may persist for a considerable distance which would certainly show “orientation.” In fact, theoretically, the probability density function is *always* oriented with respect to the origin. The second reason is that there is a direct correspondence between the type of directional sensory cue used and the nature of the directed walk, hence the terms “idiothetic” and “allothetic” were adopted.
- (3) Complex locomotor units have not been a focus of the RW literature. There does not appear to be any work which considers a general elementary step with statistically dependent angular and linear error distributions, with a general step structure consisting of a turn, step and another turn, allowing for biased and/or asymmetrical errors. Indeed even a moderately complex locomotor unit would display atypical characteristics. Larralde (1997) considered a PRW problem in terms of persistent local asymmetrical (chiral) scattering of particles. This meant that the heading distributions were biased in the egocentric reference frame. Interestingly, it was recognized that the diffusion constant had a kind of “resonance-like” property. We now know that the expected path of the general IDW follows a logarithmic spiral which gives rise to the potentially nonmonotonic (resonance-like) first and second positional moments.
- (4) Despite the explosion of problems which have been identified to fit into the RW framework, and despite the number of results which have been derived to solve those problems, there are still significant properties of CRWs and PRWs for which general solutions have not

been found. One such property is the expected radial displacement, $E(R_{\text{total}})$ (Bovet and Benhamou 1988; McCulloch and Cain 1989; Wu et al. 2000; Byers 2001; Bracher 2004). From the current work, it is clear that the directed nature of the positional distributions demand at least two separate first moments i.e., $E(X_{\text{total}})$ and $E(Y_{\text{total}})$, plus the corresponding second moments. These quantities are reported in the current work in exact, closed forms. Interestingly, the exact form of the expected radial displacement squared, $E(R_{\text{total}}^2)$, is equivalent for the CRW, PRW and simple IDW, and is relatively trivial [e.g. Eq. (2) of Kareiva and Shigesada 1983, or Appendix (A) in Marsh and Jones 1988, or Eq. (9) of Bracher 2004]. Accordingly, Sect. 6.4 of this work only reports the general form of this quantity, rather than reiterate the previously known results.

Now we focus on navigation, for which the theory of directed walks was originally developed (Cheung et al. 2007). It was demonstrated previously that in the case of a rather simple model of locomotion, it can be proven that, without a compass, medium to long range navigation is all but impossible. The simple reason lies in the fact that the positional expectation has a maximum finite limit, and worse still, the positional variances grow more rapidly than in a random walk. Indeed, the smaller the cumulative random errors, the more rapidly the variances increase asymptotically. The larger the cumulative random errors, the smaller the maximum expected displacement.

The current work extends the above findings to incorporate a very general description of locomotion, the general elementary step, which can theoretically account for any level of complexity of animal locomotion relevant to navigation. In fact the only assumption that is required is statistical independence between the error components of successive general elementary steps.

General directed walks share some distinct similarities with their more basic counterparts the simple directed walks. However, as the locomotory unit's complexity increases, so too the mathematical characterization of the evolving probability density functions (see Table 2).

7.1 Straight line navigation requires the use of a compass

The results of the present study confirm that any animal that can travel reasonable distances in an approximately straight line must be doing so with the aid of a compass. This must be true irrespective of the complexity of locomotion or whether there is a feedback system for path correction.

Regardless of the complexity or sophistication of the navigation system, there will always be sensorimotor noise. The presence of sensorimotor noise completely changes the

behaviour of a navigating animal which does not use a compass. The net progress per step decreases with successive steps; the general expected path is approximately a logarithmic spiral (which degenerates to a straight line in the absence of bias); the positional variances are also nonlinear functions of step number, sometimes with fluctuations that can result in successive minima and maxima, until parallel linear asymptotes are reached. The asymptotic probability density for the animal's position is a radially symmetric bivariate Gaussian function, centred at a finite distance from the starting point. One peculiar distinction between the simple directed walk (Cheung et al. 2007) and the general directed walk (present work) is that any bias can radically alter the magnitude of the positional uncertainty. We have shown here that extremely large biases can incur positional uncertainty in such a way that it actually increases less rapidly in the absence of a compass.

However, if the biases are moderate, and the locomotory unit makes significantly more gain in the egocentrically forward direction at each step, then the behaviour of the variance functions resembles those of the simple directed walk. Indeed, the latter is more likely to reflect biologically realistic locomotion. In essence, a forward-biased locomotory unit would result in greater positional variances in the absence of a compass, but a laterally-biased locomotory unit would result in greater positional variances in the presence of a compass.

7.2 Path integration systems are governed by the same constraints

There are suggestions in the literature that certain animals, under controlled conditions, may use purely idiothetic cues for path integration (Mittelstaedt and Mittelstaedt 1982; Etienne et al. 1996, 1998). As alluded to in Cheung et al. (2007), it should now be possible to differentiate path integration, which uses purely idiothetic cues, from one which uses allothetic directional cues. The only proviso is that a sufficiently large population of experimental trials should be conducted to have reliable estimates of positional means and variances. For example, if the mean position shifted by approximately the same distance following each step, each variance function increased linearly at its own distinct rate, and the region of positional uncertainty was small relative to that of a random walk, then the animal was almost certainly navigating *with* the use of a compass. In contrast, if the displacement of mean position became smaller and smaller with successive steps, the variance functions accelerated towards parallel asymptotes, and the region of positional uncertainty was larger than for a random walk, then the animal was almost certainly navigating *without* the use of a compass.

In the rat, there are at least two regions in the medial temporal lobe whose neurons display activity fields which seem

to be related to the animal's spatial location. Both hippocampal "place cells" (O'Keefe and Nadel 1978) and entorhinal "grid cells" (Hafting et al. 2005) have response patterns under light which are anchored to allothetic directional cues. The fact that these distinctive firing patterns persist when visible cues have been removed, have been taken to mean that idiothetic path integration continues to update the position of the animal (Quirk et al. 1990; Gothard et al. 1996; Hafting et al. 2005; McNaughton et al. 2006; Barry et al. 2007 reviewed by Jeffery 2007).

Following that interpretation and based on Cheung et al. (2007) and the current work, it is clear that the expected path of the animal in both representational and real space must have a finite length. Furthermore, the variances are likely to increase very rapidly (faster than random walks for forward-biased locomotor units). Both these properties would lead to degeneration of the association between place and neuronal activity; i.e. the maintenance of place or grid fields would be theoretically impossible. Suppose the rat tried to move between two places which corresponded to the firing peaks of a grid cell. Firstly, our results show that such a path (motor output) would degenerate rapidly without a compass. The expected measure of the same distance decreases with successive steps so that the two peaks would be expected to converge into one. Furthermore, the region of positional uncertainty would increase rapidly, probably accelerating initially and eventually approaching a steep linear function. In other words, the spatial area now associated with one grid cell activity peak would likely expand faster than a random walk.

Suppose that the animal had some allothetic directional reference for movement, but used idiothetic cues for path integration. Even then, its internal representation would succumb to the same phenomenon as described here as a general directed walk without a compass, but in representational space. Again, it would be impossible to maintain an association between place and neuronal activity. Hence, if path integration is truly idiothetic, it would be impossible to maintain spatially consistent activity fields.

Hafting et al. (2005) reported that the spike activity of grid cells persisted for 30 min in darkness after an initial lit period of only 10 min. If idiothetic path integration is nearly theoretically impossible, yet the initial orientating allothetic cue has been eliminated, how is the rat estimating its position in space? From our results, it would seem that the rats must have been using non-visual allothetic directional cues whilst moving in the dark. This conclusion is consistent with those of Dudchenko and Bruce (2005) who tried to systematically remove reliable allothetic directional information for rats in similarly restricted laboratory arenas. Yet even after significant efforts at making the allothetic cues ambiguous, they concluded that the animals still did not resort to idiothetic navigation. In essence, seemingly weak allothetic cues, at least as judged by the experimentalist,

were preferred over idiothetic cues. Although the activities of place and grid cells were not recorded in those experiments, the behavioural results suggest that rats have the ability to anchor to a wide range of allothetic cues, across sensory modalities, and importantly assess the usefulness of those cues in a dynamic way. Given existing evidence that rats can substitute one external directional cue for another (Jeffery et al. 2006), it should not be surprising if they switch from a visual cue during lit conditions, to a non-visual but still allothetic cue (such as the noise from recording equipment, the airflow from vents, or odour and tactile cues) during darkness. Save et al. (2000) showed that hippocampal place fields lose their stability if the light is turned off *and* odour cues are actively cleaned behind the moving animal. There was no obvious evidence that idiothetic cues were interrupted.

It is important to note that there are movement strategies which could incorporate idiothetic navigation for short periods, but which are allothetic in the long run. For instance, if the rat maintains and even resets its representation of heading direction by moving along walls of a confined arena, and perhaps also resets its absolute positional representation at corners, then, in principle, it could make regular, short sojourns into the middle of the arena and still curtail the accumulation of sensorimotor noise. However, based on the definitions and results of the current work, the arena itself should be considered as an allothetic directional cue. This idea is in keeping with the results of O'Keefe and Burgess (1996) who showed that subtle changes in arena configuration resulted in place fields which maintained their spatial relationship to nearby walls.

As a final point to note, most rodent models of navigation are based on data obtained from experiments in confined arenas (for obvious methodological reasons). For example, McNaughton et al. (2006) described a toroidal model of grid cells which could explain their spatially-repetitive firing fields. In their model, it was assumed that the output of path integration gave rise to a spatial phase shift of the entire set of grid cells (for each toroid). Thus in this model, the spatial regularity of the resultant firing field would depend critically on the accuracy and precision of the path integrator's output. From the analytical results presented above, it is clear that such accuracy and precision during path integration is only possible in the presence of a compass. So how can a grid field's stability be preserved for extended periods in darkness? One obvious theoretical answer is that the animal has access to non-visual compass cues, such as constant air flow direction or asymmetrical equipment noise. In the absence of all compass cues, however, path integration must be supplemented by extra positional information—such as the arena boundaries, or actively laid olfactory cues. Then in principle, the animal could re-zero its positional uncertainty each time it encountered a positional cue. However, the latter method

would only work in a confined navigational domain where the probability of re-encountering a positional cue is sufficiently large.

7.3 Artificial navigation using idiothetic path integration

As explained in Cheung et al. (2007), our results are equally applicable to the navigation of autonomous robots. Furthermore, the disastrous effects of cumulative errors in path integration systems have been recognized in studies of robot navigation (Ingemar 1991) and sophisticated techniques have been developed to try to avoid the problem (Thrun 1997, 2003). Of particular interest is the *correspondence problem* (also known as the *data association problem*). A prime example of this occurs when a robot is used to map a large cyclic environment. At the end of one cycle in physical space, the pose of the robot (position and orientation) may be associated with a large amount of uncertainty, due to an accumulation of sensorimotor noise.

The question then arises as to whether the current location corresponds to a previously visited one? This is a key question of many simultaneous localization and mapping (SLAM) algorithms (Thrun 1997, 2003; Milford 2008). The present work may offer some insights into this problem. It is clear that if the position is updated through idiothetic path integration, there is likely to be much larger positional and heading uncertainty. It is now possible to quantify the uncertainty as functions of step number or total path length. Hence for an environment of given complexity, assuming a reasonable estimate of sensorimotor noise per “step,” it should be possible to estimate the error rate following each cycle. In principle it should be possible to determine whether a given mapping task is likely to be achievable at all.

For example, suppose a robot using wheel-based odometric path integration is to map the perimeter of a 10 m × 10 m square region, travels 10 ± 1 cm every wheel cycle ($\mu \pm \sigma$), and has combined sensorimotor angular noise per cycle with σ of 2°. As a first approximation, assume the angular and linear errors are Gaussian and statistically independent. It can be shown that following one full loop around the perimeter of the square region, the average represented positional variance is about 109 m². If fully unconstrained (i.e., no knowledge of arena geometry), there is no way that the robot’s idiothetic path integration system alone would be sufficient for it to assign the current location to the starting point with any reasonable degree of confidence.

Clearly, alternative strategies must be in place to reduce the area of positional uncertainty. For instance, being able to use a compass throughout the journey reduces the average positional variance by nearly five thousand times (to 2.24 × 10⁻² m²) for identically distributed sensorimotor noise per wheel cycle. If some prior knowledge about the

environment is available, for example that the path follows the perimeter of a square arena, then the positional uncertainty may be reduced even further. This is because prior knowledge reduces the area of uncertainty in which the navigating agent *could* be located, even before any sensory information has been obtained.

7.4 Straightness and curvature of a path

It was shown in Cheung et al. (2007) that the egocentrically measured linear and angular displacements of a sequence of steps can be used to calculate an index of straightness of a path. Its relative stability compared to *D/L* (Batschelet 1981) as a measure of straightness, and its sensitivity to error distribution unlike the better known index of sinuosity (Bovet and Benhamou 1988), offers real advantages in application.

The current work offers one more important extension to the index of straightness E_{\max} . Intuitively, there are at least two reasons why a path may not be straight. Firstly, successive steps may not be aligned due to random errors. Secondly, there could be a general trend (a systematic bias) which causes a distinct curvature in the path. The former was accounted for by the indices of straightness and sinuosity described above. The absolute curvature itself is determined by the bias terms. Expressed in radians, they are natural measures of curvature and may be considered trivial.

However, estimating the relative contributions of systematic bias (curvature) and random angular errors to the overall structure of a path is not trivial. Perhaps the simplest approach would be to take the ratio of the bias to the standard deviation of the angular errors between steps,

$$\frac{\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b}{\sqrt{V(\Delta^a) + V(\Delta^b)}}.$$

However, in much the same way that Bovet and Benhamou’s sinuosity index is distribution insensitive (see Cheung et al. 2007), empirically derived measures of this type would suffer from the same limitation. Finally, there is no easy geometric interpretation of such an index.

From the results of the current work, an intuitive solution can be found. We now know that a tortuous path with random turns plus a systematic bias has an expected path which follows a logarithmic spiral. It is well known that the pitch of a logarithmic spiral defines its shape and is scale-invariant. Since the shape of the expected path is determined by the interaction of the maximum expected path length (or total length of the spiral) and the absolute curvature (bias per step), the magnitude of the pitch must relate the path length and absolute curvature. Therefore a signed pitch value, SP, is inversely related to the amount of contribution of the systematic bias compared with random turns,

$$SP = \operatorname{sgn} \left(\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b \right) \left[\frac{\pi}{2} - \left| \tan^{-1} \left(\frac{\Delta_{\text{bias}}^a + \Delta_{\text{bias}}^b}{\ln \beta_{a,b}} \right) \right| \right].$$

The greater the magnitude of pitch, the greater the relative magnitude of random turns, leading to more rapid degeneration of expected progress. Hence the spiral's tangent is angled closer to the radial line. A positive SP value represents an anticlockwise inward spiral, and vice versa for a negative SP value. Overall, SP represents a robust yet distribution sensitive measure of the relative contribution of systematic bias to the curvature of the path. However, due to the scale invariance property, a small systematic angular bias coupled with a small random angular error can yield a similar pitch to a large pair of values. This is not a problem since the maximum expected displacement may be used as an absolute index of the amount of random angular errors. In the general case, we need to be careful since the expected path is a spiral. We want the total length of the spiral path rather than the asymptotic expected position. It is obvious that the total path length, D_{total} , can be obtained directly from the positional expectations of the unbiased version of general directed walk without a compass,

$$D_{\text{total}} = \sqrt{E(X_{\text{total}})^2 + E(Y_{\text{total}})^2} = \frac{\beta_{a,b}^n - 1}{\beta_{a,b} - 1} \sqrt{\rho_a^2 + \varepsilon_a^2}.$$

Therefore, the combination of SP and D_{total} gives a succinct, robust and unambiguous description of the systematic and random angular deviations of a tortuous path.

7.5 Quantifying animal navigation paths

Navigation is an extremely important component of the total set of behavioural outputs of nearly every animal. Clearly it would be an advantage to be able to quantify that output objectively and robustly. From the results from [Cheung et al. \(2007\)](#) and the current results, we suggest that it would be instructive to quantify first and second positional moments following any navigational task. This is particularly important if the sensory inputs used during navigation are unclear. For example, some animals seem to be able to navigate relatively short distances without using a compass ([Mittelstaedt and Mittelstaedt 1982](#); [Etienne et al. 1996, 1998](#)). There are three ways in which this may be quantified on a population basis. Firstly, on repeated trials, the mean position should advance by decreasing increments, tending towards some finite asymptotic location; secondly, the positional variances should initially accelerate, with or without fluctuations, asymptotically increasing with equal but constant rates; and thirdly, in all likelihood, the asymptotic gradient of the positional variance functions would be greater than a random walk (except in the presence of extreme angular biases). Demonstrating these three properties would lend strong theoretical support for the notion that the animals are truly

carrying out idiothetic path integration. In practice, population-based methods may at times be cumbersome. Based on the principles of the current work, individual-based path quantification methods are presently being developed and tested.

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