

Animal navigation: the difficulty of moving in a straight line

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Abstract In principle, there are two strategies for navigating a straight course. One is to use an external directional reference and continually reorienting with reference to it, while the other is to infer body rotations from internal sensory information only. We show here that, while the first strategy will enable an animal or mobile agent to move arbitrarily far away from its starting point, the second strategy will not do so, even after an infinite number of steps. Thus, an external directional reference—some form of compass—is indispensable for ensuring progress away from home. This limitation must place significant constraints on the evolution of biological navigation systems. Some specific examples are discussed. An important corollary arising from the analysis of compassless navigation is that the maximum expected displacement represents a robust measure of the straightness of a path.

1 Introduction

It is well recognized that cumulative 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 that the use of an external direction reference e.g., a compass, would reduce that final uncertainty. However, the literature is sparse on any rigorous evidence that this must be so. Furthermore, the exact

details whereby cumulative errors adversely affect navigating success have not been studied analytically.

There have been numerous attempts at quantitatively describing the so-called “correlated random walk” 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).

Two common themes to these and related works are evident. Firstly, there is a common assumption that the first step may be in any allocentric direction. In other words, the first step is identical to a true random walk. It is only in the subsequent steps that the “correlation” takes effect; i.e., the allocentric heading of every step from the second onwards is correlated with the allocentric heading of the previous step. A second common theme emerges. Due to the first assumption, the positional distribution will be circularly symmetric, and the expected radial displacement from the starting position is used as a measure of the spread of the organism.

At this point, two very clear distinctions become evident between the current work and previous models of animal movement/navigation/dispersion. Firstly, in previous work, the “random” turns within the model are thought to be part of the navigation strategy of the animal; i.e., the animals are making turns intentionally (for example, as part of exploration). In contrast, the present work considers the consequences of unintended turns, e.g., sensory and/or motor errors. For example, one may ask: can the animal keep a perfect neural record of its physical turns (imperfections equate to sensory errors)? Similarly, can the animal perfectly realize its neural record in physical space (imperfections equate to motor errors)? Benhamou et al. (1990) considered the effect of superimposing random errors onto tortuous paths whose turns are intended. Their simulations certainly support

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the notion that using a compass reduces the uncertainty in position (measured as the standard deviation of the “memorized” location of home). However, it is far from a proof. Furthermore, it is difficult to disentangle the effect of the tortuous path (intended) from the random errors (unintended). Consequently, from such simulations it is not exactly clear why a compass is so important. For instance, one could question whether a compassless animal with inherently smaller random errors (sensory and motor) can outperform one with a compass but larger errors. What if errors followed statistical distributions other than those considered in the previous work, e.g., other than Gaussian or von Mises distributions? (e.g., Batschelet 1981).

A second important feature of the current work is the assumption that animals have some deliberate starting orientation rather than random orientation. For instance, a honeybee hive is often eccentric to the foraging area of its worker bees, suggesting a bias in the initial heading orientation during foraging (Capaldi et al. 2000). Furthermore, the homeward journey requires aiming for a particular spatial location rather than a random search; i.e., animals make useful net gains in particular directions rather than simply “diffusing” outward like particles. Hence the expected radial displacement is no longer useful conceptually; i.e., there has to be direction incorporated into the measure of navigational success or failure. Furthermore, an analytical form for the expected radial displacement has yet to be found. The distinction becomes even clearer when one considers the probability distribution describing the individual animal (see later).

To disentangle the effect of the compass from the path itself, we analytically compare two strategies for navigating a straight course. The first strategy is to use an external directional reference, which practically 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 1994, 1992; 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 compensate for (or prevent) unwanted deviations.

Fraenkel and Gunn (1961) seemed to recognize that cumulative turns will cause an animal to deviate from some arbitrary axis. Unfortunately, they described random turns extrinsic to the sensorimotor apparatus, responsive to the environment: “In some animals there is a *klino-kinetic* response, in which the rate of random turning, or angular velocity, depends on the intensity of stimulation.” Also, “The direction of linear movement changes for no apparent reason. In some cases these random changes of direction occur often, so that the animal never goes far in a straight line.” Since the “random” turns show quantitative dependence on environmental factors, the final behaviour may be attributed to

both a purposeful navigation mechanism as well as a random component. Is the deviation from the straight line preventing the animal from moving along a straight course (which would be obvious given there are random turns) or along *any* directed course away from the starting point? (p. 45).

Indeed, Fig. 42 (p. 105) reproduced traces from v. Buddenbrock (1917) which show paths travelled by four species of arthropods in light and dark conditions. The paths travelled with a directed light are clearly straighter than the paths travelled in darkness. Again, it is not clear whether the tortuous paths represent a purposeful searching strategy, or whether the animals are showing irrecoverable cumulative random errors. Furthermore, the nature of the tortuous paths are distinctive i.e., they show many looping structures which imply a systematic bias in the angular displacement. What if there was no bias?

This study develops a quantitative theory to address the above questions. In particular, the analysis will demonstrate the navigational consequences of cumulative errors in the presence and absence of a compass. Some examples of performance will be illustrated through computer simulation.

2 Methods

Computer simulation Monte Carlo simulations were carried out in MATLAB 6.5, using its standard function for generating normally distributed random numbers. At each iteration, two distinct arrays each containing 20,000 random floating point numbers were created and scaled by σ_Δ and σ_L . These represented the random angular and linear displacement errors which were added to the ideal step to produce the non-ideal displacement. 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 elementary locomotor 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.

In all numerical and simulation examples, parameter values were arbitrarily set to $\mu_L = 2$ linear units, $\sigma_L = 0.2$ linear units, and $\sigma_\Delta = 0.5$ radians, unless otherwise specified. The exact values of these parameters are not critical to any of the conclusions of this work.

Analytical simplifications For clarity, we have used a simplified description of locomotion so that the analytical results are transparent, whilst preserving the most important elements. We assume in this work that (i) error distributions are symmetric and unbiased (i.e., no systematic drift), (ii) step size error is independent of angular error, and (iii) the basic

repeating unit of locomotion can be described by a turn and a step. However, it can be shown that the general conclusions of this paper are valid even if these assumptions do not hold (Cheung et al., in preparation).

3 Locomotion approximated by repeating elementary steps

Consider an animal that is attempting to move along a straight line in a desired direction. The path that is actually travelled by the animal can be viewed as a sequence of elementary steps. We assume the animal's locomotion consists of repeating units of motion, whereby each 'step' is essentially a repeat of the previous 'step' but shifted by some amount. If navigation is perfect, each step is constant in length and direction. In reality, the size of each step can fluctuate, as can direction. This can be due to imperfections or noise in the motor mechanisms that mediate locomotion; e.g., the actual step of a human, the wing beat of a bee, or the tail flip of a fish, as well as in the sensory mechanisms that measure the pace and direction of locomotion.

4 Navigation with a compass

Let us begin by considering a situation in which an animal attempts to travel along a straight line in a desired direction by using an external reference direction. For simplicity, the external direction reference will be called a 'compass' and will be assumed to be stable for the duration of the journey. As shown in Fig. 1a and b, the ideal trajectory of the animal is along the axis of intended locomotion. Non-ideal trajectories have step lengths denoted by L_1, L_2, L_3, \dots , with a mean value $\mu_L = E(L)$ and standard deviation σ_L , where E denotes the expectation operator. Angular errors are denoted by $\Delta_1, \Delta_2, \Delta_3, \dots$, and characterized by standard deviation σ_Δ .

With reference to Fig. 1a, we begin by considering the expected movement of the animal along an axis (Y -axis) perpendicular to the direction of intended travel (X -axis). After n steps,

$$E(Y_{\text{total}}) = \sum_{j=1}^n E(Y_j) = \sum_{j=1}^n E(L_j \sin \Delta_j) = 0.$$

Each term $E(L_j \sin \Delta_j)$ represents the average projection of the j th step on the Y -axis, and is zero because leftward and rightward errors are symmetrically distributed. Thus, on average, the animal will not stray from the intended direction of locomotion—although, on individual runs, it may end up on one side or other of the intended axis of travel.

Using a compass at each step, we find that the expected movement of the animal along the direction of intended travel (the X -axis) after n steps is

$$\begin{aligned} E(X_{\text{total}}) &= \sum_{j=1}^n E(X_j) = \sum_{j=1}^n E(L_j \cos \Delta_j) \\ &= \sum_{j=1}^n E(L_j) E(\cos \Delta_j) = n \mu_L \beta, \end{aligned}$$

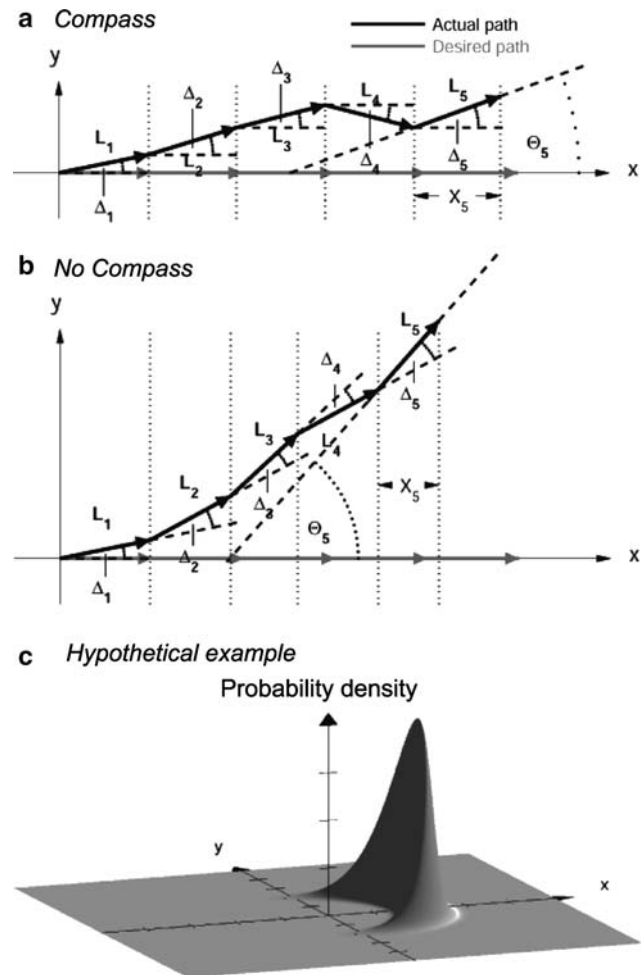


Fig. 1 Illustration of attempted navigation along a straight line **a** with and **b** without the use of a compass. The grey arrows represent the first five steps of an ideal path (along the X -axis). The black arrows represent the actual first five steps taken due to the presence of angular displacement errors, indicated by Δ at each step. L represents the step length. The allocentric heading, Θ , at step 5 is shown for each case. The vertical dotted lines show the projection of the X position of the hypothetical animal following each of the five steps. The net displacement along the X -axis is shown for step 5 in each case. **c** A hypothetical example of a probability density function for the position of an animal (or other mobile agent) following a single step starting at the origin, with intended locomotion along the X -axis. The step size is assumed to be normally distributed, with a mean value $\mu_L = 2$ linear units and a standard deviation $\sigma_L = 0.2$ linear units. The error in step direction is also assumed to be normally distributed and independent of the step size, and with a standard deviation $\sigma_\Delta = 0.5$ radians. Tick marks are shown at 1 linear unit increments (spatial axes) and 0.2 (linear unit) $^{-2}$ increments (probability density axis). This is the same distribution, following a single step, for the case with and without the use of a compass

where X_j denotes the projection of the j th step on the X -axis, and $\beta = E(\cos \Delta)$.

Since β is a constant, we see that the expected travel along the direction of intended locomotion is proportional to the number of steps, and can become arbitrarily large as the number of steps is increased. Thus, there is no limit to how far the animal can move away from its starting point.

The variance in the distance travelled along the X -axis after n steps is

$$\begin{aligned} V(X_{\text{total}}) &= \sum_{j=1}^n V(X_j) = \sum_{j=1}^n V(L_j \cos \Delta_j) \\ &= \sum_{j=1}^n \left[E(L^2 \cos^2 \Delta) - E(L \cos \Delta)^2 \right] \\ &= n\gamma(\sigma_L^2 + \mu_L^2) - n\mu_L^2\beta^2 = n(\gamma\sigma_L^2 + \mu_L^2(\gamma - \beta^2)), \end{aligned}$$

where $\gamma = E(\cos^2 \Delta)$. The variance along the Y -axis is

$$\begin{aligned} V(Y_{\text{total}}) &= \sum_{j=1}^n V(Y_j) = \sum_{j=1}^n V(L_j \sin \Delta_j) = n \left[E(L^2 \sin^2 \Delta) \right] \\ &= n \left[E(L^2) E(1 - \cos^2 \Delta) \right] = n(\mu_L^2 + \sigma_L^2)(1 - \gamma). \end{aligned}$$

Clearly, the variances (or scatters) in the distance travelled along, and perpendicular to, the intended direction increase in proportion to the number of steps—the longer the journey, the larger the variance.

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.

5 Navigation without a compass

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. Note that the first step is identical to the case with a compass (see Fig. 1c). In principle, the animal can still keep track of its direction by monitoring its motions egocentrically—that is, by inferring its turns by monitoring its limb, wing or fin movements, and/or by using signals from organs that sense rotations, without knowing absolute heading direction. Thus, the animal can start off in the desired direction and then prevent deviations from this direction by ensuring that there are no turns. In practice, however, this method will not maintain a given heading indefinitely, because noise in the motor and sensory systems will

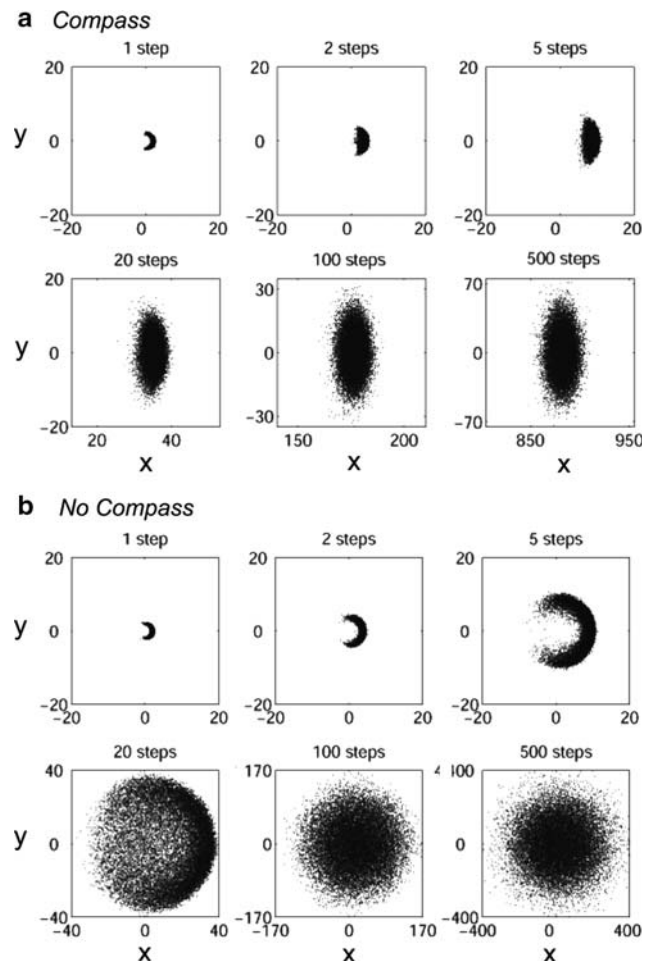


Fig. 2 Simulation examples. **a** Computer simulations of the results of compass-based navigation, showing the end points of 20,000 simulated journeys after 1 step, 2 steps, 5 steps, 20 steps, 100 steps and 500 steps. At every step, the axis of intended locomotion is along the abscissa. All 20,000 simulated journeys began at the origin (0, 0). The errors in step size and direction are assumed to be normally distributed, with $\mu_L = 2$ linear units, $\sigma_L = 0.2$ linear units, and $\sigma_\Delta = 0.5$ radians. Note the change in scale in the lower panels to accommodate the increasing means and spread of positions of the simulated agents. **b** Computer simulations of the results of navigation without a compass, showing the end points of 20,000 simulated journeys (other parameters as in part **a**)

generate errors, which will accumulate as the journey progresses.

It is important to note that we are not modelling a truly random walk, i.e., Brownian motion. In the case of Brownian motion, the particle (or agent) is free to move in any direction at each step; i.e., there is no concept of “forward”. In contrast, we are modelling a journey in which the animal attempts to progress in a straight line by continually trying to move along its current body axis. With Brownian motion, the expected position of the particle would be at the starting point, even after an infinite number of steps (which is also the case with a correlated random walk). In the case of navigation without a compass, the expected location of the animal

would be a finite distance away from the starting point, along the intended direction of travel.

Our analysis will use the same model paradigm and definitions as before. The animal begins by attempting to take the first step in the desired direction. In this process, it makes a random angular error Δ_1 of which the animal is unaware. In the second step, it strives to maintain the direction of the first step but it makes a further random error Δ_2 (see Fig. 1b) and again is unaware of this error, and so on.

Since the directional errors accumulate from step to step, the total angular error after the n th step, Θ_n , can be expressed as

$$\Theta_n = \sum_{j=1}^n \Delta_j,$$

where Δ_j is the angular error at step j .

After n steps, the expected movement perpendicular to the direction of intended travel would be

$$\begin{aligned} E(Y_{\text{total}}) &= E\left(\sum_{j=1}^n L_j \sin \Theta_j\right) = \sum_{j=1}^n E(L_j \sin \Theta_j) \\ &= \sum_{j=1}^n E(L_j)E(\sin \Theta_j) = 0. \end{aligned}$$

Since Θ_j is equally likely to be positive or negative, it follows that each term $\sin \Theta_j$ in the series on the right hand side has an expected value of zero. Therefore, $E(Y_{\text{total}})$ is zero, implying that, on average, there is no movement perpendicular to the direction of travel—although individual trajectories can end up either side of the X -axis.

The expected movement along the direction of intended travel is

$$\begin{aligned} E(X_{\text{total}}) &= E\left(\sum_{j=1}^n L_j \cos \Theta_j\right) = \sum_{j=1}^n E(L_j \cos \Theta_j) \\ &= \sum_{j=1}^n E(L_j)E(\cos \Theta_j) = \mu_L \sum_{j=1}^n E(\cos \Theta_j) \\ &= \mu_L E\left(\cos \Delta_1 + \cos(\Delta_1 + \Delta_2) + \dots + \cos(\Delta_1 + \Delta_2 + \dots + \Delta_n)\right) \\ &= \mu_L \left(E(\cos \Delta_1) + E(\cos(\Delta_1 + \Delta_2)) + \dots + E(\cos(\Delta_1 + \Delta_2 + \dots + \Delta_n)) \right). \end{aligned}$$

Now

$$\begin{aligned} \cos(\Delta_1 + \Delta_2) &= \cos \Delta_1 \cos \Delta_2 - \sin \Delta_1 \sin \Delta_2 \\ \sin(\Delta_1 + \Delta_2) &= \sin \Delta_1 \cos \Delta_2 + \cos \Delta_1 \sin \Delta_2. \end{aligned}$$

Thus,

$$\begin{aligned} \cos(\Delta_1 + \Delta_2 + \Delta_3) &= \cos \Delta_1 \cos(\Delta_2 + \Delta_3) - \sin \Delta_1 \sin(\Delta_2 + \Delta_3) \\ &= \cos \Delta_1 \cos \Delta_2 \cos \Delta_3 - \cos \Delta_1 \sin \Delta_2 \sin \Delta_3 \\ &\quad - \sin \Delta_1 \sin(\Delta_2 + \Delta_3) \end{aligned}$$

... and so on for any number of steps. We note a few important properties:

1. Elementary trigonometric identities allow us to separate the independent variables.
2. By careful inspection, there is one and only one term which does not possess a $\sin(\Delta)$ factor.
3. $\int_{-\infty}^{\infty} \sin \Delta P(\Delta) d\Delta = 0$ due to the fact that $\sin \Delta$ is an odd function (i.e., $-\sin(\Delta) = \sin(-\Delta)$) while $P(\Delta)$ is even (i.e., $P(\Delta) = P(-\Delta)$).
4. $\int_{-\infty}^{\infty} \cos \Delta P(\Delta) d\Delta = E(\cos \Delta)$ and $|E(\cos \Delta)| \leq 1$ with equality if and only if $\sigma_{\Delta}^2 = 0$.

Therefore, we can write

$$\begin{aligned} E(X_{\text{total}}) &= \mu_L \cdot \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \dots \int_{-\infty}^{\infty} \left(\cos \Delta_1 + \cos \Delta_1 \cos \Delta_2 \right. \\ &\quad \left. + \dots + \prod_{t=1}^n \cos \Delta_t + \sin \text{ terms} \right) \\ &\quad \times \prod_{t=1}^n P(\Delta_t) d\Delta_1 d\Delta_2 \dots d\Delta_n \end{aligned}$$

The sine terms reduce to:

$$\begin{aligned} \int \int \dots \int_{-\infty}^{\infty} \sin \Delta_j f(\Delta_{\text{others}}) P(\Delta_j) P(\Delta_{\text{others}}) d\Delta_j d\Delta_{\text{others}} &= \\ \int \int \dots f(\Delta_{\text{others}}) \left[\int_{-\infty}^{\infty} \sin \Delta_j P(\Delta_j) d\Delta_j \right] P(\Delta_{\text{others}}) d\Delta_{\text{others}} &= 0, \end{aligned}$$

leaving only the cosine terms. The earlier equation reduces to

$$\begin{aligned} E(X_{\text{total}}) &= \mu_L \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \dots \int_{-\infty}^{\infty} \left(\sum_{j=1}^n \prod_{t=1}^j \cos \Delta_t \right) \\ &\quad \times \prod_{t=1}^n P(\Delta_t) d\Delta_1 d\Delta_2 \dots d\Delta_n. \\ \text{term}_j &= \mu_L \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \dots \int_{-\infty}^{\infty} \prod_{t=1}^j \cos \Delta_t \\ &\quad \times \prod_{t=1}^n P(\Delta_t) d\Delta_1 d\Delta_2 \dots d\Delta_n \\ &= \mu_L \int_{-\infty}^{\infty} \dots \int_{-\infty}^{\infty} \prod_{t=2}^j \cos \Delta_t \left[\int_{-\infty}^{\infty} \cos \Delta_1 P(\Delta_1) d\Delta_1 \right] \end{aligned}$$

$$\begin{aligned}
& \times \prod_{t=2}^n P(\Delta_t) d\Delta_2 \dots d\Delta_n \\
& = \mu_L \int_{-\infty}^{\infty} \dots \int_{-\infty}^{\infty} \prod_{t=2}^j \cos \Delta_t [E(\cos \Delta_1)] \\
& \quad \times \prod_{t=2}^n P(\Delta_t) d\Delta_2 \dots d\Delta_n \\
& = \mu_L E(\cos \Delta_1) \int_{-\infty}^{\infty} \dots \int_{-\infty}^{\infty} \prod_{t=2}^j \cos \Delta_t \\
& \quad \times \prod_{t=2}^n P(\Delta_t) d\Delta_2 \dots d\Delta_n \\
& = \dots = \mu_L \prod_{t=1}^j E(\cos \Delta_t).
\end{aligned}$$

Noting that $E(\cos \Delta_1) = E(\cos \Delta_2) = \dots = E(\cos \Delta_n)$, we see that

$$E(X_{\text{total}}) = \mu_L \sum_{t=1}^n [E(\cos \Delta)]^t,$$

which is in fact a simple geometric series. If we let $\beta = E(\cos \Delta)$,

$$\begin{aligned}
E(X_{\text{total}}) &= \mu_L (\beta + \beta^2 + \beta^3 + \beta^4 + \dots + \beta^n) \\
&= \mu_L \frac{\beta - \beta^{n+1}}{1 - \beta}.
\end{aligned}$$

We see that since $\beta \leq 1$ with equality if and only if $\sigma_\Delta = 0$, as $n \rightarrow \infty$, $E(X_{\text{total}}) \rightarrow \mu_L \frac{\beta}{1-\beta}$ which is a constant independent of n .

This implies, surprisingly, that no matter how many steps the animal takes, the expected movement along the direction of intended motion will never exceed a limiting value. In other words, an animal can be moving forward egocentrically for an indefinite period of time, without making any gain in its expected allocentric position.

This limiting value is proportional to the average step size, μ_L , and depends critically on the value of β . The greater the angular error, the smaller the value of β and the smaller the limiting value.

For the example of a normally distributed Δ ,

$$\beta = E(\cos \Delta) = e^{-\frac{\sigma_\Delta^2}{2}}$$

see [Bovet and Benhamou \(1988\)](#), [Mardia \(1972\)](#), [Batschelet \(1981\)](#).

$$E(\cos^2 \Delta) = \int_{-\infty}^{\infty} \left[1 + \sum_{n=1}^{\infty} (-1)^n \frac{\Delta^{2n}}{(2n)!} \right]^2 \frac{1}{\sigma_\Delta \sqrt{2\pi}} e^{-\frac{1}{2} \left(\frac{\Delta}{\sigma_\Delta} \right)^2} d\Delta$$

We note that the expansion of $\cos^2 \Delta$, using Cauchy multiplication:

$$\begin{aligned}
\cos^2 \Delta &= 1 - \Delta^2 \left(\frac{1}{2!} + \frac{1}{2!} \right) + \Delta^4 \left(\frac{1}{4!} + \frac{1}{2!2!} + \frac{1}{4!} \right) \\
&\quad - \Delta^6 \left(\frac{1}{6!} + \frac{1}{4!2!} + \frac{1}{2!4!} + \frac{1}{6!} \right) + \dots
\end{aligned}$$

The $n+1$ 'th term of $E(\cos^2 \Delta)$ is thus:

$$\begin{aligned}
& \frac{(-1)^n 2^n \sigma_\Delta^{2n}}{\sqrt{\pi}} \left(\frac{1}{(2n)!} + \frac{1}{(2n-2)!2!} + \frac{1}{(2n-4)!4!} \right. \\
& \quad \left. + \dots + \frac{1}{(2n)!} \right) \Gamma(n + \frac{1}{2})
\end{aligned}$$

Evaluating the first few terms reveals a well known Taylor series within:

$$\begin{aligned}
E(\cos^2 \Delta) &= 1 - \sigma_\Delta^2 + \frac{2}{2!} \sigma_\Delta^4 - \frac{4}{3!} \sigma_\Delta^6 + \frac{8}{4!} \sigma_\Delta^8 \\
&\quad - \frac{16}{5!} \sigma_\Delta^{10} + \frac{32}{6!} \sigma_\Delta^{12} - \dots \\
&= \frac{1 + e^{-2\sigma_\Delta^2}}{2}
\end{aligned}$$

For completeness,

$$V(\cos \Delta) = \frac{1 + e^{-2\sigma_\Delta^2}}{2} - \left(e^{-\frac{\sigma_\Delta^2}{2}} \right)^2 = \frac{(1 - e^{-\sigma_\Delta^2})^2}{2}$$

A computer simulation of navigation without a compass is shown in Fig. 2b. We see that, for short journeys, the scatter plots are more crescent-shaped in comparison with their compass-based counterparts (Fig. 2b). More importantly, in contrast to navigation with a compass, the average distance moved along the intended direction of travel does *not* increase in proportion to the number of steps. In this example, it saturates at a value of approximately 15 linear units, which is never exceeded, regardless of the number of steps taken.

Figure 3a compares the way in which the expected movement along the intended direction, $E(X_{\text{total}})$, increases with step number for navigation with and without a compass. With a compass, the expected movement increases indefinitely, in proportion to the number of steps ($E(X_{\text{total}}) = n\mu_L\beta$). Without a compass, the expected displacement never exceeds an upper limit. Panel B shows the 99% confidence intervals for the radial distance travelled from the starting point, as a function of step number. This was obtained using Monte Carlo methods (400,000 runs). Even after 1,000 steps, there is a 99.5% chance that the animal will not travel beyond a net distance of approximately 572 linear units from its starting point. Even though the probability distribution grows wider with each step, this on its own is not sufficient to compensate for the saturating mean displacement. Indeed, it can be shown that using the error parameters in this example, the maximum possible probability density at the goal location is 10,000 fold larger when a compass is used to maintain

the heading direction. Furthermore, the ratio of the probability densities (odds ratio) continues to grow approximately linearly with increasing goal distance.

Why is it impossible for an animal to travel arbitrarily far away from its starting location when it does not possess a compass? We see that, in the absence of a compass, the animal is more and more likely to stray away from its intended direction as the number of steps increases. Therefore, after a large number of steps, the animal is just as likely to be moving back toward (or even past) its starting point, as it is to be moving further away. In fact, after a large number of steps, all directions of travel become equally likely, so that the average distance travelled along the desired direction does not increase any further.

We can derive the positional variances as follows:

$$V(X_{\text{total}}) = E(X_{\text{total}}^2) - [E(X_{\text{total}})]^2$$

$$\begin{aligned} E(X_{\text{total}}^2) &= E \left[(L_1 \cos \Delta_1 + L_2 \cos(\Delta_1 + \Delta_2) + \dots + L_n \cos(\Delta_1 + \Delta_2 + \dots + \Delta_n))^2 \right] \\ &= E \left[\begin{aligned} &L_1^2 \cos^2 \Delta_1 + 2L_1 L_2 \cos \Delta_1 \cos(\Delta_1 + \Delta_2) + \dots + 2L_1 L_n \cos \Delta_1 \cos(\Delta_1 + \Delta_2 + \dots + \Delta_n) \\ &+ L_2^2 \cos^2(\Delta_1 + \Delta_2) + \dots + 2L_2 L_n \cos(\Delta_1 + \Delta_2) \cos(\Delta_1 + \Delta_2 + \dots + \Delta_n) \\ &\vdots \\ &+ L_n^2 \cos^2(\Delta_1 + \Delta_2 + \dots + \Delta_n) \end{aligned} \right] \end{aligned}$$

$$\begin{aligned} E \left(L_m^2 \cos^2 \left(\sum_{j=1}^m \Delta_j \right) \right) &= E \left(L_m^2 \right) \frac{(2\gamma - 1)^m + 1}{2} \\ &= (\sigma_L^2 + \mu_L^2) \frac{(2\gamma - 1)^m + 1}{2} \\ &= \mu_L^2 E \left(\cos^2 \left(\sum_{j=1}^m \Delta_j \right) \right) + \sigma_L^2 \frac{(2\gamma - 1)^m + 1}{2}. \end{aligned}$$

$$\begin{aligned} E(X_{\text{total}}^2) &= \mu_L^2 E [(\cos \Delta_1 + \cos(\Delta_1 + \Delta_2) + \dots + \cos(\Delta_1 + \Delta_2 + \dots + \Delta_n))^2] + \sum_{j=1}^n \sigma_L^2 \frac{(2\gamma - 1)^j + 1}{2} \\ &= \mu_L^2 E [(\cos \Delta_1 + \cos(\Delta_1 + \Delta_2) + \dots + \cos(\Delta_1 + \Delta_2 + \dots + \Delta_n))^2] + \frac{\sigma_L^2}{2} \left[\frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{2\gamma - 2} + n \right] \\ &= \mu_L^2 E \left[\begin{aligned} &\cos^2 \Delta_1 + 2 \cos \Delta_1 \cos(\Delta_1 + \Delta_2) + \dots + 2 \cos \Delta_1 \cos(\Delta_1 + \Delta_2 + \dots + \Delta_n) \\ &+ \cos^2(\Delta_1 + \Delta_2) + \dots + 2 \cos(\Delta_1 + \Delta_2) \cos(\Delta_1 + \Delta_2 + \dots + \Delta_n) \\ &\vdots \\ &+ \cos^2(\Delta_1 + \Delta_2 + \dots + \Delta_n) \end{aligned} \right] \\ &\quad + \frac{\sigma_L^2}{2} \left[\frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{2\gamma - 2} + n \right]. \end{aligned}$$

The result of each squared term is:

$$\begin{aligned} E(\cos^2(\Delta_1 + \Delta_2 + \dots + \Delta_j)) &= E((\cos(\Delta_1 + \Delta_2 + \dots + \Delta_{j-1}) \cos \Delta_j \\ &\quad - \sin(\Delta_1 + \Delta_2 + \dots + \Delta_{j-1}) \sin \Delta_j)^2) \\ &= E \left(\begin{aligned} &\cos^2(\Delta_1 + \Delta_2 + \dots + \Delta_{j-1}) \cos^2 \Delta_j \\ &- 2 \cos(\Delta_1 + \Delta_2 + \dots + \Delta_{j-1}) \cos \Delta_j \\ &\quad \times \sin(\Delta_1 + \Delta_2 + \dots + \Delta_{j-1}) \sin \Delta_j \\ &+ \sin^2(\Delta_1 + \Delta_2 + \dots + \Delta_{j-1}) \sin^2 \Delta_j \end{aligned} \right) \\ &= E(\cos^2(\Delta_1 + \Delta_2 + \dots + \Delta_{j-1})) E(\cos^2 \Delta_j) \\ &\quad + E(\sin^2(\Delta_1 + \Delta_2 + \dots + \Delta_{j-1})) E(\sin^2 \Delta_j) \\ &= E_{j-1} \gamma + (1 - E_{j-1})(1 - \gamma) = E_{j-1}(2\gamma - 1) + (1 - \gamma). \end{aligned}$$

Via induction, we can readily show that

$$E\left(\cos^2\left(\sum_{j=1}^m \Delta_j\right)\right) = \frac{(2\gamma - 1)^m + 1}{2}.$$

The other terms are of the form ($n > m$):

$$\begin{aligned} & E\left(\cos\left(\sum_{j=1}^m \Delta_j\right) \cos\left(\sum_{j=1}^n \Delta_j\right)\right) \\ &= E\left(\cos\left(\sum_{j=1}^m \Delta_j\right) \cos\left(\sum_{j=1}^{n-1} \Delta_j\right) \cos \Delta_n\right) \\ &\quad - E\left(\cos\left(\sum_{j=1}^m \Delta_j\right) \sin\left(\sum_{j=1}^{n-1} \Delta_j\right) \sin \Delta_n\right) \\ &= E\left(\cos\left(\sum_{j=1}^m \Delta_j\right) \cos\left(\sum_{j=1}^{n-1} \Delta_j\right)\right) E(\cos \Delta_n) \\ &\quad - E\left(\cos\left(\sum_{j=1}^m \Delta_j\right) \sin\left(\sum_{j=1}^{n-1} \Delta_j\right)\right) E(\sin \Delta_n) \\ &= E\left(\cos\left(\sum_{j=1}^m \Delta_j\right) \cos\left(\sum_{j=1}^{n-1} \Delta_j\right)\right) E(\cos \Delta_n) \\ &\quad \vdots \\ &= E\left(\cos^2\left(\sum_{j=1}^m \Delta_j\right)\right) [E(\cos \Delta)]^{n-m} \\ &= \frac{(2\gamma - 1)^m + 1}{2} \beta^{n-m}, \end{aligned}$$

so that each row of terms may be expressed as a geometric series following expansion and elimination of the null terms. Doubling and then subtracting the extra diagonal term, we get

$$\begin{aligned} & \sum m^{\text{th row}} \\ &= ((2\gamma - 1)^m + 1) \frac{\beta^{n-m+1} - 1}{\beta - 1} - \frac{(2\gamma - 1)^m + 1}{2} \\ &= ((2\gamma - 1)^m + 1) \frac{\beta^{n-m+1} - \frac{\beta}{2} - \frac{1}{2}}{\beta - 1}. \end{aligned}$$

Combining the results, we have

$$\begin{aligned} & E(X_{\text{total}}^2) \\ &= \mu_L^2 \left[\frac{1}{\beta - 1} \sum_{j=1}^n (2\gamma - 1)^j \beta^{n-j+1} \right. \\ &\quad \left. - \frac{\beta + 1}{2(\beta - 1)} \sum_{j=1}^n (2\gamma - 1)^j \right. \\ &\quad \left. + \frac{1}{\beta - 1} \sum_{j=1}^n \beta^{n-j+1} - \frac{n(\beta + 1)}{2(\beta - 1)} \right] \\ &\quad + \frac{\sigma_L^2}{2} \left[\frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{2\gamma - 2} + n \right] \\ &= \mu_L^2 \left[\left(\frac{1}{\beta - 1} \right) \frac{(2\gamma - 1)^n - \beta^n}{\frac{1}{\beta} - \frac{1}{2\gamma - 1}} \right. \\ &\quad \left. - \left(\frac{\beta + 1}{4(\beta - 1)} \right) \frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{\gamma - 1} \right. \\ &\quad \left. + \left(\frac{1}{\beta - 1} \right) \frac{\beta^{n+1} - \beta}{\beta - 1} - \frac{n(\beta + 1)}{2(\beta - 1)} \right] \\ &\quad + \frac{\sigma_L^2}{2} \left[\frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{2\gamma - 2} + n \right]. \end{aligned}$$

Given that

$$[E(X_{\text{total}})]^2 = \left[\mu_L^2 \frac{\beta - \beta^{n+1}}{1 - \beta} \right]^2 = \mu_L^2 \frac{\beta^{n+1} - \beta}{(\beta - 1)^2} [\beta^{n+1} - \beta],$$

we can write

$$\begin{aligned} & V(X_{\text{total}}) \\ &= \mu_L^2 \left[\left(\frac{1}{\beta - 1} \right) \frac{(2\gamma - 1)^n - \beta^n}{\frac{1}{\beta} - \frac{1}{2\gamma - 1}} \right. \\ &\quad \left. - \left(\frac{\beta + 1}{4(\beta - 1)} \right) \frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{\gamma - 1} \right. \\ &\quad \left. + \left(\frac{1 + \beta - \beta^{n+1}}{\beta - 1} \right) \frac{\beta^{n+1} - \beta}{\beta - 1} - \frac{n(\beta + 1)}{2(\beta - 1)} \right] \\ &\quad + \frac{\sigma_L^2}{2} \left[\frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{2\gamma - 2} + n \right]. \end{aligned}$$

In a similar manner, we can show that the positional variance in the perpendicular direction is

$$\begin{aligned}
 V(Y_{\text{total}}) &= E(Y_{\text{total}}^2) - [E(Y_{\text{total}})]^2 = E(Y_{\text{total}}^2) \\
 &= E[(L_1 \sin \Delta_1 + L_2 \sin(\Delta_1 + \Delta_2) + \dots + L_n \sin(\Delta_1 + \Delta_2 + \dots + \Delta_n))^2] \\
 &= E \left[\begin{array}{l} L_1^2 \sin^2 \Delta_1 + 2L_1 L_2 \sin \Delta_1 \sin(\Delta_1 + \Delta_2) + \dots + 2L_1 L_n \sin \Delta_1 \sin(\Delta_1 + \Delta_2 + \dots + \Delta_n) \\ + L_2^2 \sin^2(\Delta_1 + \Delta_2) + \dots + 2L_2 L_n \sin(\Delta_1 + \Delta_2) \sin(\Delta_1 + \Delta_2 + \dots + \Delta_n) \\ \vdots \\ + L_n^2 \sin^2(\Delta_1 + \Delta_2 + \dots + \Delta_n) \end{array} \right] \\
 &\vdots \\
 &= \mu_L^2 E \left[\left(\begin{array}{l} \sin \Delta_1 + \sin(\Delta_1 + \Delta_2) \\ + \dots + \sin(\Delta_1 + \Delta_2 + \dots + \Delta_n) \end{array} \right)^2 \right] + \sum_{j=1}^n \sigma_L^2 \frac{1 - (2\gamma - 1)^j}{2} \\
 &= \mu_L^2 E \left[\left(\begin{array}{l} \sin \Delta_1 + \sin(\Delta_1 + \Delta_2) \\ + \dots + \sin(\Delta_1 + \Delta_2 + \dots + \Delta_n) \end{array} \right)^2 \right] + \frac{\sigma_L^2}{2} \left[n - \frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{2\gamma - 2} \right] \\
 &\vdots \\
 &= \mu_L^2 \left[\begin{array}{l} \left(\frac{1}{1 - \beta} \right) \frac{(2\gamma - 1)^n - \beta^n}{\frac{1}{\beta} - \frac{1}{2\gamma - 1}} \\ + \left(\frac{\beta + 1}{4(\beta - 1)} \right) \frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{\gamma - 1} \\ + \left(\frac{1}{\beta - 1} \right) \frac{\beta^{n+1} - \beta}{\beta - 1} - \frac{n(\beta + 1)}{2(\beta - 1)} \end{array} \right] + \frac{\sigma_L^2}{2} \left[n - \frac{(2\gamma - 1)^{n+1} - (2\gamma - 1)}{2\gamma - 2} \right].
 \end{aligned}$$

Figure 5b shows how these two variance functions increase with the step number, when no compass is available. This is in contrast to Fig. 5a, which shows the case with a compass. It is immediately obvious that lack of a compass leads to much larger variances in general (noisier navigation), but, interestingly, the variance functions have linear and parallel asymptotes. One consequence is that the ratio of the variances will approach unity. In contrast, the use of a compass results in much smaller variances (less noise), but the variance functions diverge whilst maintaining the same proportion, hence the elongated joint probability density function seen in Fig. 4a.

These variances increase with n . As n approaches infinity, it can be shown that 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.

We can derive the asymptotic distributions of X_{total} and Y_{total} by considering X_t as a time-dependent process, and showing that the elements of X_{total} satisfy the criteria for weak dependence and that the Central Limit Theorem is applicable in this context. [Note that during the first few steps, the probability density functions along and perpendicular to the axis of intended locomotion will in general be different from each other. It is only when many steps have been taken such that the heading direction probability density function is essentially flat, that the assumption of ‘identically distributed’ will hold for successive steps. The successive steps are, of course, still statistically dependent.] The criteria which must be satisfied are

- (i) Essentially stationary: $E(X_t^2) \leq M$ i.e., uniformly bounded (loosely: never infinite),

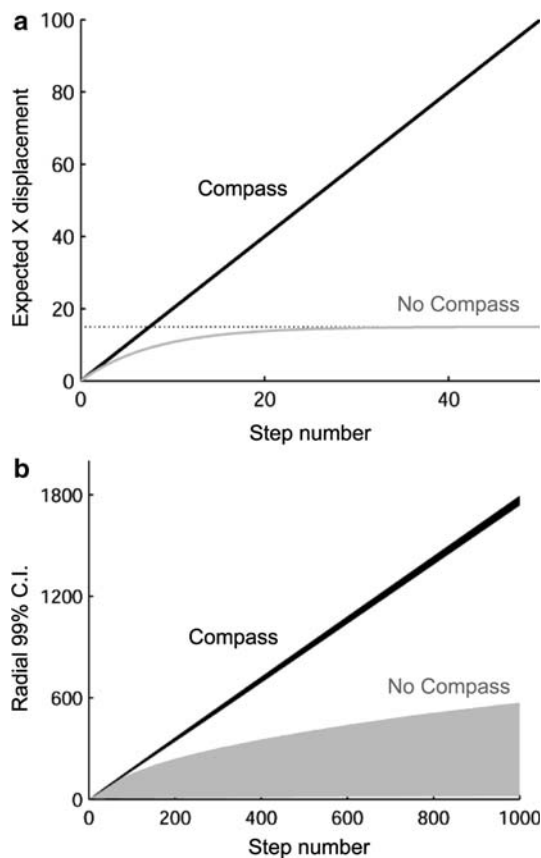


Fig. 3 Effect of not having a compass. **a** The expected movement along the intended direction with step number for navigation with a compass (black line) and without a compass (grey line) for parameter values $\mu_L = 2.0$ linear units and $\beta \approx 0.88$ (which corresponds to a normally distributed Δ with $\sigma_\Delta = 0.5$ radians). With a compass, the expected movement increases indefinitely, in proportion to step number. Without a compass, the expected displacement saturates, approaching a limiting value of 15.0 linear units (dotted black line). Note that the number of steps shown in panel **a** has been restricted to 50 in order for the important characteristics of both functions to be clearly visible. **b** Using the same parameters, the 99% confidence intervals are shown of the radial distance from the origin (starting point of journey) of both navigation with (black) and without a compass (grey) following each step. The confidence limits are estimated by Monte Carlo methods using a sample size of 400,000

- (ii) $V(X_{\text{total}}) = O(n)$ [rules out strong positive serial correlation], and
- (iii) $\frac{1}{V(X_{\text{total}})} = O(\frac{1}{n})$ [rules out strong negative serial correlation].

(ii) & (iii) can be combined loosely as: $f_{\min}(n) \leq V(X_{\text{total}}) \leq f_{\max}(n)$ where both $f_{\min}(n)$ and $f_{\max}(n)$ are of order n . This is clearly the case here since the variances asymptote to linear functions (as $n \rightarrow \infty$).

Careful examination of the variance functions show that asymptotic gradients can be found by equating 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 following linear functions in the step number n ; i.e.,

$$V(X_{\text{total}}) \approx n \left[\frac{\mu_L^2(1+\beta)}{2(1-\beta)} + \frac{\sigma_L^2}{2} \right] - \mu_L^2 \left[\frac{(2\gamma-1)(1+\beta)}{4(1-\gamma)(\beta-1)} + \frac{\beta(1+\beta)}{(1-\beta)^2} \right] - \frac{\sigma_L^2}{4} \left[\frac{2\gamma-1}{\gamma-1} \right]$$

and

$$V(Y_{\text{total}}) \approx n \left[\frac{\mu_L^2(1+\beta)}{2(1-\beta)} + \frac{\sigma_L^2}{2} \right] - \mu_L^2 \left[\frac{(2\gamma-1)(1+\beta)}{4(\gamma-1)(\beta-1)} + \frac{\beta}{(1-\beta)^2} \right] - \frac{\sigma_L^2}{4} \left[\frac{2\gamma-1}{1-\gamma} \right],$$

respectively.

It is now clear that the strongly mixing (α -mixing) condition is satisfied (Rosenblatt 1956). Hence, we may apply the central limit theorem and 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. Hence, the limiting probability density function is in fact a circular joint normal function.

For completeness, it should be noted that the variance functions will, in general, not be equal. Indeed, their difference will asymptote to

$$\lim_{n \rightarrow \infty} [V(Y_{\text{total}}) - V(X_{\text{total}})] = \mu_L^2 \left[\frac{(1+\beta)(2\gamma-1)}{2(1-\beta)(\gamma-1)} + \frac{\beta^2}{(1-\beta)^2} \right] + \frac{\sigma_L^2}{2} \left[\frac{2\gamma-1}{\gamma-1} \right].$$

Figure 4 shows asymptotic probability density functions of position for navigation with and without a compass.

In the current work, distributions of step lengths have been assumed to have finite first and second moments. This assumption guarantees that the central limit theorem applies and thus the limiting distribution is Gaussian. This is mathematically significant because the sum of independent heavy-tailed (infinite variance) distributions converge in the limit to a Lévy distribution, not a Gaussian. A Lévy distribution has infinite mean and variance.

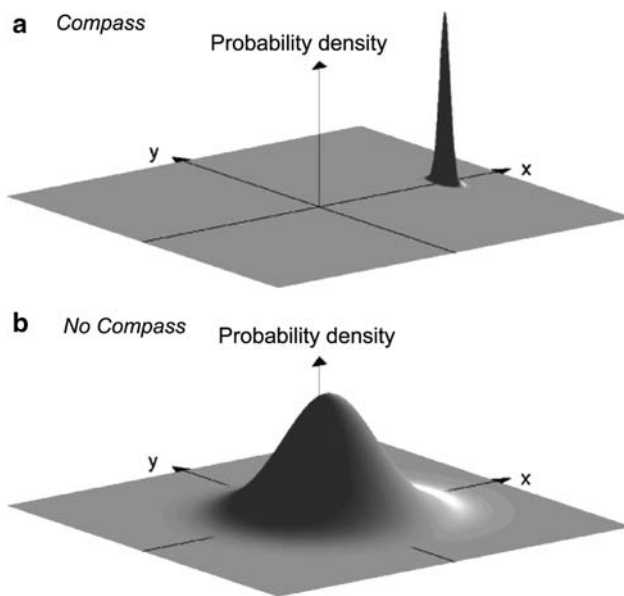


Fig. 4 Probability density functions. **a** The positional probability density function following 100 steps, using a compass. The errors in step size and direction are assumed to be normally distributed and statistically independent, with $\mu_L = 2$ linear units, $\sigma_L = 0.2$ linear units, and $\sigma_\Delta = 0.5$ radians. **b** The positional probability density function following 100 steps, without the use of a compass. The locomotor assumptions are otherwise the same as in (a). Both the 2-dimensional ($X - Y$) spatial domains shown represent 500 linear units by 500 linear units, centred about the starting position (origin). The probability density axes represent values of 4×10^{-3} (linear units) $^{-2}$ and 7×10^{-5} (linear units) $^{-2}$ respectively for panels **a** and **b**

The justification for making the assumption of finite step length is as follows. We are interested in quantifying the way in which physical movements of animals (or other navigating agents) accumulate errors or noise. A physical ‘step’ (be it terrestrial, aerial or aquatic) seems highly likely to have a finite mean and variance. In theory, an infinite step size would require an animal to expend an infinite amount of energy, and take an infinite amount of time, neither of which is plausible. Therefore, it seems implausible that the distribution of a physical ‘step’ taken by any animal may have an infinite first or second moment.

Truncated Lévy distributions, in contrast, may be more biologically plausible. For example, it appears to be the optimal step length distribution for searching for sparse targets (Viswanathan et al. 1999). By definition, a truncated Lévy distribution will have finite mean and variance. Not surprisingly, the positional distribution of a truncated Lévy flight will converge to Gaussian (Mantegna and Stanley 1994). The rate of convergence depends on the second and third moments (Shlesinger 1995).

The results of the current work will therefore be perfectly applicable to truncated Lévy distributions as any other finite distribution of step length. The only difference is that the rate of reaching asymptotic behaviour (and hence Gaussian

probability density) may be slower than many commonly encountered finite distributions e.g., Gaussian, Poisson, Rayleigh ...etc. However, the derived first and second moments will still be exact during the evolution from structured to asymptotic distributions. Furthermore, we have also simulated step lengths as full Lévy distributions (not shown here) and the results are completely analogous to the finite case i.e., the high probability density region moves approximately linearly with each step with a compass, whereas it remains close to the starting location without a compass. Although both distributions are infinitely wide, one is skewed in the direction of the goal (presence of compass), while the other is radially symmetric (absence of compass).

Interestingly, navigation without a compass produces a greater variance than does a purely random walk (i.e., Brownian motion). In other words, the uncertainty associated with an animal’s position after a finite number of steps is greater when the animal performs a directed walk without a compass, than when it executes a purely random walk. For example, using the parameters as per Fig. 1, the variance (in any direction) for attempting to move in a straight line without a compass will have exceeded that of a random walk by the 6th step. In fact, using the results derived above, it can be shown that as the number of steps increases, the variance of this directed walk will be nearly 16 times that of a random walk (along any direction).

6 General discussion

While it may seem rather obvious that an animal cannot move along a perfectly straight line without a compass, the finding that it *cannot move arbitrarily far away from home* without a compass is unexpected and has important implications.

6.1 Straight line navigation requires the use of a compass

Firstly, the results derived in this work imply that any animal that does demonstrate an ability to travel reasonable distances in an approximately straight line must be doing so with the aid of a compass. To accomplish such a task without the aid of a compass would place unrealistic demands on the animal’s ability to sense and correct unwanted turns. For example, the Saharan desert ant, which forages in a featureless, flat landscape and does not lay any pheromone trails, is able to return to its nest in a more-or-less straight line from a distance of 100 m (Wehner 1987; Wolf and Wehner 2005). If we assume a step size of 10 mm (Zollikofer 1994) and a directional error of about 2° (σ_Δ) between steps, we can calculate that the maximum possible expected distance that the ant can travel in the desired direction is less than 20 m. This calculation makes it virtually undeniable that the animal uses a compass—as early field experiments have indeed demonstrated

(Wehner 1994). Even in situations where no visual cues are available—such as spiders returning to a specific location on their web in the dark (Seyfarth et al. 1982; Görner and Claas 1985), or bumblebees moving between specific locations in the darkness of their hive (Chittka et al. 1999), it appears that animals use external directional references, such as olfactory cues, the earth's magnetic field, even information based on the mechanical properties of the web (Wehner 1992; Seyfarth et al. 1982; Görner and Claas 1985; Chittka et al. 1999). Our study demonstrates mathematically that there are powerful motivations for the use of such allocentric cues, even for relatively short journeys.

6.2 Path integration systems are governed by the same constraints

Secondly, our results have consequences not just for an animal's locomotion, but also for an animal's *perception* of how far it has travelled. Even if an animal were theoretically able to travel in a perfectly straight line without the aid of a compass (by being led along an artificial track, for example), and if its nervous system is subject to noise-related errors in *sensing* the direction of locomotion (as it undoubtedly will be), then we can see from the above analysis that the animal's path integration or “dead reckoning” system (e.g., Gallistel 1990) will suffer from the same effect of saturation. Therefore, no matter how far the animal travels in a straight line, it will never *perceive* having travelled farther than a certain limiting distance, on average. This maximum average distance will depend upon the level of noise that is prevalent in the animal's direction-sensing mechanisms. Furthermore, there is a subtlety in the way the compass must be used. For instance, a path integrator which uses the compass to measure/infer egocentric or allocentric *rotations* (as accurately and precisely as one might like), but not absolute heading direction, would still succumb to the same degenerescence. It should be emphasized that this phenomenon causes navigational problems in two ways. Firstly, the magnitude of the positional uncertainty exceeds that of navigation with a compass or even a random walk. Secondly, and perhaps less obviously, there is a systematic error between the intended and actual displacement which gets worse with every step taken.

There have been numerous examples in the literature where navigation models have been proposed without due consideration of this phenomenon, especially the systematic error. Hartmann and Wehner (1995) stated that “This cyclical neural chain provides idiothetic azimuth by integration of angular velocities and may be seen as a compass”. From the current work, it is clear that such a system would not be a useful “compass”, especially for medium to long range navigation. The authors did seem to recognize that cumulative errors will result hence the statement “So the λ compass,

in addition to being initialized at the beginning of an excursion, must also be calibrated at short intervals”. Indeed, if the recalibration occurred at every step, then there will not be any systematic error—but that reduces to using the compass to measure heading at every step. However, if the recalibration intervals were greater than one, then a systematic error would still result. The only guaranteed solution is to recalibrate *regularly* thereby effectively turning each sequence of steps between successive recalibrations into a single elementary step (the repeating unit of locomotion).

Another example is to be found in Mittelstaedt and Mittelstaedt (1982) who wrote “Rotations are measured by an inertial instrument...” and “Candidates for the first are the semicircular canals, which are known to be angular accelerometers ...” in the context of a biological path integration system. We now understand that aside from larger random errors, this type of inertial path integration system would have growing systematic errors. Therefore, unless it is complemented by some sort of search strategy with a significant range, it could not work even in theory. Certainly, in light of the present findings, it is important to be aware of the systematic error that inevitably accompanies compassless path integration, and to consider ways in which an animal might cope with this error.

Gallistel (1990) recognized that a path integration model which uses a polar representation of position requires a feedback of the current representation vector to the updating portion of the system for the next step (heavy arrows in his Fig. 4.7). Gallistel argued that this recurrent addition of noise would lead to greater errors overall, and hence this form of vector representation would be evolutionarily inferior to a Cartesian form. Although there is no direct contradiction of that study with the concepts developed here, there is a subtlety, which might have been overlooked. The exact way in which the errors accumulate is absolutely vital. Again consider the Hartmann & Wehner model as an example. The second version of their λ compass (their Fig. 5c) would in fact be no different in principle to Mittelstaedt's Cartesian (bicomponent) model, which according to Gallistel's argument is superior, if we only consider sensorimotor noise. Indeed, using Mittelstaedt and Mittelstaedt (1982) hypothesis about inertial instruments and heading direction measurement, this form of Cartesian representation would actually succumb to the systematic error and finite range described in the current work. In summary, regardless of how the net vector is represented neurally (polar, Cartesian or some other form), two critical issues remain: a) the kind of sensory information available—a compass is far superior to idiothetic cues; and b) the way in which the vector is updated from sensory information—compass heading should be used directly.

Indeed, an accurate path integrator would need to use heading direction *per se* rather than changes in heading direction. Thus it is only distance that is actually ‘integrated’.

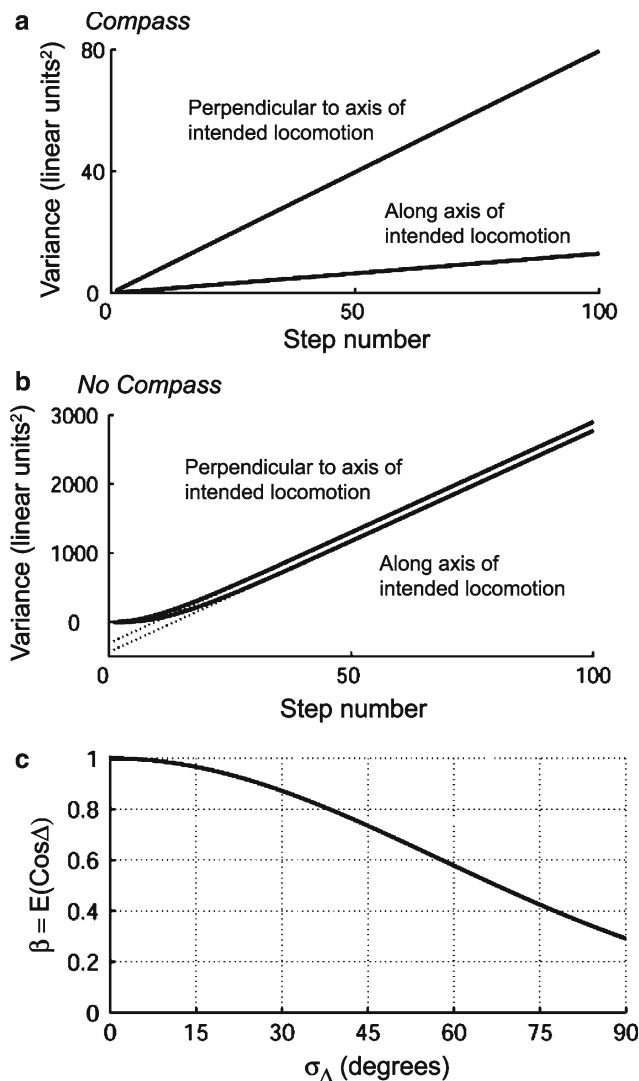


Fig. 5 Panel **a** shows how the variances along and perpendicular to the axis of intended locomotion increases with the number of steps, when using a compass at every step. The errors in step size and direction are assumed to be normally distributed and statistically independent, with $\mu_L = 2$ linear units, $\sigma_L = 0.2$ linear units, and $\sigma_\Delta = 0.5$ radians. Panel **b** shows the same without a compass. The *dotted lines* represent the derived linear asymptotes of the same functions. Panel **c** shows the expected value of $\cos(\Delta)$ when Δ is normally distributed (see text for details)

A clear example of this mechanism in action is seen in the path integration model proposed by Wittmann and Schwegler (1995) or the alternative version of the model by Hartmann and Wehner (1995) summarized in their Fig. 5c. This is an unavoidable constraint for the evolution of neural networks which need to perform accurate path integration. In fact, accurate path integration (regardless of precision) requires the combined use of both egocentric and allocentric information. In other words, accurate path integration is impossible when it is based only on egocentric cues.

6.3 Artificial navigating agents are also governed by the same constraints

Thirdly, our results are equally applicable to the navigation of autonomous robots. Robot navigation that does not use an external directional reference, but relies purely on wheel-based odometry (for example), will suffer from the same limitations that we have described above. Again, this limitation applies not only to the robot's locomotion, but also to the robot's path integration system which is meant to provide a continually updated estimate of the robot's current position. The presence of cumulative error in path integration systems has been recognized in studies of robot navigation (Ingemar 1991) and sophisticated techniques have been developed in an attempt to avoid the problem (Thrun 1997). However, to our knowledge, the extreme consequences of navigating without a compass have hitherto not been properly quantified or appreciated.

6.4 Index of straightness of a path

Fourthly, the maximum expected displacement can be used as a measure of the straightness of a path. A single value, representing a measure of straightness, can be reported in two distinct but meaningful ways:

1. $E_{\max}^a = \frac{\beta}{1-\beta}$ is a dimensionless value denoting the maximum possible expected displacement expressed as a function of the number of steps. This measure is scale independent and would allow very different sized animals to be compared directly.
2. $E_{\max}^b = \mu_L \frac{\beta}{1-\beta}$ is E_{\max}^a multiplied by the mean step length (in linear units) to give the maximum possible expected displacement in physical dimensions. This version accounts for the dimensions of the animal's gait and would be a better reflection of the environmental demands and interactions.

Intuitively, the closer E_{\max} is to 0, the less straight the path (and hence more sinuous), while the larger the value (approaching infinity), the straighter the path (and hence less sinuous). In other words, E_{\max} is consistent with the intuitive meaning of straightness, and is inversely related to sinuosity.

Straightness is often measured as D/L (Batschelet 1981), where D is the net distance between the start and current location, while L represents the length of the total path. As Bovet and Benhamou (1988) showed, this measure is very unstable because of the inherent variance of D . Furthermore, an animal using some sort of higher navigation control e.g., moving with the aid of a compass, may indeed yield a value of D much closer to L without changing the intrinsic size of the random errors i.e., the sensorimotor noise. In an attempt to account for these problems, Bovet and Benhamou developed

an index which they termed “sinuosity” which measures the angular displacements over the entire journey. They showed that an index based on the standard deviation of the angular displacements seems to be quite stable. The use of E_{\max} has a similar effect whereby $\hat{\beta} = \frac{1}{n-1} \sum_{j=1}^{n-1} \cos \Delta_j$ after n steps.

In practice, this measure has the advantage of not underestimating the values in the tails of distributions (e.g., Gaussian) when they wrap around to approximate a circular variable whereas a direct sampling of Δ values would. Analytically, there is a subtle but extremely important reason for using E_{\max} instead of any measure which only takes into account σ_{Δ} : for a given value of σ_{Δ} , the sinuosity/straightness of a path still depends on the *distribution* of Δ . A simple example will illustrate this point. Consider two angular error distributions both with unit σ_{Δ} i.e.,

$$(1) \Delta = \pm 1 \quad (2) \Delta \sim N(0, 1)$$

In both cases, Bovet & Benhamou's measure of sinuosity will give $S = 1/\sqrt{P}$ where P was defined as the mean step length (equivalent to our μ_L). So the same sinuosity index is found for the two distributions. In contrast, $\beta = \cos(1) \approx 0.54$ for (1), which gives $E_{\max} \approx 1.2P$, whereas $\beta = e^{-\frac{1}{2}} \approx 0.61$ for (2) which gives $E_{\max} \approx 1.5P$. The sinuosity is the same in both cases, but the E_{\max} value shows that the normally distributed angular displacement error results in a straighter path. This is consistent with intuition since the majority of turns are less than 1 radian in magnitude. So for practical as well as theoretical reasons, E_{\max} seems to be a useful measure of the straightness of a path.

6.5 Absence of a compass implies alternative navigational strategies

Finally, in animals which seem to navigate relatively short distances and which do not use a compass (Mittelstaedt and Mittelstaedt 1982; Etienne et al. 1996, 1998), there is now a clear question which must be addressed: How do the animals cope with this systematic error? One obvious solution would be to have very small errors (or conversely very short navigation paths) so that the total systematic error is smaller than the effective search radius of the animal. Conversely, an efficient search strategy may have evolved to cope with the large positional uncertainty which necessarily results from compassless navigation. In an experienced animal, it is plausible for some learning to take place whereby the systematic error is (at least partially) compensated; e.g., the return journey adjusted to be systematically longer (more steps) than the net home vector suggests. This method, however, requires a measure of the step number or total distance travelled, rather than a net vector, so a separate neural mechanism may well be required. In any case, if an animal is truly compassless (no external direction reference at all) during navigation, it

should be possible to use the results of our work and/or more extensive theoretical generalizations (Cheung et al. in preparation) to characterize its behaviour.

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